We are IntechOpen,
the world's leading publisher of
Open Access books
Built by scientists, for scientists

6,900
Open access books available

185,000
International authors and editors

200M
Downloads

154
Countries delivered to

Our authors are among the

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

CLARIVATE ANALYTICS
BOOK CITATION INDEX
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Chapter

ROS Regulation Mechanism for Mitigation of Abiotic Stress in Plants

Asha Kumari, Mahendar Singh Bhinda, Sachin Sharma, Manoj Kumar Chitara, Ashim Debnath, Chandan Maharana, Manoj Parihar and Binny Sharma

Abstract

Plants respond to various stresses during their lifecycle among which abiotic stress is the most severe one comprising heat, cold, drought, salinity, flooding, etc. which take a heavy toll on crop yield worldwide in every corresponding year. ROS has a dual role in abiotic stress mechanisms where, at high levels, they are toxic to cells while at the same time, the same molecule can function as a signal transducer that activates a local as well as a systemic plant defense response against stress. The most common ROS species are Hydrogen peroxide (H_2O_2), Superoxide anions (O_2-), Hydroxyl radicals ($OH-$), and Singlet oxygen ($1O_2$) which are results of physiological metabolism often controlled by enzymatic and non-enzymatic antioxidant defense systems. ROS generally accumulate in plants during abiotic and biotic stress conditions resulting in oxidative damage which ultimately leads to programmed cell death. Many ROS scavenging pathways have been well studied against stress responses. Through careful manipulation of ROS levels in plants, we can enhance stress tolerance in plants under unfavorable environmental conditions. This chapter presents an overview of ROS regulation in plants and the essential enzymes involved in the abiotic stress tolerance mechanisms which are thoroughly discussed below.

Keywords: Plants, ROS, Abiotic stress, Signal transducer, antioxidants

1. Introduction

Drought, temperature, salinity, flooding and heavy metal toxicity are the examples of abiotic stressors. These multiple abiotic stressors sometimes occur at the same time [1, 2] and cause significant reduction in crop production. To satisfy the demands of food security for sustainable development in the era of a rising population and climate change, scientists predict a vital need for a "second green revolution" to produce higher yield and yield stability under non-optimal and adverse growing conditions through a combination of approaches based on recent advances in functional genomics [3, 4]. Plants have evolved a range of biological and biochemical responses to

coping up with adverse climatic conditions, including the activation of many stress-responsive genes and the synthesis of different structural proteins via complex signaling pathways, to confer resistance to abiotic stress conditions [5]. Reactive oxygen species (ROS) are byproducts of plant metabolic processes and are produced in a range of cellular compartments including chloroplasts [6], mitochondria [7], and peroxisomes [7, 8]. ROS not only cause irreversible DNA damage and cell death, but they also serve as important signaling molecules, regulating growth in plants under stress conditions. This suggests that ROS plays a dual role in vivo depending on their level of reactivity, production site, and ability to penetrate the cell membrane [9]. Reactive oxygen species (ROS), which include hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet-}$), hydroxyl radical ($OH^{\bullet}$), and singlet oxygen ($^1O_2$), are harmful byproducts of basic metabolic processes in living organisms [9, 10]. In plants, oxygen (O_2), the source of all ROS, is stable and not very reactive [11]. Many excellent reviews have focused on ROS metabolism [9, 12], ROS sensory and signaling networks [9, 13, 14], and the involvement of ROS in developmental and stress response processes [12, 13]. The majority of these reviews, however, provided an overall retrospective for the model plant *Arabidopsis* [15]. They discussed enzymatic and non-enzymatic antioxidants and their roles in abiotic stress responses. However, the anti-oxidant system's regulation mechanisms, or even the key components involved in ROS regulation and abiotic stress resistance, has yet to be compiled in crop plants. In this chapter, we provide insight into current knowledge on the regulation of ROS homeostasis in crop plants. The genes that have been recognized in ROS homeostasis regulation affecting abiotic stress tolerance in crop plants were summarized in particular.

2. ROS role in plant growth and development

Despite the continuous efforts and gains made in agriculture development during recent decades, many stress factors continue to harm the crop growth and productivity. Most of the crop plants thrive in suboptimal environmental surroundings. Stressful conditions are the main factor preventing them from exhibiting their maximum genetic competence in terms of growth and reproduction, and as a result, plant productivity suffers as an outcome of these aberrant circumstances [15–17]. These pressures resulted in significant productivity and economic declines around the world. These stresses might be either biotic or abiotic. Pathogens (viruses, bacteria, and fungi), insects, herbivores, and rodents are all examples of biotic stresses. On the other hands, drought (water scarcity situation), salinity (high concentration of salt), cold (chilling and frost), heat (high temperature), flooding (water excess), radiation (high-intensity ultraviolet and visible light), contaminants, and toxins (heavy metals, pesticides, and aerosols), and soil nutrient deprivation are all examples of abiotic stresses [16, 18]. Any of these conditions either separately or in combinations may have varying degrees of influence on plant growth and development (**Table 1**).

Environmental factors influence plant growth and development through morphological, physiological, biochemical, and molecular alterations. The plant organelle metabolic paths are vulnerable to variation in environmental factors [13]. Tolerance can be attained by plant breeding or cultural activities that mitigate damages and require knowledge of the plant's stress response and how it affects individual plants and plant processes [42]. Various mechanisms linked with abiotic stress instruct plant cells to develop oxygen radicals and their derivatives referred to as reactive oxygen species (ROS). Furthermore, the development of reactive oxygen species (ROS) is a

Stress type	Plant Sp.	Stress condition	Loss result	Reference
Salinity	Soybean (*Glycine max* L.)	Application of (0, 33, 66 and 99 mM NaCl)	Significantly ↓ shoot length by 24%, 32% and 47% , and shoot and dry weight by 46%, 61% and 80% and 44%, 65% and 83% at 33, 66 and 99 mM NaCl respectively and root fresh, dry weight by 23%, 20% and 53%, 53% at 66 and 99 mM NaCl respectively	[19]
	Miscanthus × giganteus	NaCl concentrations (0, 2.86, 5.44, 7.96, 10.65, 14.68, 17.5, 19.97 and 22.4 dS m−1	Significantly ↓ biomass yield by 50% at 10.65 dS m−1 NaCl, root dry weight reduced by 61% at 22.4 dS m−1 NaCl	[20]
	Maize	0, 60, 120, 180 and 240 mM NaCl	Significantly ↓ in germination percentage (77.4%), germination rate (32.4%), length of radicle (79.5%) and plumule (78%), seedling length (78.1%) and seed vigor (95%) are obtained in highest level of salinity (240 mM)	[21]
	Tomato	1% and 3% NaCl	Significantly reduction in germination percentage 77.60% at 3% NaCl,	[22]
	Egg plant cultivars - Lagra Negra (LN), China-A2 (CH) and Black Beauty (BB)	NaCl (0, 50, 100, 150 and 200 mM)	Significantly ↓ survival of cultivar at 100 (50, 40, 30%), 150 (15, 0, 0) and 200 (0, 0, 0% or no survival of the plants)	[23]
	Lentil (*Lens culinaris* Medik.)	100 mM NaCl for 4 days	Significantly ↓ the growth (33%) and seedling fresh weight (44%)	[24]
Water logging	Maize var. DH605 and ZD958	Waterlogging for 3 and 6 days at third extended leaf stage (V-3, V-6), six extended leaf stage (V-3, V-6) and 10th day after flowering stage (10VT-3, 10VT-6), no waterlogging (CK)	Grain yields of DH605 in treatments V3-3, V3-6, V6-3, V6-6, 10VT-3 and 10VT-6 are 18.6 %, 30.3 %, 12.6 %, 18.8 %, 5.7 % and 13.9 % lower than in the control (CK), respectively. ZD958 yields in treatments V3-3, V3-6, V6-3, V6-6, 10VT3 and 10VT-6 are lower than CK yields by 15.6 %, 30.4 %, 13.0 %, 21.4 %, 5.9 % and 12.8 %, respectively	[25]
	Wheat	Waterlogging for 14 days at 22 days after sowing	Shoot dry weight ↓ by 37% and grain yield by 32% compared with the non-waterlogged plants	[26]
	Mung bean (*Vigna radiata*) var. MH–1K–24	Waterlogging at vegetative stage (30 days after sowing) for 3, 6 and 9 days	Photosynthetic loss at 3, 6 and 9 days are 43, 51, and 63 %, respectively, while grain yield	[27]

Stress type	Plant Sp.	Stress condition	Loss result	Reference
			loss was 20, 34 and 52 % respectively.	
	Chinese kale (*Brassica oleracea* var. *alboglabra*) and Caisin (*Brassica rapa* subsp. *parachinensis*)	Waterlogging or water deficit for 19 days in case of Chinese kale and 14 days in case of Caisin	Significantly ↓ plant fresh (90%) and dry weight (80%), leaf area (86%) and leaf number (38%) in Chinese kale; no impact on leaf number in Caisin but ↓ plant fresh and dry weights and leaf area by 60–70%	[28]
Drought/ Water deficit	Wheat	Plants are kept at normal day/ night (21/ 15°C) temperature and moisture content was maintained at 30% field capacity	Grain yield reduced by 53.05% compared to control	[29]
	Eggplant cultivars - Lagra Negra (LN), China-A2 (CH) and Black Beauty (BB)	Drought stimulated by PEG (0, 3, 8 and 10%)	↓ survival of cultivar at 3 % (90, 75, 70%), 8% (60, 45, 40%) and 10% (10, 0, 0% survival)	[23]
	Black gram (*Vigna mungo* L.) cultivar T9, KU-301 and green gram (*Vigna radiata* L.) cultivar Pratap, SG21-5 SG 21-5	A temporary rain shed are constructed in the field with PVC (polyvinyl chloride) film (of about 0.15 mm thickness and 85% of transmittance) to avoid rainfall	↓ Seed yield (T9-31.28%, KU 301- 48.52%, Pratap-37.12%, SG 21-5- 56.98%)	[30]
	Tomato genotypes viz., LE 1, LE 27, LE 57, LE 114, LE 118, LE 125, CO 3, PKM 1, TH CO 2 and TNAU TH CO 3	25 days old seedlings were transplanted and drought was imposed at first day after transplanting onwards based on IW/CPE, 0.5 IW/CPE for drought stress and 1.0 IW/CPE for control are maintained by irrigation the field at regular interval based cumulative pan evaporation.	Overall yield loss of tomato fruits up to 52 per cent under field condition, highest yield loss of 83.18 and 81.51 per cent are shown by LE 125 and LE 1 respectively.	[31]
Toxic/ heavy metals	Wheat	$CdCl_2 .H_2O$ (98%) @ 0, 5, 20, 50 and 80 mg L^{-1}	Significantly ↓ in root length (70.4%), shoot length (81.2%), percent germination (68%) and germination index (76.8%) at 80 mg L-1 Cd compared to control	[32]
	Maize	$CuSO_4·5H_2O$ @ 0, 1, 10, 100, 1000, 5000, 10000 µmol/L in Hoagland culture medium	Significantly ↓ root activity in 1 µmol/L (18.3%), 10 µmol/ L (62.7%), and then decrease slowly-slowly	[33]

