MDPI

Review

Review of the Mechanisms by Which Transcription Factors and Exogenous Substances Regulate ROS Metabolism under Abiotic Stress

Peng Liu [1,2,†], **Xiaolei Wu** [1,†], **Binbin Gong** [1,†], **Guiyun Lü** [1], **Jingrui Li** [1] **and Hongbo Gao** [1,*]

1 Key Laboratory of North China Water-Saving Irrigation Engineering, Hebei Key Laboratory of Vegetable Germplasm Innovation and Utilization, Collaborative Innovation Center of Vegetable Industry in Hebei, College of Horticulture, Hebei Agricultural University, Baoding 071000, China
2 Institute of Vegetables Research, Shandong Academy of Agricultural Sciences, Jinan 250100, China
* Correspondence: hongbogao@hebau.edu.cn
† These authors contributed equally to this work.

Abstract: Reactive oxygen species (ROS) are signaling molecules that regulate many biological processes in plants. However, excess ROS induced by biotic and abiotic stresses can destroy biological macromolecules and cause oxidative damage to plants. As the global environment continues to deteriorate, plants inevitably experience abiotic stress. Therefore, in-depth exploration of ROS metabolism and an improved understanding of its regulatory mechanisms are of great importance for regulating cultivated plant growth and developing cultivars that are resilient to abiotic stresses. This review presents current research on the generation and scavenging of ROS in plants and summarizes recent progress in elucidating transcription factor-mediated regulation of ROS metabolism. Most importantly, the effects of applying exogenous substances on ROS metabolism and the potential regulatory mechanisms at play under abiotic stress are summarized. Given the important role of ROS in plants and other organisms, our findings provide insights for optimizing cultivation patterns and for improving plant stress tolerance and growth regulation.

Keywords: ROS; abiotic stress; transcription factor; exogenous substances

## 1. ROS Metabolism under Abiotic Stress

Due to human activities, the Earth's environment has changed dramatically over the past two hundred years, and the frequency of natural disasters such as drought, waterlogging, salinity and high and low temperatures has increased. Various abiotic stresses, such as cold, heat, drought, flood, salt, excessive light, nutrient deficiency, etc., lead to the overproduction of reactive oxygen species (ROS) in plants which cause damage to proteins, lipids and DNA. Plants generate a burst of ROS in response to infection by virulent or even avirulent bacteria, fungi and viruses [1]. ROS may be critical for establishing the hypersensitivity response (HR) of plants following infection and pathogen recognition [2].

ROS are partially reduced or activated derivatives of oxygen (singlet oxygen ($^1O_2$), superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical ($OH\cdot$), alkoxy radicals ($RO^{\cdot}$), etc.) that play an important role in plant growth and development. ROS act as a signal to regulate a series of plant biological activities, such as promoting seed germination, inhibiting Arabidopsis thaliana hypocotyl elongation, tissue root structure and flowering regulation [3–9]. However, excess ROS caused by biotic and abiotic stresses leads to the destruction of macromolecules in plants [10,11]. Thus, to maintain ROS homeostasis, plants have an effective and redundant network of ROS generation and scavenging that involves ROS-producing genes, ROS scavenging-related genes and regulators of these genes.

Here, we mainly introduce the mechanisms of ROS generation and scavenging, review the response laws and mechanisms of ROS metabolism that have recently been studied

and discuss the mechanism by which exogenous substances regulate ROS metabolism under abiotic stress. This study provides a reference for the investigation of plant adaptive mechanisms and stress physiology.

O_2 preferentially accepts one electron at a time, leading to the production of ROS, which can damage cells in plants. Here, we generalize the process by which oxygen forms different ROS (Figure 1). In general, the production of ROS is accompanied by energy harvest, transmission and consumption, so ROS are mainly produced in mitochondria and chloroplasts and peroxisomes [12]. For example, O_2^- and $^1O_2$ are generated in photosystems I and II (PSI and PSII) of chloroplasts, and O_2^- is generated in the electron transport chain (ETC) of mitochondria [13]. In addition to mitochondria and chloroplasts, ROS were generated in peroxisomes, glyoxysomes and apoplasts (Figure 2) [14]. To remove excess ROS, the enzymatic and nonenzymatic antioxidant systems in the plant are initiated [15]. In the following section, we summarize the ROS generation and scavenging system in plants to further explicate the regulation of ROS metabolism.
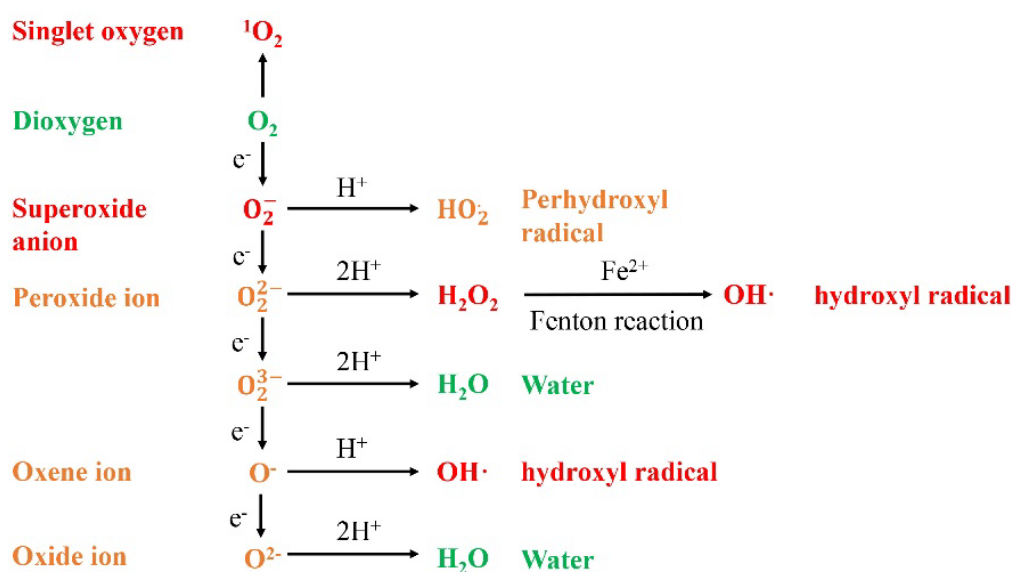

Figure 1. Generation of different ROS via energy transfer or sequential univalent reduction in ground state triplet oxygen. Red font: Singlet oxygen ($^1O_2$), superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH·) are the main forms of ROS in plants; Orange font: Intermediate products of ROS metabolism; Green font: Dioxygen (O_2) and Water (H_2O_2).

1.1. ROS Generation under Abiotic Stress

Plasma membrane RBOH is a key producer of ROS in plants [16]. Therefore, RBOH has been the subject of intensive research [17–19]. Ten *RBOH* genes (RbohA to RbohJ) were identified in Arabidopsis thaliana. However, *RBOHs* redundantly work in response to stress. ROS produced by *AtRBOHD* and *AtRBOHF* can be used as signal molecules to improve salt tolerance of Arabidopsis thaliana [20]. RBOH is structurally conserved and consists of two EF-hand motifs, six α-transmembrane helical domains (TMD-I to TMD-VI), an FAD domain and an NADPH domain. RBOH transfers electrons from NADPH to O_2 to generate O_2^- via heme in FAD, membranes and TMDs [15]. Chemical inhibitors of RBOH (such as diphenyleneiodonium) have been shown to block or impair ROS generation during biotic or abiotic stress in Arabidopsis thaliana [21]. In contrast, Ca^{2+} directly binds to the EF-hand motif to activate RBOH activity, thereby triggering the generation of ROS [22]. Calcium-dependent protein kinase (CDPK) and Ras-related C3 botulinum toxin substrate (RAC) activate RBOH through the Ca^{2+} pathway [23]. CDPK also directly phosphorylates RBOH [24]. The lipid product phosphatidic acid (PA) of phospholipase Dα1 (PLDα1) can induce *RBOHE,* and *RBOHF* express and activate RBOH and participate in ROS and nitric oxide (NO) production, and NO also regulates the metabolism of ROS as signals in

broccoli seedlings [25]. Park et al. found exogenous PA treatment increased ROS levels in Arabidopsis [26]. In addition to RBOH, plant cell wall peroxidases, peroxisomes, and glyoxysomes also catalyze the production of ROS. OH·, H_2O_2 and O_2^- are produced during fatty acid oxidation (by acyl-CoA oxidase) in peroxisomes. H_2O_2 and O_2^- are produced during photorespiration (by glycolate oxidase) in glyoxysomes, respectively [27–29]. Cell wall peroxidases catalyze H_2O_2 to O_2^- in cell membranes.
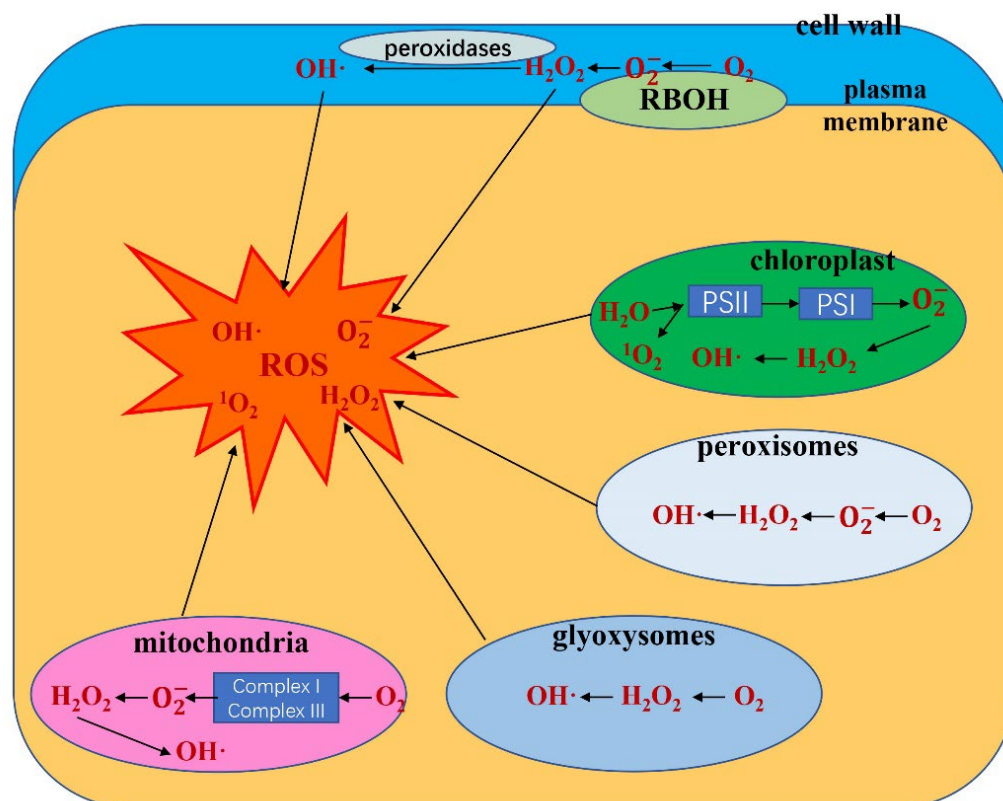
Figure 2. Model of the production and metabolic fate of various ROS (OH·, $^1O_2$, H_2O_2, O_2^-) in different cellular compartments (chloroplasts, mitochondria, peroxisomes, glyoxysomes, plasma membrane and apoplast).

RBOH is a key producer of ROS in plants, and the specific regulation of *RBOH* expression plays an important role in plant resistance to stress [30–32]. Kabała et al. reported that *CsRBOHD* and *CsRBOHF1* expression are induced at the early stages of salt stress in cucumber seedlings, and H_2O_2 is generated, which functions as a signaling molecule participating in the stress response [33]. This is consistent with the findings of Gémes et al. in tobacco [34]. In cucumber, both salt stress and the maintenance of acquired cold tolerance depend on RBOH [35]. Zhang et al. reported that *CsRbohD* is essential in resistance to cold stress in cucumber. These results suggest that *RBOHD* and *RBOHF* act as ROS signal initiators and activate antioxidant systems during plant resistance to salt and cold stress [36]. Whether *RBOH D* and *E* genes expression is regulated by other abiotic stresses and what the roles of other *RBOH*s are in abiotic stresses may remain to be explored. Another enzyme that responds to abiotic stress is oxalate oxidase. Oxalate oxidase is involved in ROS production in plant root cells during response to drought stress on maize and rice, and heavy metal ions stress on wheat [37,38]. The functions of these oxidases in plant resistance to stress require further study.

Photosynthesis and respiratory metabolism are accompanied by the production of ROS. The capacity for light capture during photosynthesis can exceed use, which can produce O_2^- and H_2O_2 through oxygen photoreduction in PSI and can form singlet oxygen by the interaction of oxygen with triplet-state chlorophyll in PSII [39–41]. To reduce the generation of ROS, photosynthetic organisms minimize overexcitation of the photosystems.

Nonphotochemical quenching (NPQ) mechanisms that dissipate energy in excess of that used by the photosynthetic electron transport chain are induced to reduce damage to the photosynthetic apparatus caused by the synthesis of ROS [42,43]. In plant mitochondria, the key sources of ROS production are NADH dehydrogenase complexes I and III and the ubiquinone pool [44,45], where O_2^- radicals are generated from the complexes as a byproduct of energy metabolism by the reduction state of the ubiquinone pool [46,47].

Abiotic stress can result in an oxidative burst and the release of ROS in the photosynthetic and respiratory systems of plants. Abiotic stress triggers a reduction in the respiration rate and inhibition of carbon assimilation, resulting in excess NADPH, which causes excess ROS [48,49]. Plants also respond to adversity stress through a series of complex physiological activities, which regulate the generation of ROS, and many hormones, such as ethylene, jasmonic acid (JA) and salicylic acid (SA), are involved in this process [50]. Hormones are commonly affected by abiotic stress, and these hormones play an important role in plant resistance to stress. Many studies have shown that hormones can regulate the production of ROS in granules and chloroplasts under stressful conditions. It has been reported that abscisic acid (ABA) directly influences photosynthetic oxygen evolution related to the functioning of PSII centers by disrupting the barley chloroplast structure [51]. Meanwhile, ABA increases the content of total carotenoids, xanthophylls and chlorophyll in leaves to ameliorate the impact of excessive excitation energy on PSII. Additionally, ABA downregulates the expression of light-harvesting chlorophyll a/b binding (*LHCB*) genes, *LHCB1-5*, which is beneficial for reducing the absorption of light energy under adverse conditions, thereby reducing the excessive synthesis of ROS in Arabidopsis [52]. Auxin, cytokinin, JA and ethylene may also play important roles in the stability of PSI and PSII, and thus in the improvement of photosynthesis and ROS balance in plants exposed to abiotic stress. During this process, the regulation of *LHCB* gene expression by these hormones is the key activity. Studies have shown that *LHCB* gene expression is regulated by these hormones [50]. However, it is not clear how hormones regulate the expression of these genes. Plant mitochondria may control ROS generation by means of energy-dissipating systems. Therefore, scholars have speculated that mitochondria may play a central role in cell adaptation to abiotic stresses [53]. However, due to a lack of suitable research methods and the specific function of mitochondria, which is energy factory of life and inevitably produces ROS, the mechanism of ROS metabolism in mitochondria under adverse conditions is still unclear.

1.2. ROS Scavenging under Abiotic Stress

The enzymatic ROS scavengers that have been reported thus far include superoxide dismutases (SODs), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), glutathione-S-transferase (GST), dehydroascorbate reductase (DHAR) and glutathione reductase (GR). SODs act as the first line of defense against ROS, dismutating O_2^- to H_2O_2. H_2O_2 is then detoxified by APX, GPX and CAT [53]. These enzymatic reactions require the participation of ascorbic acid (AsA), dehydroascorbate (MDA), glutathione (GSH), etc. AsA and GSH also regenerate through the ASA–GSH cycle (Figure 3). In addition to enzymatic ROS scavengers, nonenzymatic antioxidants include the major cellular redox buffers AsA and GSH, as well as tocopherol, flavonoids, alkaloids, vitamin E, mannitol, proline and carotenoids [54].

