



Uncovering the Role of Hormones in Enhancing Antioxidant Defense Systems in Stressed Tomato (Solanum lycopersicum) Plants

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Abstract: Tomato is one of the most important fruits worldwide. It is widely consumed due to its sensory and nutritional attributes. However, like many other industrial crops, it is affected by biotic and abiotic stress factors, reducing its metabolic and physiological processes. Tomato plants possess different mechanisms of stress responses in which hormones have a pivotal role. They are responsible for a complex signaling network, where the antioxidant system (enzymatic and non-enzymatic antioxidants) is crucial for avoiding the excessive damage caused by stress factors. In this sense, it seems that hormones such as ethylene, auxins, brassinosteroids, and salicylic, jasmonic, abscisic, and gibberellic acids, play important roles in increasing antioxidant system and reducing oxidative damage caused by different stressors. Although several studies have been conducted on the stress factors, hormones, and primary metabolites of tomato plants, the effect of endogenous and/or exogenous hormones on the secondary metabolism is still poorly studied, which is paramount for tomato growing management and secondary metabolites production. Thus, this review offers an updated overview of both endogenous biosynthesis and exogenous hormone application in the antioxidant system of tomato plants as a response to biotic and abiotic stress factors.

Keywords: tomato plants; secondary metabolism; antioxidants; phytohormones; reactive oxygen species

1. Introduction

Plants are generally subjected to biotic and abiotic stresses during their growth and development [1]. Among biological factors, microorganisms, insects, arachnids, and weeds are the most relevant, whereas radiation, salinity, floods, drought, extreme temperatures, and heavy metals are the most important abiotic stresses [2,3]. Although the genetic, molecular, and physiological mechanisms of plants against stress factors are not fully understood yet, available evidence indicates that these can cause negative, positive, or null effects on plants, and they cannot be generalized among species and stress factors [4]. Until now, it is well-known that, when plants are stressed, a complex signaling network is activated, initiating when the stress factor is perceived by protein receptors, triggering signal responses like reactive oxygen species (ROS) production, changes in basal levels of phytohormones, gene expression, kinase/phosphatase up- or downregulation, etc. [4,5].

ROS, such as hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), singlet oxygen (1O_2), hydroxyl ion (HO^-), peroxyl ion (RO_2^-), alkoxyl ion (RO^-), and organic hydroperoxide (ROOH), at basal levels, regulate plant growth and development. However, they are



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). produced at higher levels under unfavorable conditions as a defense mechanism [6]. Their excessive production needs to be counteracted by plants to prevent oxidative damage and cell death through their antioxidant defense system [1]. Secondary metabolites (phenolic compounds, terpenoids, alkaloids, glucosinolates, etc.) and antioxidant enzymes (SODs, CATs, APXs, GPXs, etc.) are mainly responsible for managing ROS, maintaining cellular homeostasis, and reducing oxidative damage in plants [7].

Hormones play a crucial role in plant growth, organ formation, reproduction, fruiting, ripening, senescence, etc. In addition, one of the most important roles is protection against biotic and abiotic stress [8–12]. Each hormone initiates a specific pathway, which integrates a complex signaling network of synergistic, additive, or antagonistic interactions, commonly called crosstalk [13]. Hormones regulate key mechanisms, including up-or downregulation of gene transcription factors involved in encoding ROS production, enzymatic and non-enzymatic antioxidants biosynthesis, regulation of redox state, osmotic adjustment, physiological changes, hormonal homeostasis, etc. [14,15]. Therefore, understanding how biotic and abiotic factors affect the biosynthesis of hormones and their responses to maintain or even increase the antioxidant immunity system of plants is of great importance.

Tomato (*Solanum lycopersicum*) is one of the most important vegetable crops worldwide [16]. Its consumption is increasing due to its sensory attributes [17], its versatility [18], and its health-promoting compounds [19]. Despite tomato being one of the most studied plants, the effect of phytohormones on the antioxidant system (AS) against biotic and abiotic factors is scarcely reported. Thus, this review aimed to offer an overview of the hormone effects on improving the AS of tomato plants when they are subjected to stress factors. To fully achieve this purpose, the following topics are covered: (i) identify the enzymatic and non-enzymatic antioxidants in tomato plants and (ii) present and discuss the individual and crosstalk hormone responses on the AS of tomato plants subjected to stress factors.

2. Enzymatic and Non-Enzymatic Antioxidants in Tomato Plants

2.1. Non-Enzymatic Antioxidant Compounds (NEACs)

2.1.1. Phenolic Compounds (PCs)

PCs are a diverse group of secondary metabolites having in common at least one benzene ring attached to one or more phenolic hydroxyl group substituents. PCs are generally classified into phenolic acids, flavonoids, xanthones, stilbenes, and lignans [20]. They are synthesized through the shikimic acid and phenylpropanoid pathways during normal growth or induced by biotic and abiotic stress factors [21]. PCs in plants can be electron or hydrogen donors to ROS molecules ($^{1}O_{2}$, $H_{2}O_{2}$, O_{2}^{-} , HO^{-} , etc.). However, PCs also can activate the antioxidant enzyme system of plants. Like in many other plant products, the PCs composition of tomato fruit depends on several conditions, such as plant tissues, variety, growth and development condition, preharvest, harvest, and postharvest management, etc. Hydroxycinnamic acids (cis ρ -coumaric acid, 4-O-caffeoylquinic acid, gallic acid, ferulic acid, and chlorogenic acid) are the most abundant PCs reported in tomato plants [22,23]. Table 1 shows the main NEACs reported in tomato fruit.

2.1.2. Carotenoids

Carotenoids are bioactive compounds belonging to the isoprenoid family; they provide yellow to red colors to fruits and vegetables [24]. Carotenoids are divided into two groups: carotenes, which contain only carbon and hydrogen in their molecular structure, and xanthophylls (XAN), which also possess oxygen in their different chemical forms [25]. All carotenoids present in fruits and vegetables are synthesized by the methylerythritol phosphate and mevalonate pathways, where, based on isopentenyl-diphosphate and dimethyl-diphosphate, lycopene is firstly synthesized, and then α -carotene or β -carotene are further produced [26]. Although carotenoids of tomato fruits are synthesized during the ripening process, on fully ripe tomatoes, lycopene (lyc) is the most abundant carotenoid,

with 80–90%, and the rest of them are β -carotene, XAN, and other carotenoids [27]. Among carotenoids, lyc is the most efficient antioxidant compound because, according to its chemical structure (11 double bonds), it can act through the quenching of singlet oxygen and scavenging for peroxyl radicals [28].

2.1.3. Vitamins

Among vitamins, E and C are the most potent antioxidants in fruits and vegetables [29]. Vitamin E is the common name given to the tocopherol (α , β , δ , and γ) and tocotrienol (α , β , δ , and γ) compounds, which are synthesized in the chloroplast by the tocochromanol pathway [30]. Among these compounds, α -tocopherol is the majoritarian tocopherol found in the mesocarp of tomato fruits, while γ -tocopherol is mainly found in seeds [31]. α -tocopherol is synthesized in the inner membrane of plastids and is responsible for protecting lipids and other membrane compounds of chloroplasts. When α -tocopherol scavenges ROS, it forms a tocopheroxyl radical, which is further reduced to tocopherol levels change during plant growth and development, as well as in response to environmental factors such as light, temperature, nutrients, etc. [30,33].

On the other hand, vitamin C, or ascorbic acid (AA), is a potent water-soluble antioxidant compound of six-carbon lactone. It is a reducing agent; therefore, it can give electrons to any free radical, changing from ascorbic acid to semidehydroascorbic acid or dehydroascorbic acids, which are more stable compounds with a short life as free radicals [34]. Even though the tomato is not the best source of AA among fruits and vegetables, its higher consumption positions it as the most important for the human diet [35]. In this sense, the AA content in tomatoes is affected by several factors, like ripening; some authors have indicated that, as the tomato reaches edible maturity, the AA increases [36]. However, some other authors have pointed out that AA increases during the ripening of tomatoes, but when the fruit is fully ripe, the AA content significantly decreases [37].

2.1.4. Glutathione (GSH)

GSH (γ -glutamyl-cysteinyl-glycine) is a key secondary metabolite for plant survival due to its role in ROS control [38]. Under normal conditions, it is commonly presented in reduced form (GSH), whereas its oxidized form (GSSH) is presented in a low amount [39]. In plants, the functions of GSH include storage of reduced sulfur, being a substrate for glutathione S-transferases for removing toxic compounds, maintaining the sulfhydryl groups of cysteine in their reduced form, and eliminating ROS generated by stress factors [39]. Contrary to the other non-enzymatic antioxidants, GSH has been less studied and quantified in tomato plants, but its concentration (Table 1) is also affected by several biotic and abiotic factors [40,41].

2.2. Antioxidant Enzymes (AEs)

2.2.1. Superoxide Dismutases (SODs)

SODs are metalloenzymes responsible for catalyzing the dismutation of superoxide radicals (O_2^-) to O_2 and H_2O_2 [42]. SODs are the principal defense against ROS, having an important role in treating oxidative stress diseases in living organisms. SODs are commonly grouped into four categories according to their metal cofactors: Cu/ZnSOD, FeSOD, MnSOD, and NiSOD [43]. However, only the first three have been widely found in lower and higher plants [44]. Cu/ZnSODs are mainly noticed in chloroplast, cytosol, and mitochondria, while FeSODs and MnSODs occur in chloroplasts and mitochondria, respectively [45]. In tomato plants, nine SOD genes (four Cu/ZnSODs, three FeSODs, and one MnSOD) have been unevenly distributed on 12 chromosomes [46]. Table 1 displays the AEs values reported in tomato plants.

2.2.2. Catalases (CATs)

CATs are AEs presented in practically all living organisms, having vital roles in plant development and as a response to different stresses [47]. Among AEs, CATs were the first to be identified, and they are considered the most potent due to their affinity for the H_2O_2 radical (the major ROS), degrading to H_2O and O_2 [48]. CATs are unique enzymes because they do not require any cellular reducing equivalent as they mainly catalyze a dismutase retort [49]. They have been found in peroxisomes, mitochondria, cytosol, and chloroplast [50,51]. Although multiple CAT isoenzymes are reported in plants, in tomatoes, two isoforms (*CAT1* and *CAT2*) are related to stress factors [52–54].

2.2.3. Ascorbate Peroxidases (APXs)

APXs are valuable components of the AEs of plants against biotic and abiotic stresses [55]. They are members of the class 1 peroxidases and have a vital role in the AsA-GSH cycle [56]. This cycle plays a principal role in plants. For example, they are used to detoxify H_2O_2 generated by the cytosol and chloroplast while maintaining ASA and GSH reserves in different cellular compartments [57]. APXs possess a higher affinity for reducing H_2O_2 by using ASA as an electron donor to H_2O and MDHA, transforming the last compound to DHA [58]. Like many other AEs, APXs increase under various stress conditions [59]. In tomato plants, seven APX gene families (*APX1, APX2, APX3, APX4, APX5, APX6,* and *APX7*) have been found [60].

2.2.4. Glutathione Peroxidases (GPXs)

GPXs are tetrameric enzymes containing seleno-cysteine (animal enzymes) or cysteine (plant enzymes) in their active site. GPXs catalyze the reduction of H₂O₂ to H₂O or alcohols by the oxidation of GSH or thioredoxin [61]. Generally, plant GPXs prefer thioredoxin as a reducing agent instead of GSH [62]. In plant cells, these enzymes are localized in chloroplast, mitochondria, cytosol, and the endoplasmic reticulum [63]. Although different reports have indicated that GPXs are upregulated under various stress factors, many others have pointed out the downregulation of GPXs against stress factors [62,64]. In tomato plants, GPXle-1 is an isoform of GPX located in mitochondria and cytoplasm. This isoenzyme is associated with oxidative stress response [65]. However, Sharma et al. [66] pointed out that *SIPRX25*, *SIPRX81*, and *SIPRX95* were upregulated in tomato plants infected with the tomato leaf curl New Delhi virus.

Table 1. Reference values of AEs and NEACs of tomato fruit.

Component	Values	Source	Reference
Phenolic acids (mg/100 g DW 1)	172.19-311.82	Low ³	[22,67,68]
TFs (mg/100 g DW)	11.67-35.19	Low	[22,67,68]
Lyc (mg/100 g FW ²)	18.6-64.98	High	[27,69]
Total carotenoids (mg/100 g FW)	7.0-19.0	Medium	[27,68]
AA $(mg/100 \text{ g FW})$	16.32-19.43	Low	[36,68]
Tocopherols (mg/100 g FW)	0.17-0.62	Low	[31,68]
AC [FRAP (mmol/100 g DW)]	1.29-2.21	Medium	[68,70,71]
AC [DPPH (mmol/100 g DW)]	0.85-1.85	Low	[67,68,70]
GSH (mg/100 g FW)	1.43-1.61	NR ⁴	[72]
PODs(U/gFW)	7.03-19.8	NR	[73,74]
SODs $(U/g FW)$	0.35-0.65	NR	[73]
CATs $(U/g FW)$	2.08-26.91	NR	[73,74]
APXs $(U/g FW)$	10.25-14.05	NR	[73,74]

¹ Dry weight; ² Fresh weight; ³ The interpretation was conducted from comparative studies performed by the cited authors. ⁴ No reported, comparative studies were not found in the available literature.

3. Hormones and Their Effects on the Antioxidant System of Tomato Plants *3.1. Ethylene (ET)*

Ethylene (C_2H_4) is a phytohormone associated with the ripening of climacteric fruits. At low concentration, it is responsible for tomato fruit's color, taste, and flavor development [75]. Therefore, ET is involved in the biosynthesis of carotenoids (lyc and β -carotene), AA, TFs, PCs, and, consequently, the AC (FRAP and DPPH assays) of tomato fruit during the ripening [70,76]. Currently, Guo [77] has indicated that the histone deacetylation gene (SIHDT1) is a negative regulator of ethylene biosynthesis genes (*ACS2*, *ACS4*, *ACO1*, and *ACO3*), and it is vital for carotenoid gene expression and its accumulation. ET is also involved in plant growth, development, and stress response, and, due to its gaseous nature, can be easily transported in plants without a carrier [78]. Thus, ET plays an important role in accelerating the transition of primary to secondary metabolism when plants are stressed [79].