Stress type	Plant Sp.	Stress condition	Loss result	Reference
	Maize (*Zea mays* L.) cultivars Run Nong 35 and Wan Dan 13	Cd (0, 75, 150, 225, 300, 375 μM)	Grain yield is reduced in the range of 4–11 % under different Cd toxicity levels	[34]
	Tomato (cultivar PKM –1)	$ZnSO_4.7H_2O$ (0, 50, 100, 150, 200 and 250 mg kg^{-1} soil)	Significantly ↓ in root length 21.86, 25.40 and 33.3 and shoot length 7.46, 26.73, 31.72%, leaf area 29.53, 45.79, 48.02, root dry weight 27.46, 37.20, 54.37 and shoot dry weight 16.78, 32.91, 41.86% @ 150, 200, 250 mg/kg^{-1} respectively	[35]
	Pepper (*Capsicum annuum* L.)	0.1mM $PbCl_2$ and 0.1 mM $CdCl_2$	Significantly ↓ in total dry mass, root dry mass and shoot dry mass under both heavy metal and in combination compered to control	[36]
	Bean (*Phaseolus vulgaris*)	Pot soil contaminated with As (III) 20, 50 mg/kg and As (V) 20, 50 mg /kg	Significantly ↓ in shoot dry weight (40.85%) in As (V), shoot biomass in As (III) 49.3% & As (V) 63.88%, Dry matter yield of roots in 20 mg/kg As (V) 34.42, 46.18, 59.87 and 50 mg/kg As (V) 43.82, 56.09, 71.67%	[37]
Heat stress/ High temperature	Maize	In pot trial 32/22 °C (max/min temperature, control), 36/26 °C, and 40/30 °C for 14 consecutive days bracketing flowering	At 40/30 °C grain yield, seed-set, and grain number significantly ↓ by 73.6, 76.4, and 77.6%	[38]
	Wheat	In field condition during hot area in Iran	Significantly ↓ in grain yield (46.63%), 1000-kernel weight (20.61%) and grain filling duration (20.42%)	[39]
	Soybean	Double crop growing season in field	Significantly ↓ seed yield (29.5%) compare to previous year	[40]
	Field pea (*Pisum sativum* L.);	Field pea crop exposed three distinct windows normal, moderately and late sowing to heat stress environment	Significantly ↓ in seed set (7–14%) and 100-seed weight (6–16%)	[41]

Table 1.
Effect of various abiotic stresses on plant growth, development and production.

crucial mechanism in higher plants, since it is used to relay cellular signaling information in reaction to fluctuating environmental conditions.

As the crop yield is depending on the plant's capability to respond to various forms of environmental stresses, most of which causes oxidative stress and increases concentration of reactive oxygen species (ROS). Increased ROS accumulation is closely

related to increased environmental stress. A variety of biotic and abiotic factors can disrupt the balance between ROS production and the scavenging process, and responsible for raising their levels in intra-cellular [10]. All of these are accountable to cause serious oxidative injury to the plants, limiting their growth parameters and revenue ultimately (**Figure 1**).

Reactive oxygen species (ROS) also play a role in a variety of processes, including cell growth, production, and comeback to biotic and abiotic environmental inducements, as well as programmed cell death and signal transduction. Stressors, hormones, growth, and a variety of additional metabolic pathways can all arouse ROS formation, which can then trigger other pathways or serve as direct defense compounds in the plant body [43]. But, when ROS synthesis exceeds cellular scavenging potential, it disturbs the cellular redox homeostasis and produce ROS [44, 45]. To counter these stresses, plants have antioxidant pathways that scavenge excess ROS and avoid cell damage. Thus, plant synthesis and quenching are out of equilibrium, resulting in yield losses due to oxidative disruption. Though, it is difficult to identify this drop to oxidative damage due to the many processes involved in ROS synthesis; however, stresses and oxidative damage are interconnected and are liable for yield reduction [46].

Therefore, understanding the oxidative appliances in plants might be an aid in the growth of plants that are best suited to their surroundings. Plants stimulate antioxidant defense mechanisms in response to stress, which helps in the continuation of cell constituent's structural integrity and, potentially reduces oxidative injury. Plant defense is aided by several antioxidant enzymes. As a result, maintaining a high antioxidant ability to abolish toxic levels of ROS has been concurrent to improved crop plant capacity towards stress tolerance.

Manipulating ROS scavenging enzyme organizations is a likely method for producing transgenic plants that are more tolerant to a variety of stress situations; however, more research is needed for this since many enzymes and isoforms are
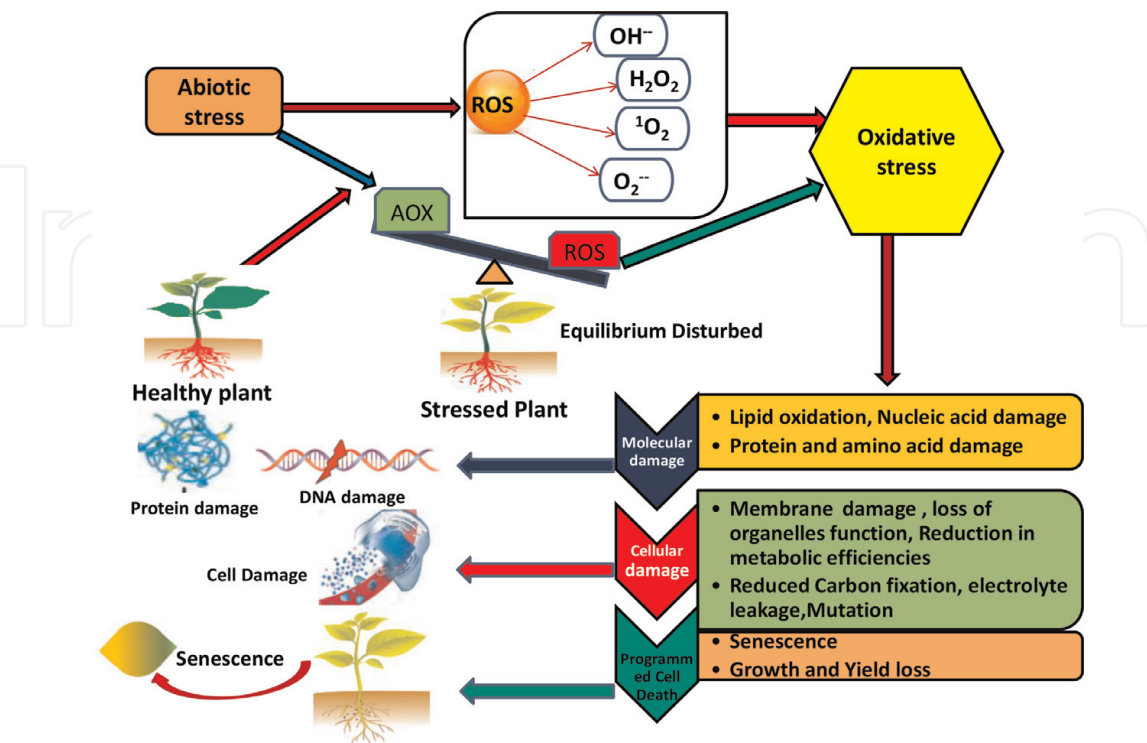

Figure 1.
Effect of oxidative stress on plant growth. ROS (Reactive oxygen species),AOX (Antioxidants).

involved, and ROS is only one of the promising issues of plant tolerance to environmental and biotic stresses [47].

2.1 Plant antioxidant defense system overview

To minimize possible harm to cellular components, as well as to sustain growth, metabolism, development, and total yield, the balance between ROS generation and removal at the intracellular level must be closely controlled and/or competently processed. Antioxidants scavenge ROS and/or regulate ROS development, either directly or indirectly [48]. This antioxidant defence system comprises low-molecular-weight non-enzymatic antioxidants and some antioxidant enzymes [49]. Non-enzymatic components include tocopherol, carotenoids, phenolic compounds, flavonoids, alkaloids, and non-protein amino acids, besides cellular redox buffers like ascorbate (AsA) and glutathione (GSH) [50–52].

Numerous antioxidant enzymes, like superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), peroxidase (POX), polyphenol oxidase (PPO), peroxiredoxins (PRXs), Thioredoxins (TRXs), and ascorbate-glutathione (AsAGSH) cycle enzymes, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) are the parts of the enzymatic components of the antioxidant defense organization [53–56]. The above non-enzymatic antioxidants function in combination with antioxidant enzymes to keep the balance between ROS synthesis and detoxification [52, 54].

3. ROS involvement in plant stress responses

The disruption of the equilibrium between the formation of reactive oxygen species (ROS) and antioxidant defense systems, resulting in an unsustainable accumulation of ROS and oxidative stress induction in the plant body, is one of the most imperative effects of environmental stresses. Both enzymatic and non-enzymatic antioxidant defense systems maintain the balance between reclamation and ROS generation when exposed to extreme environmental conditions [57]. Based on their concentration in plants, reactive oxygen species (ROS) can play both harmful and advantageous functions. ROS are unwelcome and dangerous byproducts of natural cellular metabolism at elevated amounts. But, serve as a second messenger in intracellular signaling flows that facilitate a variety of retorts in plant cells at low concentrations. It causes oxidative destruction to lipids, proteins, and DNA, resulting in changes in intrinsic membrane features such as fluidity, ion transfer, enzyme activity loss, protein crosslinking, protein synthesis inhibition, and DNA damage, all of which contribute to cell death. Thus, ROS disrupt biomolecules and cause genetically programmed cell death events at high concentrations. Higher plants have an extensive and very robust plant ROS setup, which is made up of antioxidant enzymes and antioxidant particles, that keeps ROS levels under control to avoid oxidative harm. Environmental factors like heat [58], cold [59], drought [60], Al toxicity [61], organic pollutants (OPs) [62], and pathogens [63, 64] have all been revealed to bring ROS production in plant cells.

On the other hand, changes in ROS levels over time and space are inferred as signals for a variety of biological events, including growth, development, resistance to abiotic stress factors, appropriate response towards pathogen, and cell death. The

molecular communication connected with ROS arbitrated signal transduction, which leads to gene expression management, is one of the essential early stress responses in the plant's acclamatory output. By altering the cell's redox equilibrium, ROS might function as a "second messenger," modifying the actions of particular proteins or gene expression. At any level of plant growth, the network of redox signals composes metabolism to regulate energy generation and consumption, interfering with primary signaling agents (hormones) to respond to evolving environmental nods. The consequence or fine-tuning of biological reactions to changed ROS levels is determined by interactions with other signaling molecules. Despite the recent identification of several constituents of the ROS signaling system, understanding how ROS-derived signals are incorporated to ultimately control biological processes like plant growth, development, stress adaptability as well as programmed cell death remains a challenge. To offset the negative impacts of oxidative stress, plants engage their antioxidant defense mechanism. Antioxidant defense ability, instead, vary according to plant species and genotype, stress kind, and period of exposure.