To remove excess ROS in plants under different types of adverse conditions, nonenzymatic and enzymatic antioxidant systems are activated. For example, CAT is required for removing ROS under drought conditions [55], and both SOD and POD play important roles in plant responses to various stresses. Scholars have found that SOD, POD, flavonoids, polyphenols and alkaloids respond to salt stress to scavenge ROS. However, there is controversy about the role of CAT under salt stress [56]. This may be due to the presence of other ROS scavenging systems in plants. Adverse stress induces an increase in the synthesis of plant secondary metabolites, such as flavonoids, polyphenols and alkaloids, which have high medicinal value [57–59]. Therefore, many studies have been published on the topic

of exposing plants with desirable secondary metabolites to moderate stress in order to increase the quality of black tea and tomato [60,61].

$$O_2^- \xrightarrow{\text{SOD}} H_2O_2 \xrightarrow{\text{CAT}} H_2O + \tfrac{1}{2}O_2$$
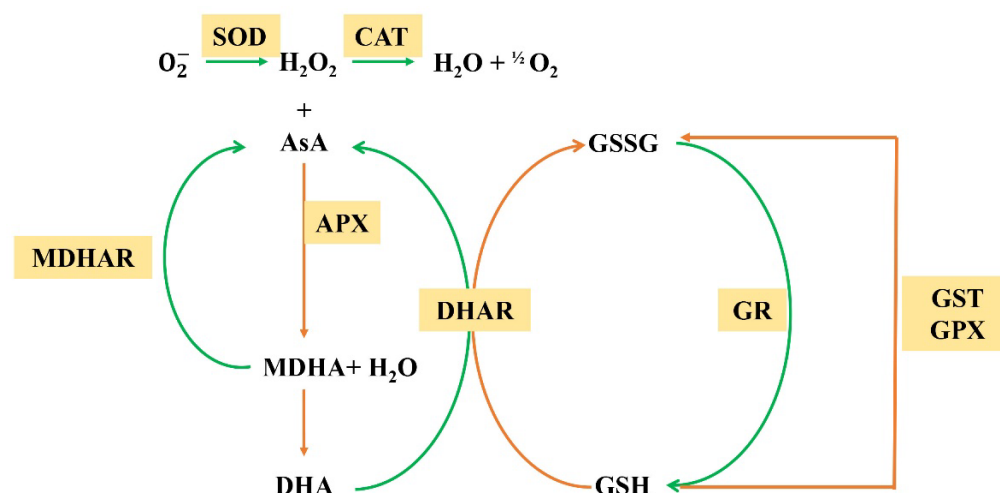
Figure 3. Model of the ASA–GSH cycle. The orange line indicates oxidation reaction and the green line indicates reduction reaction.

2. The Function of Transcription Factors in ROS Metabolism under Abiotic Stress

ROS homeostasis in plants is regulated by a complex and redundant network, and transcription factors (TFs) play an important role in this network. TFs are proteins that can bind to target gene promoters and that regulate the expression of target genes. There are many transcription factors in plants, such as ethylene response factor (AP2/ERF), WRKY, NAC and MYB, that regulate the metabolism of ROS. We found that AP2/ERF, WRKY and NAC mainly regulate the enzymatic antioxidant system, which resists oxidative stress caused by adversity. In addition, bHLH, MYB, bZIP and Dof regulate nonenzymatic antioxidant systems, such as tocopherol, flavonoid, proline and carotenoid metabolism. Undoubtedly, these transcription factor families can regulate both enzymatic and nonenzymatic antioxidant systems. The generation of ROS is also regulated by transcription factors, such as tobacco bHLH123 and Arabidopsis ERF74, which activate *NtRbohE* and *RbohD*, respectively (Table 1) [62,63].

With the popularization of transgenic technology, the functions of many transcription factor genes in plants under abiotic stress have been identified. Many studies have shown that overexpression of *AtWRKY30*, *BdWRKY36*, *SbWRKY30*, *SpWRKY1*, *ZmWRKY40* and *ZmWRKY106* increased the activities of POD, CAT, SOD and some stress related genes (*RD29A*, *HSP90* (*heat shot protein 90*), *DREB2A*, *DREB2B*, *CuZnSOD*, *NCED1* (*Nine cis epoxycarotenoid dioxygenase 1*), *NCED3*, *NCED6*, *LEA5*, *NtP5CS*, and decreased the content of ROS under drought stress [64–69]. This indicates that WRKY TFs regulate plant drought resistance by improving the capacity of scavenging ROS. Scholars found that tomato JUNGBRUNNEN1 and SlNAC2 promote *SlDREB1*, *SlDREB2*, *SlDELLA* and glutathione biosynthesis genes to reduce drought-induced accumulation of ROS in tomato, respectively [70,71]. In addition, Niu et al. found that the expression levels of multiple genes regulating ROS production and scavenging were regulated by BnaNAC55 in *Brassica napus* L. [72]. That suggested that NAC TFs regulates plant drought resistance by regulating ROS production and scavenging. Relevant scholars found that NtERF172 and JERF3 induced *NtCAT* and *SOD* expression to decrease drought tolerance through the regulation of CAT-mediated H_2O_2 homeostasis in tobacco [73,74]. Much research has shown that GbMYB5 and TaMyb1D regulated the expression of genes encoding antioxidant enzymes and activity of antioxidant enzymes under drought stress in cotton and tobacco, respectively [75,76]. Furthermore, PbrMYB21 of Pyrus betulaefolia could regulate polyamine accumulation, which is also a mechanism by which plants eliminate reactive oxygen species induced by drought stress [77]. This indicated that MYB TFs can activate both enzymatic

and nonenzymatic antioxidant systems. Peanut AhbHLH112 and apple *MdbHLH130* act as a positive regulator of drought stress responses through ROS-scavenging in tobacco [73,78]. From these studies, it can be seen that transcription factors can regulate the homeostasis of ROS under drought stress through hormone metabolism and enzymatic antioxidant systems. In addition to WRKY, NAC, AP2/ERF, MYB and bHLH TFs, there are many TFs involved in the regulation of ROS metabolism under drought stress. For instance, TaBZR2 directly interacts with the gene promoter to activate the expression of *TaGST1* to scavenge drought-induced superoxide anions in tobacco [79]. However, the target genes of many transcription factors in the clearing of drought-induced oxidative stress are still unclear.

The lack of oxygen in plants caused by prolonged flooding is the main cause of plant waterlogging. Meng et al. found that 34 WRKY genes were regulated by waterlogging in apple [80]. However, the function of these differentially expressed genes on flood tolerances remains unknown. Liu et al. found that WRKY33 enhanced the expression of hypoxia-responsive genes and alleviated oxidative stress in Arabidopsis [81]. RAP2.12, an ERF TF, induced HRU1, which modulates ROS production in Arabidopsis [82]. Park et al. found that AtERF71/HRE2-overexpressing transgenic Arabidopsis showed tolerance to flooding stress, exhibiting lower levels of ROS [83]. Rice OsEBP89 and Arabidopsis AtERF71 play an important role in alleviating oxidative stress caused by flooding [83,84]. However, the reason for the decrease in ROS is still unknown. At present, there are few published studies on the responses of transcription factors to hypoxia and waterlogging, and much research is still needed.

Salt stress can cause poor plant growth and development. Overexpression of *Ah-WRKY75*, *FtWRKY46*, *HbWRKY82*, *MfWRKY70* and *PcWRKY33* could improve the salt tolerance of peanut and Arabidopsis [85–89]. The activation of antioxidant enzymes, such as SOD, POD and CAT, is the main reason for the improvement in salt tolerance of WRKY TFs plants. In addition, ROS-related genes (*RbohD*, *CSD1*, *CSD2*, *FSD3*) and hormone signaling genes (*EIN3*, *ABF3*, *ABF4*) are induced in *HbWRKY82* expression plants, and ROS signals and ABA signals may activate antioxidant enzymes. *CaNAC46, GmNAC06, GmNAC065, MbNAC25* and *RtNAC100* play an important role in eliminating ROS induced by salt stress [90–94]. Overexpression of *CaNAC46, GmNAC06, GmNAC065, MbNAC25* and *RtNAC10* induced the antioxidant enzymes genes express, activated antioxidant enzymes and promoted proline accumulation in Arabidopsis, soybean and recretohalophyte Reaumuria trigyna. There have been reports that overexpression of *LcERF056*, *GhERF13.12*, *ZmEREB20* and *SlERF84* are helpful to alleviate oxidative damage induced by salt stress [95–98]. LcERF056 could bind to cis-element GCC box or DRE of ROS-related genes in Lotus corniculatus [98]. Overexpression of *GhERF13.12* and *ZmEREB20* induced proline biosynthesis and ROS scavenging genes express in upland cotton and Arabidopsis. *SlERF84* gives transgenic tomato a better ROS-scavenging capability. This indicates that ERF TFs can activate the ROS scavenging system. Genetic evidence suggested that *MYB49*, *SlMYB102* and *TaMYB86B* can enhance the ability of tomato and tobacco to scavenge ROS under salt stress [99–101]. NtbHLH123 directly regulates *RBOHE* expression and acts as a molecular switch to control an Rboh-dependent mechanism in response to salt stress in tobacco [62]. Peanut AhbHLH112 directly and specifically binds to and activates the promoter of the *POD* gene. *BvBHLH93* induced the expression of antioxidant genes *SOD* and *POD* and repressed the expression of *RbohD* and *RbohF* in Arabidopsis [102]. There are reports that indicated that bHLH TFs can regulate the production and clearance of ROS under salt stress. PeSTZ1 confers salt stress tolerance by regulating the expression of *PeZAT12* and *PeAPX2* in poplar [103]. Many TFs respond to salt stress and regulate ROS metabolism, and many studies have revealed that the expression of these transcription factors can cause changes in the ROS level [90,99]. However, the mechanism by which TFs regulate the metabolism of ROS under salt stress remains unclear.

Appropriate temperature is a necessary condition for plant growth. Low temperature will cause damage to plants and can even cause production failure in severe cases. Fei et al. found that *KoWRKY40* transgenic Arabidopsis exhibited higher proline content, SOD, POD

and CAT activities, and lower H_2O_2 content than wild-type Arabidopsis under cold stress conditions [104]. *CaNAC064*, *MbNAC25* improved SOD, POD and CAT activities, and scavenging capability of ROS in peppers and Arabidopsis [94,105]. He et al. reported that PeSTZ1 enhances freezing tolerance through modulation of ROS scavenging by directly regulating *PeAPX2* in poplar [103]. Additionally, MYB, ERF and bHLH TFs can directly regulate the expression of ascorbic acid, flavonoid, phenol and anthocyanin synthesis genes to resist low temperature-induced oxidative stress [106–109]. During this process, the expression of these transcription factors is regulated by hormonal signals such as ethylene. This has important implications for our full comprehension of plant resistance to cold stress.

As global temperatures rise, high or extreme heat is becoming increasingly common. *ZmWRKY106*, *ERF74* and *MYB44* activated antioxidant enzymes, and play an important role in scavenging ROS under heat stress on maize, Arabidopsis and Xanthoceras sorbifolium [64,69,110]. Singh et al. reported that under heat stress, *EcDREB2A* overexpression also resulted in increased antioxidant enzymes activity with decreased ROS content in tobacco [111]. Heat shock transcription factors (HSFs) regulate the expression levels of heat shock proteins and play an important role in plant high temperature stress. LlHsfA4 upregulated *APX2* expression to resist heat stress in lilies [112]. However, ZmHsf08 negatively regulates abiotic stress responses of maize [113]. ZmWRKY106, BZR1, OsSPL7 and other transcription factors play an important role in ROS balance under heat stress [69,114,115]. This showed that TFs could alleviate the oxidative damage caused by high temperatures by activating antioxidant enzymes. However, most of the recent research on this topic only covers the function of these transcription factors; the specific functional mechanism is still unclear.

Table 1. Transcription factors that participate in the metabolism of ROS.

Transcription Factor Family	Genes Name	Description
WRKY	*AhWRKY75* [85]	Peanut *AhWRKY75* gene conferred salt tolerance in transgenic peanut lines by improving the efficiency of the ROS scavenging system and photosynthesis.
	EjWRKY17 [118]	Overexpression of Eriobotrya japonica *EjWRKY17* led to enhanced drought tolerance in transgenic Arabidopsis, which was lower levels of ROS.
	FtWRKY46 [89]	Overexpression of Tartary buckwheat *FtWRKY46* enhanced the stress tolerance of transgenic Tartary buckwheat by modulating ROS clearance and stress-related gene expression.
	HbWRKY82 [88]	Hevea brasiliensis *HbWRKY82* regulated the transcriptional expression of ROS-related genes (*RbohD, CSD1, CSD2, FSD3*) against salt and drought stress in Hevea brasiliensis.
	KoWRKY40 [104]	Mangrove plant K. obovate *KoWRKY40* transgenic Arabidopsis exhibited higher proline content, SOD, POD and CAT activities, and lower H_2O_2 content under cold stress conditions.
	MfWRKY70 [87]	Myrothamnus flabellifolia *MfWRKY70* could significantly increase tolerance to drought, osmotic and salinity stresses by enhancing the antioxidant enzyme system and maintaining ROS homeostasis in Myrothamnus flabellifolia.
	PcWRKY33 [86]	Polygonum cuspidatum *PcWRKY33* negatively regulates the salt tolerance by increasing the level of cellular ROS in Arabidopsis thaliana.
	WRKY33 [119]	Arabidopsis thaliana *WRKY33* can bind to and activate *RAP2.2* and activate towards *RAP2.2* to increase hypoxia tolerance of Arabidopsis thaliana.
	ZmWRKY40 [68]	Overexpression of maize *ZmWRKY40* improved drought tolerance in transgenic Arabidopsis by enhancing the activities of POD and CAT under drought stress.
	ZmWRKY79 [120]	Maize *ZmWRKY79* boost ROS scavenging to result in less H_2O_2 and MDA accumulation and increased antioxidant enzyme activities under drought stress in Arabidopsis.
	ZmWRKY106 [69]	Overexpression of maize *ZmWRKY106* improved the tolerance to drought and heat in transgenic Arabidopsis by reducing ROS content in transgenic lines by enhancing the activities of SOD, POD and CAT under drought stress.

Table 1. *Cont.*

Transcription Factor Family	Genes Name	Description
NAC	*CaNAC46* [92]	Overexpression of Capsicum annuum *CaNAC46* improved the tolerance of transgenic Arabidopsis thaliana plants to drought and salt stresses by promoting the expression of *SOD* and *POD*.
	CaNAC064 [105]	The Capsicum annuum *CaNAC064*-overexpressing Arabidopsis plants exhibited lower MDA content, chilling injury index under cold stress.
	GmNAC06 [90]	Soybean *GmNAC06* could cause the accumulation of proline and glycine betaine to alleviate or avoid the negative effects of ROS in soybean.
	GmNAC065 [93]	Soybean *GmNAC065* expression shows a phenotype associated with enhanced oxidative performance and higher carotenoid contents under salt stress in Arabidopsis.
	GmNAC085 [121]	Soybean *GmNAC085* mediated drought resistance in transgenic Arabidopsis plants, with higher activities of antioxidant enzymes responsible for scavenging hydrogen peroxide or superoxide radicals.
	MbNAC25 [94]	Overexpressing *Malus baccata* (L.) Borkh *MbNAC25* Arabidopsis plants showed enhanced tolerance against cold and drought salinity by increasing proline content, the activities of antioxidant enzymes SOD, POD and CAT.
	ONAC066 [122]	Overexpression of rice *ONAC066* in transgenic rice improved drought and oxidative stress tolerance, accompanied with increased contents of proline, decreased accumulation of ROS in rice.
	RtNAC100 [91]	R. trigyna *RtNAC100* overexpression aggravated salt-induced PCD in transgenic R. trigyna lines by promoting ROS.
AP2/ERF	*ERF6* [123]	Arabidopsis ERF6 functions as a transcriptional activator and suppressor of genes in response to drought stress and decreased ROS content in Arabidopsis.
	ERF96 [124]	Arabidopsis *ERF96*-overexpressing Arabidopsis lines exhibited the significant increases in CAT and GPX activities as well as the glutathione (GSH) content, while having a decrease in ROS accumulation compared to WT.
	ERF74 [63]	Arabidopsis *ERF74*-overexpressing Arabidopsis lines showed enhanced tolerance to drought, high light, heat and aluminum stresses, and induction of stress marker genes and ROS-scavenging enzyme genes is dependent on the *ERF74-RbohD*-ROS signal pathway.
	LcERF056 [98]	Lotus corniculatus *LcERF056* plays important roles in salt tolerance in Lotus corniculatus by modulating ROS-related genes
	GhERF13.12 [96]	*GhERF13.12* from Gossypium hirsutum transgenic Arabidopsis showed enhanced salt stress tolerance and enhanced expression of genes participating in proline biosynthesis, and ROS scavenging.
	ZmEREB20 [95]	Maize *ZmEREB20* positively regulated salt tolerance through the molecular mechanism associated with ROS scavenging in maize.
	SlERF84 [97]	Overexpression of tomato *SlERF84* in Arabidopsis endows transgenic plants enhanced tolerance to drought and salt stress.
MYB	*CmMYB012* [125]	*CmMYB012* from Chrysanthemum morifolium was also found to inhibit anthocyanin biosynthesis by suppressing the expression of *CmCHS, CmDFR, CmANS* and *CmUFGT* against heat stress on Chrysanthemum morifolium.
	MdMYB23 [126]	Transgenic apple calli and Arabidopsis with overexpression of *MdMYB23* from apple exhibited increased cold tolerance through active *MdANR* to promote proanthocyanidin accumulation and ROS scavenging.
	MYB44 [110]	Suppression of *XsMYB44* expression via virus-induced gene silencing weakened yellowhorn tolerance to both individual and combined drought and heat stress and increased ROS levels and decreased antioxidant enzyme activities and proline content.
	MYB49 [100]	Overexpression of *SlMYB49* in tomato significantly enhanced the resistance of tomato to salt and drought stress and decreased accumulation of ROS.
	PlMYB108 [127]	Overexpression of *PlMYB108* from Herbaceous Peony in tobacco plants, showed that the flavonoid content, antioxidant enzyme activities, and photosynthesis were markedly elevated to confer drought stress.
	SlMYB102 [99]	The overexpression of *SlMYB102* in tomato maintained lower ROS generation and increased the activity of ROS scavenging enzymes, the accumulation of antioxidants and proline was higher under salt stress.
	TaMYB86B [128]	Wheat *TaMYB86B* influences the salt tolerance of wheat by regulating the ion homeostasis to maintain an appropriate osmotic balance and decrease ROS levels.