The effect of ET has been evaluated against biotic and abiotic stresses such as NaCl, CO₂, CdCl₂, microorganisms, cold temperature, etc., in seeds, plants, and/or tomato fruits, indicating that ET effects are time-, tissue-, dose-, and stressor-dependent [80,81]. Overall, results have indicated that, when tomato plants are stressed, ERFs, especially B1, E2, E3, F1, and F5, are upregulated by ROS production, increasing the AS [82,83]. However, some conflicting results are reported in the literature (Table 2). For example, tomato cells or plants treated with NaCl (0–250 mM) showed a higher positive correlation between ET accumulation and oxidative damage (EL, MI, or ROS) [84-86]. Nevertheless, in a recent study, tomato plants with over-expressing SIMAPK3 showed higher results of AEs (PRX, SOD, APX, and CAT) and lower values of OD than control and SIMAPK3 knock-out plants when NaCl (100 mM/L) was applied. The increase in AEs is attributed to the expression of genes related to ET biosynthesis [87]. Similarly, Gharbi et al. [88] indicated that S. chilense showed higher ET production compared to S. lycopersicum when they were stressed with NaCl (125 mM). The higher ET production was related to the increase in SIERF5, SIJERF1, and SIERF3 gene expression, causing low OD evaluated by MDA production. This study also indicated that tomato plants treated with AVG (aminoethoxyvinylglycine, ET inhibitor) had higher OD in leaf and root than untreated plants. Nevertheless, neither OD nor AEs was affected by ET in wild-type Micro-Tom and its Nr mutant when they were submitted to NaCl (100 mM) and CdCl₂ (0.5 mM) as stressors [89]. These contradictory results may be explained since (1) tomato plants initiate the biosynthesis of ERFs in one tissue while suppressing its production in others; (2) ERFs are stress-dependent (one set for cold and heat, and another for salt, water, and flooding stresses), and (3) the possible activation of other hormones signaling pathways [83,87].

Regarding biotic stress factors, the information reported in the literature indicates more consistent results. Tian et al. [90] stated that ET reduces some transcription factors while increasing others in tomato plants against cotton ballworm (*Helocoverpa zea*) invasion, reducing PIN2 and PPOF gene expression, but inducing SA biosynthesis via ERF1 and PR1 upregulation. Overproducing ET tomato seeds (Micro-Tom variety) inoculated with mycorrhiza (*Glomus clarum*) produced higher values of transcription genes, such as CuZnSOD, CAT, and TPX1, related to AEs production [91]. Similarly, NEACs (AA and GSH) were increased in wild-type tomato seeds (LA0162) inoculated with *Bacillus megaterium* (PGPB) compared to its Nr counterpart, suggesting the intervention of ET in NEACs biosynthesis [92]. Recent studies have indicated that, when tomato plants were inoculated with *Fusarium oxysporum* or its toxin (fusaric acid), upregulation of ET key stress responses genes was observed (SIERF1, SIERF4, SIERF5, SIERF9, and SIERF11), which may reduce the OD in tomato plants [93,94].

The effect of ET in tomato fruit has also been evaluated during the cold storage (28–45 days at 7–8 °C). Results indicated that despite the ET increase being accompanied by an increment of lyc content, a significant reduction of AA, PCs, and AC was observed [95,96]. Similarly, when tomato fruits were stored for a long time period (35 days at 4 °C), higher ET and AEs were synthesized (associated with a higher expression of SlCBF1), and less OD

(MDA and EL) were detected compared to antisense SIACS2 [14]. Therefore, an inverse correlation may exist between ET biosynthesis and OD, EAs, and NEACs. This tendency was corroborated by the evaluation of ET (dipped into 0.01% ethephon for 10 min) during the storage (2 °C for 20 h). The findings indicated a significant reduction of OD (MDA and EL) in treated tomato fruit [97]. Moreover, tomatoes at the breaker stage treated with ethephon solution (1.0 g/L, exogenous application) and stored at 25 °C increased their MDA, O_2 -, and H_2O_2 after 1, 2, and 6 days of storage, respectively [73]. Thus, it is possible to infer that ET treatment significantly improves the AS when tomato fruits are stressed, for instance, during low storage temperatures. On the contrary, ET treatment may induce OD [72,98].

3.2. Salicylic Acid (SA)

SA is a natural phenolic compound (2-hydroxybenzoic acid) essential for signaling plant hormone immunity [99]. SA plays pivotal roles in plants in functions like stress tolerance, seed germination, DNA damage/repair, thermogenesis, increasing yield, etc. [100]. The exogenous application of SA induces the well-known SAR in different plant species against microbial pathogens such as viruses, fungi, and oomycetes, and some abiotic stress like salinity, drought, and heavy metals (Table 3) [101–104]. For example, when NaCl was applied as a stressor, exogenous SA application (0.1–1.0 mM) reduced EL [105], MDA [106], H₂O₂, and TBARS by increasing AEs such as SOD, GPX, APX, GR, and CAT [107,108]. The above-mentioned is probably caused by upregulating the expression of *HKT 1;2, NHX*, and *SOS1* genes, which regulate stress tolerance due to high salinity concentration [109,110].

During the growth of tomato plants at low temperature (10 °C), exogenous SA (0.5 and 1.0 mM) applied in two varieties (Streenb and Floridat) of tomato seedlings at 15 and 30 days after transplanting (one-true leaf stage) significantly increased AEs (PRX and PPO) and AC and reduced the OD indicators, such as MDA and EL, in leaf and root of tomato plants in a dose-dependent manner. It is worthy of interest that the H_2O_2 application displayed better AEs and OD responses than SA [111]. This result corroborates the idea that exogenous application or endogenous biosynthesis of ROS due to stress factors improves the AS of tomato plants. The effect of SA application during the tomato plant growth was evaluated against high-temperature exposure (42 °C for 36 h). The results indicated that SA increased AEs (SOD, CAT, PRX, APX), carotenoids, and proline and reduced EL, H₂O₂, and MDA [112]. They pointed out that SA supplementation improves the photosynthesis apparatus, proline production, and ROS management, important factors in avoiding OD. Moreover, the application of SA during tomato plant growth at low temperatures also improves the NEACs (AA and lyc) of tomato fruit [113]. The beneficial effect of SA in the tomato plant during its growth is time- and dose-dependent, showing an increase in AA, PCs, TFs, and AC as the dose of SA increases from 0 to 450 ppm; however, higher concentration was detrimental for tomato plants [114]. Moreover, some studies have indicated that, 24 h after SA application (0.2 and 1.0 mM), an increase in oxidative parameters is observed, which may trigger SAR [115,116]. For instance, SA application induces SAR in tomato plants against Alternaria solani [117,118], Fusarium oxysporum [119–121], Xanthomonas vesicatoria [122], Potato virus X [103], Tomato yellow leaf curl virus, Orobanche [123], Ralstonia solanacearum [124], *Tomato mottle mosaic virus* [125], and nematodes [126].

SA (0, 1, and 2 mM) was also applied to alleviate the effect of cold storage (cell membrane damage) on tomato fruit at the green mature stage. Results indicated that OD (MDA, EL, lipoxygenase, and phospholipase enzymes) was reduced probably due to the P5CS2 upregulation, which is responsible for proline production [127]. Moreover, SA application as a postharvest treatment of tomato fruit delayed the AA losses and lyc production during the storage at low temperature, which is associated with its antagonism effect on the ripening and senescence process caused by ET [128–130].

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
ET ²	Roma and Patio/microshoots	3 weeks old	NaCl (0-200 mM)	OD increases as ET increases.	EL = 23–80% MI = 0–73% ET = 0.043–0.733 μ/Lh	[84]
ET ²	Rio fuego/cells	4 to 5 days after subculture	NaCl (250 nM)	ROS increases as ET increases	$H_2DCFDA = 430-643\%$ ET = 0.199-0.160 nL/g	[85]
ET ²	Rio fuego/roots	6 weeks old	NaCl (100–250 mM)	ROS increases as ET increases	H ₂ DCFDA = 103–133.4% EL = 117.90–428.66% ET = 2.22–4.15 nL/g	[86]
ET ²	Ailsa Craig and OE.MAPK3-5/roots	6 weeks old	NaCl (100 mM)	AEs and OD were increased in OE.MAPK3-5 tomato plants	POD = 103.58% SOD = 21.57% APX = 11.34% CAT = 48.90% MDA = 39.02% $H_2O_2 = -48.6\%$	[87]
ET ²	Ailsa Craig/roots and leaves	23-day-old seedlings	NaCl (125 mM)	Lower ET production in <i>S. lycopersicum</i> than in <i>S. chilense</i> produces higher OD	MDA = 36.15–59.67% ⁴ ; 36.07–57.86% ⁵	[88]
ET ²	Micro-Tom, epi, and Nr/roots	23 days old	Glomus clarum (10 g)	AEs increase in inoculated tomato plants	Cu/ZnSOD = 513.33% APX = 106.66% CAT = 59.46%	[91]
ET ²	WT and Nr/roots	8 weeks old	PGPB (10 ⁻⁷ CFU/mL)	PGPB increases NEACs in tomato plants	AA = 8.61–54.34% GSH = 24.28–37.90%	[92]
ET ²	WT and Nr/leaves	6 to 7 weeks old	Fusaric acid (0.1–1.0 mM)	MDA was higher in Nr tomato plants and increased as FA increased	MDA = 2.17-55.4%	[94]
ET ²	Valouro/fruits	Ripe stage	Cold storage (7 \pm 0.5 °C) for 35 days	Some NEACs were reduced as ET increased	ET = 51.74% AC = -16.2% AA = -55.18% PCs = -23.73% Lyc = 92.0%	[96]

Table 2. Effect of ET on antioxidant system of tomato plants under biotic and abiotic stress.

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
ET ²	Calnegre/fruits	Breaker stage	Cold storage (8 \pm 1 °C) for 28 days	After 28 days, ET and lyc increased, while AA was reduced.	ET = 57.35–268.9% Lyc = 22.8–42.4% AA = -(54.9–63.4)%	[95]
ET ²	WT and antisense SIACS2/fruits	Mature green stage	Cold storage (4 °C) for 35 days	MDA and EL were less in WT tomato compared to antisense SIACS2	ET = 564.1% MDA = -37.3% EL = -31.7%	[14]
ET ³ (0.01%)	Lichun/fruits	Mature green stage	Cold storage (2 \pm 1 °C) for up to 3 weeks	Tomato fruit treated with ET presented less OD than untreated and 1-MCP treated	MDA = -(3.3-21.4)% EL = -(39.4-66.6)%	[97]
ET ³ (100 μL/L)	BHN-602/fruits	Mature green stage	ET treatment and storage temperature (20 °C vs. 35 °C for 48 h)	ET treatment and higher temperature of storage increase NEACs	Lyc = 8.8% Carotenoids = 11.6% PCs = 5.6% AC (FRAP) = 13.8%	[98]

¹ Concentration; ² Endogenous; ³ Exogenous; ⁴ Roots; ⁵ Leaves.

 Table 3. Effect of SA on antioxidant system of tomato plants under abiotic stress.

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition Results		Values	Reference
SA ² (0.1 mM)	Roma/roots	7-week-old	NaCl (150–200 mM)	SA application reduces OD	EL = -(32-44%)	[105]
SA ² (0.01 mM)	Super Marmande/roots and leaves	35 days old	NaCl (100 mM)	SA application reduces OD	MDA = -(43.49-50.14)% ³ and -(23.62-25.88)% ⁴	[106]
SA ² (0.1 mM)	Hezuo 903/leaves	47 days old	NaCl (100 mM) for 14 days	SA application improves the AEs and reduces OD	$\begin{array}{l} {\rm GSH}=60.1\%\\ {\rm H_2O_2}=-47.2\%\\ {\rm TBARS}=-53.9\%\\ {\rm SOD}=31.6\%\\ {\rm CAT}=41.5\%\\ {\rm APX}=29.60\%\\ {\rm GPX}=-25.06\%\\ {\rm DHAR}=76.0\% \end{array}$	[107]

	Table 3. Cont.					
Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
SA ² (1 mM)	Rio fuego/leaves	31 days old	NaCl (100 mM) for 7 days	SA application improves AEs	SOD = 46.8% $CAT = 109.9%$ $APX = 494.9%$ $GR = 52.9%$ $AA = 29.5%$ $GSH = 52.6%$	[108]
SA ² (100 mM)	Pusa ruby/leaves	75 days old	NaCl (250 mM) for 3 days	SA reduces the OD and increases the AEs	EL = -74.6% SOD = 158.8% CAT = 137.3% APX = 166.6% GR = 172.7%	[110]
SA 2 (0.5 and 1.0 mM)	Streenb and Floridat/leaves and roots	80 days old	Growth under low temperature (10 °C)	SA applied increases AS and reduces OD	$POD = 7.5-42.2\%^{3};$ $15.8-34.0\%^{4}$ $PPO = 14.2-50.1\%^{3};$ $18.7-39.8\%^{4}$ $AC = 21.4-31.6\%^{3};$ $19.9-28.9\%^{4}$ $MDA = -(13.6-33.3\%)^{3}$ $EL = -(4.3-12.6\%)^{3}$	[111]
SA ² (200 ppm)	Super strain B/fruits	3 months old	Growth under changing temperatures (7.8–32.3 °C)	SA increases NEACs	AA = 20.6% Lyc = 8.4%	[113]
SA ² (1 mM) Hezuo 903/le		8 days after, with leaves	Heat stress (42 °C for 36 h)	SA reduces OD and improves AS	$\begin{array}{l} EL = -27.8\% \\ H_2O_2 = -22.7\% \\ MDA = -28.1\% \\ SOD = 22.2\% \\ CAT = 100.3\% \\ APX = 32.1\% \\ POD = 61.6\% \end{array}$	[112]

	Table 3. Cont.					
Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
SA ² (1 or 2 mM)	Newton/fruits	Mature green stage	Cold storage (1 °C) for 3 weeks	SA reduces OD	EL = -13.94% MDA = -2.2% LOX = -(33.6-45.4)%	[127]
SA ² (4-mM foliar-applied plus 1-, 2-, or 4-mM by dipping 5 min)	Baraka/fruits	NP ⁵	Cold storage (10 °C) for 40 days	SA application reduces OD and increases AA, without the effect of the concentration used (1, 2, or 4 mM)	EL = -(46.6-48.0%) AA = 336.6-403.3% APX = 447.6-455.5%	[128]
SA ² (0.2–1.2 mM)	Samrudhi/fruits	Mature (pink to light red color)	Cold storage /4–5 °C) for 21 days	As increased SA concentration, AA increases but reduces NEACs	AA = 17.9–58.3% Lyc = -(4.6–32.1)% β-carotene = -(10.2-42.5)%	[129]

		,			-(10.2-42.5)%	
SA ² (0.5–2 mM)	Durinta/fruits	Pink maturity	5 or 20 $^{\circ}\mathrm{C}$ for 20 days	As increased SA concentration reduces Lyc regardless of the storage temperature	Lyc = -(18.2-21.1)%	[130]

¹ Concentration; ² Exogenous; ³ Leaves; ⁴ Roots; ⁵ NP: Not provided.