3.1 ROS involvement in water stress

Water stress is a common environmental restriction that plants frequently faced during their lives, restricting survival, reproduction, and ultimately productivity. Drought stress causes stomata closing, decrease CO_2 entrance, and compromised photosynthetic rate, as well as discrepancy in the light acquire and usage and changed photochemistry in chloroplasts, triggering ROS excessive formation [49, 65]. The production of reactive oxygen species (ROS), which is assumed to lead to cellular injury, is one of the main and serious alterations due to drought stress. Though, a signaling function for ROS in activating the ROS scavenging mechanism, which might award defence or resistance to stress, has recently been discovered. This scavenging system is made up of antioxidant enzymes including SOD, catalase, and peroxidases, as well as antioxidant substances such as ascorbate and reduced glutathione; the oxidative load is largely governed by the balance between ROS formation and scavenging. Drought stress undoubtedly causes ROS production as a primary plant reaction, which might be regulated by hormones such as ABA and ethylene, which may also perform a downstream function. Unless ROS scavenging by antioxidant systems is disrupted, a high amount of ROS might exacerbate stress made harm to most cellular components [66].

3.2 Plant antioxidant defense against drought

According to Nahar et al. [67], a drought exposed *V. radiate* seedlings had lower AsA/DHA and GSH/GSSG ratios, but higher APX, GR, GPX, and GST activities, compared to control, which added to drought, persuaded oxidative loss tolerance. Rady et al. [68] reported raised H_2O_2 (26.2 percent) and O_2 (51 percent) production, as well as elevated SOD, CAT, and APX activities by 110 percent, 66 percent, and 77 percent, respectively and also considerably amplified AsA, GSH, and -tocopherol level, in *S. Lycopersicum* cv. *Login* 935 treated to drought stress (60 percent FC for 20 days). Improved tolerance for drought stress via the antioxidant framework regulation has also been demonstrated in several chemical priming techniques. Antoniou et al. [69], who found that pre-treatment of *M. sativa* plants with melatonin led to enhanced CAT activity and lower H_2O_2 amount relative to untreated plants.

3.3 ROS involvement in salinity stress

Salinity carries oxidative stress by striking various impediments like ion toxicity, osmotic stress, nutritional deficiency, and toxicity, all of which leading to ROS overproduction and oxidative stress [70].

Rehman et al. [71] identified a 2.5- and 3-fold rise in H_2O_2 generation, as well as a 2- and a 3-fold upsurge in thiobarbituric acid reactive substances (TBARS) concentration, under 100 and 200 mM sodium chloride (NaCl) salinity conditions, respectively, compared to control which exhibits salt-induced oxidative stress.

3.4 Plant antioxidant defense against salinity

Many plant studies have revealed that regulating the antioxidant mechanism reduces the impact of salt stress in various plant species. Researchers have shown that antioxidant enzyme activity varies according to salt level, exposure length, and plant developmental stages [72, 73]. Vighi et al. [74] found a difference in response between salt-tolerant (BRS Bojuru) and salt-sensitive (BRS Pampa) rice cultivars and established that the OsAPX3, OsGR2, OsGR3, and OsSOD3-Cu/Zn genes were the main differentiator markers among these two genotypes. Alzahrani et al. [75] revealed elevated SOD, CAT, GR, and AsA stages in faba bean genotypes, when H_2O_2 levels rose beyond 90% under salinity stress, indicating the control of antioxidant response during salt stress and its alleviation.

Alsahli et al. [76] observed that a 2-fold increase in SOD, CAT, and APX activity and lowered 3-fold H_2O_2 in comparison to untreated control plants when salicylic acid (SA) was applied under salt-stressed in wheat.

Similarly, the antioxidant responses under salt stress conditions were controlled in sour orange through exogenous application of polyamines as reported by Tanou et al. [77], whereas in sorghum with simultaneous treatment of jasmonic acid (JA) and humic acid boosted APX activity, resultant in salt tolerance revealed by Ali et al. [78].

3.5 Plant antioxidant defense against high temperature

Plants' antioxidant defense mechanisms are triggered in response to high temperature (HT) stress [79, 80] although antioxidant capability varies amongst species as well as resistant and susceptible genotypes [81]. Reduced SOD and CAT activity, as well as repressed OsSOD, OsCAT, and OsAPX2 expression resulted in a 1.27-fold increased H_2O_2 accumulation in germinating rice seeds in high-temperature stress, according to Liu et al. [82]. Sarkar et al. [83] discovered increased CAT and POX activities in wheat genotypes during high-temperature stress (30^oC).

3.6 Plant antioxidant defense against low temperature

Low-temperature stress causes plants to activate their antioxidant defense appliance to counteract negative consequences. Cucumber (*C. sativus* cv. *Xinyan* 4) seedlings were open to low-temperature stress (15/8°C day/night) for the period of 8 days and reported that 3- and 2-fold increased Cu-ZnSOD and Fe-SOD activities, respectively, in response to increased H_2O_2 and O_2^*-production [84]. Besides, after low-temperature stress, *Cynodondactylon*, *Capsella bursa pastoris*, and *Citrus reticulata* showed considerably enhanced CAT activity [85–87]. Higher APX activity was seen in *Jatropha macrocarpa* in reaction to increase H_2O_2, which enhanced low-temperature

stress tolerance, but lower APX activity (>6-fold) in *J. curcas* was connected to enhanced sensitivity under low-temperature circumstances [88]. Cheng et al. [89] studied *Citrulluslanatus* by exposing low-temperature stress (10/5 0C, 7 days) and found that the antioxidant defence system was activated, with GSH/GSSG and AsA/DHA ratios increasing considerably just a day after exposure in comparison to the control trial. Wang et al. [90] reported increased AsA and GSH levels in transgenic apple seedlings under low temperature stress in response to elevated H_2O_2 concentration ($8^{\circ}C$, 12 hours). Han et al. [91] subjected 14-days old rice seedlings to low temperature ($12^{\circ}C$, 6 days) stress and found increased H_2O_2 content and O_2^{*-} accumulation, as well as enlarged SOD and CAT activity and also increased GSH/GSSG ratio.

3.7 Plant antioxidant defense against flooding

Numerous crop species have displayed their capability to continue under the flooded or waterlogged situation for brief or even extended durations through triggering antioxidant defense mechanisms. An experiment was conducted by Li et al. [92], using18 maize genotypes which were subjected to waterlogged conditions and revealed that after 2 days of stress, 12 genotypes had 19–57 percent greater SOD activity, 13 genotypes had 19.16–106.96 percent greater POD activity, and only 9 genotypes had 26–57 percent greater CAT activity. In sesame seedlings under waterlogged conditions, lower AsA content, while higher GSH and GSSG content, as well as H_2O_2 content, was detected in a time-dependent way [93]. During extended (8 days) WL stress, although, AsA-GSH cycle enzymes were not controlled similarly, with considerably increased APX and MDHAR activity and considerably decreased DHAR and GR activity.

Furthermore, Park and Lee [94] found that when the Antarctic plants. *antarctica* was exposed to waterlogged (for 7 days), it accumulated about 52 percent more H_2O_2 and had 91 percent more CAT activity than controls.

3.8 Plant antioxidant defense against toxic metals

Metal toxicity tolerance is favorably coupled with improved antioxidant activity towards ROS detoxification and metal chelation [95, 96]. GST, one of the most important antioxidants, aids GSH in reducing metal toxicity by conjugating with them [97]. GSH also acts as a cytosolic predecessor of phytochelatins (PC), which are metal binders and catalyse the shuttle of metal ions and other xenobiotic that expedites the compound passage into the cell vacuole [81, 98]. The undertaking of cytosolic metals/metalloids ions into the vacuole in passive form lessens cellular toxicity [95]. Furthermore, both GST and GSH play a role in the accumulation of certain flavonoids (anthocyanin), which are metal binders and might follow a similar path to the vacuole [99, 100].

4. ROS generation and removal in the plants

Reactive oxygen species (ROS) are a broad term that includes the radical and non-radical form of species, formed due to incomplete oxygen metabolism. Radical species include superoxide radical (O_2•_), hydroxyl radical (•OH), alkoxyl (RO•) and peroxyl (ROO•) while non- radical species contains hydrogen peroxide (H_2O_2), singlet

oxygen (1O2), ozone (O3), and hypochlorous acid (HClO). Oxygen is a fundamental element found in the Earth's crust that evolved billions of years ago. Oxygen molecules (O2) are not only crucial for metabolism and respiration but also support life forms on the Earth. O2 are mainly evolved through the photosynthetic activities of cyanobacteria in ancient times. ROS are partially reduced or activated derivatives of oxygen molecules that are highly reactive and toxic and can cause potential damage to the plants which includes cellular destruction, damage to plant metabolism and growth along with damage to DNA, RNA, proteins, and lipids. Plants perform various metabolic processes viz., namely photosynthesis, respiration which leads to the production of reactive oxygen species in various cell organelles like mitochondria [7], peroxisomes [8], chloroplasts [6], etc. They are an unavoidable phenomenon that leads to the production of oxidative stress in plants. ROS can also be produced during abiotic and biotic stress responses in plants. Besides this, the presence of free metals (Fe, Cu, Mn) derived from the metallo-protein complex phenomenon also contributes to ROS production. The production of ROS is stimulated by many factors namely physiological responses in the plant cell organelles, hormonal signaling, pathogen attack, gravitropism which produces free radicals inside plants [101]. The stoichiometry of ROS reveals that oxygen contains two unpaired electrons in their outermost shell having similar spin quantum numbers. However, oxygen molecules can accept a single electron at a time in its outermost orbit due to spin restriction, resulting in the formation of ROS which is highly reactive and active in subsequent reactions [102]. ROS are atoms or groups of atoms that possess at least one unpaired electron. Oxygen is an indispensable part of aerobic reactions in the plant system and molecular reduction of O2 leads to the formation of reactive oxygen species various cell organelles which are highly reactive as of molecular oxygen. Photosynthesis is a crucial metabolic process performed by the plants in the chloroplast of plant cells due to the localization of photosynthetic apparatus in the chloroplast. Although the photosynthetic process is highly influenced by the generation of ROS (O2.-&1O2), the formation of superoxide radicals is associated with PSI. The photolysis of water molecules is a crucial phenomenon in the PSII system of photosynthesis which produces O2 thus favoring superoxide radical formation reaction in PSI of photosynthesis. Also, auto-oxidation of Iron-sulfur protein results in O2.- production in the subsequent process due to abundant Fred and low NADP. Furthermore, reduced Fd reacts with superoxide radicals to form H2O2 in the illuminated chloroplast [103]. However, the regulation of ROS production during photosynthetic processes has been enunciated in several studies [53, 58, 104]. Singlet oxygen is also produced in PSII during photosynthetic processes. However, the root and stems of rice plants mainly produced O2-Which might relate to their subsequent environment for adaptation [105]. Additionally, superoxide radicals can be generated during PSII by auto-oxidation of PSII electron acceptors and PQ [106]. The ROS formation in illuminated chloroplast occurs mainly due to stress conditions followed by the closing of stomata. The partial reduction of O2 molecule in the respiratory chain occurs in chloroplast which consists of NADPH dehydrogenase and terminal oxidase is termed as chlororespiration. This phenomenon is also a major source of ROS production in the chloroplast. The peroxisomes also mediate the formation of O2.-through ETC using NADH as an electron donor. Peroxisomes are single membrane-bound organelle that performs certain major functions in the plants like fatty acid β- oxidation, regulation of glyoxylate cycle, photorespiration, metabolism of ROS & ureides, etc. [107–109]. Additionally, peroxisomes also regulate the generation of ROS via various metabolic functions. For instance, H2O2 production in the peroxisomes facilitated the regulation of the photosynthetic carbon oxidation cycle in C3