Table 1. *Cont.*

Transcription Factor Family	Genes Name	Description
bHLH	*AhbHLH112* [78]	The overexpression of *AhbHLH112* from peanut improves the drought tolerance of transgenic Arabidopsis plants both in seedling and adult stages through directly activating the *POD* gene.
	bHLH123 [62]	Overexpression of *NtbHLH123* from tobacco resulted in greater resistance to salt stress on tobacco through the *NtbHLH123-NtRbohE* signaling pathway.
	BvbHLH93 [102]	Overexpression of sugar beet B*vBHLH93* in Arabidopsis enhanced the activities of antioxidant enzymes by positively regulating the expression of antioxidant genes SOD and POD to against to salt stress.
	MdbHLH130 [73]	Overexpression of apple *MdbHLH130* in tobacco led to lower ROS accumulation and upregulation of the expression of some ROS-scavenging under drought stress.
	MfbHLH38 [116]	Heterologous expression of M. flabellifolia *MfbHLH38* in Arabidopsis improved the tolerance to drought and salinity stresses, decreased proline and ROS accumulation and increased antioxidant enzyme activities
	MfPIF1 [117]	Overexpression of *MfPIF1* from M. flabellifolia in Arabidopsis thaliana led to enhanced drought and salinity tolerance, which was attributed to higher contents of proline and activities of antioxidant enzymes, as well as lower ROS accumulation in transgenic lines.
	OsWIH2 [129]	Heterologous expression of *OsWIH2* in rice resulted in significantly higher drought tolerance, probably due to the decreased ROS accumulation under drought stress.
	PYE, ILR 3 [130]	Arabidopsis *ILR3* and *PYE* confer photoprotection during Fe deficiency to prevent the accumulation of singlet oxygen and repair of the photosynthetic machinery.
	CaSBP12 [131]	Silencing the *CaSBP12* gene enhanced pepper plant tolerance to salt stress and decreased accumulation of ROS.
	CsHB5 [132]	Heterologous expression of *CsHB5* in citrus calli upregulated the expression of ROS-related genes and increased the content of H_2O_2 to against to senescence.
	HY5 [133]	Arabidopsis *ELONGATED HYPOCOTYL5* as a major transcription factor required for activation of the detoxification program under high N.
Other families	*MdZAT10* [134]	Heterologous expression of *MdZAT10* in apple calli decreased the expression level of *MdAPX2* and increased sensitivity to drought stress.
	MdHB7-like [135]	Heterologous expression of *MdHB7-like* reduced ROS under salt stress.
	OsMADS57 [136]	Overexpression of rice *OsMADS57* in both Arabidopsis thaliana and rice could improve their salt tolerance by increasing the activities of antioxidative enzymes.
	ZAT18 [137]	Heterologous expression of *ZAT18* in Arabidopsis improved drought tolerance and exhibited a lower content of ROS and higher antioxidant enzyme activities.

Multiple abiotic stresses occur simultaneously in the natural environment. Many transcription factors can help plants cope with multiple abiotic stresses that occur simultaneously. *HbWRKY82*, *CaNAC46*, *MYB49*, *AhbHLH112*, *MfbHLH38* and *MfPIF1* could alleviate oxidative damage caused by drought and salt stresses [78,88,92,100,116,117]. *ZmWRKY106* and *MYB44* also responded to drought and heat stresses [69,110]. *ERF74, 75* also help plants cope with drought, heat, excessive light and aluminum stresses [63].

The complex transcriptional regulatory network of ROS metabolism composed of these transcription factors plays an important role in the resistance to various abiotic stresses. However, the mechanism by which these transcription factors regulate ROS metabolism needs further exploration, which will provide new ideas for solving problems such as the crop yield reduction caused by abiotic stress.

3. The Mechanism by Which Exogenous Substances Regulate ROS Metabolism

Although plants have an efficient ROS regulation system, ROS are still inevitably produced in large amounts during an oxidative burst when plants are under stress conditions, and plants are inevitably damaged by ROS. Therefore, exploring the mechanism of ROS metabolism regulation via exogenous substances is of great significance for improving cultivated plant resistance to stress.

3.1. Plant Growth Regulators

3.1.1. Epibrassinolide (EBR)

Brassinolide (BRs) is an important phytosterol hormone, which regulates plant growth and development and improves plant resistance to abiotic stresses. In view of the low content of plant-synthesized brassinolide, cheap and efficient synthetic EBR is applied to agricultural production. Fan et al. found that application of EBR can regulate the xylem development of masson pine and accelerate its timber formation [138]. Zhang et al. found that application of EBR is good for the leaf size and expansion of tobacco [139]. Studies have shown that exogenous BR improves the activities of SOD, CAT, POD and APX; promotes the accumulation of AsA and GSH; and increases Fv/Fm, Φ (PSII) and qP [140–142]. Exogenous EBR regulates endogenous hormones by activating BR biosynthetic genes at the transcript level, which increases antioxidant enzyme capacity levels and reduces the overproduction of ROS [143]. A BR receptor, BRASSINOSTEROID-INSENSITIVE 1 (BRI1), negatively regulates antioxidant capacity [144]. BRASSINAZOLE RESISTANT 1 (BZR1), the critical regulator of the BR response, binds to the promoters of *FERONIA2* (*FER2*) and *FER3* and induces their expression. BZR1 regulates ROS scavenging through *RBOH1*-dependent ROS signaling, which is at least partially mediated by FER2 and FER3 [114]. Although it has long been reported that exogenous EBR can improve plant antioxidant capacity, a comprehensive analysis of the regulation of ROS metabolism by exogenous EBR still remains a challenge.

3.1.2. GR24

Strigolactone (SL) is a new type of plant hormone that plays an important role in the regulation of lateral growth and ROS metabolism in plants. GR24 is used in agricultural production as an artificial strigolactone analog. Several studies shown that GR24 facilitates light harvest and accumulation of anthocyanins in grapevine berries and tomato [145,146]. GR24 strengthens the enzyme activities of SOD, POD and CAT; promotes the accumulation of proline, GSH, AsA and GABA; and enhances the electron transport rate in PSII and PSI, the nonphotochemical quenching, the oxidized plastoquinone pool size and the ratio of the quantum yield of cyclic electron flow to Y (II) [147–150]. Interestingly, the AsA content in plants in turn affects endogenous SL metabolism in rice [151]. SL is believed to function in conjunction with ABA and JA [152,153]. NO signaling plays important roles in SL-regulated ROS metabolism [147]. However, the detailed mechanism by which SL regulates ROS metabolism is not fully clear. Furthermore, the appropriate SL dose application for different crops is also not clear.

3.1.3. Abscisic Acid (ABA)

Abscisic acid (ABA), as a hormone, has been intensively studied in order to elucidate its role in plant growth and material metabolism regulation and defense against abiotic stresses. Exogenous application of ABA reduces cold-induced oxidative stress by enhancing the activities of both enzymatic and nonenzymatic antioxidants in maize [154]. The cross-talk of both ABA and NO is believed to increase oxidative stress tolerance in plants, and NO may act downstream of ABA [155]. Furthermore, ABA triggers NO production and enhances counteracting oxidative stress [156]. However, how ABA regulates NO production to relieve oxidative stress still needs to be clarified. In contrast, in Arabidopsis, exogenous ABA inhibits AsA synthesis to promote the accumulation of ROS [157]. Therefore, the effect of exogenous ABA on the metabolism of ROS needs to be further explored.

3.1.4. Salicylic Acid (SA)

Salicylic acid (SA), as a hormone, has been intensively studied in order to elucidate its role in plant growth and material metabolism regulation and defense against biotic and abiotic stresses. Schussler et al. proposed that abscisic acid (ABA) may stimulate sucrose transport into filling seeds of legumes, potentially regulating seed growth rate [158]. Wang et al. reported that exogenous ABA application promotes anthocyanin and sugar

accumulation in grape berry [159]. Furthermore, many studies have shown that SA induces the generation of ROS by inhibiting mitochondrial complex III enzymatic activity and by activating RBOH [160,161]. In addition, SA blocks electron flow from the substrate dehydrogenases to the ubiquinone pool and triggers H_2O_2 generation [162]. Meanwhile, SA directly binds to CAT and APX, inhibiting their activities in tobacco and mammalian [163]. Subsequently, the ROS generated by SA activation acts as a signal, enhancing *StSABP2*, *StSOD* and *StAPX* expression and SOD, POD and CAT activities and upregulating the ASA-GSH cycle [39,164–168]. Therefore, the novel action of SA in ROS metabolism will likely continue to be unveiled.

3.1.5. Ethephon

Ethylene (ETH) is the only known gaseous plant hormone, so exogenous liquid ethephon, rather than gaseous ETH, has been used for plant growth regulation. Exogenous ethylene application could promote female flower differentiation of horticultural crops. Exogenous ethylene promotes mango fruit peel color transformation by regulating the degradation of chlorophyll and synthesis of anthocyanin and fructan accumulation in chicory [169,170]. Some scholars have found that exogenous application of ethephon can increase the content of H_2O_2 and can increase the activity of antioxidant enzymes and the content of antioxidant substances [74,171–175]. Jiang et al. found that ETH signaling upregulates RBOH expression, and that ROS accumulate in *RBOH* mutants. These findings suggest that ETH signaling has the potential to enhance antioxidant system activity by activating ROS signaling. Too much ETH, however, can cause oxidative stress [176]. Ethylene's ability to regulate ROS metabolism has been widely studied, but the effect of ETH doses on ROS metabolism is still unclear. Moreover, the precise molecular mechanisms by which ETH tunes the ROS scavenging and ROS production machinery to maintain proper ROS levels remain unclear.

3.2. Inorganic Substances

3.2.1. Ca^{2+}

As an essential medium element of plants, calcium participates in many life processes. Hou et al. found that exogenous Ca^{2+} application had a significant effect on *Brassica napus* height, root length, biomass accumulation and root structure formation, especially on the growth and development of coarse roots [177]. Ca^{2+} is the universal secondary messenger in plant stress signaling. Many studies have shown that exogenous Ca^{2+} is beneficial for plants in scavenging ROS [178–180]. In general, exogenous calcium stimulates the production of ROS, which acts as a signal to activate the ROS scavenging system in plants to avoid oxidative damage [36]. Calcium ions enhance RBOH activity and promote the production of plasma membrane ROS, which act as a signal to activate antioxidant enzymes (i.e., POD, CAT and SOD) and the antioxidant system of the AsA-GSH cycle in potato tuber [181]. Moreover, the Ca^{2+}/calmodulin system activates glutamate decarboxylase (GAD) in the cytosol, and concomitantly, gamma-aminobutyric acid (GABA) levels increase of soybean [182]. GABA, as a signal, can activate the ROS scavenging system in plants. Meanwhile, exogenous calcium alleviates PSII photoinhibition caused by ROS mainly by promoting carbon fixation, CEF, xanthophyll cycles, PQ pools, and ATPase activity, which affects the oxidative bursts that produce large amounts of ROS, as mentioned in Section 1.1 [183]. However, the mechanism by which calcium regulates GABA and the photosynthetic system still needs to be elucidated. In addition, calcium also directly regulates the ROS scavenging system. A Ca^{2+}-sensor, RESISTANCE OF RICE TO DISEASES1 (ROD1), directly scavenges ROS via catalase activation in Arabidopsis [184].

3.2.2. Sodium Nitroprusside (SNP)

Many studies have shown that exogenous nitric oxide (NO) provides protection against oxidative membrane damage for photosynthetic pigments, AsA-GSH and proline [185–190]. Notably, SNP acts as a donor of exogenous NO. NO is not only an ROS scav-

enger itself but also regulates the metabolism of ROS by functioning as a signal [191,192]. As a signal, NO combines with GSH to form *S*-nitrosoglutathione (GSNO) [193]. GSNO is transported in the phloem and activates the antioxidant system in the plant [194]. Transcriptome analysis has found that exogenous NO downregulates RBOH expression and upregulates *CAT*, *POD* and antioxidant synthesis gene expression in alfalfa seedlings [195]. After overexpression of the neuronal NO synthase gene *nNOS*, the expression levels of zinc finger protein transcription factors and C-repeat binding transcription factor (CBF) transcription factors increased, which indicated that zinc finger protein transcription factors and CBF transcription factors may be involved in NO regulation of the expression of antioxidant-related genes. Meanwhile, two ABA receptor genes, *AtPYL4* and *AtPYL5*, are also involved in NO-induced ROS scavenging in Arabidopsis [196]. However, the mechanism by which exogenous NO can improve the antioxidant capacity of plants still requires further research.

3.2.3. Other Inorganic Substances

Jia et al. reported that exogenous phosphorus reduced lipid peroxidation effects on SOD, CAT and POD activities of perennial ryegrass [197]. On the other hand, phosphorus also affects the plant photosynthesis system and thus affects the generation of ROS. H_2S is another inorganic substance of interest, as it can enhance plant tolerance to salt and heavy metal stresses by regulating Na^+/K^+ homeostasis and the uptake and transport of metal ions. H_2S also promotes the H_2S-Cys cycle balance under abiotic stress and enhances the roles of the cycle in the regulation of the antioxidant system in the alternative respiratory pathway, and in heavy metal chelator synthesis [198].

3.3. Organic Substances

3.3.1. Gamma-Aminobutyric Acid (GABA)

As a signaling molecule, GABA can regulate many physiological processes, including growth, development and stress responses. Xie et al. found that GABA negatively regulates adventitious root development in poplar and respiratory rate titratable acidity of apple but improves morphological growth of maize [199–201]. Many studies have shown that exogenous GABA elevates plant stress tolerance by improving photosynthesis, inhibiting ROS generation, and activating antioxidant enzymes [202–206]. Exogenous GABA application induces an increase in endogenous GABA. The potential mechanisms by which exogenous GABA alleviates oxidative injury may be related to the enhancement of plant antioxidant systems, which results in reductions in malondialdehyde (MDA) and ROS levels, and to proline accumulation-mediated osmoregulation. In contrast, Bouche et al. reported that in GABA-deficient mutant Arabidopsis with the *succinic semialdehyde dehydrogenase* (*ssadh*) phenotype, the level of ROS was significantly increased, and the mutants behaved abnormally and were more sensitive to stress [207]. Wang et al. proposed a potential mechanism whereby exogenous GABA mitigates oxidative damage caused by hypoxia in melon plants by accelerating polyamine biosynthesis and transformation to prevent polyamine degradation [205]. It has also been reported that exogenous GABA plays an antioxidant role by promoting *glutathione transferase* (*GST*) gene expression and enhancing GSH peroxidase activity to catalyze the binding reaction of GSH with various electrophilic exogenous chemicals. However, how GABA activates the ROS scavenging system remains unclear.