3.3. Jasmonates

Jasmonic acid (JA) and its methyl ester (MeJA) exist naturally in a wide range of higher plants when they are stressed [131], triggering the hyperproduction of various secondary metabolites [132]. Both have been applied in seeds and leaves during plant growth and as a postharvest treatment against stress factors (Table 4). Tomato plants inoculated with nematodes and molds and treated with exogenous JA or MeJA showed higher expression of AEs (SOD, PRX, CAT, and GPX) and NEACs (AA, PCs, GSH, carotenoids, tocopherols, and some flavonoids) by upregulation of some antioxidant genes, such as *PAL5, C4H, CHS*, and *FLS*, which are related to the phenolic biosynthesis pathways (kaempferol, quercetin, xanthophylls, anthocyanins, and salicylic acid mainly) [10,133–136]. In this sense, despite microorganisms improving the AS of tomato plants by SAR, their application also increased the OD. Nevertheless, JA or MeJA application significantly improves AS and reduces OD to a level that is even less than in uninfected plants. Similar behavior was observed when salt was used as a stressing agent [131,137].

Moreover, when tomato plants were submitted to cold stress, MeJA application significantly reduced OD (MDA and EL) by increasing putrescine biosynthesis through upregulation of *ACD1*. It is important to highlight that, at room temperature, putrescine content did not change between treatments [138]. In this sense, SOD, POD, and GST (the enzyme responsible for reducing GSH) are the main enzymes responsible for avoiding the OD, while PCs were not affected, suggesting the use of other NEACs as an antioxidant against the OD [9,139], which was partially corroborated by Ding et al. [138].

Jasmonates were also applied to tomato fruit during off-vine ripening to evaluate their effects as postharvest treatment. Tomatoes stored under volatilized MeJA (44.8 μ L/L) for 1 week (13 °C) showed an increase in AA, PCs, lyc, and β -carotene after 1 week of retail [140]. Moreover, at a lower temperature (2 °C), tomato fruit treated with MeJA (0.05 mM vapor phase 12 h at 20 °C) significantly increased AEs (SOD, PRX, CAT, and APX) and lyc content and reduced OD by increasing the expression of *SIMYC2* (helix–loop–helix transcription factor, which is the master regulator of JA mediated response) [141]. In the same way, tomato fruit at the mature green stage inoculated with gray mold (*Botrytis cinerea*) and treated with exogenous MeJA induces endogenous JA biosynthesis and ET production. The treatment caused an increase in enzymes (PAL, C4H, 4CL) related to the synthesis of PCs and POD (an enzyme responsible for inducing lignification of cell walls, reducing fungal invasion). Moreover, low relative expression of the SIMYC2 transcription factor was reported, which is interesting because, under some stress conditions such as cold and wound, it is promptly transcribed as a stress response mechanism. However, under pathogen attack, it is a negative regulator of JA response [142,143].

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 Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
 MeJA ² (1 mM)	Beta/seedlings	15 days old	Microorganism (<i>Alternaria porri</i> f. sp. <i>Solani</i>)	MeJA application increases NEACs	PCs= 17.1-21.5% ATH= 12.6-14.1%	[144]
JA ² (0.01–100 nM)	Pusa Ruby/seedlings	7 days old	Microorganism (Meloidogyne incognita)	MeJA application reduces OD and increases AEs	$\begin{array}{l} O_2{}^- = -(17.8{-}30.9)\%\\ \mathrm{SOD} = 19.3{-}43.0\%\\ \mathrm{POD} = 15.4{-}48.6\%\\ \mathrm{CAT} = 14.5{-}52.5\%\\ \mathrm{APX} = 1.4{-}29.5\%\\ \mathrm{DHAR} = 18.8{-}51.9\\ \mathrm{GST} = -(24.5{-}35.5)\%\\ \mathrm{GR} = 14.5{-}70.3\%\\ \mathrm{PPO} = -(10.9{-}43.8)\%\\ \end{array}$	[136]
JA ² (0.01–100 nM)	Pusa Ruby/seedlings	7 days old	Microorganism (Meloidogyne incognita)	MeJA application reduces OD and increases NEACs	$\begin{array}{l} H_2O_2 = -(15.2 - 40.7)\%\\ GSH = 18.8 - 63.1\%\\ Carotenoids = \\ 25.9 - 48.7\%\\ TFs = 20.3 - 56.7\%\\ ATH = 33.3 - 80.1\%\\ XAN = -(8.8) - 94.7\%\\ AA = 7.9 - 28.9\%\\ Tocopherols = 7.7 - 21.4\%\\ PCs = 27.5 - 80.9\%\\ \end{array}$	[135]
MeJA ² (0–60 μM)	Rio Grande and Savera/leaves	50 days old	Seeds dipped into NaCl (5%) for 10 min	MeJA increases AEs	CAT = 6.0–30.2% PRX = 5.3–25.1%	[131]
JA ³	Castlemart and its JA-deficient mutant/leaves	45 days old	CdCl ₂ (5–50 mg/kg soil)	WT tomato showed less OD and higher AEs compared to its JA-deficient mutant	MDA = -26.9% EL = -27.6% H ₂ O ₂ = -21.1% SOD = 29.5% POD = 28.9% CAT = 243.6%	[9]

Table 4. Effect of JA or MeJA on antioxidant system of tomato plants under biotic and abiotic stress.

	Table 4. Cont.					
Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
JA ² (1 nM)	NP ⁴ /leaves	55 days old	NaCl (200 mM)	JA treatment reduces OD and increases AS	$\begin{array}{l} H_2O_2 = -35.2\% \\ MDA = -22.4\% \\ AA = 40.3\% \\ GSH = 8.6\% \\ TF = 74.3\% \\ SOD = 19.4\% \\ CAT = 27.6\% \\ APX = 20\% \\ GR = 22.4\% \end{array}$	[137]
MeJA ² (100 µM)	MicroTom/leaves	4-leaf stage	Cold stress (4 $^{\circ}$ C) for 24 h	MeJA increases putrescine and reduces OD	MDA = -41.6% EL = -19.8%	[138]
MeJA ² (44.8 μL/L)	Carousel/fruits	NP ⁴	Cold storage (13 °C)	After 2-weeks of storage (13 °C) MeJA improved NEACs	AA = 50% PCs = 87.4% Lyc = 177.8% β-carotene = 43.3%	[140]
MeJA ² (0.05 mM)	Badun/fruits	Mature green	Cold storage (2 $^{\circ}$ C) for 28 days	MeJA treatment showed less OD and higher AS than silencing MeJA	MDA = -(39.7-70.3)% SOD = 39.9-62.0% POD = 47.7-63.6% CAT = 36.6-54.6% APX = 42.6-53.9% Lyc = 24.1-51.9%	[141]

¹ Concentration; ² Exogenous; ³ Endogenous; ⁴ NP: Not provided.

3.4. Abscisic Acid (ABA)

The plant hormone ABA has been associated with the ripening process of fruits and vegetables [79,145]. However, it is also a hormone for stress management in tomato seeds, plants, and fruits (Table 5). It is noteworthy that most of the studies about ABA effects on tomato plants have been conducted to understand how it affects the stress response against abiotic stress factors [116,146–150]. ABA improves stress resistance by closing the stomata of plant leaves, reducing the OD, and increasing the AEs (CAT, APX, and GR) in tomato roots and shoots. This response deals with the ROS imbalance caused by salt and drought stress [151]; meanwhile, Cd accumulation decreased in tomato plants due to ABA inhibiting iron-regulated transporter 1, which shows divalent cations like Cd. The results were corroborated when exogenous ABA application significantly alleviated the OD caused by salt [152], heat [8], and drought [153–155] by inducing the AsA-GSH cycle and promoting the AEs biosynthesis (SOD, POD, CAT, APX, and GR) [152]. Moreover, Zhou et al. [8,156] indicated that ABA application improves the RBOH1 transcription, which increases the stress resistance of the tomato plant against cold, heat, drought, and salinity. In this sense, a study conducted by Wang et al. [157] pointed out that exogenous ABA applications significantly influence ABA signaling pathway genes related to transcription factors (SISnRK2, SIAREB, and SIPP2C) associated with biotic and abiotic stress responses [155].

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference			
ABA ² (50 μM)	LA1698/leaves	Seedlings	NaCl (200 mM)	ABA application reduces OD and increases AS	$\begin{array}{l} MDA = -35.6\% \\ H_2O_2 = -29.6\% \\ SOD = 3.1\% \\ POD = 17.1\% \\ CAT = 3.8\% \\ GR = 138.7\% \\ APX = -20.5\% \\ AA = 40.4\% \\ GSH = 5.8\% \end{array}$	[152]			
ABA ³	Rheinlands/leaves	74 days old	NaCl (100 and 250 mM)	Silencing ABA mutants present lower NEACs	Carotenoids= -(60.6-74.6%)	[116]			
ABA ³	Ailsa Craig/roots	13 days old	NaCl (150 mM)	Silencing ABA mutants reduce AEs and increase OD	APX = -33.9% CAT = -24.2% MDA = 40.3%	[150]			
ABA ² (50 μM)	PKM1/leaves	7 days after 4-fully-expanded- leaves stage.	Drought (7 days)	ABA application reduces OD and increases AE	$\begin{array}{l} H_2O_2 = -57.0\% \\ SOD = 10.2\% \\ CAT = 233.3\% \\ APX = 26.8\% \\ GR = 6.0\% \end{array}$	[154]			
ABA ² (150 μM)	Micro-Tom/leaves	1 month	Drought (6 days)	ABA increases AEs compared to untreated plants	SOD = 6.2% CAT = 17.8% APX = 32.0%	[155]			
	1 Concentration: 2 Excensus: 3 Endegenous								

Table 5. Effect of ABA on antioxidant system of tomato plants under abiotic stress.

Concentration; ² Exogenous; ³ Endogenous.

3.5. Gibberellic Acid (GA)

GA is a diterpenoid carboxylic acid belonging to the gibberellin family. Among GAs, GA₃ acts as a natural plant growth regulator against biotic and abiotic stress factors by preventing lipid peroxidation and regulating AS [158,159]. Results of exogenous GA application to tomato plants (Table 6) indicated that some NEACs (PCs, TFs, and GSH) and AEs (SOD, PPO, and APX) were upregulated in tomato plants stressed with NaCl [160,161]. Interestingly, carotenoids were not affected by the application of GA, probably due to both compounds being derived from geranylgeranyl diphosphate [146,161]. Regarding other abiotic stresses, such as cadmium or heat conditions, the results indicated that GA (0–10 μ M, exogenous application) used in tomato plants (30-days-old) alleviates the damage caused by heavy metals such as Cd (0–20 μ M). In this aspect, MDA was reduced, and CAT, GPX, and APX were increased in a dose-dependent manner [162]. In the same way, the application of GA (100 ppm) significantly improves CAT and PRX during treatments of tomato seedlings at low (10 °C) and high (45 °C) temperatures [163]. On the other hand, some reductions in metabolic (transpiration) and physiological (plant growth, stomatal

closure, xylem vessel proliferation, and expansion) processes were observed in tomato

GA biosynthesis deficient mutants exposed to drought conditions [164,165]. This response is a defense adaptation mechanism of plants to reduce the stress damage caused by the overproduction of H_2O_2 [166].

Table 6. Effect of GA on antioxidant system of tomato plants under	abiotic stress.

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
GA ² (0.4–0.6 mM)	BF1 and UC82B/leaves	45 days old	NaCl (200 mM)	GA improves AS	$\begin{array}{c} APX = 0-9.6\% \\ PPO = 15.1-16.0\% \\ SOD = 32.1-59.2\% \\ TFs = 18.8-100\% \\ PCs = 10.7-19.1\% \\ Carotenoids = 294.4-1980\% \end{array}$	[161]
GA ² (100 μM)	NP ⁴ /leaves	3 weeks old	NaCl (250 mM)	GA application improves AS	GSH = 99.6% MDA = -13.3%	[160]
GA ³	Micro-Tom and procera mutant/shoots	30 days old	Drought (7 days)	GA production reduces MDA, but induces H ₂ O ₂	$\begin{array}{l} MDA = -18.6\% \\ H_2O_2 = 41.1\% \end{array}$	[166]
GA ² (10 μM)	CH/roots	60 days old	Cd (20 µM)	GA application reduces OD and increases AEs	CAT = 9.3% GPX = 20.9% APX = 12.9% MDA = -38.7%	[162]
GA ² (100 ppm)	Fayrouz, Aziza and N23-48/shoot	6 weeks old	Temperature of growth when tomato shoots were exposed to 10 and 45 °C	GA increases the AE	CAT = 1.5–13.9% APX = 9.2–56.7%	[163]

¹ Concentration; ² Endogenous; ³ Exogenous; ⁴ Not provided.

3.6. Auxins

Auxins are phytohormones that play the most relevant role in plant development and growth [167]. Among auxins, IAA is the most detected auxin; however, naphthaleneacetic acid (NAA), indole-3-butyric acid (IBA), 4-chloroindole-3-acetic acid, and phenylacetic acid are also present in lower amounts [168]. Despite auxins being related to physiological processes, recent studies have indicated that they are implicated in responses against biotic and abiotic stress factors (Table 7). IAA has been applied to tomato seeds to evaluate their effects against Cd [169], salinity [170], heat stress [171], phytotoxins (benzoic and vanillic acids) [172,173], and parasite plants [123]. IAA improves the redox status of the plants by increasing AEs (SOD, CAT, PRX, APX, GPX, and those related to the AsA-GSH cycle) and NEACs (carotenoids, TFs, PC, tocopherols, and AC), and reducing some OD indicators like EL, MDA, and H_2O_2 production. It is interesting to note that IAA effects are dose-dependent because, at low concentrations (<5 μ M), an increase in AS is reported, which is caused by an increase in H_2O_2 production [169,171,174,175]. However, when increasing IAA concentration, no effect of IAA was observed in unstressed plants, which was probably caused by a reduction in H_2O_2 biosynthesis [123,173].

3.7. Brassinosteroids (BRs)

BRs are a group of polyhydroxy steroidal phytohormones present in different parts of plants [176]. BRs participate in diverse physiological and developmental processes, such as growth, seed germination, rhizogenesis, senescence, and resistance against various abiotic and biotic stresses [177]. The exogenous application (Table 8) of BRs significantly increases the AEs (SOD, CAT, GR, and APX) and NEACs (PCs, TFs, carotenoids, and GSH/GSSG and ASA/DHA ratios) of tomato plants by inducing enzymes related to the secondary metabolisms of plants (GST, G6PDH, SKDH, and PAL) [8,178,179]. In vivo assays indicated that tomato leaves treated with exogenous BRs and incubated at 40 °C showed a higher increase (p < 0.05) in the AEs (SOD, POX, and CAT) compared to leaves placed at 25 °C [180]. Later, in vivo assays corroborated that SOD, APX, GPOD, and CAT enzymes were upregulated and OD was reduced (H₂O₂ and MDA) by BR application [181]. In this aspect, Zhou et al. [8] indicated that BRs induce RBOH1-NADPH oxidase activation to produce H₂O₂, triggering stress tolerance by the upregulation of other hormones, such as ABA.