plants. During the carbon oxidation cycle, oxygenation of RuBP (mediated by RuBisCO) regenerates NADP+ and harbors a major sink of electrons which in turn prevents photoinactivation of PSII in the case when CO2 concentration is lacking. Due to which RuBisCO stimulates oxygenation in place of carboxylation as temperature elevates. The glycolate thus generated by oxygenation of RuBisCO suffers oxidation upon translocation to peroxisomes from chloroplast produces H2O2 as a by-product in the cells [102, 110]. Photorespiration is a metabolic process that occurs in chloroplast, mitochondria & peroxisomes. It includes phosphoglycolate metabolism which involves light-dependent O2 uptake & CO2 release with peroxisomal glycolate oxidase generating (H2O2) in the cells. The mitochondrial metabolism generated a considerable amount of ROS like H2O2, hydroxyl radicals, superoxide, etc. In the plants, mitochondria regulate aerobic respiration includes ETC (electron transport chain), which formulates ROS production in the mitochondrial membrane. However, the mitochondria bestow the limited ROS production in plants possibly due to the presence of alternative oxidase (AOX) that catalyzes the tetravalent reduction of O2 by ubiquinone [10]. The series of metabolic reactions in mitochondria leads to the formation of ROS inside the organelle. The flavoprotein region of NADH dehydrogenase encourages the production of O2- anions during mitochondrial electron transport (MET). One of the effective inhibitors of MET antimycin A enhances the ROS production by blocking electron flow after ubiquinone and the reduced ubiquinone undergoes auto-oxidation by contributing electron to O2, forming O2- [111]. Additionally, researchers studied that ubiquinone also contributes to H2O2 production in MET [112, 113]. Several mitochondrial enzymes like aconitase and 1-galactono-γ lactone dehydrogenase (GAL) also contribute to ROS generation. Furthermore, the O2- also gets converted into stable form H2O2 by the mitochondrial form of SOD (Mn-SOD). H2O2 is further transformed to (OH.) through Fenton reaction which is removed by ascorbate- glutathione cycle enzyme in plant system. Such OH molecules are liable to mutations in ETC of the mitochondrial genome. ROS generation in mitochondria also possesses negative effects on proteins by oxidation, cleavage, degradation of backbones [106]. Mitochondrial dysfunction due to excessive ROS production under unfavorable circumstances induces PCD (programmed cell death) and necrosis in the plants. The respiratory burst oxidase homologue (RBOH) synonymous with membrane-bound NADPH oxidase (NOX) in the plants also contributes to O2.-formation through electron through from intracellular NADPH across the plasma membrane to O2 in apoplast [103]. NADPH oxidase has a well-established role in stress responses in plants. Neill et al, 2002 studied that RBOH- dependent O2.—generation enunciates lipid peroxidation, PCD. NADPH oxidase induces membrane damage, favors oxidative burst, and reduces plant metabolic and growth-related activities under certain undesirable conditions. The plant cell wall is a site of redox reactions which enables the H2O2- dependent reactions and consists of malate dehydrogenase and NADH oxidase. NADPH-dependent microsomal electron transport is also a potential source of superoxides in the plant system. O2– formation in microsomes is mainly progressed by auto-oxidation of cytochrome P-450 reductase and/or auto-oxidation of oxycytochrome –P-450 complex [114]. Thus, the plant system involves efficient methods of ROS production in different responses. Different cellular compartments enunciate constant ROS production as a byproduct of redox and aerobic reactions. It is interesting to know that under favourable conditions plant maintains redox homeostasis and counteract with ROS production strategies within its system. The system of higher plants is complex and posses various regulatory processes. It is important to understand that controlled ROS generation and oxidative

burst can be a fundamental part of the plant signaling and defense mechanism. Future acknowledgments and researches should be directed towards the detailed study of ROS production in various aspects in plants with its signaling implications with references to various molecules present in the plant system. Plants possess a peculiar ROS scavenging system to maintain ROS homeostasis and redox signaling in their system during oxidative stress. However, disrupted protective mechanisms in response to oxidative burst may affect ROS-mediated redox homeostasis and cause cell death in the plants [11]. It is well-acquainted fact that plant produces a considerable amount of ROS during various metabolic processes in several cell organelles like chloroplast, mitochondria, plasma membrane and many more. They are an inexorable part of plant metabolism which play important role in redox signaling under environmental stresses [115]. To accomplish ROS removal from plant system plants consists of several ROS scavenging system which can be categorized into enzymatic and non-n enzymatic defense mechanism. Plants contain various antioxidant enzymes to mediate ROS scavenging mechanism which includes superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), catalase (CAT), monodehydroascorbate reductase (MDHAR or MDAR), dehydroascorbate reductase (DHAR or DAR) and glutathione reductase (GR) (**Figure 2**). These antioxidant enzymes ensure plant survival by minimizing the deleterious effect of ROS and prevent its overaccumulation. SOD (1.15.1.1) is a ubiquitous enzyme that plays a
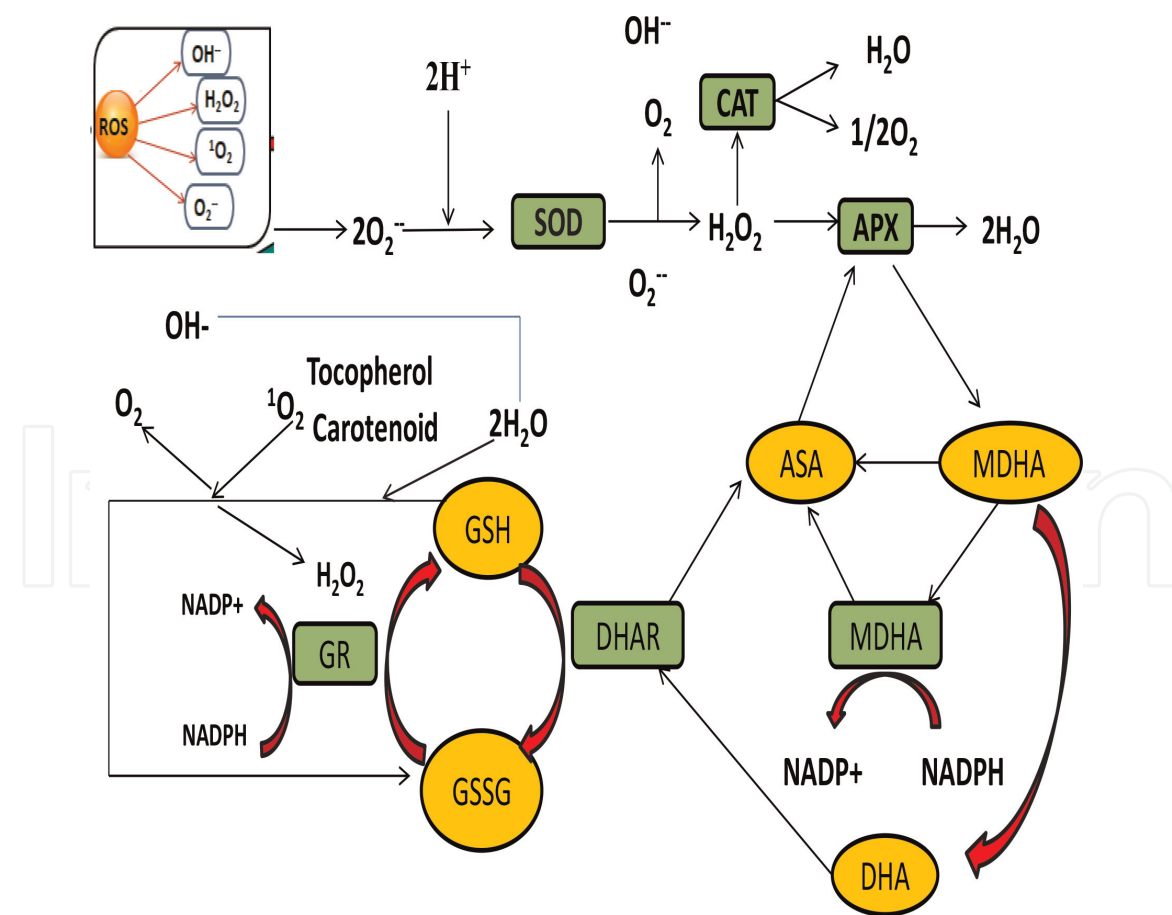

Figure 2.
Enzymatic and Non enzymatic Antioxidant mechanism to defend oxidative stressEnzymatic and non-enzymatic antioxidants in algae.ASC(Ascorbate),APX,(Ascorbate peroxidase),CAT Catalase, DHA Dehydroascorbate, GSH (Glutathione), GR Glutathione reductase , GSSG (Glutathione disulfide),MDHA (Monodehydroascorbate),SOD (Superoxide dismutase),DHA (Dehydroascorbate).