3.3.2. Polyamines

Polyamines, putrescine (Put), spermidine (Spd) and spermine (Spm), are widely present in plants and are closely related to plant growth and development. Qu et al. found that exogenous Put significantly ameliorated the losses of Chl and improved photochemical capability and prevented membrane impairment of *Nephrolepis cordifolia* [208]. Tavallali et al. reported exogenous Spd significantly increased levels of phenolic and flavonoid compounds in pot marigold [209]. Polyamines can not only scavenge ROS directly through disproportionation

reactions [210] but can also increase the content of antioxidant substances by increasing the activity of antioxidant enzymes [211]. Moreover, exogenous application of polyamines can maintain the activity of PSII of helianthus tuberosus and can reduce the production of ROS in PSI at the end of the chloroplast electron transport chain [212]. Moreover, polyamines inhibit RBOH activity and reduce the accumulation of hydrogen peroxide of cucumber cultivars [213]. However, the mechanism by which polyamines act as signals to activate the antioxidant system and regulate the expression of RBOH still needs further exploration.

3.3.3. Melatonin

Melatonin is a small molecule indoleamine substance, which has important functions in animals and plants. Xiao et al. found that 20 μM melatonin treatment optimally promotes cotton seed germination [214]. Melatonin increases the activities of various antioxidant enzymes and the levels of antioxidants such as AsA, GSH and phenolic compounds, thereby reducing ROS accumulation and alleviating oxidative damage induced by drought, chilling and aluminum stress [215–217]. However, the mechanism by which melatonin, as a signaling substance, regulates the metabolism of ROS under abiotic stress still needs to be further explored.

3.3.4. Sugars

Many studies have shown that sucrose, trehalose and chitosan can alleviate oxidative damage caused by abiotic stress [218–221]. Van den Ende et al. reported that sucrose and sucrose oligosaccharides are involved in stabilizing membrane-associated peroxidases and NADPH oxidases in Arabidopsis [219]. Trehalose plays an important role in resistance to adversity and abiotic stress, and these reports indicate that trehalose can enhance antioxidant systems, activate photosynthesis and protect cell structure [222,223]. Wang et al. reported that exogenous chitosan can improve photosynthetic capacity and antioxidant enzyme activity of banana plants and can reduce ROS induced by chilling injury [224]. Sugars are easy to obtain, are inexpensive and can be widely used in agricultural production. Therefore, it is important to analyze the mechanism by which sugars regulate ROS metabolism under stress. Furthermore, Tan et al. found exogenous sucrose could effectively promote vitamin C, sucrose and fructose contents of pea sprouts [225].

3.3.5. Other Organic Substances

Exogenous proline, L-carnitine, p-coumaric acid and GSH can alleviate oxidative damage caused by abiotic stress on salvia hispanica, Arabidopsis and barley seedlings [226–229]. However, the mechanism by which these exogenous substances regulate the metabolism of ROS under adverse conditions still needs to be further explored.

4. Conclusions and Perspectives

Because ROS play a dual role in plants, both as toxic byproducts and as signaling molecules, the ROS synthesis and ROS scavenging machineries are tightly regulated to achieve appropriate levels of ROS at different developmental stages and in different growing environments. However, with the deterioration of the natural environment, abiotic and biotic stresses such as drought, waterlogging, salinity and alkalinity disrupt the ROS balance in plants, which causes oxidative stress to the plant. Through transgenic technology, we can regulate the expression of TFs, reduce the oxidative damage caused by abiotic stress and improve the ability of plants to resist abiotic stress. On the other hand, the use of exogenous substances to regulate the generation and scavenging of ROS in plants has been widely studied with the aim of alleviating oxidative damage caused by biotic and abiotic stresses in cultivated plants (Figure 4). However, many questions remain unanswered, among which are the following:
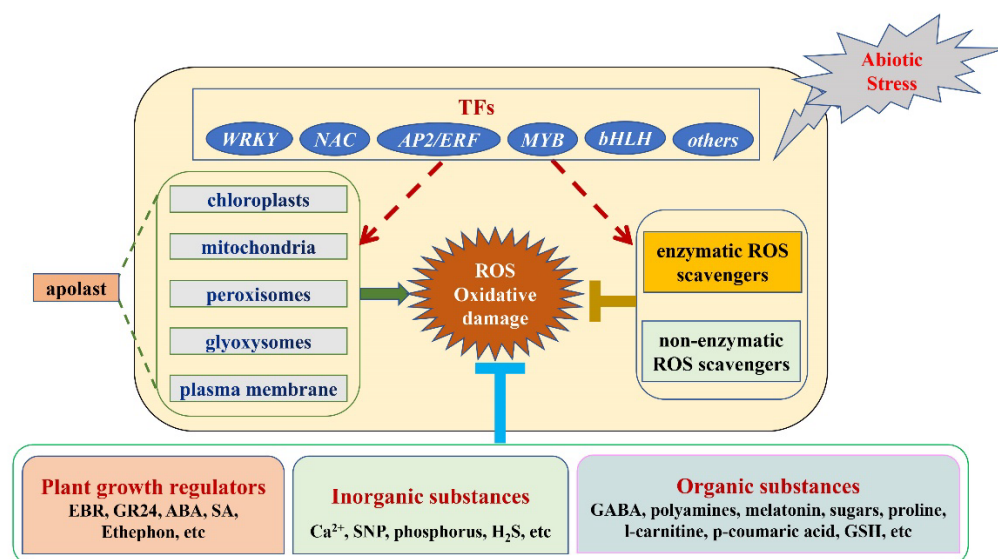
Figure 4. The model of transcription factors and exogenous substances regulate ROS metabolism under abiotic stress.

(1) Are there previously undiscovered forms of ROS and ROS generation and scavenging systems in plants?

(2) Although many transcription factors have been found to be involved in the regulation of ROS metabolism resistance to abiotic stress, specifically how they regulate ROS metabolism to resist abiotic stress is still unclear, and much work is still needed in this area.

(3) Although most of the aforementioned studies have shown that many exogenous substances can regulate the metabolism of ROS in plants in response to abiotic factors, there are some differences in the findings, which may be due to differences in the plant species and the amount of exogenously applied substances used in the studies. These divergent results require further investigation. The economic and environmental sustainability of applying these exogenous substances also needs to be considered. Most recent studies in this area have been on the effects of a single exogenous substance on the regulation of ROS. There are few reports on the effects of two or more exogenous additives on plant resistance to oxidative stress and ROS production; thus, additional research is needed. Furthermore, it is of great value to elucidate more types of exogenous substances and comprehensively evaluate their effects on the generation and scavenging of ROS in plants.

Such studies will further deepen our understanding of the role of ROS metabolism under abiotic stress in plants and may provide insights for developing new cultivation models.

Author Contributions: H.G. helped in the supervision, structuring, arranging of sub-topics, outlay conceptualization and overall shaping of the manuscript. P.L. and X.W. wrote the manuscript. P.L., X.W., B.G., G.L. and J.L. checked and revised the manuscript. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest: The authors declare that they have no conflict of interest.

References

1. Torres, M.A. ROS in biotic interactions. *Physiol. Plant.* **2010**, *138*, 414–429. [CrossRef] [PubMed]
2. Zurbriggen, M.D.; Carrillo, N.; Hajirezaei, M.-R. ROS signaling in the hypersensitive response: When, where and what for? *Plant Signal. Behav.* **2010**, *5*, 393–396. [CrossRef] [PubMed]

3. Oracz, K.; Karpiński, S. Phytohormones Signaling Pathways and ROS Involvement in Seed Germination. *Front. Plant Sci.* **2016**, *7*, 864. [CrossRef] [PubMed]

4. Ju, H.-W.; Koh, E.-J.; Kim, S.-H.; Kim, K.-I.; Lee, H.; Hong, S.-W. Glucosamine causes overproduction of reactive oxygen species, leading to repression of hypocotyl elongation through a hexokinase-mediated mechanism in Arabidopsis. *J. Plant Physiol.* **2009**, *166*, 203–212. [CrossRef] [PubMed]

5. Tsukagoshi, H.; Busch, W.; Benfey, P.N. Transcriptional Regulation of ROS Controls Transition from Proliferation to Differentiation in the Root. *Cell* **2010**, *143*, 606–616. [CrossRef] [PubMed]

6. Mhamdi, A.; Van Breusegem, F. Reactive oxygen species in plant development. *Development* **2018**, *145*, dev164376. [CrossRef] [PubMed]

7. Bailly, C. The signalling role of ROS in the regulation of seed germination and dormancy. *Biochem. J.* **2019**, *476*, 3019–3032. [CrossRef] [PubMed]

8. Prakash, V.; Vishwakarma, K.; Singh, V.; Rai, P.; Ramawat, N.; Tripathi, D.K.; Sharma, S. NO and ROS implications in organization of root system architecture. *Physiol. Plant.* **2019**, *168*, 473–489. [CrossRef] [PubMed]

9. Schippers, J.H.; Foyer, C.H.; van Dongen, J.T. Redox regulation in shoot growth, SAM maintenance and flowering. *Curr. Opin. Plant Biol.* **2016**, *29*, 121–128. [CrossRef] [PubMed]

10. Nadarajah, K.K. ROS Homeostasis in Abiotic Stress Tolerance in Plants. *Int. J. Mol. Sci.* **2020**, *21*, 5208. [CrossRef] [PubMed]

11. del Río, L.A. ROS and RNS in plant physiology: An overview. *J. Exp. Bot.* **2015**, *66*, 2827–2837. [CrossRef] [PubMed]

12. Zhu, J.-K. Abiotic Stress Signaling and Responses in Plants. *Cell* **2016**, *167*, 313–324. [CrossRef] [PubMed]

13. Singh, R.; Singh, S.; Parihar, P.; Mishra, R.K.; Tripathi, D.K.; Singh, V.P.; Chauhan, D.K.; Prasad, S.M. Reactive Oxygen Species (ROS): Beneficial Companions of Plant' Developmental Processes. *Front. Plant Sci.* **2016**, *7*, 1299. [CrossRef] [PubMed]

14. Mittler, R. ROS Are Good. *Trends Plant Sci.* **2017**, *22*, 11–19. [CrossRef]

15. Kadota, Y.; Shirasu, K.; Zipfel, C. Regulation of the NADPH Oxidase RBOHD During Plant Immunity. *Plant Cell Physiol.* **2015**, *56*, 1472–1480. [CrossRef]

16. Cheng, X.; Li, G.; Manzoor, M.A.; Wang, H.; Abdullah, M.; Su, X.; Zhang, J.; Jiang, T.; Jin, Q.; Cai, Y.; et al. In Silico Genome-Wide Analysis of Respiratory Burst Oxidase Homolog (RBOH) Family Genes in Five Fruit-Producing Trees, and Potential Functional Analysis on Lignification of Stone Cells in Chinese White Pear. *Cells* **2019**, *8*, 520. [CrossRef]

17. Sun, H.; Cao, X.; Wang, X.; Zhang, W.; Li, W.; Wang, X.; Liu, S.; Lyu, D. RBOH-dependent hydrogen peroxide signaling mediates melatonin-induced anthocyanin biosynthesis in red pear fruit. *Plant Sci.* **2021**, *313*, 111093. [CrossRef]

18. Chu-Puga, A.; González-Gordo, S.; Rodríguez-Ruiz, M.; Palma, J.M.; Corpas, F.J. NADPH Oxidase (Rboh) Activity is Up Regulated during Sweet Pepper (*Capsicum annuum* L.) Fruit Ripening. *Antioxidants* **2019**, *8*, 9. [CrossRef]

19. Orman-Ligeza, B.; Parizot, B.; de Rycke, R.; Fernandez, A.; Himschoot, E.; Van Breusegem, F.; Bennett, M.J.; Périlleux, C.; Beeckman, T.; Draye, X. RBOH-mediated ROS production facilitates lateral root emergence in Arabidopsis. *Development* **2016**, *143*, 3328–3339. [CrossRef]

20. Liu, B.; Sun, L.; Ma, L.; Hao, F.-S. Both AtrbohD and AtrbohF are essential for mediating responses to oxygen deficiency in Arabidopsis. *Plant Cell Rep.* **2017**, *36*, 947–957. [CrossRef]

21. Ren, X.; Wang, M.; Wang, Y.; Huang, A. Superoxide anion generation response to wound in Arabidopsis hypocotyl cutting. *Plant Signal. Behav.* **2020**, *16*, 1848086. [CrossRef] [PubMed]

22. Kurusu, T.; Kuchitsu, K.; Tada, Y. Plant signaling networks involving Ca2+ and Rboh/Nox-mediated ROS production under salinity stress. *Front. Plant Sci.* **2015**, *6*, 427. [CrossRef]

23. Asai, S.; Ichikawa, T.; Nomura, H.; Kobayashi, M.; Kamiyoshihara, Y.; Mori, H.; Kadota, Y.; Zipfel, C.; Jones, J.D.G.; Yoshioka, H. The Variable Domain of a Plant Calcium-dependent Protein Kinase (CDPK) Confers Subcellular Localization and Substrate Recognition for NADPH Oxidase. *J. Biol. Chem.* **2013**, *288*, 14332–14340. [CrossRef] [PubMed]

24. Kobayashi, M.; Ohura, I.; Kawakita, K.; Yokota, N.; Fujiwara, M.; Shimamoto, K.; Doke, N.; Yoshioka, H. Calcium-Dependent Protein Kinases Regulate the Production of Reactive Oxygen Species by Potato NADPH Oxidase. *Plant Cell* **2007**, *19*, 1065–1080. [CrossRef] [PubMed]

25. Jakubowicz, M.; Gałgańska, H.; Nowak, W.; Sadowski, J. Exogenously induced expression of ethylene biosynthesis, ethylene perception, phospholipase D, and Rboh-oxidase genes in broccoli seedlings. *J. Exp. Bot.* **2010**, *61*, 3475–3491. [CrossRef] [PubMed]

26. Park, J.; Gu, Y.; Lee, Y.; Yang, Z.; Lee, Y. Phosphatidic Acid Induces Leaf Cell Death in Arabidopsis by Activating the Rho-Related Small G Protein GTPase-Mediated Pathway of Reactive Oxygen Species Generation. *Plant Physiol.* **2004**, *134*, 129–136. [CrossRef]

27. Gilroy, S.; Białasek, M.; Suzuki, N.; Górecka, M.; Devireddy, A.R.; Karpiński, S.; Mittler, R. ROS, Calcium, and Electric Signals: Key Mediators of Rapid Systemic Signaling in Plants. *Plant Physiol.* **2016**, *171*, 1606–1615. [CrossRef]

28. Kerchev, P.; Waszczak, C.; Lewandowska, A.; Willems, P.; Shapiguzov, A.; Li, Z.; Alseekh, S.; Mühlenbock, P.; Hoeberichts, F.A.; Huang, J.; et al. Lack of GLYCOLATE OXIDASE1, but Not GLYCOLATE OXIDASE2, Attenuates the Photorespiratory Phenotype of CATALASE2-Deficient Arabidopsis. *Plant Physiol.* **2016**, *171*, 1704–1719. [CrossRef]

29. Rodríguez-Serrano, M.; Romero-Puertas, M.C.; Sanz-Fernández, M.; Hu, J.; Sandalio, L.M. Peroxisomes Extend Peroxules in a Fast Response to Stress via a Reactive Oxygen Species-Mediated Induction of the Peroxin PEX11a. *Plant Physiol.* **2016**, *171*, 1665–1674. [CrossRef]

30. Hou, J.; Xia, X.J.; Zhou, Y.H.; Shi, K.; Chen, Z.X.; Yu, J.Q. RBOH1-dependent H2O2 production and subsequent activation of MPK1/2 play an important role in acclimation-induced cross-tolerance in tomato. *J. Exp. Bot.* **2014**, *65*, 595–607.