Hormone (C ¹)	Variety/Tomato Part	Age	Stress condition	Results	Values	Reference
IAA ² (50 μM)	Roots/cv. Navoday	30 days old	Cd (100 μM)	AS was improved and OD was reduced in IAA treated plants	Carotenoids = 8.1% APX = 28.0% GR = 99.4% AA = 99.3% GSH = 133.3% $O_2^- = -32.0\%$ $H_2O_2 = -27.1\%$ MDA = 37.1% EL = 52.6%	[169]
IAA, NAA ² (100 mg/L)	UC82B/leaves	NP ³	NaCl (200 mM)	IAA increases CAT activity	CAT= 274.1-311.1%	[170]
IAA ² (50 nM)	Five Star F-1 hybrid/leaves	17 days old after seed germination	Heat shock (38 °C for 4 h)	IAA reduces OD and increases AE	MDA = -38.5% EL = 20.5% CAT = 9.6% POD = 7.7% SOD = 16.5%	[171]
IAA ² (1 mM)	Pusa ruby/leaves	First fully expandedleaves	Benzoic acid (0.5–1 mM)	IAA reduces OD and increases AE	$\begin{array}{l} \text{Carotenoids} = 32.4-62.6\%\\ \text{EL} = -(21.4-30.4)\%\\ \text{MDA} = -(19.7-28.3)\%\\ \text{SOD} = 31.7-40.5\%\\ \text{CAT} = 66.1-97.3\%\\ \text{APX} = 54.1-57.7\%\\ \text{GPX} = 45.8-50.7\% \end{array}$	[172]
IAA ² (1 mM)	Pusa ruby/leaves	Fully expanded leaves	Vanillic acid (0.5–1 mM)	IAA reduces OD and increases AS	$\begin{array}{l} \text{Carotenoids} = 13.8-27.3\%\\ \text{MDA} = -(9.8-13.0)\%\\ \text{EL} = -(31.6-55.3)\%\\ \text{H}_2\text{O}_2 = -(3.4-18.5)\%\\ \text{SOD} = 21.6-28.0\%\\ \text{CAT} = 21.4-28.9\%\\ \text{APX} = 31.8-34.5\%\\ \text{GPX} = 42.0-52.1\%\\ \text{PCs} = 23.1-41.0\%\\ \text{ATH} = 15.3-34.7\% \end{array}$	[173]

Table 7. Effect of auxins on antioxidant system of tomato plants under biotic and abiotic stress.

Hormone (C¹)

Table 7. Cont.					
Variety/Tomato Part	Age	Stress condition	Results	Values	Reference
				AC = 131.2% 4; 80.0% ⁵	
				PCs = 48.4% 4; 46.1% ⁵	

IAA ² (0.09 mM)	NP ⁴ /root and shoot	60 days old	Orobanche ramose L. infection	IAA application improves AS and reduces OD	$PCs = 48.4\% 4; 46.1\%^{5}$ $PCs = 48.4\% 4; 46.1\%^{5}$ $TFs = 115.9\% 4; 63.2\%^{5}$ $To copherols = 40.6\%^{4}; 40.6\%^{5}$ $ASA = 21.7\%^{4}; 20.6\%^{5}$ $GSH = 27.5\%^{4}; 168.8\%^{5}$ $H_{2}O_{2} = -8.1\%^{4}; -26.2\%^{5}$ $MDA = -17.1\%^{4}; -24.5\%^{5}$ $CAT = 37.2\%^{4}; 31.1\%^{5}$ $POX = 31.0\%^{4}; 33.0\%^{5}$ $SOD = 40.1\%^{4}; 26.4\%^{5}$	[123]	
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¹ Concentration; ² Exogenous; ³ Not provided; ⁴ Root; ⁵ Shoot.

Table 8. Effect of BRs on antioxidant system of tomato plants under abiotic stress.

Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
BRs ² (100 nM)	Hezuo 903/roots	50 days old	Polychlorinated biphenyls	BRs increases AS and reduces OD	Carotenoids = $4.4-10.5\%$ $H_2O_2 = \cdot(13.3-20.9)\%$ $O_2^- = -(16.5-36.0)\%$ MDA = $-(7.5-8.7)\%$ SOD = $15.2-30.2\%$ POD = $64.7-152.8\%$ CAT = $15.1-20.0\%$ APX = $35.9-56.6\%$ GR = $59.0-140\%$	[178]
BRs ² (10.6 nM)	Amalia/leaves	21 days old	Temperature (25–40 °C)	BRs increases AEs	SOD = 58.2–81.1% POD = 12.1–50.5% CAT = 36.2–84.9%	[180]

	Table 8. Cont.					
Hormone (C ¹)	Variety/Tomato Part	Age	Stress Condition	Results	Values	Reference
BRs ² (0.01–1 mg/L)	9021/leaves	55 days old	Temperature (25–40 °C) for 8 days	As increase temperature, the BRs significantly improve the AEs and OD	SOD = 12.9-13.0% APX = 13.0-35.7% CAT = 23.4-89.2% H ₂ O ₂ = -(26.6-33.8)% MDA = -(8.4-33.6)%	[181]
BRs ² (100 nM)	Hezuo 903/roots	50 days-old	Phenanthrene (300 µM)	Foliar application of BRs improves AS and reduces OD	PCs = 5.9% TF = 10.5% MDA = -13.3% AC(DPPH) = 15.6%	[179]
BRs ² (10 ⁻⁸ M)	K-25 and Sarvodya/leaves and fruit	60 days old and mature fruit	Cd (100 μM)	BRs improves AS (except AA)	$\begin{array}{c} \text{SOD} = 18.6 - 27.9\%\ ^3 \\ \text{POX} = 26.0 - 34.6\%\ ^3 \\ \text{CAT} = 9.8 - 14.6\%\ ^3 \\ \text{Lyc} = 19.5 - 22.1\%\ ^4 \\ \beta\text{-carotene} = 8.6 - 14.8\%\ ^4 \\ \text{AA} = -(15.6 - 19.5)\%\ ^4 \end{array}$	[182]
BRs ² (10–7 M)	K-21/leaves	40 days old	Cr (10 mg/kg soil)	BRs reduces OD and increase AS	$\begin{array}{l} H_2O_2 = -50\% \\ MDA = -49.3\% \\ EL = -28.8\% \\ MG = -30.9\% \\ SOD = 27.3\% \\ CAT = 19.7\% \\ GST = 54.5\% \\ APX = 37.0\% \\ GR = 48.9\% \\ AA = 31.8\% \\ GSH = 17.6\% \\ TF = 60.6\% \end{array}$	[141]
BRs 2 (1 and 3 $\mu M)$	EC-652652 and EC-620419/leaves	67 days old	Drought	BRs reduce OD and AS	$\begin{array}{l} H_2O_2 = -(16.626.1)\%\\ \text{SOD} = 8.735.5\%\\ \text{Lyc} = 4.116.0\% \end{array}$	[183]
	¹ Concentration; ² Exoger	nous; ³ Leave; ⁴ Fruits.				

Regarding drought and heavy metal stress (Cd and Cr), BR application improves AS and reduces OD in tomato plants when it was applied in a foliar manner [41,182,183]. In this sense, heavy metals may induce ROS, affecting DNA, proteins, and pigments, and stimulate lipid peroxidation of the cell wall. However, BR application alleviates the oxidative stress because BR upregulates GSH, AsA, and proline, which neutralize free radicals caused by heavy metals. It is noteworthy BR's effect in tomato fruit was also beneficial for improving lyc and β -carotene due to BR accelerating the ripening process [184].

4. Crosstalk among Hormones against Oxidative Damage Caused by Stress Factors

So far, this manuscript has described the effect of individual hormones on AS of stressed tomato plants. However, crosstalk between hormones has also been reported in studies dealing with tomato mutants altered in their hormonal pathways. Information on hormonal crosstalk resulting from responses to stressors is scarce, and valuable information is presented in Figure 1. In this sense, some controversial information was described on the hormonal effects when they interact. SA application in tomato plants under salt or nematode stress (*Ralstonia solanacearum*) significantly reduced ET biosynthesis and EL and increased AEs [110,124]. Moreover, its application significantly increased some hormones (ABA, GA₃, IAA, and JA) and reduced the OD caused by cold temperature growth [111,185] and *R. solanacearum* [124].

On the other hand, MeJA application significantly increased ET and NEACs biosynthesis in a dose-dependent manner when it was applied against microorganisms in tomato seeds and plants [144]. Interestingly, ERFs genes (ERF1, ERF5, and ERF.C4), well-known as stress response factors associated with ET signaling, were upregulated by SA, MeJA, and ABA [80,82,90,124]. In tomato fruit, exogenous application of hormones (MeJA, BRs, and ABA) showed a positive effect on ET during the tomato fruit ripening [12,44,186]. In this aspect, the increase in ET production induced by ABA application was through the upregulation of the LeACS2, LeACS4, LeACC1, LeGR, and LeETR6 genes [186]. Moreover, Hu et al. [187] and Vardhini and Rao [184] pointed out that BRs promote the synthesis of AC by upregulating ET biosynthesis and signaling in a dose-dependent manner. The authors theorized that AC is increased by BR regulated by the BZR1 transcription factor, which directly regulates several genes involved in ET biosynthesis and signaling. Conversely, IAA application significantly reduced ET biosynthesis and, consequently, the ripening process, causing a reduction in lyc and α , β , and δ carotenes by downregulating the *PSY1*, *PSY3*, PDS, ZISO, and CrtiSO genes and chlorophyllase 1-3 [188]. Interestingly, IAA significantly improves ABA content in tomato fruit [189]; however, this ABA increment (3-6 days) positively affects ET synthesis, as previously described [186].

Ethephon applied to tomato leaves significantly increased (2.6–10.6 times) SA content compared to control, while treatment with MeJA did not affect SA content. Interestingly, when ethephon was applied, MeJA content was reduced by decreasing PIN2 and PPOF gene expression, two well-characterized wounding and insect response genes in tomato plants [90]. On the other hand, Zhou et al. [8] pointed out that BRs can induce H_2O_2 production in tomato plants, triggering ABA biosynthesis, which increases H₂O₂ production, improving stress tolerance. Thus, ABA biosynthesis was stimulated by the oxidative stress (epigallocatechin-3-gallate) in tomato plants, increasing OD and AE by the upregulation of the NCED1 and NCED2 genes [190]. They also indicated that, while ABA increases, GA showed a reduction, indicating an antagonist behavior between these hormones. ABA application did not present any effect on IAA when it was applied to mitigate salt stress damage. In an interesting study conducted by Heidari et al. [191], tomato seedling growth at low temperatures showed a reduction in GA₃ and IAA in both resistant and sensitive cold tomato species, while ABA increased in both species. These results confirm the theory about the negative effect of some hormones on each other. However, there exist several interaction nodes among hormones responsible for their up- or downregulation.



Figure 1. Effect of hormones and their interaction on enzymatic and non-enzymatic antioxidant systems to alleviate the biotic and abiotic stressors in tomato plants.

5. Conclusions

This review shows that hormones play a pivotal role in the antioxidant response of tomato plants against biotic and abiotic stresses. Tomato plants contain different enzymatic and non-enzymatic antioxidant compounds, which can be regulated by hormones. In general, it seems that, under normal conditions, hormones are found at basal levels; however, under stress conditions, the interaction between ROS and hormones generates a loop, which increases the antioxidant system and alleviates oxidative damage. Moreover, as has been described, some hormones presented a positive, negative, or null effect among them, showing their impacts on molecular and genetic signaling. This review is valuable to clarify some important questions about hormones and their effects on oxidative damage in tomato plants. Nevertheless, further studies are needed to clarify the hormone effects on improving antioxidant responses against stress factors and how to take advantage of promoting resistance or increasing health-promoting compounds found in tomato plants.

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Abbreviations

AA	Ascorbic acid
ABA	Abscisic acid
ABTS	2,2'-azino-bis-3-ethylbenzthiazoline-6-sulphonic acid
AC	Antioxidant capacity
AEs	Antioxidant enzymes
APXs	Ascorbate peroxidases
ATH	Anthocyanins
AS	Antioxidant system
ASA	Ascorbate
AsA-GSH	Ascorbate-Glutathione
BRs	Brassinosteroids
CATs	Catalases
CHS	Chalcone synthase
C4H	Cinnamate 4-hydroxylase
DHA	Dehydroascorbate
DHAR	Dehydroascorbate reductase
DPPH	2,2-difenil-1-picrilhidrazilo
EL	Electrolyte leakage
ET	Ethylene
ERFs	Ethylene response factors
GST	Glutathione-S-transferase
G6PDH	Glucose-6-phosphate dehydrogenase
FRAP	Ferric reducing antioxidant power
GA	Gibberellic acid
GPXs	Glutathione peroxidases
GR	Glutathione reductase
GSH	Glutathione
H ₂ DCFDA	2',7'-dichlorofluorescein diacetate
IAA	Indole-3-acetic acid
IBA	Indole-3-butyric acid
JA	Jasmonic acid
MDA	Malondialdehyde
Lyc	Lycopene
MDHA	Monodehydroascorbate
MeJA	Methyl jasmonic acid
MG	Methylglyoxal
MI	Membrane injury
NAA	Naphthaleneacetic acid
NEACs	Non-enzymatic antioxidant compounds
Nr	Never ripe
OD	Oxidative damage
PGPB	Plant growth-promoting bacteria
LOX	Lysyl oxidase
PAL	Phenylalanine ammonia-lyase
PCs	Phenolic compounds
POD	guaiacol peroxidase
PPO	Polyphenol oxidase

PRXs	Peroxidases
ROS	Reactive oxygen species
RP	Reducing power
SA	Salicylic acid
SAR	Systemic acquired resistance
SKDH	Shikimate dehydrogenase
SIMAPK3	Nitrogen-activated protein kinase
SODs	Superoxide dismutases
TBARS	Thiobarbituric acid reactive substances
TFs	Total flavonoids
XAN	Xanthophylls