significant role in plant protection against oxidative stress. It catalyzes the dismutation of O2—to O2 and H2O. SOD has several isoforms and can be categorized as FeSOD, MnSOD, NiSOD, Cu/Zn SOD based on metal cofactors associated with the enzymes. The Arabidopsis genome contains three FeSOD (FSD1, FSD2, FSD3), one MnSOD (MSD1), and three Cu/Zn SOD (CSD1, CSD2, CSD3) type of genes [116, 117]. Similarly, the tomato genome consists of four Cu/Zn SOD, three FeSOD, and one MnSOD [118]. SOD gene family also have been discovered in many plant species like Musa acuminate, Sorghum bicolor, Populus trichocarpa, potato, pea, wheat, etc. However, transgenic approaches have also been described to study SOD responses in plants [10]. SOD isozymes have also been compartmentalized into mitochondria [119], peroxisomes [9], cytosol [116, 120], thylakoids [116, 121]. In plants, SOD is found in roots, leaves, fruits, and seeds where it functions significantly in the environment and oxidative stresses [122], photooxidative stress [123, 124], lateral root growth [119], germination [120], chloroplast development and flowering [121, 125]. Catalases (CAT) (E.C. 1.11.1.6) are a versatile antioxidant that helps in ROS scavenging mechanism in plants. They are ion containing homotetrameric proteins that catalyze the decomposition of H2O2 to H2O and O2 during the photorespiration process along with detoxification of H2O2[126]. Catalases are involved in antioxidant defense mechanism have been enunciated in many studies [127–132]. They also mediate in various physiological processes [45, 133–135]. The oxidative stress in plant cells can be maintained by enzymes of ascorbate- glutathione cycle. Ascorbate peroxidase (APX) (E.C.1.11.1.11) is another class of antioxidant enzyme that plays a vital role in scavenging H2O2 in chloroplast and cytosol in the plants. They are categorized into various forms based on their localization which is mainly chloroplast stromal soluble form (sAPX), chloroplast thylakoid bound form (tAPX), cytosolic form (cAPX) and glyoxisome membrane form (gmAPX) [136, 137]. They are heme-containing peroxidases possessing nine putative APX genes identified in Arabidopsis in cytosolic, chloroplast and peroxisomal regions of plant cells [138, 139] and sAPX in mitochondria [140]. They detoxify H2O2 through electron transfer from ascorbate to form monodehydroascorbate (MDHA). APX possesses several metabolic functions in H2O2 scavenging, plant responses to environmental stress, photoprotection, and plant development [115]. Another enzyme of ascorbate- glutathione cycle MDHAR (E. C.1.6.5.4) catalyzes the reverse reduction of MDHA to ascorbate in the presence of NAD(P)H [141] Foyer & Noctor, 2011). MDHAR is mainly localized in the cytosol, peroxisomes, mitochondria, and chloroplast. MDHAR is involved in stress tolerance, plant physiological processes, senescence, interaction, with endophytes has been explored in various studies [115, 142, 143]. DHAR is another enzyme that brings about the regeneration of ascorbate from DHA. DHARs (E.C.1.8.5.1) are monomeric enzymes that are identified in the Arabidopsis genome as DHAR1 and DHAR2 (cytosol), DHAR3 (chloroplast) [144]. Similar to APX, DHAR is also involved in the regulation of defense against environmental stress in various species [145, 146]. Glutathione reductase (GR) (E.C.1.6.4.2) is another potent enzyme mainly localized in chloroplast, mitochondria and cytosol. It catalyzes the reduction of glutathione and contains FAD-binding domain & NADPH- binding domain which carries out an enzymatic activity. Isozymes of GR have been widely studied in Arabidopsis which plays a vital role in various plant physiological responses [115].

The non-enzymatic antioxidant defense mechanism includes several low molecular mass ROS scavenging molecules like glutathione, ascorbic acid (AsA), flavonoids, carotenoids, tocopherols, alkaloids which aid in the removal of H2O2, singlet oxygen, and other ROS molecules. The antioxidant defense mechanism of AsA during

oxidative burst has been well acquainted through several studies. AsA (commonly known as Vit C) is water-soluble, localized in many plant cell organelles stimulates the quenching superoxide hydroxyl radicals and singlet oxygen produced during oxidative stress. Despite these, it also reduces H_2O_2 to H_2O via ascorbate peroxidase reaction [147]. AsA regulates antioxidant defense mechanisms in response to various environmental stresses [148]. The non-enzymatic antioxidant system functions along with an enzymatic system to counteract the negative effect of ROS in plants. Reduced glutathione (GSH) is another class of low M.W thiol tripeptide antioxidant molecule commonly dominated in the cytosol, ER, mitochondria, chloroplast, vacuoles, peroxisomes & apoplast. GSH mediates multiple functions in plants. It plays a vital role in plant physiological functions like cell differentiation, growth, senescence, and many more. Precisely, it is also known for its antioxidant defense system in oxidative stress. It scavenges H_2O_2, $1O_2$, $OH.$, $O_2.-$, and reduces them to produce GSSG as a by-product. GSSG can also be generated through GSH. GSH plays a crucial part in regenerating AsA via the ascorbate- glutathione cycle. GSSG gets converted to GSH through denovo synthesis or by GR. Similar to glutathione another potential antioxidant molecule also includes proline, amino acids, alkaloids, polyamines, terpenes, amines, phenolics like compounds that scavenge ROS in plants. Carotenoids, on the other hand, are a group of lipophilic antioxidants that are present in a wide variety of organisms including plants. They have a well-established role in photosynthesis and protect photosynthetic machinery in response to ROS production. They scavenge $1O_2$, thus preventing generation by reacting with $3Chl^*$ and excited Chl (Chl^*), regulates the xanthophylls cycle. Similar to carotenoids, α- tocopherol is also a protector of the cell membrane in response to ROS production. α- tocopherol quench excess energy, safeguard lipids, and scavenges ROS formed during photosynthesis. It usually reacts with lipid radicals $RO.$, $ROO.$ And RO^* at membrane- water interface and gets reduced to TOH. Which is then interacts with GSH & AA [149]. Flavonoids like flavonols, flavones, isoflavones, and anthocyanins are diverse in the plant kingdom and also plays a crucial role in the various physiological process mainly pigmentation in flowers, fruits, and seeds. They mitigate the negative effects of ROS produced in plants during photosynthesis. Additionally, they also scavenges$1O_2$ along with repairing chloroplast membrane [150].

5. ROS regulation with genes and tolerance to abiotic stress tolerance in crops

Plants are evolved with multiple signaling pathways to control various sets of genes for generating different classes of protein to cope up with abiotic stress. These highly regulated genes play a very important role in ROS activation and regulation. Functional genomics helps us to identify more than 1000 stress-responsive genes in plants [151]. These genes have been characterized into different classes such as protein kinases and phosphatases, transcription factors, enzymes, molecular chaperones, and other functional proteins. The different genes involved in the regulation of ROS homeostasis and response to abiotic stresses have been categorized in plants (**Figure 3**; **Table 2**).

5.1 Protein kinases and phosphatases

Mitogen-activated protein kinases (MAPK) are the important gene groups in ROS signaling and regulation. Many studies have been conducted in plants on MAPK
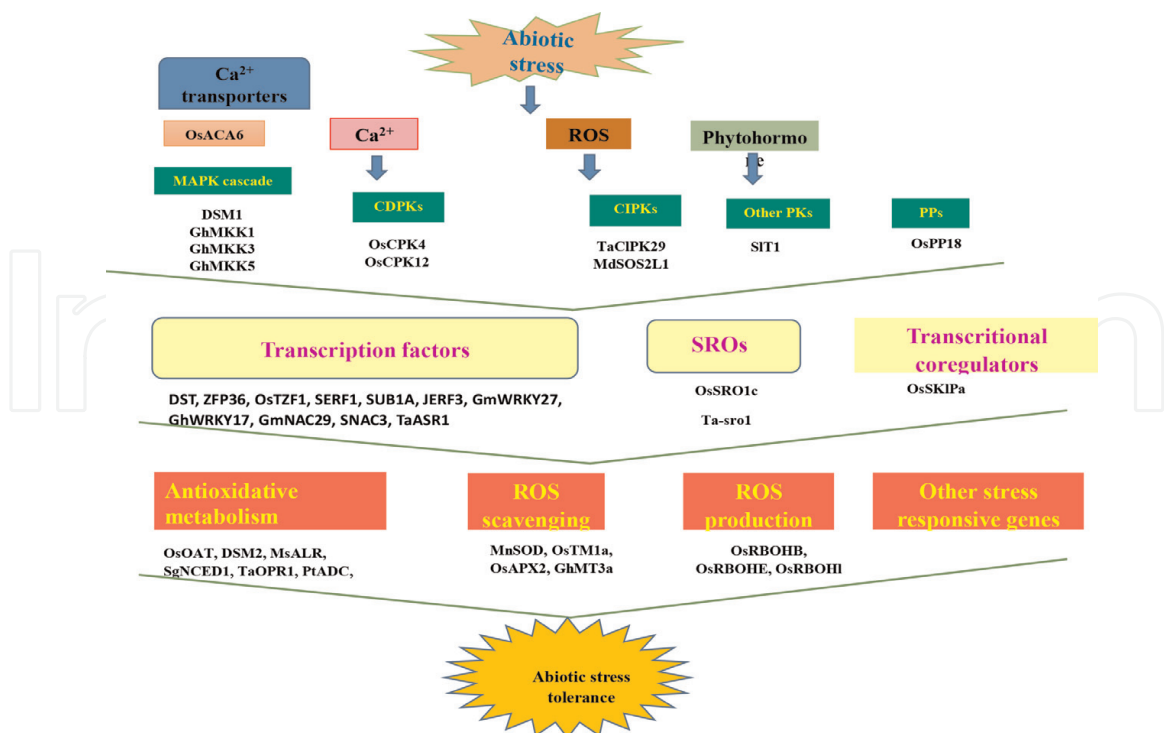
Figure 3.
Representative diagram showing several major genes/factors involved in ROS regulation and provides abiotic stress tolerance response in plants. Abbreviations: calcium-dependent protein kinase (CDPK); calcineurin B-like protein-interacting protein kinase (CIPK); mitogen-activated protein kinase (MAPK); protein kinase (PK); similar to RCD one (SRO).

cascades [174]. In cotton, two MAPK kinases (MAPKKs) have been characterized (GhMKK1 and GhMKK5) which are responsible for the homeostasis of ROS and abiotic stress tolerance [152]. Due to overexpression of GhMKK1 in tobacco, tolerance to salt and drought stresses have been observed by exhibiting ROS scavenging along with activities of antioxidant enzymes [175]. In transgenic tobacco plants, when BnMKK1 gene has been introduced, it triggers ABA signaling and leads to drought sensitivity and water loss [158] whereas GhMKK5 gene reduces salt and other abiotic stresses [152]. Plants showing overexpression of GhMKK5 leads to the up-regulation of ROS-related genes resulted in hypersensitive reaction with an accumulation of H2O2 [176]. In another study, a gene called GhMKK3 helps in regulating drought tolerance. Overexpression of this gene in tobacco induces stomatal closure due to activation of ABA-responsive gene along with a reduction in stomatal numbers [153, 177]. In some cases, two or more genes (GhMKK3 and HgPIP1) work together in connection with HgMPK7 gene for the production of drought and ABA-activated MAPK modules [178]. A drought-hypersensitive mutant1 (DSM1) of MAPK gene has been identified in rice which shows the sensitive response to oxidative stress [154]. In rice plants, two calcium-dependent protein kinase (CDPK) genes, OsCPK12 and OsCPK4 enhance tolerance to salt and drought stress respectively [155]. CBL-interacting protein kinase (CIPK) gene TaCIPK29 in wheat also is salt tolerance with ROS regulation mechanism (**Table 3**).