31. Torres, M.A.; Dangl, J.L.; Jones, J.D.G. Arabidopsis gp91phox homologues AtrbohD and AtrbohF are required for accumulation of reactive oxygen intermediates in the plant defense response. *Proc. Natl. Acad. Sci. USA* **2002**, *99*, 517–522. [CrossRef] [PubMed]

32. Kwak, J.M.; Mori, I.C.; Pei, Z.; Leonhardt, N.; Torres, M.A.; Dangl, J.L.; Bloom, R.E.; Bodde, S.; Jones, J.D.; Schroeder, J.I. NADPH oxidase AtrbohD and AtrbohF genes function in ROS-dependent ABA signaling in Arabidopsis. *EMBO J.* **2003**, *22*, 2623–2633. [CrossRef] [PubMed]

33. Kabała, K.; Reda, M.; Wdowikowska, A.; Janicka, M. Role of Plasma Membrane NADPH Oxidase in Response to Salt Stress in Cucumber Seedlings. *Antioxidants* **2022**, *11*, 1534. [CrossRef] [PubMed]

34. Gémes, K.; Kim, Y.J.; Park, K.Y.; Moschou, P.N.; Andronis, E.; Valassaki, C.; Roussis, A.; Roubelakis-Angelakis, K.A. An NADPH-Oxidase/Polyamine Oxidase Feedback Loop Controls Oxidative Burst Under Salinity. *Plant Physiol.* **2016**, *172*, 1418–1431. [CrossRef]

35. Di, Q.; Li, Y.; Li, S.; Shi, A.; Zhou, M.; Ren, H.; Yan, Y.; He, C.; Wang, J.; Sun, M.; et al. Photosynthesis Mediated by *RBOH*-Dependent Signaling Is Essential for Cold Stress Memory. *Antioxidants* **2022**, *11*, 969. [CrossRef]

36. Zhang, X.; Bian, A.; Li, T.; Ren, L.; Li, L.; Su, Y.; Zhang, Q. ROS and calcium oscillations are required for polarized root hair growth. *Plant Signal. Behav.* **2022**, *17*, 2106410. [CrossRef]

37. Voothuluru, P.; Thompson, H.J.; Flint-Garcia, S.A.; Sharp, R.E. Genetic variability of oxalate oxidase activity and elongation in water-stressed primary roots of diverse maize and rice lines. *Plant Signal. Behav.* **2013**, *8*, e23454. [CrossRef]

38. Berna, A.; Bernier, F. Regulation by biotic and abiotic stress of a wheat germin gene encoding oxalate oxidase, a H_2O_2-producing enzyme. *Plant Mol. Biol.* **1999**, *39*, 539–549. [CrossRef]

39. Li, Z.; Wakao, S.; Fischer, B.B.; Niyogi, K.K. Sensing and Responding to Excess Light. *Annu. Rev. Plant Biol.* **2009**, *60*, 239–260. [CrossRef]

40. Murchie, E.H.; Niyogi, K.K. Manipulation of Photoprotection to Improve Plant Photosynthesis. *Plant Physiol.* **2011**, *155*, 86–92. [CrossRef]

41. Noctor, G.; Foyer, C.H. Ascorbate and glutathione: Keeping active oxygen under control. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1998**, *49*, 249–279. [CrossRef] [PubMed]

42. Müller, P.; Li, X.-P.; Niyogi, K.K. Non-Photochemical Quenching. A Response to Excess Light Energy. *Plant Physiol.* **2001**, *125*, 1558–1566. [CrossRef] [PubMed]

43. Ruban, A.V. Nonphotochemical Chlorophyll Fluorescence Quenching: Mechanism and Effectiveness in Protecting Plants from Photodamage. *Plant Physiol.* **2016**, *170*, 1903–1916. [CrossRef]

44. Marchi, S.; Giorgi, C.; Suski, J.M.; Agnoletto, C.; Bononi, A.; Bonora, M.; De Marchi, E.; Missiroli, S.; Patergnani, S.; Poletti, F.; et al. Mitochondria-Ros Crosstalk in the Control of Cell Death and Aging. *J. Signal Transduct.* **2011**, *2012*, 1–17. [CrossRef] [PubMed]

45. Steffens, B.; Steffens, B. The role of ethylene and ROS in salinity, heavy metal, and flooding responses in rice. *Front. Plant Sci.* **2014**, *5*, 685. [CrossRef] [PubMed]

46. Rhoads, D.M.; Umbach, A.L.; Subbaiah, C.C.; Siedow, J.N. Mitochondrial Reactive Oxygen Species. Contribution to Oxidative Stress and Interorganellar Signaling. *Plant Physiol.* **2006**, *141*, 357–366. [CrossRef] [PubMed]

47. Dröse, S.; Brandt, U. Molecular Mechanisms of Superoxide Production by the Mitochondrial Respiratory Chain. In *Advances in Experimental Medicine and Biology*; Springer: Berlin/Heidelberg, Germany, 2012; Volume 748, pp. 145–169. [CrossRef]

48. Foyer, C.H.; Noctor, G. Redox homeostasis and antioxidant signaling: A metabolic interface between stress perception and physiological responses. *Plant Cell.* **2005**, *17*, 1866–1875. [CrossRef] [PubMed]

49. Takahashi, S.; Murata, N. How do environmental stresses accelerate photoinhibition? *Trends Plant Sci.* **2008**, *13*, 178–182. [CrossRef]

50. Gururani, M.A.; Venkatesh, J.; Tran, L.S.P. Regulation of Photosynthesis during Abiotic Stress-Induced Photoinhibition. *Mol. Plant* **2015**, *8*, 1304–1320. [CrossRef]

51. Maslenkova, L.T.; Zanev, Y.; Popova, L.P. Effect of abscisic acid on the photosynthetic oxygen evolution in barley chloroplasts. *Photosyn. Res.* **1989**, *21*, 45–50. [CrossRef]

52. Xu, Y.H.; Liu, R.; Yan, L.; Liu, Z.Q.; Jiang, S.C.; Shen, Y.Y.; Wang, X.F.; Zhang, D.P. Light-harvesting chlorophyll a/b-binding proteins are required for stomatal response to abscisic acid in Arabidopsis. *J. Exp. Bot.* **2012**, *63*, 1095–1106. [CrossRef] [PubMed]

53. Gill, S.S.; Tuteja, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.* **2010**, *48*, 909–930. [CrossRef] [PubMed]

54. Ahmad, P.; Jaleel, C.A.; Salem, M.A.; Nabi, G.; Sharma, S. Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. *Crit. Rev. Biotechnol.* **2010**, *30*, 161–175. [CrossRef] [PubMed]

55. Harb, A.; Krishnan, A.; Ambavaram, M.M.; Pereira, A. Molecular and Physiological Analysis of Drought Stress in Arabidopsis Reveals Early Responses Leading to Acclimation in Plant Growth. *Plant Physiol.* **2010**, *154*, 1254–1271. [CrossRef]

56. Elsawy, H.I.; Mekawy, A.; Elhity, M.A.; Abdel-Dayem, S.M.; Abdelaziz, M.N.; Assaha, D.V.; Ueda, A.; Saneoka, H. Differential responses of two Egyptian barley (*Hordeum vulgare* L.) cultivars to salt stress. *Plant Physiol. Biochem.* **2018**, *127*, 425–435. [CrossRef]

57. Petrussa, E.; Braidot, E.; Zancani, M.; Peresson, C.; Bertolini, A.; Patui, S.; Vianello, A. Plant Flavonoids—Biosynthesis, Transport and Involvement in Stress Responses. *Int. J. Mol. Sci.* **2013**, *14*, 14950–14973. [CrossRef]

58. Kaling, M.; Kanawati, B.; Ghirardo, A.; Albert, A.; Winkler, J.B.; Heller, W.; Barta, C.; Loreto, F.; Schmitt-Kopplin, P.; Schnitzler, J.-P. UV-B mediated metabolic rearrangements in poplar revealed by non-targeted metabolomics. *Plant Cell Environ.* **2014**, *38*, 892–904. [CrossRef]

59. Abouzeid, S.; Beutling, U.; Selmar, D. Stress-induced modification of indole alkaloids:Phytomodificines as a new category of specialized metabolites. *Phytochemistry* **2018**, *159*, 102–107. [CrossRef]

60. Nomura, M.; Ma, W.Y.; Huang, C.; Yang, C.S.; Bowden, G.T.; Miyamoto, K.I.; Dong, Z. Inhibition of ultraviolet B-induced AP-1 activation by theaflavins from black tea. *Mol Carcinog.* **2000**, *28*, 148–155. [CrossRef]

61. Alseekh, S.; Ofner, I.; Liu, Z.; Osorio, S.; Vallarino, J.; Last, R.L.; Zamir, D.; Tohge, T.; Fernie, A.R. Quantitative trait loci analysis of seed-specialized metabolites reveals seed-specific flavonols and differential regulation of glycoalkaloid content in tomato. *Plant J.* **2020**, *103*, 2007–2024. [CrossRef]

62. Liu, D.; Li, Y.-Y.; Zhou, Z.-C.; Xiang, X.; Liu, X.; Wang, J.; Hu, Z.-R.; Xiang, S.-P.; Li, W.; Xiao, Q.-Z.; et al. Tobacco transcription factor bHLH123 improves salt tolerance by activating NADPH oxidase *NtRbohE* expression. *Plant Physiol.* **2021**, *186*, 1706–1720. [CrossRef] [PubMed]

63. Yao, Y.; He, R.J.; Xie, Q.L.; Zhao, X.H.; Deng, X.M.; He, J.B.; Song, L.; He, J.; Marchant, A.; Chen, X.Y.; et al. ETHYLENE RESPONSE FACTOR 74 (ERF74) plays an essential role in controlling a respiratory burst oxidase homolog D (RbohD)-dependent mechanism in response to different stresses in Arabidopsis. *New Phytol.* **2017**, *213*, 1667–1681. [CrossRef] [PubMed]

64. El-Esawi, M.A.; Al-Ghamdi, A.A.; Ali, H.M.; Ahmad, M. Overexpression of AtWRKY30 Transcription Factor Enhances Heat and Drought Stress Tolerance in Wheat (*Triticum aestivum* L.). *Genes* **2019**, *10*, 163. [CrossRef] [PubMed]

65. Sun, J.; Hu, W.; Zhou, R.; Wang, L.; Wang, X.; Wang, Q.; Feng, Z.; Li, Y.; Qiu, D.; He, G.; et al. The Brachypodium distachyon BdWRKY36 gene confers tolerance to drought stress in transgenic tobacco plants. *Plant Cell Rep.* **2014**, *34*, 23–35. [CrossRef] [PubMed]

66. Yang, Z.; Chi, X.; Guo, F.; Jin, X.; Luo, H.; Hawar, A.; Chen, Y.; Feng, K.; Wang, B.; Qi, J.; et al. SbWRKY30 enhances the drought tolerance of plants and regulates a drought stress-responsive gene, SbRD19, in sorghum. *J. Plant Physiol.* **2020**, *246–247*, 153142. [CrossRef]

67. Li, J.-B.; Luan, Y.-S.; Liu, Z. Overexpression of *SpWRKY1* promotes resistance to *Phytophthora nicotianae* and tolerance to salt and drought stress in transgenic tobacco. *Physiol. Plant.* **2015**, *155*, 248–266. [CrossRef]

68. Wang, C.-T.; Ru, J.-N.; Liu, Y.-W.; Yang, J.-F.; Li, M.; Xu, Z.-S.; Fu, J.-D. The Maize WRKY Transcription Factor ZmWRKY40 Confers Drought Resistance in Transgenic Arabidopsis. *Int. J. Mol. Sci.* **2018**, *19*, 2580. [CrossRef]

69. Wang, C.-T.; Ru, J.-N.; Liu, Y.-W.; Li, M.; Zhao, D.; Yang, J.-F.; Fu, J.-D.; Xu, Z.-S. Maize WRKY Transcription Factor ZmWRKY106 Confers Drought and Heat Tolerance in Transgenic Plants. *Int. J. Mol. Sci.* **2018**, *19*, 3046. [CrossRef]

70. Thirumalaikumar, V.P.; Devkar, V.; Mehterov, N.; Ali, S.; Ozgur, R.; Turkan, I.; Mueller-Roeber, B.; Balazadeh, S. NAC transcription factor JUNGBRUNNEN1 enhances drought tolerance in tomato. *Plant Biotechnol. J.* **2017**, *16*, 354–366. [CrossRef]

71. Borgohain, P.; Saha, B.; Agrahari, R.; Chowardhara, B.; Sahoo, S.; van der Vyver, C.; Panda, S.K. SlNAC2 overexpression in Arabidopsis results in enhanced abiotic stress tolerance with alteration in glutathione metabolism. *Protoplasma* **2019**, *256*, 1065–1077. [CrossRef]

72. Niu, F.; Wang, C.; Yan, J.; Guo, X.; Wu, F.; Yang, B.; Deyholos, M.K.; Jiang, Y.-Q. Functional characterization of NAC55 transcription factor from oilseed rape (*Brassica napus* L.) as a novel transcriptional activator modulating reactive oxygen species accumulation and cell death. *Plant Mol. Biol.* **2016**, *92*, 89–104. [CrossRef] [PubMed]

73. Zhao, Q.; Fan, Z.; Qiu, L.; Che, Q.; Wang, T.; Li, Y.; Wang, Y. MdbHLH130, an Apple bHLH Transcription Factor, Confers Water Stress Resistance by Regulating Stomatal Closure and ROS Homeostasis in Transgenic Tobacco. *Front. Plant Sci.* **2020**, *11*, 543696. [CrossRef] [PubMed]

74. Wu, L.; Zhang, Z.; Zhang, H.; Wang, X.-C.; Huang, R. Transcriptional Modulation of Ethylene Response Factor Protein JERF3 in the Oxidative Stress Response Enhances Tolerance of Tobacco Seedlings to Salt, Drought, and Freezing. *Plant Physiol.* **2008**, *148*, 1953–1963. [CrossRef] [PubMed]

75. Chen, T.; Li, W.; Hu, X.; Guo, J.; Liu, A.; Zhang, B. A Cotton MYB Transcription Factor, GbMYB5, is Positively Involved in Plant Adaptive Response to Drought Stress. *Plant Cell Physiol.* **2015**, *56*, 917–929. [CrossRef] [PubMed]

76. Wei, Q.; Zhang, F.; Sun, F.; Luo, Q.; Wang, R.; Hu, R.; Chen, M.; Chang, J.; Yang, G.; He, G. A wheat MYB transcriptional repressor TaMyb1D regulates phenylpropanoid metabolism and enhances tolerance to drought and oxidative stresses in transgenic tobacco plants. *Plant Sci.* **2017**, *265*, 112–123. [CrossRef]

77. Li, K.; Xing, C.; Yao, Z.; Huang, X. *PbrMYB21*, a novel MYB protein of *Pyrus betulaefolia*, functions in drought tolerance and modulates polyamine levels by regulating arginine decarboxylase gene. *Plant Biotechnol. J.* **2017**, *15*, 1186–1203. [CrossRef]

78. Li, C.; Yan, C.; Sun, Q.; Wang, J.; Yuan, C.; Mou, Y.; Shan, S.; Zhao, X. The bHLH transcription factor AhbHLH112 improves the drought tolerance of peanut. *BMC Plant Biol.* **2021**, *21*, 540. [CrossRef]

79. Cui, X.-Y.; Gao, Y.; Guo, J.; Yu, T.-F.; Zheng, W.-J.; Liu, Y.-W.; Chen, J.; Xu, Z.-S.; Ma, Y.-Z. BES/BZR Transcription Factor TaBZR2 Positively Regulates Drought Responses by Activation of *TaGST1*. *Plant Physiol.* **2019**, *180*, 605–620. [CrossRef]

80. Meng, D.; Li, Y.; Bai, Y.; Li, M.; Cheng, L. Genome-wide identification and characterization of WRKY transcriptional factor family in apple and analysis of their responses to waterlogging and drought stress. *Plant Physiol. Biochem.* **2016**, *103*, 71–83. [CrossRef]

81. Liu, B.; Jiang, Y.; Tang, H.; Tong, S.; Lou, S.; Shao, C.; Zhang, J.; Song, Y.; Chen, N.; Bi, H.; et al. The ubiquitin E3 ligase SR1 modulates the submergence response by degrading phosphorylated WRKY33 in *Arabidopsis*. *Plant Cell* **2021**, *33*, 1771–1789. [CrossRef]

82. Gonzali, S.; Loreti, E.; Cardarelli, F.; Novi, G.; Parlanti, S.; Pucciariello, C.; Bassolino, L.; Banti, V.; Licausi, F.; Perata, P. Universal stress protein HRU1 mediates ROS homeostasis under anoxia. *Nat. Plants* **2015**, *1*, 15151. [CrossRef] [PubMed]

83. Park, H.-Y.; Seok, H.-Y.; Woo, D.-H.; Lee, S.-Y.; Tarte, V.N.; Lee, E.-H.; Lee, C.-H.; Moon, Y.-H. AtERF71/HRE2 transcription factor mediates osmotic stress response as well as hypoxia response in Arabidopsis. *Biochem. Biophys. Res. Commun.* **2011**, *414*, 135–141. [CrossRef] [PubMed]

84. Fukao, T.; Yeung, E.; Bailey-Serres, J. The Submergence Tolerance Regulator SUB1A Mediates Crosstalk between Submergence and Drought Tolerance in Rice. *Plant Cell* **2011**, *23*, 412–427. [CrossRef] [PubMed]