References

- 1. Laxa, M.; Liebthal, M.; Telman, W.; Chibani, K.; Dietz, K.-J. The role of the plant antioxidant system in drought tolerance. *Antioxidants* **2019**, *8*, 94. [CrossRef] [PubMed]
- 2. Gull, A.; Lone, A.A.; Wani, N.U.I. Biotic and abiotic stresses in plants. *Abiotic Biotic Stress Plants* 2019, 1–6. [CrossRef]
- Liu, M.-Y.; Li, Q.; Ding, W.-Y.; Dong, L.-W.; Deng, M.; Chen, J.H.; Tian, X.; Tian, X.; Hashem, A.; Al-Arjani, F.; et al. Arbuscular mycorrhizal fungi inoculation impacts expression of aquaporins and salt overly sensitive genes and enhances tolerance of salt stress in tomato. *Chem. Biol. Technol. Agric.* 2023, 10, 5. [CrossRef]
- 4. Ramegowda, V.; Senthil-Kumar, M. The interactive effects of simultaneous biotic and abiotic stresses on plants: Mechanistic understanding from drought and pathogen combination. *J. Plant Physiol.* **2015**, *176*, 47–54. [CrossRef]
- Devireddy, A.R.; Zandalinas, S.I.; Fichman, Y.; Mittler, R. Integration of reactive oxygen species and hormone signaling during abiotic stress. *Plant J.* 2021, 105, 459–476. [CrossRef] [PubMed]
- 6. Qi, J.; Wang, J.; Gong, Z.; Zhou, J.-M. Apoplastic ROS signaling in plant immunity. *Curr. Opin. Plant Biol.* 2017, 38, 92–100. [CrossRef]
- 7. Caverzan, A.; Piasecki, C.; Chavarria, G.; Stewart, C.N., Jr.; Vargas, L. Defenses against ROS in crops and weeds: The effects of interference and herbicides. *Int. J. Mol. Sci.* 2019, 20, 1086. [CrossRef]
- 8. Zhou, J.; Wang, J.; Li, X.; Xia, X.-J.; Zhou, Y.-H.; Shi, K.; Chen, Z.; Yu, J.-Q. H₂O₂ mediates the crosstalk of brassinosteroid and abscisic acid in tomato responses to heat and oxidative stresses. *J. Exp. Bot.* **2014**, *65*, 4371–4383. [CrossRef]
- 9. Zhao, S.; Ma, Q.; Xu, X.; Li, G.; Hao, L. Tomato jasmonic acid-deficient mutant *spr2* seedling response to cadmium stress. *J. Plant Growth Regul.* **2016**, *35*, 603–610. [CrossRef]
- Wang, Q.; Chen, X.; Chai, X.; Xue, D.; Zheng, W.; Shi, Y.; Wang, A. The involvement of jasmonic acid, ethylene, and salicylic acid in the signaling pathway of *Clonostachys rosea*-induced resistance to gray mold disease in tomato. *Phytopathology* 2019, 109, 1102–1114. [CrossRef]
- 11. Tao, X.; Wu, Q.; Li, J.; Cai, L.; Mao, L.; Luo, Z.; Li, L.; Ying, T. Exogenous methyl jasmonate regulates sucrose metabolism in tomato during postharvest ripening. *Postharvest Biol. Technol.* **2021**, *181*, 111639. [CrossRef]
- 12. Tao, X.; Wu, Q.; Li, J.; Wang, D.; Nassarawa, S.S.; Ying, T. Ethylene biosynthesis and signal transduction are enhanced during accelerated ripening of postharvest tomato treated with exogenous methyl jasmonate. *Sci. Hortic.* **2021**, *281*, 109965. [CrossRef]
- Aerts, N.; Mendes, M.P.; Van Wees, S.C.M. Multiple levels of crosstalk in hormone networks regulating plant defense. *Plant J.* 2021, 105, 489–504. [CrossRef] [PubMed]
- 14. Yu, W.; Sheng, J.; Zhao, R.; Wang, Q.; Ma, P.; Shen, L. Ethylene biosynthesis is involved in regulating chilling tolerance and *SlCBF1* gene expression in tomato fruit. *Postharvest Biol. Technol.* **2019**, *149*, 139–147. [CrossRef]
- 15. Shiraz, M.; Sami, F.; Siddiqui, H.; Yusuf, M.; Hayat, S. Interaction of auxin and nitric oxide improved photosynthetic efficiency and antioxidant system of *Brassica juncea* plants under salt stress. *J. Plant Growth Regul.* **2020**, *40*, 2379–2389. [CrossRef]
- 16. FAO. Food and Agriculture Organization of the United Nations. FAOSTAT Database. 2017. Available online: https://www.fao. org/faostat/en/#search/tomato (accessed on 3 February 2022).
- Špika, M.J.; Dumičić, G.; Bubola, B.K.; Soldo, B.; Ban, S.G.; Selak, G.V.; Ljubenkov, I.; Mandušić, M.; Žanić, K. Modification of the sensory profile and volatile aroma compounds of tomato fruits by the scion × rootstock interactive effect. *Front. Plant Sci.* 2021, *11*, 616431. [CrossRef]
- Galhardo, R.; Ferraz, E.A. Tomatoes and tomato products as dietary sources of antioxidants. *Food Rev. Int.* 2009, 25, 313–325. [CrossRef]
- 19. Fanasca, S.; Colla, G.; Rouphael, Y.; Saccardo, F.; Maiani, G.; Venneria, E.; Azzini, E. Evolution of nutritional value of two tomato genotypes grown in soilless culture as affected by macrocation proportions. *HortScience* **2006**, *41*, 1584–1588. [CrossRef]
- Luna-Guevara, M.L.; Luna-Guevara, J.J.; Hernández-Carranza, P.; Ruíz-Espinosa, H.; Ochoa-Velasco, C.E. Phenolic compounds: A good choice against chronic degenerative diseases. In *Studies in Natural Products Chemistry*; Atta-ur-Rahman, F.R.S., Ed.; University of Karachi: Karachi, Pakistan, 2018; Volume 59, pp. 79–108. [CrossRef]
- Marchiosi, R.; dos Santos, W.D.; Constantin, R.P.; de Lima, R.B.; Soares, A.R.; Finger-Teixeira, A.; Mota, T.R.; de Oliveira, D.M.; Foletto-Felipe, M.P.; Abrahão, J.; et al. Biosynthesis and metabolic actions of simple phenolic acids in plants. *Phytochem. Rev.* 2020, 19, 865–906. [CrossRef]

- Gómez-Romero, M.; Segura-Carretero, A.; Fernández-Gutiérrez, A. Metabolite profiling and quantification of phenolic compounds in methanol extracts of tomato fruit. *Phytochemistry* 2010, 71, 1848–1864. [CrossRef]
- Barros, L.; Dueñas, M.; Pinela, J.; Carvalho, A.M.; Buelga, C.S.; Ferreira, I.C.F.R. Characterization and quantification of phenolic compounds in four tomato (*Lycopersicon esculentum* L.) farmers' varieties in Northeastern Portugal homegardens. *Plant Foods Hum. Nutr.* 2012, *67*, 229–234. [CrossRef] [PubMed]
- 24. Pérez-Llorca, M.; Muñoz, P.; Müller, M.; Munné-Bosch, S. Biosynthesis, metabolism and function of auxin, salicylic acid and melatonin in climacteric and non-climacteric fruits. *Front. Plant Sci.* **2019**, *10*, 136. [CrossRef] [PubMed]
- Story, E.N.; Kopec, R.E.; Schwartz, S.J.; Harris, G.K. An update on the health effects of tomato lycopene. *Annu. Rev. Food Sci. Technol.* 2010, 1, 189–210. [CrossRef] [PubMed]
- Xie, B.-X.; Wei, J.-J.; Zhang, Y.-T.; Song, S.-W.; Su, W.; Sun, G.-W.; Hao, Y.-W.; Liu, H.-C. Supplemental blue and red light promote lycopene synthesis in tomato fruits. J. Integr. Agric. 2019, 18, 590–598. [CrossRef]
- Inbaraj, B.; Chen, B.H. Carotenoids in tomato plants. In *Tomatoes and Tomato Products*; CRC Press: Boca Raton, FL, USA, 2008; pp. 133–164.
- Brandt, S.; Pék, Z.; Barna, É.; Lugasi, A.; Helyes, L. Lycopene content and colour of ripening tomatoes as affected by environmental conditions. J. Sci. Food Agric. 2006, 86, 568–572. [CrossRef]
- 29. Jideani, A.I.O.; Silungwe, H.; Takalani, T.; Omolola, A.O.; Udeh, H.O.; Anyasi, T.A. Antioxidant-rich natural fruit and vegetable products and human health. *Int. J. Food Prop.* **2021**, *24*, 41–67. [CrossRef]
- 30. Abbasi, A.R.; Hajirezaei, M.; Hofius, D.; Sonnewald, U.; Voll, L.M. Specific roles of alpha- and gamma-tocopherol in abiotic stress responses of transgenic tobacco. *Plant Physiol.* 2007, 143, 1720–1738. [CrossRef]
- Raiola, A.; Tenore, G.C.; Barone, A.; Frusciante, L.; Rigano, M.M. Vitamin E content and composition in tomato fruits: Beneficial roles and bio-fortification. *Int. J. Mol. Sci.* 2015, 16, 29250–29264. [CrossRef]
- Štolfa, I.; Žuna, P.T.; Špoljarić, D. Abiotic stress response in plants: The relevance of tocopherols. In Antioxidants and Antioxidant Enzymes in Higher Plants; Hupa, D., Palma, J., Corpa, F., Eds.; Springer: Cham, Switzerland, 2018; pp. 233–252.
- Almeida, J.; da Azevedo, M.S.; Spicher, L.; Glauser, G.; Dorp, K.V.; Guyer, L.; del Carranza, A.V.; Asis, R.; de Souza, A.P.; Buckeridge, M.; et al. Down-regulation of tomato PHYTOL KINASE strongly impairs tocopherol biosynthesis and affects prenyllipid metabolism in an organ-specific manner. *J. Exp. Bot.* 2016, 67, 919–934. [CrossRef]
- 34. Du, J.; Cullen, J.J.; Buettner, G.R. Ascorbic acid: Chemistry, biology and the treatment of cancer. *Biochim. Biophys. Acta* 2012, 1826, 443–457. [CrossRef]
- 35. Fenech, M.; Amaya, I.; Valpuesta, V.; Botella, M.A. Vitamin C content in fruits: Biosynthesis and regulation. *Front. Plant Sci.* 2019, 9, 2006. [CrossRef]
- Valšíková-Frey, M.; Komár, P.; Rehuš, M. The effect of varieties and degree of ripeness on vitamin C content in tomato fruits. *Acta Hortic. Regiotect.* 2017, 20, 44–48. [CrossRef]
- 37. Del Giudice, R.; Raiola, A.; Tenore, G.C.; Frusciante, L.; Barone, A.; Monti, D.M.; Rigano, M.M. Antioxidant bioactive compounds in tomato fruits at different ripening stages and their effects on normal and cancer cells. J. Funct. Foods 2015, 18, 83–94. [CrossRef]
- Dorion, S.; Ouellet, J.C.; Rivoal, J. Glutathione metabolism in plants under stress: Beyond reactive oxygen species detoxification. *Metabolites* 2021, 11, 641. [CrossRef] [PubMed]
- 39. Ammar, W.B.; Mediouni, C.; Tray, B.; Ghorbel, M.H.; Jemal, F. Glutathione and phytochelatin contents in tomato plants exposed to cadmium. *Biol. Plant.* **2008**, *52*, 314–320. [CrossRef]
- Kuźniak, E.; Skłodowska, M. Compartment-specific role of the ascorbate–glutathione cycle in the response of tomato leaf cells to Botrytis cinerea infection. J. Exp. Bot. 2005, 56, 921–933. [CrossRef]
- Jan, S.; Noman, A.; Kaya, C.; Ashraf, M.; Nasser, A.M.; Ahmad, P. 24-Epibrassinolide alleviates the injurious effects of Cr(VI) toxicity in tomato plants: Insights into growth, physio-biochemical attributes, antioxidant activity and regulation of ascorbate–glutathione and glyoxalase cycles. J. Plant Growth Regul. 2020, 39, 1587–1604. [CrossRef]
- 42. Zhao, H.; Zhang, R.; Yan, X.; Fan, K. Superoxide dismutase nanozymes: An emerging star for anti-oxidation. *J. Mater. Chem. B* 2021, *9*, 6939–6957. [CrossRef]
- Su, W.; Raza, A.; Gao, A.; Jia, Z.; Zhang, Y.; Hussain, M.A.; Mehmood, S.S.; Cheng, Y.; Lv, Y.; Zou, X. Genome-wide analysis and expression profile of superoxide dismutase (SOD) gene family in rapeseed (*Brassica napus* L.) under different hormones and abiotic stress conditions. *Antioxidants* 2021, 10, 1182. [CrossRef]
- Li, X.; Tsuta, M.; Hayakawa, F.; Nakano, Y.; Kazami, Y.; Ikehata, A. Estimating the sensory qualities of tomatoes using visible and near-infrared spectroscopy and interpretation based on gas chromatography-mass spectrometry metabolomics. *Food Chem.* 2021, 343, 128470. [CrossRef]
- 45. Wang, W.; Xia, M.; Chen, J.; Deng, F.; Yuan, R.; Zhang, X.; Shen, F. Genome-wide analysis of superoxide dismutase gene family in *Gossypium raimondii* and *G. arboretum*. *Plant Gene* **2016**, *6*, 18–29. [CrossRef]
- 46. Feng, K.; Yu, J.; Cheng, Y.; Ruan, M.; Wang, R.; Ye, Q.; Zhou, G.; Li, Z.; Yao, Z.; Yang, Y.; et al. The *SOD* gene family in tomato: Identification, phylogenetic relationships, and expression patterns. *Front. Plant Sci.* **2016**, *7*, 1279. [CrossRef]
- 47. Zhang, Y.; Zheng, L.; Yun, L.; Ji, L.; Li, G.; Ji, M.; Shi, Y.; Zheng, X. Catalase (CAT) gene family in wheat (*Triticum aestivum* L.): Evolution, expression pattern and function analysis. *Int. J. Mol. Sci.* **2022**, *23*, 542. [CrossRef] [PubMed]
- Alfonso-Prieto, M.; Biarnés, X.; Vidossich, P.; Rovira, C. The molecular mechanism of the catalase reaction. J. Am. Chem. Soc. 2009, 131, 11751–11761. [CrossRef] [PubMed]