In transgenic tobacco, activities of ROS- scavenging enzymes have been increased along with the expression of transporter genes which leads to abiotic stress (salt stress) tolerance [156]. Another CIPK gene (MdSOS2L1) showed abiotic stress (salt tolerance) tolerance in crops like tomato and apple. Increased antioxidant metabolites (malate, procyanidin) and ROS scavenging enzymes are the mechanisms found after

Functional Class	Functional Protein	Genes involved	Plant concern	Abiotic Stress Resistance	ROS regulation	Reference
Protein Kinase and phosphatase						
MAPKs	MAPKK	GhMKK1	G.hirsutum	Drought and salt stress	ROS scavenging	[152, 153, 175]
	MAPKKK	DSM1	O. sativa	Drought stress	ROS scavenging	[154]
CDPK	Calcium-dependent protein kinase	OsCPK12	O. sativa	Salt stress	ROS production and scavenging	[155]
	Calcium-dependent protein kinase	OsCPK4	O. sativa	Drought and salt stress	ROS scavenging.	
CIPK	CBL-interacting protein kinase	TaCIPK29	T. aestivum	Salt stress	ROS scavenging	[156]
	CBL-interacting protein kinase	MdSOS2L1	Malus x domestica	Salt stress	ROS scavenging; antioxidative metabolism	[157]
Protein phosphatase	Protein phosphatase 2C	OsPP18	O. sativa	Drought and oxidative stress	ROS scavenging	[158]
Transcription factors						
AP2/ERF	ERF	SERF1	O. sativa	Salt stress	ROS signaling	[159]
	ERF	SUB1A	O. sativa	Drought, submerge and oxidative stress	ROS scavenging	[160]
	ERF	JERF3	S.lycopersicum	Drought, salt and freezing stress	ROS scavenging	[161]
Zinc finger	C2H2 zinc finger	DST	O. sativa	Drought and salt stress	ROS scavenging	[162]
	C2H2 zinc finger	ZFP36	O. sativa	Drought and oxidative stress	ABA-induced antioxidant defense	[163]
	CCCH zinc finger	OsTZF1	O. sativa	Drought, salt and oxidative stress	ROS scavenging	[164]
NAC	NAC	GmNAC29	G. max	Drought and salt stress	ROS production	[165]
	NAC	SNAC3	O. sativa	Drought, heat and oxidative stress	ROS scavenging	[166]
WRKY	WRKY	GmWRKY27	G. max	ROS production	Drought and salt stress	[165]

Functional Class	Functional Protein	Genes involved	Plant concern	Abiotic Stress Resistance	ROS regulation	Reference
	WRKY	*GhWRKY17*	*G. hirsutum*	ROS scavenging	Drought and salt stress	[167]
Other nuclear proteins						
SRO protein	SRO	*OsSRO1c*	*O. sativa*	Drought and oxidative stress	ROS scavenging	[168]
	SRO	*Ta-sro1*	*T. aestivum*	Osmotic, salt and oxidative stress	ROS production and scavenging	[33]
ABA metabolism	Carotene hydroxylase	DSM2	*O. sativa*	Drought and oxidative stress	antioxidative metabolism	[169]
	9-cis-epoxycarotenoid	*SgNCED1*	*S. guianensis*	Drought and salt stress	ABA-induced antioxidant defense	[170]
ROS scavenging	MnSOD	*MnSOD*	*N. plumbaginifolia*	Drought stress	ROS scavenging	[171]
	APX	*OsAPX2*	*O. sativa*	Drought, salt and cold stresses	ROS scavenging	[172]
Calcium transporters	type IIB Ca2+ATPase	*OsACA6*	*O. sativa*	Drought and salt stress	ROS scavenging	[173]

Table 2.
Major representative genes of crops involves in abiotic stress tolerance through ROS regulation.

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
For salt stress plants are applied 12 dS m^{-1} NaCl after 2 weeks of germination	Pot	Maize	Se application (20 mg/L)	Improved shoot fresh and dry weight compared to control	[179]
For salt stress each pot pre-treated with 150 mM of NaCl for four weeks before AM fungus treatment	Pot	Rice	AM fungus *Claroideoglomus etunicatum* (isolate EEZ 163) @ 700 infective propagules per pot at sowing time just below rice seedlings	Significantly ↑ shoot dry weight (156%), root length (63%) under 150 mM NaCl concentration compared to un-inoculated control plants	[180]
For salt stress seedling are dip into Hoagland's medium containing 200 mM salt solution	Pot	Wheat	Seedling allowing in Hoagland's medium containing 200 mM salt solution and 5 ml PGP bacterial solution (*Bacillus* sp. (EN1), *Zhihengliuella* sp. (EN3), *S. succinus* (EN4), *Bacillus gibsonii* (EN6), *Oceanobacillus* sp. (EN8), *Halomonas* sp. (IA), and *Thalassobacillus* sp. (ID), *Halobacillus* sp) @ 1×10^9 cfu mL^{-1}	Significantly ↑growth rates of the plants are 67.5%, 64.4%, 62.2%, 76.3%, 70.6%, 73.5% and 78.1% for EN1, EN3, EN4, EN6, EN8, IA and ID as well as ↑ total fresh weight and length of root and shoot of wheat seedlings compared to control	[181]
Irrigated by saline water with 5 salinity levels: S1: 2 dS m^{-1}, S2: 4 dS m^{-1}, S3: 6 dS m^{-1}, S4: 8 dS m^{-1}, and S5: 10 dS m^{-1}	Pot	Tomato	Nano-fertilizer consisting of 79.19% CaCO$_3$ and 4.62% MgCO$_3$% areapplied through foliar spraying in three concentrations: N1: 0.5 g L^{-1}, N2: 0.75 g L^{-1}, and N3: 1 g L^{-1}.	Significantly ↑ average number of clusters and flowering, fruit set (especially in N1/S1: 65%), yield of fruit compare to control (N0/S1: 26% fruit set)	[182]
Marigold seedlings were exposed to four levels of drought stresses (100% (D$_0$), 75% (D$_1$), 50% (D$_2$), and 25% (D$_3$) according to water	Pot	Marigold	The inoculum (5 g of soil containing spores of AM fungi *Glomus constrictum* Trappe) are placed 3 cm below the surface of the soil (before sowing) to	Significantly ↑ plant height (7.7, 4.9, 5.5 and 16.2%), dry weight of shoot (19.14, 25.6, 5.88 and 31%) and flower (42.6, 9.6 and 21.8%,	[183]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
holding capacity of the soil			produce mycorrhizal pants	respectively) compared to non-AM inoculated plant	
For water stress plants are supplied 50%, 75%, 100% water after germination	Pot	Sorghum	Surface sterilized seeds are dipped in inoculums (*Streptomyces laurentii* EU-LWT3-69 and *Penicillium* sp. strain EU-DSF-10) for 2 h and sown in pot	Significantly ↑ plant root and shoot length, dry weight of biomass compared to un-inoculated plants	[184]
Exposure of inoculated plant to a 8-week drought-stress	Pot	Timothy (Phleum pratense L.)	At 3 weeks post seeding, each seedling was inoculated by pipetting 0.5 mL of phosphate buffer containing 10^6 CFU of *B. subtilis* strain B26	Significantly ↑ in shoot and root biomass by 26.6 and 63.8% compared to un-inoculated plants	[185]
For salt stress, 150 mM NaCl applied after 5 weeks of transplantation or at 5 to 6 leaf stage, and For drought stress, plant supplied of half of the water required for normal irrigation	Pot	Cucumber (*Cucumis sativus*) (cv. Cador, cv. Venus)	Foliar spray with Si (2.25 mM) as K_2SiO_3 to stressed plant at 10 days interval	Significantly ↑ in the R/S ratio by > 20 % in Cador and about 15 % in Venus cultivars	[186]
For flooding stress, 8 weeks older plants are flooded with deionised water for 15 days	Pot	*Ocimum sanctum*	Seedling treated with ACC deaminase-containing rhizobacteria bacterial inoculum of Fd2 (*Ach romobacte rxylosoxidans*), Bac5 (*Serratia ureilytica*), Oci9 (*Herbaspirillum seropedicae*) and Oci13 (*Ochrobac trum rhizosphaerae*) @ 10^8 CFU/ml before imposing stress	Significantly ↑ in fresh weight Fd2 (46.5%) followed by Oci13 (45.1%), Bac5 (26.5%) and Oci9 (16.6%), root weight in Fd2 (37%), shoot length 76.3, 41.1, 31.3 and 19.7%, number of leaves is 41.9, 37.7, 16 and 11%, number of nodes in Fd2 (72%) Bac5 (66%), Oci9 (33%) and Oci13 (27%) respectively.	[187]
For flooding stress, 5 month older	Pot	Muscadine Grape	control (aerated plants), aerated +	Si significantly ↑ the dry weight of	[188]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
plants are induced flooding/hypoxia stress by limiting the oxygen supply to the nutrient solution in hydroponic units		(*Muscadinia rotundifolia* Michx.)	Si (250 ppm), aerated + SiNP (250 ppm), hypoxia stress, hypoxia stress + Si (250 ppm), and hypoxia stress + SiNPs (250 ppm)	root, shoot, and total weight 20, 30 and 15%, Si + hypoxia stress ↑ 125, 120 and 125%, SiNPs + control ↑ 30, 46 and 20% and overall improvement is 155% compared to untreated control	
Heat stress treatment imposed on plants after 4 weeks of emergence and raised temperature by 2°C each day to avoid osmotic shock until the desired temperature level (45±2°C) are achieved	Pot	Tomato	Plants are sprayed 45 days after sowing with sulphur (S) @ 2, 4, 6, and 8 ppm for 2 times at 15 and 22 days after heat induction	In thermo tolerant cultivar @ 6 ppm S significantly ↑ maximum shoot (38.3 cm) and root (12.3 cm) length, shoot fresh (46.65g) and dry (14.57g) weights, average root fresh (12.21g) and dry (6.44g) weight, and in thermo sensitive cultivar fresh weight of fruit (42.1g), shoot fresh (42.14g) and dry (13.16g) weight, root fresh (12.21g) and dry (5.3g) weight compared to @ 2, 4, 8 ppm and untreated control	[189]
Heat stress treatment in Pot: at squaring, flowering and ball formation Field: April (medium temperature), early May (high temperature) and mild-June (optimum temperature) at squaring, flowering and boll formation stage	Pot and field	Cotton	Foliar spray of K, Zn and B @ 1.5, 0.2 and 0.1 % one day before heat treatment	Pot: Significantly ↑ seed cotton yield (SCY) in K (21%) Zn (16%) and B (7%) and average ball weight compared to control Field: Significantly ↑ seed cotton yield (SCY) in April (15%) and May (17%) thermal regimes and average ball weight compared to control in both year	[190]
For heat stress treatment at V$_3$	Pot	Soybean	2 days after transplantation,	Significantly ↑ in shoot length	[191]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
stage plants are exposed for 5 and 10 days			50 ml of freshly diluted *Bacillus cereus* SA1 culture (10^9 CFU/mL) are inoculated to each pot and repeated further 2 times after 5 days	(15.08%), root length (14.63%), fresh and dry weight (27.28 and 12.39%, respectively) after 5and similar pattern followed by 10 days	
1 week after bacterial drench treatment, each pot are watered with 20 ml tap water and then heat and drought stressed by withholding watering for 5-7 days at 35°C in a growth chamber	Pot	Chinese cabbage	Seedlings (four-leaf stage) were drenched with bacterial suspensions (*Bacillus aryabhattai* H26-2 and H30-3) @ 10^7 cells/ml, 1 ml/g of potting mixture	Significantly ↑ in fresh weight (2.4% in H30-3) and number of lateral root (10.95 and 1.5% in H30-3 and H26-2, respectively) compare to control	[192]
For drought stress pots are irrigated with 80, 60 and 40% of water holding capacity for 60 days	Pot	Common bean (*Phaseolus vulgaris* L)	Before sowing seeds are treated with H_2O_2 for 4 hour	Significantly ↑ in root (8.15, 2.72%) and shoot (21.09, 10.52%) length, root fresh (25, 10%) and dry (31.25, 15.38%) weight, shoot fresh (21.12, 6.6%) and dry (21.68, 5.79%) weight in 60 and 40% WHC, respectively.	[193]
Drought stress induced in the pots artificially by irrigating the pot with a PEG-6000 (g/L of water) nutrient solution	Pot	Black gram and garden pea	Seed treatment with bacterial inoculum in individual with RJ12, RJ15 and RJ46 and in consortium with RJ12+RJ15, RJ12+RJ46, RJ15+RJ46 (1×10^8 CFU^{-1})	Significantly ↑ in germination percentage (3-13, 7.7-17%), root length (21.15-55, 48.27-64.7%) and shoot length (26.66-35.67, 13.33-22.15%) varies in both crop plant respectively	[194]
For cold stress treatment pot are kept at 8±2°C for 60 days	Pot	Wheat	Seed treatment with charcoal based inoculum of the bacterial (*Pseudomonad*) culture 10^8 cfu g^{-1}	Significantly ↑ in shoot (4.7-26.1%), root length (27.9–70.5%), root (1.04–2.04-fold), and shoot biomass (1.25–1.66-fold) as compare to control	[195]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
For cold-stress 40 day old seedlings are transferred at 15/10°C (day/night) for two weeks	Pot	Cucumber	Each pot inoculated with 10 g of the AM fungi *R. irregularis*	Significantly ↑ shoot (7%) and root (25%) dry matter per gram compared to control	[196]
Heavy metal stress of Cadmium ($CdSO_4 \cdot 8H_2O$) treatments (0, 100 and 200 mg/l)	Pot	Mustard	SA (1.0 mM) are sprayed in the evening (10 ml/plant) to plants mixed with tween-20 every alternate day from the 1st day of treatment up to day 45	Significantly ↑ shoot (7%) and root (5%) fresh weight and Shoot and root dry weight (5%) @ 200 mg/l and 1 mM SA concentration compared to control	[197]
For heavy metal stress of Cr, plants after 30 days of germination, both soil and sand pots are irrigated with Cr as K2Cr2O7 solution (500 ml pot^{-1}) of 0, 0.25, and 0.5 mM in 7-day interval	Pot	Wheat	Glycinebetaine in 0.1 % Tween-20 solution are applied at 0 and 100 mM on the leaves until runoff at both tillering and booting vegetative stages	Significantly ↑ plant height, root length, kernel length, and number of tillers per plant compared to control	[198]
For heavy metal stress of Hg, seedlings are treated with $HgCl_2$ at 60 and 100 μM concentration for 7 days	Pot	Rice	Application of different combination with $HgCl_2$ of SNPs @ 100, 200 μM or KNO_2 @ 200 μM or $K_4Fe(CN)_6$ @ 200 μM or TIBA 1 μM	Significantly ↑ shoot and root length compare in all treatments to Hg treated plant	[199]
For heavy metal stress of Al, plants are treated with Al (500 μM) + salicyclic acid at different concentration for 2 weeks in Hoagland solution	Pot	Tomato var. SIRI and GOWRI	Application of salicyclic acid (SA) @ 100, 250 and 500 μM concentration on seedling which is mix in Hoagland for 2 weeks	Significantly ↑ plant growth in SIRI (65-85%) and GOWRI (20-55%)	[200]