85. Zhu, H.; Jiang, Y.; Guo, Y.; Huang, J.; Zhou, M.; Tang, Y.; Sui, J.; Wang, J.; Qiao, L. A novel salt inducible WRKY transcription factor gene, AhWRKY75, confers salt tolerance in transgenic peanut. *Plant Physiol. Biochem.* **2021**, *160*, 175–183. [CrossRef]

86. Bao, W.; Wang, X.; Chen, M.; Chai, T.; Wang, H. A WRKY transcription factor, PcWRKY33, from Polygonum cuspidatum reduces salt tolerance in transgenic Arabidopsis thaliana. *Plant Cell Rep.* **2018**, *37*, 1033–1048. [CrossRef]

87. Xiang, X.-Y.; Chen, J.; Xu, W.-X.; Qiu, J.-R.; Song, L.; Wang, J.-T.; Tang, R.; Chen, D.; Jiang, C.-Z.; Huang, Z. Dehydration-Induced WRKY Transcriptional Factor MfWRKY70 of *Myrothamnus flabellifolia* Enhanced Drought and Salinity Tolerance in *Arabidopsis*. *Biomolecules* **2021**, *11*, 327. [CrossRef]

88. Kang, G.; Yan, D.; Chen, X.; Yang, L.; Zeng, R. HbWRKY82, a novel IIc WRKY transcription factor from Hevea brasiliensis associated with abiotic stress tolerance and leaf senescence in Arabidopsis. *Physiol. Plant.* **2020**, *171*, 151–160. [CrossRef]

89. Lv, B.; Wu, Q.; Wang, A.; Li, Q.; Dong, Q.; Yang, J.; Zhao, H.; Wang, X.; Chen, H.; Li, C. A WRKY transcription factor, FtWRKY46, from Tartary buckwheat improves salt tolerance in transgenic Arabidopsis thaliana. *Plant Physiol. Biochem.* **2019**, *147*, 43–53. [CrossRef]

90. Li, M.; Chen, R.; Jiang, Q.; Sun, X.; Zhang, H.; Hu, Z. GmNAC06, a NAC domain transcription factor enhances salt stress tolerance in soybean. *Plant Mol. Biol.* **2020**, *105*, 333–345. [CrossRef]

91. Ma, B.; Liu, X.; Guo, S.; Xie, X.; Zhang, J.; Wang, J.; Zheng, L.; Wang, Y. RtNAC100 involved in the regulation of ROS, Na+ accumulation and induced salt-related PCD through MeJA signal pathways in recretohalophyte Reaumuria trigyna. *Plant Sci.* **2021**, *310*, 110976. [CrossRef]

92. Ma, J.; Wang, L.-Y.; Dai, J.-X.; Wang, Y.; Lin, D. The NAC-type transcription factor CaNAC46 regulates the salt and drought tolerance of transgenic Arabidopsis thaliana. *BMC Plant Biol.* **2021**, *21*, 11. [CrossRef] [PubMed]

93. Melo, B.P.; Lourenço-Tessutti, I.T.; Fraga, O.T.; Pinheiro, L.B.; Lins, C.B.D.J.; Morgante, C.V.; Engler, J.A.; Reis, P.A.B.; Grossi-De-Sá, M.F.; Fontes, E.P.B. Contrasting roles of GmNAC065 and GmNAC085 in natural senescence, plant development, multiple stresses and cell death responses. *Sci. Rep.* **2021**, *11*, 11178. [CrossRef] [PubMed]

94. Han, D.; Du, M.; Zhou, Z.; Wang, S.; Li, T.; Han, J.; Xu, T.; Yang, G. Overexpression of a *Malus baccata* NAC Transcription Factor Gene MbNAC25 Increases Cold and Salinity Tolerance in Arabidopsis. *Int. J. Mol. Sci.* **2020**, *21*, 1198. [CrossRef] [PubMed]

95. Fu, J.; Zhu, C.; Wang, C.; Liu, L.; Shen, Q.; Xu, D.; Wang, Q. Maize transcription factor ZmEREB20 enhanced salt tolerance in transgenic Arabidopsis. *Plant Physiol. Biochem.* **2020**, *159*, 257–267. [CrossRef]

96. Lu, L.; Qanmber, G.; Li, J.; Pu, M.; Chen, G.; Li, S.; Liu, L.; Qin, W.; Ma, S.; Wang, Y.; et al. Identification and Characterization of the ERF Subfamily B3 Group Revealed GhERF13.12 Improves Salt Tolerance in Upland Cotton. *Front. Plant Sci.* **2021**, *12*, 705883. [CrossRef]

97. Li, Z.; Tian, Y.; Xu, J.; Fu, X.; Gao, J.; Wang, B.; Han, H.; Wang, L.; Peng, R.; Yao, Q. A tomato ERF transcription factor, SlERF84, confers enhanced tolerance to drought and salt stress but negatively regulates immunity against Pseudomonas syringae pv. tomato DC3000. *Plant Physiol. Biochem.* **2018**, *132*, 683–695. [CrossRef]

98. Wang, D.; Sun, Z.; Hu, X.; Xiong, J.; Hu, L.; Xu, Y.; Tang, Y.; Wu, Y. The key regulator LcERF056 enhances salt tolerance by modulating reactive oxygen species-related genes in Lotus corniculatus. *BMC Plant Biol.* **2021**, *21*, 605. [CrossRef]

99. Zhang, X.; Chen, L.; Shi, Q.; Ren, Z. SlMYB102, an R2R3-type MYB gene, confers salt tolerance in transgenic tomato. *Plant Sci.* **2019**, *291*, 110356. [CrossRef]

100. Cui, J.; Jiang, N.; Zhou, X.; Hou, X.; Yang, G.; Meng, J.; Luan, Y. Tomato MYB49 enhances resistance to Phytophthora infestans and tolerance to water deficit and salt stress. *Planta* **2018**, *248*, 1487–1503. [CrossRef]

101. Zhu, X.; Li, X.; He, Q.; Guo, D.; Liu, C.; Cao, J.; Wu, Z.; Kang, Z.; Wang, X. TaMYB29: A Novel R2R3-MYB Transcription Factor Involved in Wheat Defense Against Stripe Rust. *Front. Plant Sci.* **2021**, *12*, 783388. [CrossRef]

102. Wang, Y.; Wang, S.; Tian, Y.; Wang, Q.; Chen, S.; Li, H.; Ma, C.; Li, H. Functional Characterization of a Sugar Beet *BvbHLH93* Transcription Factor in Salt Stress Tolerance. *Int. J. Mol. Sci.* **2021**, *22*, 3669. [CrossRef] [PubMed]

103. He, F.; Niu, M.-X.; Feng, C.-H.; Li, H.-G.; Su, Y.; Su, W.-L.; Pang, H.; Yang, Y.; Yu, X.; Wang, H.-L.; et al. PeSTZ1 confers salt stress tolerance by scavenging the accumulation of ROS through regulating the expression of PeZAT12 and PeAPX2 in Populus. *Tree Physiol.* **2020**, *40*, 1292–1311. [CrossRef] [PubMed]

104. Fei, J.; Wang, Y.-S.; Cheng, H.; Su, Y.-B.; Zhong, Y.-J.; Zheng, L. The Kandelia obovata transcription factor KoWRKY40 enhances cold tolerance in transgenic Arabidopsis. *BMC Plant Biol.* **2022**, *22*, 274. [CrossRef] [PubMed]

105. Hou, X.-M.; Zhang, H.-F.; Liu, S.-Y.; Wang, X.-K.; Zhang, Y.-M.; Meng, Y.-C.; Luo, D.; Chen, R.-G. The NAC transcription factor CaNAC064 is a regulator of cold stress tolerance in peppers. *Plant Sci.* **2020**, *291*, 110346. [CrossRef] [PubMed]

106. Xing, C.; Liu, Y.; Zhao, L.; Zhang, S.; Huang, X. A novel MYB transcription factor regulates ascorbic acid synthesis and affects cold tolerance. *Plant Cell Environ.* **2018**, *42*, 832–845. [CrossRef] [PubMed]

107. Lattanzio, V.; Di Venere, D.; Linsalata, V.; Bertolini, P.; Ippolito, A.; Salerno, M. Low Temperature Metabolism of Apple Phenolics and Quiescence of *Phlyctaena vagabunda*. *J. Agric. Food Chem.* **2001**, *49*, 5817–5821. [CrossRef]

108. An, J.-P.; Wang, X.-F.; Zhang, X.-W.; Xu, H.-F.; Bi, S.-Q.; You, C.-X.; Hao, Y.-J. An apple MYB transcription factor regulates cold tolerance and anthocyanin accumulation and undergoes MIEL1-mediated degradation. *Plant Biotechnol. J.* **2019**, *18*, 337–353. [CrossRef]

109. Fang, H.; Dong, Y.; Yue, X.; Hu, J.; Jiang, S.; Xu, H.; Wang, Y.; Su, M.; Zhang, J.; Zhang, Z.; et al. The B-box zinc finger protein MdBBX20 integrates anthocyanin accumulation in response to ultraviolet radiation and low temperature. *Plant Cell Environ.* **2019**, *42*, 2090–2104. [CrossRef]

110. Li, J.; Zhao, S.; Yu, X.; Du, W.; Li, H.; Sun, Y.; Sun, H.; Ruan, C. Role of Xanthoceras sorbifolium MYB44 in tolerance to combined drought and heat stress via modulation of stomatal closure and ROS homeostasis. *Plant Physiol. Biochem.* **2021**, *162*, 410–420. [CrossRef]

111. Singh, S.; Chopperla, R.; Shingote, P.; Chhapekar, S.S.; Deshmukh, R.; Khan, S.; Padaria, J.C.; Sharma, T.R.; Solanke, A.U. Overexpression of EcDREB2A transcription factor from finger millet in tobacco enhances tolerance to heat stress through ROS scavenging. *J. Biotechnol.* **2021**, *336*, 10–24. [CrossRef]

112. Wang, C.; Zhou, Y.; Yang, X.; Zhang, B.; Xu, F.; Wang, Y.; Song, C.; Yi, M.; Ma, N.; Zhou, X.; et al. The Heat Stress Transcription Factor LlHsfA4 Enhanced Basic Thermotolerance through Regulating ROS Metabolism in Lilies (*Lilium Longiflorum*). *Int. J. Mol. Sci.* **2022**, *23*, 572. [CrossRef] [PubMed]

113. Wang, J.; Chen, L.; Long, Y.; Si, W.; Cheng, B.; Jiang, H. A Novel Heat Shock Transcription Factor (*ZmHsf08*) Negatively Regulates Salt and Drought Stress Responses in Maize. *Int. J. Mol. Sci.* **2021**, *22*, 11922. [CrossRef] [PubMed]

114. Yin, Y.; Qin, K.; Song, X.; Zhang, Q.; Zhou, Y.; Xia, X.; Yu, J. BZR1 Transcription Factor Regulates Heat Stress Tolerance Through FERONIA Receptor-Like Kinase-Mediated Reactive Oxygen Species Signaling in Tomato. *Plant Cell Physiol.* **2018**, *59*, 2239–2254. [CrossRef] [PubMed]

115. Hoang, T.V.; Vo, K.T.X.; Rahman, M.; Choi, S.-H.; Jeon, J.-S. Heat stress transcription factor OsSPL7 plays a critical role in reactive oxygen species balance and stress responses in rice. *Plant Sci.* **2019**, *289*, 110273. [CrossRef] [PubMed]

116. Qiu, J.-R.; Huang, Z.; Xiang, X.-Y.; Xu, W.-X.; Wang, J.-T.; Chen, J.; Song, L.; Xiao, Y.; Li, X.; Ma, J.; et al. MfbHLH38, a Myrothamnus flabellifolia bHLH transcription factor, confers tolerance to drought and salinity stresses in Arabidopsis. *BMC Plant Biol.* **2020**, *20*, 542. [CrossRef]

117. Qiu, J.-R.; Xiang, X.-Y.; Wang, J.-T.; Xu, W.-X.; Chen, J.; Xiao, Y.; Jiang, C.-Z.; Huang, Z. MfPIF1 of Resurrection Plant Myrothamnus flabellifolia Plays a Positive Regulatory Role in Responding to Drought and Salinity Stresses in Arabidopsis. *Int. J. Mol. Sci.* **2020**, *21*, 3011. [CrossRef]

118. Wang, D.; Chen, Q.; Chen, W.; Liu, X.; Xia, Y.; Guo, Q.; Jing, D.; Liang, G. A WRKY Transcription Factor, EjWRKY17, from *Eriobotrya japonica* Enhances Drought Tolerance in Transgenic *Arabidopsis*. *Int. J. Mol. Sci.* **2021**, *22*, 5593. [CrossRef]

119. Tang, H.; Bi, H.; Liu, B.; Lou, S.; Song, Y.; Tong, S.; Chen, N.; Jiang, Y.; Liu, J.; Liu, H.; et al. WRKY33 interacts with WRKY12 protein to up-regulate *RAP2. 2* during submergence induced hypoxia response in *Arabidopsis thaliana*. *New Phytol.* **2020**, *229*, 106–125. [CrossRef]

120. Gulzar, F.; Fu, J.; Zhu, C.; Yan, J.; Li, X.; Meraj, T.A.; Shen, Q.; Hassan, B.; Wang, Q. Maize WRKY Transcription Factor *ZmWRKY79* Positively Regulates Drought Tolerance through Elevating ABA Biosynthesis. *Int. J. Mol. Sci.* **2021**, *22*, 10080. [CrossRef]

121. Hoang, X.L.T.; Chuong, N.N.; Hoa, T.T.K.; Doan, H.; Van, P.H.P.; Trang, L.D.M.; Huyen, P.N.T.; Le, D.T.; Tran, L.-S.P.; Thao, N.P. The Drought-Mediated Soybean GmNAC085 Functions as a Positive Regulator of Plant Response to Salinity. *Int. J. Mol. Sci.* **2021**, *22*, 8986. [CrossRef]

122. Yuan, X.; Wang, H.; Cai, J.; Bi, Y.; Li, D.; Song, F. Rice NAC transcription factor ONAC066 functions as a positive regulator of drought and oxidative stress response. *BMC Plant Biol.* **2019**, *19*, 278. [CrossRef]

123. Sewelam, N.; Kazan, K.; Thomas-Hall, S.R.; Kidd, B.N.; Manners, J.M.; Schenk, P.M. Ethylene Response Factor 6 Is a Regulator of Reactive Oxygen Species Signaling in Arabidopsis. *PLoS ONE* **2013**, *8*, e70289. [CrossRef] [PubMed]

124. Jiang, L.; Yang, J.; Liu, C.; Chen, Z.; Yao, Z.; Cao, S. Overexpression of ethylene response factor ERF96 gene enhances selenium tolerance in Arabidopsis. *Plant Physiol. Biochem.* **2020**, *149*, 294–300. [CrossRef] [PubMed]

125. Zhou, L.-J.; Geng, Z.; Wang, Y.; Wang, Y.; Liu, S.; Chen, C.; Song, A.; Jiang, J.; Chen, S.; Chen, F. A novel transcription factor CmMYB012 inhibits flavone and anthocyanin biosynthesis in response to high temperatures in chrysanthemum. *Hortic. Res.* **2021**, *8*, 248. [CrossRef]

126. An, J.-P.; Li, R.; Qu, F.-J.; You, C.-X.; Wang, X.-F.; Hao, Y.-J. R2R3-MYB transcription factor MdMYB23 is involved in the cold tolerance and proanthocyanidin accumulation in apple. *Plant J.* **2018**, *96*, 562–577. [CrossRef] [PubMed]

127. Wu, Y.; Li, T.; Cheng, Z.; Zhao, D.; Tao, J. R2R3-MYB Transcription Factor *PlMYB108* Confers Drought Tolerance in Herbaceous Peony (*Paeonia lactiflora* Pall.). *Int. J. Mol. Sci.* **2021**, *22*, 11884. [CrossRef] [PubMed]

128. Song, Y.; Yang, W.; Fan, H.; Zhang, X.; Sui, N. TaMYB86B encodes a R2R3-type MYB transcription factor and enhances salt tolerance in wheat. *Plant Sci.* **2020**, *300*, 110624. [CrossRef] [PubMed]

129. Gu, X.; Gao, S.; Li, J.; Song, P.; Zhang, Q.; Guo, J.; Wang, X.; Han, X.; Wang, X.; Zhu, Y.; et al. The bHLH transcription factor regulated gene OsWIH2 is a positive regulator of drought tolerance in rice. *Plant Physiol. Biochem.* **2021**, *169*, 269–279. [CrossRef]