- Chaudhry, U.K.; Gökçe, Z.N.Ö.; Gökçe, A.F. Drought and salt stress effects on biochemical changes and gene expression of photosystem II and catalase genes in selected onion cultivars. *Biologia* 2021, 76, 3107–3121. [CrossRef]
- Raza, A.; Su, W.; Gao, A.; Mehmood, S.S.; Hussain, M.A.; Nie, W.; Lv, Y.; Zou, X.; Zhang, X. Catalase (CAT) gene family in rapeseed (*Brassica napus* L.): Genome-wide analysis, identification, and expression pattern in response to multiple hormones and abiotic stress conditions. *Int. J. Mol. Sci.* 2021, 22, 4281. [CrossRef]
- 51. Kafeel, S.; Hashim, Z.; Fawwad, A.; Nuzhat, N.S. Predisposition of *SOD1*, *GPX1*, *CAT* genetic variants and their haplotypes in cataractogenesis of type 2 diabetes mellitus in Pakistan. *Acta Diabetol.* **2022**, *59*, 623–632. [CrossRef]
- Kabir, M.H.; Wang, M.H. Functional studies on two catalase genes from tomato (*Solanum lycopersicum* L.). J. Hortic. Sci. Biotechnol. 2011, 86, 84–90. [CrossRef]
- 53. Shoja, H.H.M.; Khezriani, T.; Kolahi, M.; Mohajel, K.E.; Yazdi, M. Morphologic and anatomic response, catalase gene expression in drought varieties of tomato and bioinformatics analyses of microarray studies of the catalase gene. *Res. Sq.* **2016**, 1–23. [CrossRef]
- 54. Hu, J.; Chen, G.; Yin, W.; Cui, B.; Yu, X.; Lu, Y.; Hu, Z. Silencing of *SlHB2* improves drought, salt stress tolerance, and induces stress-related gene expression in tomato. *J. Plant Growth Regul.* **2017**, *36*, 578–589. [CrossRef]
- 55. Kuo, E.Y.H.; Cai, M.S.; Lee, T.M. Ascorbate peroxidase 4 plays a role in the tolerance of *Chlamydomonas reinhardtii* to photooxidative stress. *Sci. Rep.* **2020**, *10*, 13287. [CrossRef] [PubMed]
- 56. Tyagi, S.; Shumayla; Chandra, V.P.; Singh, K.; Kumar, S.U. Molecular characterization of ascorbate peroxidase (APX) and APX-related (APX-R) genes in *Triticum aestivum* L. *Genomics* **2020**, *112*, 4208–4223. [CrossRef] [PubMed]
- 57. Omoarelojie, L.O.; Kulkarni, M.G.; Finnie, J.F.; Staden, J.V. Biostimulants and the modulation of plant antioxidant systems and properties. In *Biostimulants for Crops from Seed Germination to Plant Development*; Shubhpriya Gupta, S., Van Staden, J., Eds.; Academic Press: Cambridge, MA, USA, 2021; pp. 333–363. [CrossRef]
- Liu, J.-X.; Feng, K.; Duan, A.Q.; Li, H.; Yang, Q.Q.; Xu, Z.S.; Xiong, A.-S. Isolation, purification and characterization of an ascorbate peroxidase from celery and overexpression of the *AgAPX1* gene enhanced ascorbate content and drought tolerance in *Arabidopsis*. *BMC Plant Biol.* 2019, 19, 488. [CrossRef] [PubMed]
- Ozyigit, I.I.; Filiz, E.; Vatansever, R.; Kurtoglu, K.Y.; Koc, I.; Öztürk, M.X.; Anjum, N.A. Identification and comparative analysis of H₂O₂-scavenging enzymes (ascorbate peroxidase and glutathione peroxidase) in selected plants employing bioinformatics approaches. *Front. Plant Sci.* 2016, 7, 301. [CrossRef]
- 60. Najami, N.; Janda, T.; Barriah, W.; Kayam, G.; Tal, M.; Guy, M.; Volokita, M. Ascorbate peroxidase gene family in tomato: Its identification and characterization. *Mol. Genet. Genom.* **2008**, *279*, 171–182. [CrossRef] [PubMed]
- Akbudak, M.A.; Filiz, E.; Vatansever, R.; Kontbay, K. Genome-wide identification and expression profiling of ascorbate peroxidase (*APX*) and glutathione peroxidase (*GPX*) genes under drought stress in sorghum (*Sorghum bicolor* L.). *J. Plant Growth Regul.* 2018, 37, 925–936. [CrossRef]
- Riyazuddin, R.; Bela, K.; Horváth, E.; Rigó, G.; Gallé, Á.; Szabados, L.; Fehér, A.; Csiszár, J. Overexpression of the *Arabidopsis* glutathione peroxidase-like 5 gene (*AtGPXL5*) resulted in altered plant development and redox status. *Environ. Exp. Bot.* 2019, 167, 103849. [CrossRef]
- 63. Paiva, A.L.S.; Passaia, G.; Lobo, A.K.M.; Jardim-Messeder, D.; Silveira, J.A.G.; Margis-Pinheiro, M. Mitochondrial glutathione peroxidase (*OsGPX3*) has a crucial role in rice protection against salt stress. *Environ. Exp. Bot.* **2019**, *158*, 12–21. [CrossRef]
- 64. Herbette, S.; de Labrouhe, D.T.; Drevet, J.R.; Roeckel-Drevet, P. Transgenic tomatoes showing higher glutathione peroxydase antioxidant activity are more resistant to an abiotic stress but more susceptible to biotic stresses. *Plant Sci.* **2011**, *180*, 548–553. [CrossRef]
- 65. Karpuz, B.; Çakir, Ö. Effect of proteasome inhibitor MG132 on the expression of oxidative metabolism related genes in tomato. *Food Sci. Technol. Camp.* **2021**, *42*, e52420. [CrossRef]
- Sharma, N.; Muthamilarasan, M.; Dulani, P.; Prasad, M. Genomic dissection of ROS detoxifying enzyme encoding genes for their role in antioxidative defense mechanism against Tomato leaf curl New Delhi virus infection in tomato. *Genomics* 2021, 113, 889–899. [CrossRef] [PubMed]
- 67. Chandra, S.; Khan, S.; Avula, B.; Lata, H.; Yng, M.H.; ElSohly, M.A.; Khan, I.A. Assessment of total phenolic and flavonoid content, antioxidant properties, and yield of aeroponically and conventionally grown leafy vegetables and fruit crops: A comparative study. *Evid.-Based Complement. Altern. Med.* 2014, 2014, 253875. [CrossRef] [PubMed]
- Cömert, E.D.; Mogol, B.A.; Gökmen, V. Relationship between color and antioxidant capacity of fruits and vegetables. *Curr. Res. Food Sci.* 2020, 2, 1–10. [CrossRef] [PubMed]
- 69. Martínez-Valverde, I.; Periago, M.J.; Provan, G.; Chesson, A. Phenolic compounds, lycopene and antioxidant activity in commercial varieties of tomato (*Lycopersicum esculentum*). J. Sci. Food Agric. 2002, 82, 323–330. [CrossRef]
- 70. Bhandari, S.R.; Lee, J.G. Ripening-dependent changes in antioxidants, color attributes, and antioxidant activity of seven tomato (*Solanum lycopersicum* L.) cultivars. *J. Anal. Methods Chem.* **2016**, 2016, 5498618. [CrossRef]
- Ou, B.; Huang, D.; Hampsch-Woodill, M.; Flanagan, J.A.; Deemer, E.K. Analysis of antioxidant activities of common vegetables employing oxygen radical absorbance capacity (ORAC) and ferric reducing antioxidant power (FRAP) assays: A comparative study. J. Agric. Food Chem. 2002, 50, 3122–3128. [CrossRef]
- 72. Zhu, Z.; Chen, Y.; Shi, G.; Zhang, X. Selenium delays tomato fruit ripening by inhibiting ethylene biosynthesis and enhancing the antioxidant defense system. *Food Chem.* **2017**, *219*, 179–184. [CrossRef]

- 73. Yao, G.F.; Wei, Z.-Z.; Li, T.-T.; Tang, J.; Huang, Z.Q.; Yang, F.; Li, Y.-H.; Han, Z.; Hu, F.; Hu, L.-Y.; et al. Modulation of enhanced antioxidant activity by hydrogen sulfide antagonization of ethylene in tomato fruit ripening. *J. Agric. Food Chem.* **2018**, *66*, 10380–10387. [CrossRef]
- 74. Tao, X.; Wu, Q.; Aalim, H.; Li, L.; Mao, L.; Luo, Z.; Ying, T. Effects of exogenous abscisic acid on bioactive components and antioxidant capacity of postharvest tomato during ripening. *Molecules* **2020**, *25*, 1346. [CrossRef]
- 75. Basso, A.; Moreira, R.d.F.P.M.; José, H.J. Effect of operational conditions on photocatalytic ethylene degradation applied to control tomato ripening. *J. Photochem. Photobiol. A Chem.* **2018**, 367, 294–301. [CrossRef]
- Nour, V.; Trandafir, I.; Ionica, M.E. Evolution of antioxidant activity and bioactive compounds in tomato (*Lycopersicon esculentum* Mill.) fruits during growth and ripening. *J. Appl. Bot. Food Qual.* 2014, 87, 97–103. [CrossRef]
- 77. Guo, J.-E. Histone deacetylase gene *SlHDT1* regulates tomato fruit ripening by affecting carotenoid accumulation and ethylene biosynthesis. *Plant Sci.* **2022**, *318*, 111235. [CrossRef]
- 78. Prol, F.V.; López-Gresa, M.P.; Rodrigo, I.; Bellés, J.M.; Lisón, P. Ethylene is involved in symptom development and ribosomal stress of tomato plants upon citrus exocortis viroid infection. *Plants* **2020**, *9*, 582. [CrossRef]
- 79. Li, Y.; Lu, Y.; Li, L.; Chu, Z.; Zhang, H.; Li, H.; Fernie, A.R.; Ouyang, B. Impairment of hormone pathways results in a general disturbance of fruit primary metabolism in tomato. *Food Chem.* **2019**, 274, 170–179. [CrossRef]
- Klay, I.; Pirrello, J.; Riahi, L.; Bernadac, A.; Cherif, A.; Bouzayen, M.; Bouzid, S. Ethylene response factor *SI-ERF.B.3* is responsive to abiotic stresses and mediates salt and cold stress response regulation in tomato. *Sci. World J.* 2014, 2014, 167681. [CrossRef] [PubMed]
- 81. Pan, C.; Zhang, H.; Ma, Q.; Fan, F.; Fu, R.; Ahammed, G.J.; Yu, J.; Shi, K. Role of ethylene biosynthesis and signaling in elevated CO₂-induced heat stress response in tomato. *Planta* **2019**, *250*, 563–572. [CrossRef]
- 82. Pan, Y.; Seymour, G.B.; Lu, C.; Hu, Z.; Chen, X.; Chen, G. An ethylene response factor (ERF5) promoting adaptation to drought and salt tolerance in tomato. *Plant Cell Rep.* **2012**, *31*, 349–360. [CrossRef]
- 83. Klay, I.; Gouia, S.; Liu, M.; Mila, I.; Khoudi, H.; Bernadac, A.; Bouzayen, M.; Pirrello, J. Ethylene response factors (ERF) are differentially regulated by different abiotic stress types in tomato plants. *Plant Sci.* **2018**, *274*, 137–145. [CrossRef]
- 84. Shibli, R.A.; Kushad, M.; Yousef, G.G.; Lila, M.A. Physiological and biochemical responses of tomato microshoots to induced salinity stress with associated ethylene accumulation. *Plant Growth Regul.* **2007**, *51*, 159–169. [CrossRef]
- 85. Poór, P.; Kovács, J.; Szopkó, D.; Tari, I. Ethylene signaling in salt stress- and salicylic acid-induced programmed cell death in tomato suspension cells. *Protoplasma* **2013**, 250, 273–284. [CrossRef]
- 86. Poór, P.; Borbély, P.; Kovács, J.; Szepesi, A.; Takács, Z.; Tari, I. Opposite extremes in ethylene/nitric oxide ratio induce cell death in suspension culture and root apices of tomato exposed to salt stress. *Acta Biol. Hung.* **2014**, *65*, 428–438. [CrossRef]
- Shu, P.; Li, Y.; Li, Z.; Xiang, L.; Sheng, J.; Shen, L. Ferulic acid enhances chilling tolerance in tomato fruit by up-regulating the gene expression of CBF transcriptional pathway in MAPK3-dependent manner. *Postharvest Biol. Technol.* 2022, 185, 111775. [CrossRef]
- Gharbi, E.; Martínez, J.P.; Benahmed, H.; Lepoint, G.; Vanpee, B.; Quinet, M.; Lutts, S. Inhibition of ethylene synthesis reduces salt-tolerance in tomato wild relative species *Solanum chilense*. J. Plant Physiol. 2017, 210, 24–37. [CrossRef]
- Monteiro, C.C.; Carvalho, R.F.; Gratão, P.L.; Carvalho, G.; Tezotto, T.; Medici, L.O.; Peres, L.E.P.; Azevedo, R.A. Biochemical responses of the ethylene-insensitive *Never ripe* tomato mutant subjected to cadmium and sodium stresses. *Environ. Exp. Bot.* 2011, *71*, 306–320. [CrossRef]
- 90. Tian, D.; Peiffer, M.; De Moraes, C.M.; Felton, G.W. Roles of ethylene and jasmonic acid in systemic induced defense in tomato (*Solanum lycopersicum*) against *Helicoverpa zea*. *Planta* **2014**, 239, 577–589. [CrossRef]
- 91. Fracetto, G.G.M.; Peres, L.E.P.; Mehdy, M.C.; Lambais, M.R. Tomato ethylene mutants exhibit differences in arbuscular mycorrhiza development and levels of plant defense-related transcripts. *Symbiosis* **2013**, *60*, 155–167. [CrossRef]
- 92. Ibort, P.; Imai, H.; Uemura, M.; Aroca, R. Proteomic analysis reveals that tomato interaction with plant growth promoting bacteria is highly determined by ethylene perception. *J. Plant Physiol.* **2018**, *220*, 43–59. [CrossRef]
- 93. Gao, Y.; Li, S.-J.; Zhang, S.W.; Feng, T.; Zhang, Z.-Y.; Luo, S.-J.; Mao, H.-Y.; Borkovich, K.A.; Ouyang, S.-Q. *Sly*miR482e-3p mediates tomato wilt disease by modulating ethylene response pathway. *Plant Biotechnol. J.* **2021**, *19*, 17. [CrossRef]
- 94. Iqbal, N.; Czékus, Z.; Ördög, A.; Poór, P. Ethylene-dependent effects of fusaric acid on the photosynthetic activity of tomato plants. *Photosynthetica* 2021, *59*, 337–348. [CrossRef]
- 95. Martínez-Romero, D.; Guillén, F.; Castillo, S.; Zapata, P.J.; Valero, D.; Serrano, M. Effect of ethylene concentration on quality parameters of fresh tomatoes stored using a carbon-heat hybrid ethylene scrubber. *Postharvest Biol. Technol.* **2009**, *51*, 206–211. [CrossRef]
- 96. Mansourbahmani, S.; Ghareyazie, B.; Zarinnia, V.; Kalatejari, S.; Mohammadi, R.S. Study on the efficiency of ethylene scavengers on the maintenance of postharvest quality of tomato fruit. *J. Food Meas. Charact.* **2018**, *12*, 691–701. [CrossRef]
- 97. Zhao, D.; Shen, L.; Fan, B.; Yu, M.; Zheng, Y.; Lv, S.; Sheng, J. Ethylene and cold participate in the regulation of *LeCBF1* gene expression in postharvest tomato fruits. *FEBS Lett.* **2009**, *583*, 3329–3334. [CrossRef] [PubMed]
- Loayza, F.E.; Brecht, J.K.; Simonne, A.H.; Plotto, A.; Baldwin, E.A.; Bai, J.; Lon-Kan, E. Synergy between hot water treatment and high temperature ethylene treatment in promoting antioxidants in mature-green tomatoes. *Postharvest Biol. Technol.* 2020, 170, 111314. [CrossRef]
- 99. Cornelia, P.; Adriana, C.; Iulia, V.N. Studies regarding the influence of exogenous salicylic acid treatment on some bioactive compounds of two varieties of cherry tomatoes. *Nat. Resour. Sustain. Dev.* **2018**, *8*, 67–75. [CrossRef]