Table 3.
Various management options to control various abiotic stresses in plants

molecular characterization of MdSOS2L1 gene [157]. In many cellular functions, protein phosphatase plays a crucial role in signal transduction with a process called dephosphorylation. A protein phosphatase gene, OsPP18 (PP2C) has been identified

in rice crops, which shows drought resistance response via ABA-independent pathways and regulating ROS homeostasis [158]. PPC2 genes have been identified and characterized in the genome of *Medicagotruncatula* [201]. Genome studies in Brassica [202] maize, tomato, and Arabidopsis also indicated the presence of PP2C gene families, responsible for abiotic stress tolerance [203, 204]. Among the two subfamilies of PP2C, subfamily A is used in ABA-dependent stress responses and B subfamily is MAPK regulators [205].

5.2 Transcriptional factors

Transcriptional factors (TFs) play an important role as a regulatory protein that could change the expression of stress-responsive genes and enhance tolerance to abiotic stress in plants. There are many studies on transcription factors that show their role in abiotic stress management in plants [206–208]. In-plant abiotic stress responses, members of AP2/ERF, zinc finger, NAC, and WRKY families have been identified and characterized to play a major role in the regulation of ROS homeostasis [209–211]. AP2/ERF (APETALA2/ethylene response factor) group of transcription factors regulates various abiotic stress responses and are found in certain rice varieties. They can acclimatize in stress conditions and minimize the energies consumed via gibberellin and ethylene responsiveness [212]. Although in the early stage of abiotic stresses, ROS levels act as an adaptation signal but the key components of ROS signaling are still unknown. In rice, ERF transcription factor SERF1 plays a very important role in molecular signaling (H2O2 mediated response) during the resistance response against salinity tolerance [159]. Another factor SUB1A reduces gibberellin response and ethylene production in submerged rice genotypes and conserves carbohydrates for future use. After the flooding subsides, plants go through severe leaf desiccation [204] which leads to ROS accumulation in plant tissues [206]. SUB1A boosts submergence tolerance by activating ROS-scavenging genes and also induces ABA responsiveness while activating stress genes [160, 213]. The JERF3 gene was also found to be involved in abiotic stress tolerance in tomato (*S. Lycopersicum*) by modulating ROS regulation and also influence the expression of genes involved in oxidative, osmotic stress responses which ultimately reduces ROS accumulation [161].

Zinc finger domains(s) were reported to be one of the most important transcription factors used in ROS regulation for abiotic stress tolerance in Arabidopsis and other plant species [214]. Based on the location and number of protein residues, zinc finger proteins are classified into several groups such as C2H2, CCCH, C2C2, and C3HC4 [211]. Gene DST accumulates H2O2 in the guard cell of the rice plant and enhances abiotic stress (drought and salt) tolerance while increasing the closure of stomata [162]. In rice crops, two other zinc finger proteins (ZFP179 and ZFP36) also help in the regulation of ROS homeostasis and abiotic stress tolerance [163, 215]. Another protein OSTZF1 enhances the expression of ROS-scavenging enzymes and genes responsible for redox homeostasis which helps in modulating abiotic stress resistance [164].

TF families also include the NAC group, which is one of the largest TF families with approximately 300 members among rice and Arabidopsis [216, 217]. This group of TFs helps in abiotic stress tolerance through ROS regulation. In Soybean, GmNAC2 transcription factor involves in signaling pathways of ROS and modulate the expression of ROS-scavenging genes [218]. Another NAC TF gene-SNAC3 has been identified in rice crops which regulates positively during drought stress and high temperature enhances abiotic stress tolerance by controlling ROS-related enzymes [219].

Another TF family WRKY is widely involved in Arabidopsis and Rice which has more than 100 genes only in these two plants [208]. These WRKY genes regulate both biotic and abiotic stress responses [220]. The WRKY transcription family is consists of a highly conserved region WRKYGQK heptapeptide at the C terminus and at the N- terminus a zinc-finger motif is present. These WRKY domains bind to W-box in the promoter regions and regulate various physiological responses [201, 221]. In rice WRKY genes reduces the oxidative stress tolerance effects by enhancing ROS and ABA functions. In transgenic soybean, the GmWRKY27 gene enhances drought and salt tolerance response by reducing ROS levels [165]. Another WRKY gene-GhWRKY17 in cotton involves abiotic stress tolerance by regulating ROS level and also by modifying ABA signaling pathways [167].

5.3 SRO proteins

SRO proteins which are also known as SIMILAR TO RCD ONE, are characterized as plant-specific proteins. Their domain characterization shows that they contain a C-terminal RCD1-SRO-TAF4 (RST) domain, N-terminal WWE domain, and a poly (ADP-ribose) polymerase catalytic (PARP) domain. In rice, the OsSRO1c gene targets abiotic stress (drought) related transcription factor (SNAC1), accumulates H_2O_2 in plant cells which leads to a reduction in water loss by reducing stomatal aperture [168]. OsNAC5 and ONAC095 have also been found to enhance drought and oxidative stress tolerance in rice [7]. In wheat crops, overexpression of the Ta-sro1 gene helps in cellular homeostasis with the regulation of ROS (through ROS-mediated enzymes) and provides salinity tolerance [208].

5.4 ABA metabolism-related proteins

Abscisic acid (ABA) plays an important role as a phytohormone that induces abiotic stress tolerance response in plants. In rice during drought condition, mutant gene dsm2 have been identified which synthesize β-carotene hydroxylase which is a precursor of ABA. Overexpression of *DSM2* enhances stress-related ABA-responsive gene expression and increases xanthophylls which lead to resistance response in abiotic and oxidative stresses [169]. In ABA catabolism, another hydroxylase-encoding gene-OsABA8ox3 is involved and controls oxidative stress under abiotic stress conditions [209]. In transgenic tobacco plants, overexpression of *the SgNCED1* gene (9-*cis*-epoxycarotenoid dioxygenase gene from *Stylosanthesguianensis*) increases ABA content and provides tolerance response to salt and drought stresses. This tolerance response is associated with the inducing production of NO and H_2O_2 along with the activation of ROS-scavenging enzymes [170].

5.5 ROS-scavenging proteins/enzymes

The presence of ROS-scavenging enzymes such as SOD, APX, and CAT in every cellular compartment of crop plants helps in ROS detoxification and protects against several abiotic stresses [52]. In water scarcity condition, improved yield and survival rate is observed in transgenic alfalfa crop due to the presence of MnSOD gene [171]. In transgenic rice plants under cold stress conditions, APX gene- OsAPX1 shows an increased percentage of spikelet fertility whereas overexpression of OsAPX2gene increased drought stress tolerance as compared with wild-type plants [172].

5.6 Ca2+ transporters and binding proteins

For the growth, development, and stress tolerance in plants, Calcium (Ca2+) controls several signaling pathways. P-type Ca2+ATPases or antiporters maintain the basal cytosolic level by regulating the influx and efflux of Ca2+ across the membranes. In rice crops, OsACA6 gene has been isolated and characterized. In tobacco plants, overexpression of the OsACA6 gene reduces ROS accumulation and induces expression of stress-responsive genes which leads to drought and salinity tolerance [173]. In transgenic lines, this gene controls cellular ion homeostasis and ROS-scavenging pathways which give tolerance response to Cd2+ stress [222].