130. Akmakjian, G.Z.; Riaz, N.; Guerinot, M.L. Photoprotection during iron deficiency is mediated by the bHLH transcription factors PYE and ILR3. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2024918118. [CrossRef]

131. Zhang, H.-X.; Zhu, W.-C.; Feng, X.-H.; Jin, J.-H.; Wei, A.-M.; Gong, Z.-H. Transcription Factor CaSBP12 Negatively Regulates Salt Stress Tolerance in Pepper (*Capsicum annuum* L.). *Int. J. Mol. Sci.* **2020**, *21*, 444. [CrossRef]

132. Zhang, Y.; Zhang, Y.; Sun, Q.; Lu, S.; Chai, L.; Ye, J.; Deng, X. Citrus transcription factor CsHB5 regulates abscisic acid biosynthetic genes and promotes senescence. *Plant J.* **2021**, *108*, 151–168. [CrossRef] [PubMed]

133. Bellegarde, F.; Maghiaoui, A.; Boucherez, J.; Krouk, G.; Lejay, L.; Bach, L.; Gojon, A.; Martin, A. The Chromatin Factor HNI9 and ELONGATED HYPOCOTYL5 Maintain ROS Homeostasis under High Nitrogen Provision. *Plant Physiol.* **2019**, *180*, 582–592. [CrossRef] [PubMed]

134. Yang, K.; Li, C.-Y.; An, J.-P.; Wang, D.-R.; Wang, X.; Wang, C.-K.; You, C.-X. The C2H2-type zinc finger transcription factor MdZAT10 negatively regulates drought tolerance in apple. *Plant Physiol. Biochem.* **2021**, *167*, 390–399. [CrossRef] [PubMed]

135. Zhao, S.; Wang, H.; Jia, X.; Gao, H.; Mao, K.; Ma, F. The HD-Zip I transcription factor *MdHB7 -like* confers tolerance to salinity in transgenic apple (*Malus domestica*). *Physiol. Plant.* **2021**, *172*, 1452–1464. [CrossRef]

136. Wu, J.; Yu, C.; Huang, L.; Gan, Y. A rice transcription factor, *OsMADS57*, positively regulates high salinity tolerance in transgenic *Arabidopsis thaliana* and *Oryza sativa* plants. *Physiol. Plant.* **2021**, *173*, 1120–1135. [CrossRef]

137. Yin, M.; Wang, Y.; Zhang, L.; Li, J.; Quan, W.; Yang, L.; Wang, Q.; Chan, Z. The Arabidopsis Cys2/His2 zinc finger transcription factor ZAT18 is a positive regulator of plant tolerance to drought stress. *J. Exp. Bot.* **2017**, *68*, 2991–3005. [CrossRef]

138. Fan, F.; Zhou, Z.; Qin, H.; Tan, J.; Ding, G. Exogenous Brassinosteroid Facilitates Xylem Development in *Pinus massoniana* Seedlings. *Int. J. Mol. Sci.* **2021**, *22*, 7615. [CrossRef]

139. Zhang, J.; Zhang, Y.; Khan, R.; Wu, X.; Zhou, L.; Xu, N.; Du, S.; Ma, X. Exogenous application of brassinosteroids regulates tobacco leaf size and expansion via modulation of endogenous hormones content and gene expression. *Physiol. Mol. Biol. Plants* **2021**, *27*, 847–860. [CrossRef]

140. Zeng, G.; Gao, F.; Li, C.; Li, D.; Xi, Z. Characterization of 24-epibrassinolide-mediated modulation of the drought stress responses: Morphophysiology, antioxidant metabolism and hormones in grapevine (*Vitis vinifera* L.). *Plant Physiol. Biochem.* **2022**, *184*, 98–111. [CrossRef]

141. Zhang, Y.; Liao, H. Epibrassinolide improves the growth performance of Sedum lineare upon Zn stress through boosting antioxidative capacities. *PLoS ONE* **2021**, *16*, e0257172. [CrossRef]

142. Alam, P.; Kohli, S.K.; Al Balawi, T.; Altalayan, F.; Alam, P.; Ashraf, M.; Bhardwaj, R.; Ahmad, P. Foliar Application of 24-Epibrassinolide Improves Growth, Ascorbate-Glutathione Cycle, and Glyoxalase System in Brown Mustard (*Brassica juncea* (L.) Czern.) Under Cadmium Toxicity. *Plants* **2020**, *9*, 1487. [CrossRef] [PubMed]

143. Anwar, A.; Bai, L.; Miao, L.; Liu, Y.; Li, S.; Yu, X.; Li, Y. 24-Epibrassinolide Ameliorates Endogenous Hormone Levels to Enhance Low-Temperature Stress Tolerance in Cucumber Seedlings. *Int. J. Mol. Sci.* **2018**, *19*, 2497. [CrossRef] [PubMed]

144. Nie, S.; Huang, S.; Wang, S.; Mao, Y.; Liu, J.; Ma, R.; Wang, X. Enhanced brassinosteroid signaling intensity via SlBRI1 overexpression negatively regulates drought resistance in a manner opposite of that via exogenous BR application in tomato. *Plant Physiol. Biochem.* **2019**, *138*, 36–47. [CrossRef]

145. Ferrero, M.; Pagliarani, C.; Novák, O.; Ferrandino, A.; Cardinale, F.; Visentin, I.; Schubert, A. Exogenous strigolactone interacts with abscisic acid-mediated accumulation of anthocyanins in grapevine berries. *J. Exp. Bot.* **2018**, *69*, 2391–2401. [CrossRef]

146. Mayzlish-Gati, E.; LekKala, S.P.; Resnick, N.; Wininger, S.; Bhattacharya, C.; Lemcoff, J.H.; Kapulnik, Y.; Koltai, H. Strigolactones are positive regulators of light-harvesting genes in tomato. *J. Exp. Bot.* **2010**, *61*, 3129–3136. [CrossRef] [PubMed]

147. Qiu, C.-W.; Zhang, C.; Wang, N.-H.; Mao, W.; Wu, F. Strigolactone GR24 improves cadmium tolerance by regulating cadmium uptake, nitric oxide signaling and antioxidant metabolism in barley (*Hordeum vulgare* L.). *Environ. Pollut.* **2021**, *273*, 116486. [CrossRef] [PubMed]

148. Zheng, X.; Li, Y.; Xi, X.; Ma, C.; Sun, Z.; Yang, X.; Li, X.; Tian, Y.; Wang, C. Exogenous Strigolactones alleviate KCl stress by regulating photosynthesis, ROS migration and ion transport in Malus hupehensis Rehd. *Plant Physiol. Biochem.* **2020**, *159*, 113–122. [CrossRef]

149. Song, X.; Zhao, Y.; Han, B.; Li, T.; Zhao, P.; Xu, J.-W.; Yu, X. Strigolactone mediates jasmonic acid-induced lipid production in microalga *Monoraphidium* sp. QLY-1 under nitrogen deficiency conditions. *Bioresour. Technol.* **2020**, *306*, 123107. [CrossRef]

150. Lu, T.; Yu, H.; Li, Q.; Chai, L.; Jiang, W. Improving plant growth and alleviating photosynthetic inhibition and oxidative stress from low-light stress with exogenous GR24 in tomato (*Solanum lycopersicum* L.) seedlings. *Front Plant. Sci.* **2019**, *10*, 490. [CrossRef]

151. Yu, L.; Gao, B.; Li, Y.; Tan, W.; Li, M.; Zhou, L.; Peng, C.; Xiao, L.; Liu, Y. The synthesis of strigolactone is affected by endogenous ascorbic acid in transgenic rice for l-galactono-1, 4-lactone dehydrogenase suppressed or overexpressing. *J. Plant Physiol.* **2020**, *246–247*, 153139. [CrossRef]

152. Min, Z.; Li, R.; Chen, L.; Zhang, Y.; Li, Z.; Liu, M.; Ju, Y.; Fang, Y. Alleviation of drought stress in grapevine by foliar-applied strigolactones. *Plant Physiol. Biochem.* **2018**, *135*, 99–110. [CrossRef] [PubMed]

153. Pérez, S.G.; Gutiérrez, J.; Garcia-Garcia, F.; Osuna, D.; Dopazo, J.; Lorenzo, O.; Revuelta, J.L.; Arellano, J.B. Early Transcriptional Defense Responses in Arabidopsis Cell Suspension Culture under High-Light Conditions. *Plant Physiol.* **2011**, *156*, 1439–1456. [CrossRef] [PubMed]

154. Yao, C.; Zhang, F.; Sun, X.; Shang, D.; He, F.; Li, X.; Jiang, X. Effects of S-Abscisic Acid (S-ABA) on Seed Germination, Seedling Growth, and Asr1 Gene Expression Under Drought Stress in Maize. *J. Plant Growth Regul.* **2019**, *38*, 1300–1313. [CrossRef]

155. Wu, S.; Hu, C.; Tan, Q.; Zhao, X.; Xu, S.; Xia, Y.; Sun, X. Nitric oxide acts downstream of abscisic acid in molybdenum-induced oxidative tolerance in wheat. *Plant Cell Rep.* **2018**, *37*, 599–610. [CrossRef]

156. Dong, N.; Qi, J.; Li, Y.; Chen, Y.; Hao, Y. Effects of Abscisic Acid and Nitric Oxide on Chilling Resistance and Activation of the Antioxidant System in Walnut Shoots In Vitro. *J. Am. Soc. Hortic. Sci. Am. Soc. Hortic. Sci.* **2017**, *142*, 376–384. [CrossRef]

157. Yu, Y.; Wang, J.; Li, S.; Kakan, X.; Zhou, Y.; Miao, Y.; Wang, F.; Qin, H.; Huang, R. Ascorbic Acid Integrates the Antagonistic Modulation of Ethylene and Abscisic Acid in the Accumulation of Reactive Oxygen Species. *Plant Physiol.* **2019**, *179*, 1861–1875. [CrossRef]

158. Wang, L.; Brouard, E.; Prodhomme, D.; Hilbert, G.; Renaud, C.; Petit, J.-P.; Edwards, E.; Betts, A.; Delrot, S.; Ollat, N.; et al. Regulation of anthocyanin and sugar accumulation in grape berry through carbon limitation and exogenous ABA application. *Food Res. Int.* **2022**, *160*, 111478. [CrossRef]

159. Schussler, J.R.; Brenner, M.L.; Brun, W.A. Relationship of Endogenous Abscisic Acid to Sucrose Level and Seed Growth Rate of Soybeans. *Plant Physiol.* **1991**, *96*, 1308–1313. [CrossRef]

160. Liu, R.; Cao, P.; Ren, A.; Wang, S.; Yang, T.; Zhu, T.; Shi, L.; Zhu, J.; Jiang, A.-L.; Zhao, M.-W. SA inhibits complex III activity to generate reactive oxygen species and thereby induces GA overproduction in Ganoderma lucidum. *Redox Biol.* **2018**, *16*, 388–400. [CrossRef]

161. Yang, X.; Chen, Z.; Yin, X.; Wang, Y.; Yang, Y.; Yang, Y. Genome-Wide Survey Indicates Diverse Physiological Roles of *Dendrobium officinale* Calcium-Dependent Protein Kinase Genes. *Int. J. Mol. Sci.* **2022**, *23*, 1298. [CrossRef]

162. Norman, C.; Howell, K.A.; Millar, A.H.; Whelan, J.M.; Day, D.A. Salicylic Acid Is an Uncoupler and Inhibitor of Mitochondrial Electron Transport. *Plant Physiol.* **2004**, *134*, 492–501. [CrossRef]

163. Durner, J.; Klessig, D.F. Salicylic Acid Is a Modulator of Tobacco and Mammalian Catalases. *J. Biol. Chem.* **1996**, *271*, 28492–28501. [CrossRef]

164. Guo, B.; Liang, Y.; Zhu, Y.; Zhao, F. Role of salicylic acid in alleviating oxidative damage in rice roots (*Oryza sativa*) subjected to cadmium stress. *Environ. Pollut.* **2007**, *147*, 743–749. [CrossRef] [PubMed]

165. Guo, B.; Liang, Y.; Zhu, Y. Does salicylic acid regulate antioxidant defense system, cell death, cadmium uptake and partitioning to acquire cadmium tolerance in rice? *J. Plant Physiol.* **2009**, *166*, 20–31. [CrossRef] [PubMed]

166. Kaya, C. Salicylic acid-induced hydrogen sulphide improves lead stress tolerance in pepper plants by upraising the ascorbate-glutathione cycle. *Physiol. Plant.* **2020**, *173*, 8–19. [CrossRef]

167. Kaya, C. Nitrate reductase is required for salicylic acid-induced water stress tolerance of pepper by upraising the AsA-GSH pathway and glyoxalase system. *Physiol. Plant.* **2020**, *172*, 351–370. [CrossRef] [PubMed]

168. Kaya, C.; Ashraf, M.; Alyemeni, M.N.; Ahmad, P. The role of endogenous nitric oxide in salicylic acid-induced up-regulation of ascorbate-glutathione cycle involved in salinity tolerance of pepper (*Capsicum annuum* L.) plants. *Plant Physiol. Biochem.* **2019**, *147*, 10–20. [CrossRef]

169. Chen, M.; Gu, H.; Wang, L.; Shao, Y.; Li, R.; Li, W. Exogenous Ethylene Promotes Peel Color Transformation by Regulating the Degradation of Chlorophyll and Synthesis of Anthocyanin in Postharvest Mango Fruit. *Front. Nutr.* **2022**, *9*, 911542. [CrossRef] [PubMed]

170. Mohammadi, F.; Naghavi, M.R.; Peighambari, S.A.; Dehaghi, N.K.; Khaldari, I.; Bravi, E.; Marconi, O.; Perretti, G. Abscisic acid crosstalk with auxin and ethylene in biosynthesis and degradation of inulin-type fructans in chicory. *Plant Biol.* **2021**, *23*, 636–642. [CrossRef]

171. Jung, J.Y.; Shin, R.; Schachtman, D.P. Ethylene mediates response and tolerance to potassium deprivation in Arabidopsis. *Plant Cell* **2009**, *21*, 607–621. [CrossRef]

172. Schachtman, D.P. The role of ethylene in plant responses to K+ deficiency. *Front Plant Sci.* **2015**, *6*, 1153. [CrossRef] [PubMed]

173. Wilkinson, S.; Davies, W.J. Ozone suppresses soil drying- and abscisic acid (ABA)-induced stomatal closure via an ethylene-dependent mechanism. *Plant Cell Environ.* **2009**, *32*, 949–959. [CrossRef] [PubMed]

174. He, J.; Yue, X.; Wang, R.; Zhang, Y. Ethylene mediates UV-B-induced stomatal closure via peroxidase-dependent hydrogen peroxide synthesis in *Vicia faba* L. *J. Exp. Bot.* **2011**, *62*, 2657–2666. [CrossRef] [PubMed]

175. Peng, J.; Li, Z.; Wen, X.; Li, W.; Shi, H.; Yang, L.; Zhu, H.; Guo, H. Salt-induced stabilization of EIN3/EIL1 confers salinity tolerance by deterring ROS accumulation in Arabidopsis. *PLoS Genet.* **2014**, *10*, e1004664. [CrossRef]

176. Wang, Y.; Yuan, M.; Li, Z.; Niu, Y.; Jin, Q.; Zhu, B.; Xu, Y. Effects of ethylene biosynthesis and signaling on oxidative stress and antioxidant defense system in Nelumbo nucifera G. under cadmium exposure. *Environ. Sci. Pollut. Res.* **2020**, *27*, 40156–40170. [CrossRef]

177. Hou, J.; Riaz, M.; Yan, L.; Lu, K.; Jiang, C. Effect of exogenous l-aspartate nano-calcium on root growth, calcium forms and cell wall metabolism of *Brassica napus* L. *NanoImpact* **2022**, *27*, 100415. [CrossRef]

178. Ban, Q.; Liu, T.; Ning, K.; Fan, J.; Cui, Q.; Guo, Y.; Zai, X. Effect of calcium treatment on the browning of harvested eggplant fruits and its relation to the metabolisms of reactive oxygen species (ROS) and phenolics. *Food Sci. Nutr.* **2021**, *9*, 5567–5574. [CrossRef]

179. He, L.; Li, B.; Lu, X.; Yuan, L.; Yang, Y.; Yuan, Y.; Du, J.; Guo, S. The effect of exogenous calcium on mitochondria, respiratory metabolism enzymes and ion transport in cucumber roots under hypoxia. *Sci. Rep.* **2015**, *5*, 11391. [CrossRef]