- Klessig, D.F.; Choi, H.W.; Dempsey, D.M.A. Systemic acquired resistance and salicylic acid: Past, present, and future. *Curr. Rev.* 2018, *31*, 871–888. [CrossRef]
- 101. Baby, J.; Jini, D.; Sujatha, S. Insight into the role of exogenous salicylic acid on plants grown under salt environment. *Asian J. Crop Sci.* **2010**, *2*, 226–235. [CrossRef]
- 102. Surapu, V.; Ediga, A.; Meriga, B. Salicylic acid alleviates aluminum toxicity in tomato seedlings (*Lycopersicum esculentum* Mill.) through activation of antioxidant defense system and proline biosynthesis. *Adv. Biosci. Biotechnol.* **2014**, *5*, 777–789. [CrossRef]
- 103. Falcioni, T.; Ferrio, J.P.; del Cueto, A.I.; Giné, J.; Achón, M.A.; Medina, V. Effect of salicylic acid treatment on tomato plant physiology and tolerance to potato virus X infection. *Eur. J. Plant Pathol.* **2014**, *138*, 331–345. [CrossRef]
- 104. da Lobato, A.K.S.; Barbosa, M.A.M.; Alsahli, A.A.; Lima, E.J.A.; da Silva, B.R.S.D. Exogenous salicylic acid alleviates the negative impacts on production components, biomass and gas exchange in tomato plants under water deficit improving redox status and anatomical responses. *Physiol. Plant.* 2020, 172, 869–881. [CrossRef]
- 105. Stevens, J.; Senaratna, T.; Sivasithamparam, K. Salicylic acid induces salinity tolerance in tomato (*Lycopersicon esculentum* cv. Roma): Associated changes in gas exchange, water relations and membrane stabilisation. *Plant Growth Regul.* 2006, 49, 77–83. [CrossRef]
- 106. Manaa, A.; Gharbi, E.; Mimouni, H.; Wasti, S.; Aschi-Smiti, S.; Lutts, S.; Ahmed, H.B. Simultaneous application of salicylic acid and calcium improves salt tolerance in two contrasting tomato (*Solanum lycopersicum*) cultivars. S. Afr. J. Bot. 2014, 95, 32–39. [CrossRef]
- He, Y.; Zhu, Z.J. Exogenous salicylic acid alleviates NaCl toxicity and increases antioxidative enzyme activity in *Lycopersicon* esculentum. Biol. Plant. 2008, 52, 792–795. [CrossRef]
- 108. Tari, I.; Csiszár, J.; Horváth, E.; Poór, P.; Takács, Z.; Szepesi, Á. The alleviation of the adverse effects of salt stress in the tomato plant by salicylic acid shows a time- and organ-specific antioxidant response. Acta Biol. Crac. Ser. Bot. 2015, 57, 21–30. [CrossRef]
- 109. Jaime-Pérez, N.; Pineda, B.; García-Sogo, B.; Atares, A.; Athman, A.; Byrt, C.S.; Olías, R.; Asins, M.J.; Gilliham, M.; Moreno, V.; et al. The sodium transporter encoded by the *HKT1*;2 gene modulates sodium/potassium homeostasis in tomato shoots under salinity. *Plant Cell Environ.* 2017, 40, 658–671. [CrossRef] [PubMed]
- 110. Rao, Y.R.; Ansari, M.W.; Sahoo, R.K.; Wattal, R.K.; Tuteja, N.; Kumar, V.R. Salicylic acid modulates ACS, NHX1, sos1 and HKT1; 2 expression to regulate ethylene overproduction and Na⁺ ions toxicity that leads to improved physiological status and enhanced salinity stress tolerance in tomato plants cv. Pusa Ruby. *Plant Signal. Behav.* 2021, 16, 1950888. [CrossRef] [PubMed]
- Orabi, S.A.; Dawood, M.; Salman, S. Comparative study between the physiological role of hydrogen peroxide and salicylic acid in alleviating the harmful effect of low temperature on tomato plants grown under sand-ponic culture. *Sci. Agric.* 2015, *9*, 49–59. [CrossRef]
- 112. Jahan, M.S.; Wang, Y.; Shu, S.; Zhong, M.; Chen, Z.; Wu, J.; Sun, J.; Guo, S. Exogenous salicylic acid increases the heat tolerance in Tomato (*Solanum lycopersicum* L) by enhancing photosynthesis efficiency and improving antioxidant defense system through scavenging of reactive oxygen species. *Sci. Hortic.* 2019, 247, 421–429. [CrossRef]
- Ahmed, H.I.; Shabana, A.I.; Elsayed, A.Y. Chilling tolerance enhancement in tomato (*Solanum lycopersicum*) plant by spraying of some anti-stress compounds. J. Plant Prod. 2016, 7, 185–195. [CrossRef]
- 114. Javanmardi, J.; Akbari, N. Salicylic acid at different plant growth stages affects secondary metabolites and phisico-chemical parameters of greenhouse tomato. *Adv. Hortic. Sci.* **2016**, *30*, 151–157. [CrossRef]
- 115. Kovács, J.; Poór, P.; Szepesi, Á.; Tari, I. Salicylic acid induced cysteine protease activity during programmed cell death in tomato plants. *Acta Biol. Hung.* **2016**, *67*, 148–158. [CrossRef] [PubMed]
- 116. Poór, P.; Borbély, P.; Czékus, Z.; Takács, Z.; Ördög, A.; Popović, B.; Tari, I. Comparison of changes in water status and photosynthetic parameters in wild type and abscisic acid-deficient *sitiens* mutant of tomato (*Solanum lycopersicum* cv. Rheinlands Ruhm) exposed to sublethal and lethal salt stress. *J. Plant Physiol.* **2019**, *232*, 130–140. [CrossRef] [PubMed]
- Spletzer, M.E.; Enyedi, A.J. Salicylic acid induces resistance to *Alternaria solani* in hydroponically grown tomato. *Phytopathology* 1999, *89*, 722–727. [CrossRef] [PubMed]
- 118. Adss, I.; Hamza, H.; Hafez, E.; Heikal, H. Enhancing tomato fruits post-harvest resistance by salicylic acid and hydrogen peroxide elicitors against rot caused by *Alternaria solani*. J. Agric. Chem. Biotechnol. 2017, 8, 1–8. [CrossRef]
- 119. Ojha, S.; Chatterjee, N.C. Induction of resistance in tomato plants against *Fusarium oxysporum* F. SP. Lycopersici mediated through salicylic acid and Trichoderma harzianum. *J. Plant Prot. Res.* **2012**, *52*, 220–225. [CrossRef]
- 120. Jendoubi, W.; Harbaoui, K.; Hamada, W. Salicylic acid-induced resistance against Fusarium oxysporum f.s.pradicis lycopercisi in hydroponic grown tomato plants. J. *New. Sci.* 2015, *21*, 985–995.
- 121. Zehra, A.; Meena, M.; Dubey, M.K.; Aamir, M.; Upadhyay, R.S. Synergistic effects of plant defense elicitors and *Trichoderma harzianum* on enhanced induction of antioxidant defense system in tomato against Fusarium wilt disease. *Bot. Stud.* 2017, 58, 44. [CrossRef]
- 122. Ibrahim, Y.E. Activities of antioxidants enzymes in salicylic acid treated tomato against Xanthomonas vesicatoria. *Afr. J. Microbiol. Res.* **2012**, *6*, 5678–5682. [CrossRef]
- 123. Madany, M.M.Y.; Zinta, G.; Abuelsoud, W.; Hozzein, W.N.; Selim, S.; Asard, H.; Elgawad, H.A. Hormonal seed-priming improves tomato resistance against broomrape infection. *J. Plant Physiol.* **2020**, 250, 153184. [CrossRef]
- Jiang, N.H.; Zhang, S.H. Effects of combined application of potassium silicate and salicylic acid on the defense response of hydroponically grown tomato plants to *Ralstonia solanacearum* infection. *Sustainability* 2021, 13, 3750. [CrossRef]

- 125. Nagai, A.; Torres, P.B.; Duarte, L.M.L.; Chaves, A.L.R.; Macedo, A.F.; Floh, E.I.S.; de Oliveira, L.F.; Zuccarelli, R.; dos Santos, D.Y.A.C. Signaling pathway played by salicylic acid, gentisic acid, nitric oxide, polyamines and non-enzymatic antioxidants in compatible and incompatible *Solanum*-tomato mottle mosaic virus interactions. *Plant Sci.* 2020, 290, 110274. [CrossRef]
- Udalova, Z.V.; Zinovieva, S.V. Effect of salicylic acid on the oxidative and photosynthetic processes in tomato plants at invasion with root-knot nematode meloidogyne incognita (Kofoid Et White, 1919) Chitwood, 1949. Dokl. Biochem. Biophys. 2019, 488, 350–353. [CrossRef] [PubMed]
- 127. Aghdam, M.S.; Mohammadkhani, N. Enhancement of chilling stress tolerance of tomato fruit by postharvest brassinolide treatment. *Food Bioprocess Technol.* 2014, 7, 909–914. [CrossRef]
- 128. Baninaiem, E.; Mirzaaliandastjerdi, A.M.; Rastegar, S.; Abbaszade, K.H. Effect of pre- and postharvest salicylic acid treatment on quality characteristics of tomato during cold storage. *Adv. Hortic. Sci.* **2016**, *30*, 183–192. [CrossRef]
- 129. Mandal, D.; Hazarika, T.K. Salicylic acid maintained quality and enhanced shelf life of tomato 'Samrudhi' at refrigerated storage. *Acta Hortic.* **2018**, *1210*, 207–212. [CrossRef]
- Ünal, S.; Küçükbasmaci, Ö.A.; Sabir, F.K. Salicylic acid treatments for extending postharvest quality of tomatoes maintained at different storage temperatures. *Selcuk. J. Agric. Food Sci.* 2021, 35, 35–141. [CrossRef]
- 131. Manan, A.; Ayyub, C.M.; Aslam Pervez, M.; Ahmad, R. Methyl jasmonate brings about resistance against salinity stressed tomato plants by altering biochemical and physiological processes. *Pak. J. Agric. Sci.* **2016**, *53*, 35–41. [CrossRef]
- 132. Singh, A.; Dwivedi, A. Methyl-jasmonate and salicylic acid as potent elicitors for secondary metabolite production in medicinal plants: A review. *J. Pharmacogn. Phytochem.* **2018**, *7*, 750–757.
- Chen, H.; Jones, A.D.; Howe, G.A. Constitutive activation of the jasmonate signaling pathway enhances the production of secondary metabolites in tomato. FEBS Lett. 2006, 580, 2540–2546. [CrossRef]
- Król, P.; Igielski, R.; Pollmann, S.; Kępczyńska, E. Priming of seeds with methyl jasmonate induced resistance to hemi-biotroph *Fusarium oxysporum f.sp. lycopersici in tomato via 12-oxo-phytodienoic acid, salicylic acid, and flavonol accumulation. J. Plant Physiol.* 2015, 179, 122–132. [CrossRef]
- Bali, S.; Kaur, P.; Sharma, A.; Ohri, P.; Bhardwaj, R.; Alyemeni, M.N.; Wijaya, L.; Ahmad, P. Jasmonic acid-induced tolerance to root-knot nematodes in tomato plants through altered photosynthetic and antioxidative defense mechanisms. *Protoplasma* 2018, 255, 471–484. [CrossRef]
- 136. Bali, S.; Kaur, P.; Jamwal, V.L.; Gandhi, S.G.; Sharma, A.; Ohri, P.; Bhardwaj, R.; Ali, M.A.; Ahmad, P. Seed priming with jasmonic acid counteracts root knot nematode infection in tomato by modulating the activity and expression of antioxidative enzymes. *Biomolecules* 2020, 10, 98. [CrossRef]
- 137. Ahmad, P.; Ahanger, A.M.; Alyemeni, M.N.; Wijaya, L.; Alam, P.; Ashraf, M. Mitigation of sodium chloride toxicity in *Solanum lycopersicum* L. by supplementation of jasmonic acid and nitric oxide. *J. Plant Interact.* **2018**, *13*, 64–72. [CrossRef]
- 138. Ding, F.; Wang, C.; Xu, N.; Wang, M.; Zhang, S. Jasmonic acid-regulated putrescine biosynthesis attenuates cold-induced oxidative stress in tomato plants. *Sci. Hortic.* **2021**, *288*, 110373. [CrossRef]
- Abouelsaad, I.; Renault, S. Enhanced oxidative stress in the jasmonic acid-deficient tomato mutant def-1 exposed to NaCl stress. J. Plant Physiol. 2018, 226, 136–144. [CrossRef] [PubMed]
- 140. Tzortzakis, N.G.; Economakis, C. Maintaining postharvest quality of the tomato fruit by employing methyl jasmonate and ethanol vapor treatment. *J. Food Qual.* 2007, *30*, 567–580. [CrossRef]
- 141. Min, D.; Li, F.; Zhang, X.; Cui, X.; Shu, P.; Dong, L.; Ren, C. *SlMYC2* Involved in methyl jasmonate-induced tomato fruit chilling tolerance. *J. Agric. Food Chem.* **2018**, *66*, 3110–3117. [CrossRef]
- 142. Yu, W.; Yu, M.; Zhao, R.; Sheng, J.; Li, Y.; Shen, L. Ethylene perception is associated with the methyl-jasmonate-mediated immune response against *Botrytis cinerea* in tomato fruit. *J. Agric. Food Chem.* **2019**, *67*, 6725–6735. [CrossRef] [PubMed]
- 143. Liu, C.; Chen, L.; Zhao, R.; Li, R.; Zhang, S.; Yu, W.; Sheng, J.; Shen, L. Melatonin induces disease resistance to *Botrytis cinerea* in tomato fruit by activating jasmonic acid signaling pathway. *J. Agric. Food Chem.* **2021**, *67*, 6116–6124. [CrossRef]
- 144. Kępczyńska, E.; Król, P. The phytohormone methyl jasmonate as an activator of induced resistance against the necrotroph *Alternaria porri* f. sp. solani in tomato plants. *J. Plant Interact.* **2012**, *7*, 307–315. [CrossRef]
- 145. Mou, W.; Li, D.; Luo, Z.; Mao, L.; Ying, T. Transcriptomic analysis reveals possible influences of ABA on secondary metabolism of pigments, flavonoids and antioxidants in tomato fruit during ripening. *PLoS ONE* **2015**, *10*, e0129598. [CrossRef]
- 146. Maggio, A.; Barbieri, G.; Raimondi, G.; De Pascale, S. Contrasting effects of GA₃ treatments on tomato plants exposed to increasing salinity. *J. Plant Growth Regul.* 2010, 29, 63–72. [CrossRef]
- 147. Pompeu, G.B.; Vilhena, M.B.; Gratão, P.L.; Carvalho, R.F.; Rossi, M.L.; Martinelli, A.P.; Azevedo, R.A. Abscisic acid-deficient *sit* tomato mutant responses to cadmium-induced stress. *Protoplasma* **2017**, 254, 771–783. [CrossRef]
- 148. Diao, Q.; Song, Y.; Shi, D.; Qi, H. Interaction of polyamines, abscisic acid, nitric oxide, and hydrogen peroxide under chilling stress in tomato (*Lycopersicon esculentum* Mill.) Seedlings. *Front. Plant Sci.* **2017**, *8*, 203. [CrossRef] [PubMed]
- 149. Feng, Y.; Chen, X.; He, Y.; Kou, X.; Xue, Z. Effects of exogenous trehalose on the metabolism of sugar and abscisic acid in tomato seedlings under salt stress. *Trans. Tianjin Univ.* 2019, 25, 451–471. [CrossRef]
- Santos, M.P.; Zandonadi, D.B.; de Sá, A.F.; Costa, E.P.; de Oliveira, C.J.L.; Perez, L.E.P.; Façanha, A.R.; Bressan-Smith, R. Abscisic acid-nitric oxide and auxin interaction modulates salt stress response in tomato roots. *Theor. Exp. Plant Physiol.* 2020, 32, 301–313. [CrossRef]

- Hossain, M.A.; Bhattacharjee, S.; Armin, S.-M.; Qian, P.; Xin, W.; Li, H.-Y.; Burritt, D.J.; Fujita, M.; Tran, L.-S.P. Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: Insights from ROS detoxification and scavenging. *Front. Plant Sci.* 2015, 6, 420. [CrossRef]
- 152. Hu, E.; Liu, M.; Zhou, R.; Jiang, F.; Sun, M.; Wen, J.; Zhu, Z.; Wu, Z. Relationship between melatonin and abscisic acid in response to salt stress of tomato. *Sci. Hortic.* **2021**, *285*, 110176. [CrossRef]
- 153. Zeinali, L.; Heidari, R.; Rahmani, F.; Khara, J. Drought tolerance induced by foliar application of abscisic acid and sulfonamide compounds in tomato. *J. Stress Physiol. Biochem.* **2014**, *10*, 326–334.
- 154. Ramasamy, S.; Nandagopal, J.G.T.; Balasubramanian, M.; Girija, S. Effect of abscisic acid and selenium foliar sprays on drought mitigation in tomato (*Solanum lycopersicum L.*). *Mater. Today Proc.* **2022**, *48*, 191–195. [CrossRef]
- 155. Yan, M.; Yao, Y.; Mou, K.; Dan, Y.; Li, W.; Wang, C.; Liao, W. The involvement of abscisic acid in hydrogen gas-enhanced drought resistance in tomato seedlings. *Sci. Hortic.* **2022**, 292, 110631. [CrossRef]
- 156. Zhou, J.; Xia, X.-J.; Zhou, Y.-H.; Shi, K.; Chen, Z.; 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. [CrossRef]
- 157. Wang, Y.; Tao, X.; Tang, X.-M.; Xiao, L.; Sun, J.-L.; Yan, X.-F.; Li, D.; Deng, H.-Y.; Ma, X.-R. Comparative transcriptome analysis of tomato (*Solanum lycopersicum*) in response to exogenous abscisic acid. *BMC Genom.* **2013**, *14*, 841. [CrossRef] [PubMed]
- 158. Colebrook, E.H.; Thomas, S.G.; Phillips, A.L.; Hedden, P. The role of gibberellin signalling in plant responses to abiotic stress. *J. Exp. Biol.* **2014**, *217*, 67–75. [CrossRef] [PubMed]
- 159. Camara, M.C.; Vandenberghe, L.P.S.; Rodrigues, C.; de Oliveira, J.; Faulds, C.; Bertrand, E.; Soccol, C.R. Current advances in gibberellic acid (GA₃) production, patented technologies and potential applications. *Planta* 2018, 248, 1049–1062. [CrossRef] [PubMed]
- Halo, B.A.; Khan, A.L.; Waqas, M.; Al-Harrasi, A.; Hussain, J.; Ali, L.; Adnan, M.; Lee, I.-J. Endophytic bacteria (*Sphingomonas* sp. LK11) and gibberellin can improve *Solanum lycopersicum* growth and oxidative stress under salinity. *J. Plant Interact.* 2015, 10, 117–125. [CrossRef]
- Esan, A.M.; Olaiya, C.O.; Anifowose, L.O.; Lana, I.O.; Ailenokhuoria, B.V.; Fagbami, O.; Adeyemi, H.R.Y. Effect of plant growthpromoting rhizobacteria and gibberellic acid on salt stress tolerance in tomato genotypes. *Afr. Crop Sci. J.* 2020, 28, 341–362. [CrossRef]
- Khavari-Nejad, R.A.; Najafi, F.; Ranjbari, M. The effects of GA₃ application on growth, lipid peroxidation, antioxidant enzymes activities, and sugars levels of cadmium stressed tomato (*Lycopersicon esculentum* Mill. Cv. CH) plants. *Rom. J. Biol.*—*Plant Biol.* **2013**, *58*, 51–60.
- 163. Haroun, S.A.; Gamel, R.M.E.; Bashasha, J.A.; Aldrussi, I.A. Protective role of β-sitosterol or gibberellic acid to *Lycopersicum* esculentum cultivars under temperature stress. *Egypt. J. Bot.* 2018, *58*, 233–247. [CrossRef]
- 164. Omena-Garcia, R.P.; Martins, A.O.; Medeiros, D.B.; Vallarino, J.G.; Ribeiro, D.M.; Fernie, A.R.; Araújo, W.L.; Nunes-Nesi, A. Growth and metabolic adjustments in response to gibberellin deficiency in drought stressed tomato plants. *Environ. Exp. Bot.* 2019, 159, 95–107. [CrossRef]
- 165. Illouz-Eliaz, N.; Nissan, I.; Nir, I.; Ramon, U.; Shohat, H.; Weiss, D. Mutations in the tomato gibberellin receptors suppress xylem proliferation and reduce water loss under water-deficit conditions. *J. Exp. Bot.* **2020**, *71*, 3603–3612. [CrossRef]
- 166. Gaion, L.A.; Monteiro, C.C.; Cruz, F.J.R.; Rossatto, D.R.; López-Díaz, I.; Carrera, E.; Lima, J.E.; Peres, L.E.P.; Carvalho, R.F. Constitutive gibberellin response in grafted tomato modulates root-to-shoot signaling under drought stress. *J. Plant Physiol.* 2018, 221, 11–21. [CrossRef]
- 167. Zhao, Y. Auxin biosynthesis and its role in plant development. Annu. Rev. Plant Biol. 2010, 61, 49-64. [CrossRef]
- Vega-Celedón, P.; Martínez, C.H.; González, M.; Seeger, M. Biosíntesis de ácido indol-3-acético y promoción del crecimiento de plantas por bacterias. *Cultiv. Trop.* 2016, 37, 33–39. [CrossRef]
- Khan, M.Y.; Prakash, V.; Yadav, V.; Chauhan, D.K.; Prasad, S.M.; Ramawat, N.; Singh, V.P.; Tripathi, D.K.; Sharma, S. Regulation of cadmium toxicity in roots of tomato by indole acetic acid with special emphasis on reactive oxygen species production and their scavenging. *Plant Physiol. Biochem.* 2019, 142, 193–201. [CrossRef] [PubMed]
- 170. Olaiya, C.O.; Anyanwu, G.O. Antistressful action of two auxin analogues on antioxidant enzymes and minerals in tomato (*Solanum Lycopersicon*). *Int. J. Biotechnol. Biochem.* **2013**, *9*, 145–156.
- Siddiqui, M.H.; Alamri, S.A.; Al-Khaishany, M.Y.Y.; Al-Qutami, M.A.; Ali, H.M.; Khan, M.N. Sodium nitroprusside and indole acetic acidimprove the tolerance of tomato plants to heat stress by protecting against DNA damage. *J. Plant Interact.* 2017, 12, 177–186. [CrossRef]
- Deen, S.; Singh, N.B. Alleviation of allelopathic stress of benzoic acid by indole acetic acid in *Solanum lycopersicum*. *Sci. Hortic.* 2015, 192, 211–217. [CrossRef]
- 173. Niharika, K.; Singh, N.B.; Khare, S.; Singh, A.; Yadav, V.; Yadav, R.K. Attenuation of vanillic acid toxicity by foliar application withindole-3-acetic acid in tomato seedlings. *Int. J. Veg. Sci.* 2021, *28*, 211–232. [CrossRef]
- 174. Tyburski, J.; Dunajska, K.; Mazurek, P.; Piotrowska, B.; Tretyn, A. Exogenous auxin regulates H₂O₂ metabolism in roots of tomato (*Lycopersicon esculentum* Mill.) seedlings affecting the expression and activity of CuZn-superoxide dismutase, catalase, and peroxidase. *Acta Physiol. Plant* 2009, *31*, 249–260. [CrossRef]

- 175. Ivanchenko, M.G.; den Os, D.; Monshausen, G.B.; Dubrovsky, J.G.; Bednárová, A.; Krishnan, N. Auxin increases the hydrogen peroxide (H₂O₂) concentration in tomato (*Solanum lycopersicum*) root tips while inhibiting root growth. *Ann. Bot.* 2013, 112, 1107–1116. [CrossRef]
- 176. Basit, F.; Liu, J.; An, J.; Chen, M.; He, C.; Zhu, X.; Li, Z.; Hu, J.; Guan, Y. Brassinosteroids as a multidimensional regulator of plant physiological and molecular responses under various environmental stresses. *Environ. Sci. Pollut. Res.* 2021, 28, 44768–44779. [CrossRef] [PubMed]
- 177. Anwar, A.; Liu, Y.; Dong, R.; Bai, L.; Yu, X.; Li, Y. The physiological and molecular mechanism of brassinosteroid in response to stress: A review. *Biol. Res.* 2018, *51*, 46. [CrossRef] [PubMed]
- 178. Ahammed, G.J.; Ruan, Y.P.; Zhou, J.; Xia, X.J.; Shi, K.; Zhou, Y.H.; Yu, J.Q. Brassinosteroid alleviates polychlorinated biphenylsinduced oxidative stress by enhancing antioxidant enzymes activity in tomato. *Chemosphere* 2013, 90, 2645–2653. [CrossRef] [PubMed]
- 179. Ahammed, G.J.; Zhou, Y.H.; Xia, X.J.; Mao, W.H.; Shi, K.; Yu, J.Q. Brassinosteroid regulates secondary metabolism in tomato towards enhanced tolerance to phenanthrene. *Biol. Plant.* **2013**, *57*, 154–158. [CrossRef]
- Mazorra, L.M.; Núñez, M.; Hechavarria, M.; Coll, F.; Sánchez-Blanco, M.J. Influence of brassinosteroids on antioxidant enzymes activity in tomato under different temperatures. *Biol. Plant* 2002, 45, 593–596. [CrossRef]
- Ogweno, J.O.; Song, X.S.; Shi, K.; Hu, W.H.; Mao, W.H.; Zhou, Y.H.; Yu, J.Q.; Nogués, S. Brassinosteroids alleviate heat-induced inhibition of photosynthesis by increasing carboxylation efficiency and enhancing antioxidant systems in *Lycopersicon esculentum*. *J. Plant Growth Regul.* 2008, 27, 49–57. [CrossRef]
- Hayat, S.; Hasan, S.A.; Hayat, Q.; Ahmad, A. Brassinosteroids protect *Lycopersicon esculentum* from cadmium toxicity applied as shotgun approach. *Protoplasma* 2010, 239, 3–14. [CrossRef]
- 183. Jangid, K.K.; Dwivedi, P. Physiological and biochemical changes by nitric oxide and brassinosteroid in tomato (*Lycopersicon esculentum* Mill.) under drought stress. *Acta Physiol. Plant* **2017**, *39*, 73. [CrossRef]
- 184. Vardhini, B.V.; Rao, S.S.R. Acceleration of ripening of tomato pericarp discs by brassinosteroids. *Phytochemistry* **2002**, *61*, 843–847. [CrossRef]
- 185. Ding, Y.; Sheng, J.; Li, S.; Nie, Y.; Zhao, J.; Zhu, Z.; Wang, Z.; Tang, X. The role of gibberellins in the mitigation of chilling injury in cherry tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biol. Technol.* **2015**, *101*, 88–95. [CrossRef]
- 186. Mou, W.; Li, D.; Bu, J.; Jiang, U.; Ullah, Z.; Luo, Z.; Mao, L.; Ying, T. Comprehensive analysis of ABA effects on ethylene biosynthesis and signaling during tomato fruit ripening. *PLoS ONE* **2016**, *11*, e0154072. [CrossRef] [PubMed]
- 187. Hu, S.; Liu, L.; Li, S.; Shao, Z.; Meng, F.; Liu, H.; Duan, W.; Liang, D.; Zhu, C.; Xu, T.; et al. Regulation of fruit ripening by the brassinosteroid biosynthetic gene *SlCYP90B3* via an ethylene-dependent pathway in tomato. *Hortic. Res.* 2020, 7, 163. [CrossRef] [PubMed]
- 188. Su, L.; Diretto, G.; Purgatto, E.; Danoun, S.; Zouine, M.; Li, Z.; Roustan, J.P.; Bouzayen, M.; Giuliano, G.; Chervin, C. Carotenoid accumulation during tomato fruit ripening is modulated by the auxin-ethylene balance. *BMC Plant Biol.* 2015, 15, 114. [CrossRef] [PubMed]
- Li, M.; Ahammed, G.J.; Li, C.; Bao, X.; Yu, J.; Huang, C.; Yin, H.; Zhou, J. Brassinosteroid ameliorates zinc oxide nanoparticlesinduced oxidative stress by improving antioxidant potential and redox homeostasis in tomato seedling. *Front. Plant Sci.* 2016, 7, 615. [CrossRef] [PubMed]
- 190. Ahammed, G.J.; Li, Y.; Cheng, Y.; Liu, A.; Chen, S.; Li, X. Abscisic acid and gibberellins act antagonistically to mediate epigallocatechin3gallateretarded seed germination and early seedling growth in tomato. *J. Plant Growth Regul.* **2020**, *39*, 1414–1424. [CrossRef]
- 191. Heidari, P.; Entazari, M.; Ebrahimi, A.; Ahmadizadeh, M.; Vannozzi, A.; Palumbo, F.; Barcaccia, G. Exogenous EBR ameliorates endogenous hormone contents in tomato species under low-temperature stress. *Horticulturae* **2021**, *7*, 84. [CrossRef]

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