180. Erinle, K.O.; Jiang, Z.; Ma, B.; Li, J.; Chen, Y.; Ur-Rehman, K.; Shahla, A.; Zhang, Y. Exogenous calcium induces tolerance to atrazine stress in Pennisetum seedlings and promotes photosynthetic activity, antioxidant enzymes and psbA gene transcripts. *Ecotoxicol. Environ. Saf.* **2016**, *132*, 403–412. [CrossRef]

181. Rui, Z.; Huali, X.; Min, S.; Yang, B.; Mina, N.; Yuanyuan, Z.; Haitao, L.; Prusky, D.; Xiaoyan, C. Mechanism of Ca2+-mediated NOX modulated in ROS metabolism induced by T-2 toxin in potato tuber. *Food Chem.* **2020**, *317*, 126416. [CrossRef]

182. Snedden, W.A.; Arazi, T.; Fromm, H.; Shelp, B.J. Calcium/Calmodulin Activation of Soybean Glutamate Decarboxylase. *Plant Physiol.* **1995**, *108*, 543–549. [CrossRef] [PubMed]

183. Zhang, G.; Liu, Y.; Ni, Y.; Meng, Z.; Lu, T.; Li, T. Exogenous Calcium Alleviates Low Night Temperature Stress on the Photosynthetic Apparatus of Tomato Leaves. *PLoS ONE* **2014**, *9*, e97322. [CrossRef] [PubMed]

184. Gao, M.; He, Y.; Yin, X.; Zhong, X.; Yan, B.; Wu, Y.; Chen, J.; Li, X.; Zhai, K.; Huang, Y.; et al. Ca2+ sensor-mediated ROS scavenging suppresses rice immunity and is exploited by a fungal effector. *Cell* **2021**, *184*, 5391–5404.e17. [CrossRef] [PubMed]

185. Siddiqui, M.H.; Alamri, S.; Alsubaie, Q.D.; Ali, H.M.; Khan, M.N.; Al-Ghamdi, A.; Ibrahim, A.A.; Alsadon, A. Exogenous nitric oxide alleviates sulfur deficiency-induced oxidative damage in tomato seedlings. *Nitric Oxide* **2019**, *94*, 95–107. [CrossRef] [PubMed]

186. Silveira, N.M.; Frungillo, L.; Marcos, F.C.C.; Pelegrino, M.T.; Miranda, M.T.; Seabra, A.B.; Salgado, I.; Machado, E.C.; Ribeiro, R.V. Exogenous nitric oxide improves sugarcane growth and photosynthesis under water deficit. *Planta* **2016**, *244*, 181–190. [CrossRef]

187. Mahjoubi, Y.; Rzigui, T.; Kharbech, O.; Mohamed, S.N.; Abaza, L.; Chaoui, A.; Nouairi, I.; Djebali, W. Exogenous nitric oxide alleviates manganese toxicity in bean plants by modulating photosynthesis in relation to leaf lipid composition. *Protoplasma* **2021**, *259*, 949–964. [CrossRef] [PubMed]

188. Shao, R.; Zheng, H.; Jia, S.; Jiang, Y.; Yang, Q.; Kang, G. Nitric Oxide Enhancing Resistance to PEG-Induced Water Deficiency is Associated with the Primary Photosynthesis Reaction in *Triticum aestivum* L. *Int. J. Mol. Sci.* **2018**, *19*, 2819. [CrossRef]

189. Soliman, M.; Alhaithloul, H.A.; Hakeem, K.R.; Alharbi, B.M.; El-Esawi, M.; Elkelish, A. Exogenous Nitric Oxide Mitigates Nickel-Induced Oxidative Damage in Eggplant by Upregulating Antioxidants, Osmolyte Metabolism, and Glyoxalase Systems. *Plants* **2019**, *8*, 562. [CrossRef]

190. Gautam, H.; Sehar, Z.; Rehman, T.; Hussain, A.; AlAjmi, M.; Khan, N. Nitric Oxide Enhances Photosynthetic Nitrogen and Sulfur-Use Efficiency and Activity of Ascorbate-Glutathione Cycle to Reduce High Temperature Stress-Induced Oxidative Stress in Rice (*Oryza sativa* L.) Plants. *Biomolecules* **2021**, *11*, 305. [CrossRef]

191. Savvides, A.; Ali, S.; Tester, M.; Fotopoulos, V. Chemical Priming of Plants Against Multiple Abiotic Stresses: Mission Possible? *Trends Plant Sci.* **2016**, *21*, 329–340. [CrossRef]

192. Molassiotis, A.; Tanou, G.; Diamantidis, G. NO says more than 'YES' to salt tolerance: Salt priming and systemic nitric oxide signaling in plants. *Plant Signal. Behav.* **2010**, *5*, 209–212. [CrossRef] [PubMed]

193. Valderrama, R.; Corpas, F.J.; Carreras, A.; Fernández-Ocaña, A.; Chaki, M.; Luque, F.; Gómez-Rodríguez, M.V.; Colmenero-Varea, P.; Del Río, L.A.; Barroso, J.B. Nitrosative stress in plants. *FEBS Lett.* **2007**, *581*, 453–461. [CrossRef] [PubMed]

194. Van Bel, A.J.E.; Gaupels, F. Pathogen-induced resistance and alarm signals in the phloem. *Mol. Plant Pathol.* **2004**, *5*, 495–504. [CrossRef] [PubMed]

195. Zhao, Y.; Wei, X.; Ji, X.; Ma, W. Endogenous NO-mediated transcripts involved in photosynthesis and carbohydrate metabolism in alfalfa (*Medicago sativa* L.) seedlings under drought stress. *Plant Physiol. Biochem.* **2019**, *141*, 456–465. [CrossRef] [PubMed]

196. Shi, H.; Ye, T.; Zhu, J.-K.; Chan, Z. Constitutive production of nitric oxide leads to enhanced drought stress resistance and extensive transcriptional reprogramming in Arabidopsis. *J. Exp. Bot.* **2014**, *65*, 4119–4131. [CrossRef] [PubMed]

197. Jia, H.; Hou, D.; O'Connor, D.; Pan, S.; Zhu, J.; Bolan, N.S.; Mulder, J. Exogenous phosphorus treatment facilitates chelation-mediated cadmium detoxification in perennial ryegrass (*Lolium perenne* L.). *J. Hazard. Mater.* **2019**, *389*, 121849. [CrossRef] [PubMed]

198. Huang, D.; Huo, J.; Liao, W. Hydrogen sulfide: Roles in plant abiotic stress response and crosstalk with other signals. *Plant Sci.* **2020**, *302*, 110733. [CrossRef] [PubMed]

199. Xie, T.; Ji, J.; Chen, W.; Yue, J.; Du, C.; Sun, J.; Chen, L.; Jiang, Z.; Shi, S. GABA negatively regulates adventitious root development in poplar. *J. Exp. Bot.* **2019**, *71*, 1459–1474. [CrossRef]

200. Li, W.; Liu, J.; Ashraf, U.; Li, G.; Li, Y.; Lu, W.; Gao, L.; Han, F.; Hu, J. Exogenous γ-aminobutyric Acid (GABA) Application Improved Early Growth, Net Photosynthesis, and Associated Physio-Biochemical Events in Maize. *Front. Plant Sci.* **2016**, *7*, 919. [CrossRef]

201. Li, C.; Zhu, J.; Sun, L.; Cheng, Y.; Hou, J.; Fan, Y.; Ge, Y. Exogenous γ-aminobutyric acid maintains fruit quality of apples through regulation of ethylene anabolism and polyamine metabolism. *Plant Physiol. Biochem.* **2021**, *169*, 92–101. [CrossRef]

202. Chen, X.; Li, N.; Liu, C.; Wang, H.; Li, Y.; Xie, Y.; Ma, F.; Liang, J.; Li, C. Exogenous GABA improves the resistance of apple seedlings to long-term drought stress by enhancing GABA shunt and secondary cell wall biosynthesis. *Tree Physiol.* **2022**, tpac096. [CrossRef] [PubMed]

203. Ashraf, U.; Mahmood, S.; Anjum, S.A.; Abbas, R.N.; Rasul, F.; Iqbal, J.; Mo, Z.; Tang, X. Exogenous Gamma-Aminobutyric Acid Application Induced Modulations in the Performance of Aromatic Rice Under Lead Toxicity. *Front. Plant Sci.* **2022**, *13*, 933694. [CrossRef] [PubMed]

204. Fan, L.; Wu, X.; Tian, Z.; Jia, K.; Pan, Y.; Li, J.; Gao, H. Comparative proteomic analysis of gamma-aminobutyric acid responses in hypoxia-treated and untreated melon roots. *Phytochemistry* **2015**, *116*, 28–37. [CrossRef] [PubMed]

205. Wang, C.; Fan, L.; Gao, H.; Wu, X.; Li, J.; Lv, G.; Gong, B. Polyamine biosynthesis and degradation are modulated by exogenous gamma-aminobutyric acid in root-zone hypoxia-stressed melon roots. *Plant Physiol. Biochem.* **2014**, *82*, 17–26. [CrossRef]

206. Zhu, X.; Liao, J.; Xia, X.; Xiong, F.; Li, Y.; Shen, J.; Wen, B.; Ma, Y.; Wang, Y.; Fang, W. Physiological and iTRAQ-based proteomic analyses reveal the function of exogenous γ-aminobutyric acid (GABA) in improving tea plant (*Camellia sinensis* L.) tolerance at cold temperature. *BMC Plant Biol.* **2019**, *19*, 1–20. [CrossRef]

207. Bouché, N.; Fait, A.; Bouchez, D.; Møller, S.G.; Fromm, H. Mitochondrial succinic-semialdehyde dehydrogenase of the γ-aminobutyrate shunt is required to restrict levels of reactive oxygen intermediates in plants. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 6843–6848. [CrossRef]

208. Qu, Y.; Jiang, L.; Wuyun, T.; Mu, S.; Xie, F.; Chen, Y.; Zhang, L. Effects of Exogenous Putrescine on Delaying Senescence of Cut Foliage of Nephrolepis cordifolia. *Front. Plant Sci.* **2020**, *11*, 933694. [CrossRef]

209. Tavallali, V.; Alhavi, N.; Gholami, H.; Abarghuei, F.M. Developmental and phytochemical changes in pot marigold (*Calendula officinalis* L.) using exogenous application of polyamines. *Plant Physiol. Biochem.* **2022**, *183*, 128–137. [CrossRef]

210. Aziz, A.; Larher, F. Changes in polyamine titers associated with the proline response and osmotic adjustment of rape leaf discs submitted to osmotic stresses. *Plant Sci.* **1995**, *112*, 175–186. [CrossRef]

211. Drolet, G.; Dumbroff, E.B.; Legge, R.L.; Thompson, J.E. Radical scavenging properties of polyamines. *Phytochemistry* **1986**, *25*, 367–371. [CrossRef]

212. Dondini, L.; Del Duca, S.; Dall'Agata, L.; Bassi, R.; Gastaldelli, M.; Della Mea, M.; Serafini-Fracassini, D. Suborganellar localisation and effect of light on Helianthus tuberosus chloroplast transglutaminases and their substrates. *Planta* **2003**, *217*, 84–95. [CrossRef] [PubMed]

213. Shen, W.; Tachibana, N.S. Involvement of Polyamines in the Chilling Tolerance of Cucumber Cultivars. *Plant Physiol.* **2000**, *124*, 431–439. [CrossRef] [PubMed]

214. Xiao, S.; Liu, L.; Wang, H.; Li, D.; Bai, Z.; Zhang, Y.; Sun, H.; Zhang, K.; Li, C. Exogenous melatonin accelerates seed germination in cotton (*Gossypium hirsutum* L.). *PLoS ONE* **2019**, *14*, e0216575. [CrossRef] [PubMed]

215. Zhang, N.; Zhang, H.J.; Sun, Q.Q.; Cao, Y.Y.; Li, X.; Zhao, B.; Wu, P.; Guo, Y.D. Proteomic analysis reveals a role of melatonin in promoting cucumber seed germination under high salinity by regulating energy production. *Sci. Rep.* **2017**, *7*, 503. [CrossRef] [PubMed]

216. Li, C.; He, Q.; Zhang, F.; Yu, J.; Li, C.; Zhao, T.; Zhang, Y.; Xie, Q.; Su, B.; Mei, L.; et al. Melatonin enhances cotton immunity to *Verticillium* wilt via manipulating lignin and gossypol biosynthesis. *Plant J.* **2019**, *100*, 784–800. [CrossRef]

217. Weeda, S.; Na Zhang, N.; Zhao, X.; Ndip, G.; Guo, Y.; Buck, G.A.; Fu, C.; Ren, S. Arabidopsis Transcriptome Analysis Reveals Key Roles of Melatonin in Plant Defense Systems. *PLoS ONE* **2014**, *9*, e93462. [CrossRef]

218. Ramel, F.; Sulmon, C.; Bogard, M.; Couée, I.; Gouesbet, G. Differential patterns of reactive oxygen species and antioxidative mechanisms during atrazine injury and sucrose-induced tolerance in Arabidopsis thaliana plantlets. *BMC Plant Biol.* **2009**, *9*, 28. [CrossRef]

219. Van Den Ende, W.; Valluru, R. Sucrose, sucrosyl oligosaccharides, and oxidative stress: Scavenging and salvaging? *J. Exp. Bot.* **2009**, *60*, 9–18. [CrossRef]

220. Huang, C.; Tian, Y.; Zhang, B.; Hassan, M.J.; Li, Z.; Zhu, Y. Chitosan (CTS) Alleviates Heat-Induced Leaf Senescence in Creeping Bentgrass by Regulating Chlorophyll Metabolism, Antioxidant Defense, and the Heat Shock Pathway. *Molecules* **2021**, *26*, 5337. [CrossRef]

221. Zhao, D.-Q.; Li, T.-T.; Hao, Z.-J.; Cheng, M.-L.; Tao, J. Exogenous trehalose confers high temperature stress tolerance to herbaceous peony by enhancing antioxidant systems, activating photosynthesis, and protecting cell structure. *Cell Stress Chaperon* **2019**, *24*, 247–257. [CrossRef]

222. Rohman, M.; Islam, R.; Monsur, M.B.; Amiruzzaman, M.; Fujita, M.; Hasanuzzaman, M. Trehalose Protects Maize Plants from Salt Stress and Phosphorus Deficiency. *Plants* **2019**, *8*, 568. [CrossRef] [PubMed]

223. Mostofa, M.G.; Hossain, M.A.; Fujita, M.; Tran, L.-S.P. Physiological and biochemical mechanisms associated with trehalose-induced copper-stress tolerance in rice. *Sci. Rep.* **2015**, *5*, 11433. [CrossRef] [PubMed]

224. Wang, A.; Li, J.; Al-Huqail, A.A.; Al-Harbi, M.S.; Ali, E.F.; Wang, J.; Ding, Z.; Rekaby, S.A.; Ghoneim, A.M.; Eissa, M.A. Mechanisms of Chitosan Nanoparticles in the Regulation of Cold Stress Resistance in Banana Plants. *Nanomaterials* **2021**, *11*, 2670. [CrossRef] [PubMed]

225. Tan, C.; Zhang, L.; Duan, X.; Chai, X.; Huang, R.; Kang, Y.; Yang, X. Effects of exogenous sucrose and selenium on plant growth, quality, and sugar metabolism of pea sprouts. *J. Sci. Food Agric.* **2021**, *102*, 2855–2863. [CrossRef]

226. Nkomo, M.; Gokul, A.; Keyster, M.; Klein, A. Exogenous p-Coumaric Acid Improves *Salvia hispanica* L. Seedling Shoot Growth. *Plants* **2019**, *8*, 546. [CrossRef]

227. Xiang, C.; Werner, B.L.; Christensen, E.M.; Oliver, D.J. The Biological Functions of Glutathione Revisited in Arabidopsis Transgenic Plants with Altered Glutathione Levels. *Plant Physiol.* **2001**, *126*, 564–574. [CrossRef]

228. Hayat, S.; Hayat, Q.; Alyemeni, M.N.; Wani, A.S.; Pichtel, J.; Ahmad, A. Role of proline under changing environments: A review. *Plant Signal. Behav.* **2012**, *7*, 1456–1466. [CrossRef]

229. Oney-Birol, S. Exogenous L-Carnitine Promotes Plant Growth and Cell Division by Mitigating Genotoxic Damage of Salt Stress. *Sci. Rep.* **2019**, *9*, 17229. [CrossRef]