6. Conclusion and future prospects

In the field of plant stress and ROS production, key sources, mechanism and various antioxidant enzymes to counteract the ROS are well reported. However, ROS homeostasis, signal transduction and interaction among various cellular compartments towards signaling are largely unknown and need to be addressed. Many studied reported that many antioxidant remain involve in ROS regulation but their inter and intra compartmental coordination to adjust ROS during stress condition is poorly understood. Therefore, to develop a conceptual and comprehensive framework, a combination of transcriptome, proteome, and metabolome approaches is required to understand ROS development, signaling pathways and their management.

Plants need robust and comprehensive adaption mechanisms to combat under stress conditions. For better stress resistance and ROS homeostasis many specific genes responsible for stress resistance has been identified in rice and transgenic plants. However, most of the ROS associated genes are studied for the expression of antioxidant enzymes activity and large field scale testing of transgenic plants for stress tolerance is very limited. Thus, in order to improve the abiotic stress tolerance by homeostasis of ROS, functions of associated genes and mechanism to control the ROS signaling pathways require detailed investigation. In future, these ROS associated genes and QTLs can be used in breeding and genetic engineering programme for the development of abiotic stress resistance cultivar.

Author details

Asha Kumari[1], Mahendar Singh Bhinda[1], Sachin Sharma[3], Manoj Kumar Chitara[4], Ashim Debnath[2], Chandan Maharana[1], Manoj Parihar[1*] and Binny Sharma[5]

1 ICAR—Vivekananda Parvatiya Krishi Anushandhan Sansthan, Almora, Uttarakhand, India

2 Department of Genetics and Plant Breeding, College of Agriculture, Acharya Narendra Deva University of Agriculture and Technology, Ayodhya, Uttar Pradesh, India

3 Department of Soil Science and Agricultural Chemistry, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

4 Department of Plant Pathology, College of Agriculture, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

5 Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, Uttar Pradesh, India

*Address all correspondence to: manojbhu7@gmail.com

IntechOpen

References

[1] Mittler R, Blumwald, E. Genetic engineering for modern agriculture: challenges and perspectives. Annual Review of Plant Biology. 2010;61:443–462. doi: 10.1146/annurev-arplant-042809-112116

[2] Hu H,Xiong, L. Genetic engineering and breeding of drought-resistant crops. Annual Review of Plant Biology. 2014;65:715–741. doi: 10.1146/annurev-arplant-050213-040000

[3] Zhang A, Jiang M, Zhang J, Ding H, Xu S, Hu X, et al. Nitric oxide induced by hydrogen peroxide mediates abscisic acid-induced activation of the mitogen-activated protein kinase cascade involved in antioxidant defense in maize leaves. New Phytologist. 2007;175:36–50. doi: 10.1111/j.1469-8137.2007.02071.x

[4] Eckardt NA, Cominelli E, Galbiati M, Tonelli C. The future of science: food and water for life. The Plant Cell. 2009;21:368–372. doi: 10.1105/tpc.109.066209

[5] Hirayama T, Shinozaki K. Research on plant abiotic stress responses in the post-genome era: past, present and future. The Plant Journal. 2010;61:1041–1052. doi: 10.1111/j.1365-313X.2010.04124.x

[6] Dietz KJ, Turkan I, Krieger-Liszkay A. Redox- and reactive oxygen species-dependent signaling into and out of the photosynthesizing chloroplast. Plant Physiology2016;171:1541–1550. doi: 10.1104/pp.16.00375.

[7] Huang S, Van Aken O, Schwarzländer M, Belt K, Millar AH. The roles of mitochondrial reactive oxygen species in cellular signaling and stress response in plants.Plant physiology. 2016;171(3):1551-1559.

[8] Sandalio LM, Romero-Puertas MC. Peroxisomes sense and respond to environmental cues by regulating ROS and RNS signaling networks. Annals of Botany. 2015;116:475–485. doi: 10.1093/aob/mcv074.

[9] Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell& Environment. 2010;33:453–467. doi: 10.1111/j.1365-3040.2009.02041.x

[10] Apel K, Hirt H.Reactive oxygen species: metabolism, oxidative stress, signal transduction. Annual Review of Plant Biology. 2004;55:373-399.

[11] Mittler R. ROS are good. Trends in Plant Science. 2017;22:11–19. doi: 10.1016/j.tplants.2016.08.002

[12] Noctor G, Mhamdi A, Foyer CH. The roles of reactive oxygen metabolism in drought: not so cut and dried. Plant Physiology. 2014;164:1636–1648. doi: 10.1104/pp.113.233478

[13] Suzuki N, Koussevitzky S, Mittler R, Miller G. ROS and redox signalling in the response of plants to abiotic stress. Plant, Cell &Environment. 2012;35(2):259-270. DOI: 10.1111/j.1365-3040.201102336.x

[14] Baxter A, Mittler R, Suzuki N. ROS as key players in plant stress signaling. J of Experimental Botany. 2014;65:1229–1240. doi: 10.1093/jxb/ert375

[15] Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry. 2010;48(12):909-930. DOI: 10.1016/j.plaphy.2010.08.016

[16] Mahajan S, Tuteja N. Cold, salinity and drought stresses: an overview. Archives of Biochemistry and Biophysics. 2005;444:139-158. DOI: 10.1016/j.abb.2005.10.018

[17] Atkinson NJ, Urwin PE. The interaction of plant biotic and abiotic stresses: from genes to the field. Journal of Experimental Botany. 2012;63(10): 3523-3544. DOI: 10.1093/jxb/ers100

[18] Cancado GMA. The importance of genetic diversity to manage abiotic stress. In: Shanker A, editor. Abiotic Stress in Plants - Mechanisms and Adaptations.InTechOpen;2011. pp. 351-366. DOI: 10.5772/22397

[19] Weisany W, Sohrabi Y, Heidari G, Siosemardeh A, Ghassemi-Golezani K. Changes in antioxidant enzymes activity and plant performance by salinity stress and zinc application in soybean (*'Glycine max*'L.). Plant Omics. 2012;5(2):60.

[20] Stavridou E, Hastings A, Webster RJ, Robson PR. The impact of soil salinity on the yield, composition and physiology of the bioenergy grass *Miscanthus×giganteus*. GCB Bioenergy. 2017;9(1):92-104.

[21] Khodarahmpour Z, Ifar M, Motamedi M. Effects of NaCl salinity on maize (*Zea mays* L.) at germination and early seedling stage. African Journal of Biotechnology. 2012;11(2):298-304.

[22] Singh J, Sastry ED, Singh V. Effect of salinity on tomato (*Lycopersicon esculentum* Mill.) during seed germination stage. Physiology and Molecular Biology of Plants. 2012;18(1):45-50.

[23] Zayova E, Philipov P, Nedev T, Stoeva D. Response of in vitro cultivated eggplant (*Solanum melongena* L.) to salt and drought stress. AgroLife Scientific Journal. 2017;6(1):276-282.

[24] Hossain MS, Alam MU, Rahman A, Hasanuzzaman M, Nahar K, Al Mahmud J, Fujita M. Use of iso-osmotic solution to understand salt stress responses in lentil (*Lens culinaris* Medik.). South African Journal of Botany. 2017;113:346-354.

[25] Ren B, Zhang J, Dong S, Liu P, Zhao B. Effects of duration of waterlogging at different growth stages on grain growth of summer maize (*Zea mays* L.) under field conditions. Journal of Agronomy and Crop Science. 2016; 202(6):564-575.

[26] Robertson D, Zhang H, Palta JA, Colmer T, Turner NC.Waterlogging affects the growth, development of tillers, yield of wheat through a severe, but transient, N deficiency. Crop and Pasture Science. 2009;60(6):578-586.

[27] Kumar P, Pal M, Joshi R, Sairam, RK. Yield, growth and physiological responses of mung bean [*Vigna radiata* (L.) Wilczek] genotypes to waterlogging at vegetative stage. Physiology and Molecular Biology of Plants. 2013;19(2): 209-220.

[28] Issarakraisila M, Ma Q, Turner DW. Photosynthetic and growth responses of juvenile Chinese kale (*Brassica oleracea* var. *alboglabra*) and Caisin (*Brassica rapa* subsp. *parachinensis*) to waterlogging and water deficit. Scientia horticulturae. 2007;111(2):107-113.

[29] Qaseem MF, Qureshi R,Shaheen H. Effects of pre-anthesis drought, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress. Scientific reports. 2019;9(1):1-12.

[30] Baroowa B, Gogoi N. Morpho-physiological and Yield responses of Black gram (*Vigna mungo* L.) and Green

gram (*Vigna radiata* L.) genotypes under Drought at different Growth stages. Research Journal of Recent Sciences. 2016;5(2):43-50.

[31] Sivakumar R, Nandhitha GK, Nithila S. Impact of drought on chlorophyll, soluble protein, abscisic acid, yield and quality characters of contrasting genotypes of tomato (*Solanum lycopersicum*). Current Journal of Applied Science and Technology.2017;21(5):1-10.

[32] Ahmad I, Akhtar MJ, Zahir ZA, Jamil A. Effect of cadmium on seed germination and seedling growth of four wheat (*Triticum aestivum* L.) cultivars. Pakistan Journal of Botany. 2012;44(5): 1569-1574.

[33] Liu JJ, Wei Z, Li JH.Effects of copper on leaf membrane structure and root activity of maize seedling. Botanical Studies. 2014;55(1):1-6.

[34] Anjum SA, Tanveer M, Hussain S, Bao M, Wang L, Khan I, et al. Cadmium toxicity in Maize (*Zea mays* L.): consequences on antioxidative systems, reactive oxygen species and cadmium accumulation. Environmental Science and Pollution Research. 2015;22(21): 17022-17030.

[35] Vijayarengan P,Mahalakshmi G. Zinc toxicity in tomato plants. World Applied Sciences Journal. 2013;24(5): 649-653.

[36] Kaya, C., Akram, N. A., Sürücü, A. and Ashraf, M. (2019). Alleviating effect of nitric oxide on oxidative stress and antioxidant defence system in pepper (Capsicum annuum L.) plants exposed to cadmium and lead toxicity applied separately or in combination. Scientia Horticulturae, 255, 52-60.

[37] Chandra S, Saha R, Pal P. Assessment of arsenic toxicity and tolerance

characteristics of bean plants (*Phaseolus vulgaris*) exposed to different species of arsenic. Journal of Plant Nutrition. 2018; 41(3):340-347.

[38] Wang Y, Tao H, Tian B, Sheng D, Xu C, Zhou H, et al. Flowering dynamics, pollen, pistil contribution to grain yield in response to high temperature during maize flowering. Environmental and Experimental Botany. 2019;158:80-88.

[39] Modarresi M, Mohammadi V, Zali A, Mardi M. Response of wheat yield and yield related traits to high temperature. Cereal Research Communications. 2010; 38(1):23-31.

[40] Bihter ONAT, Bakal H, Gulluoglu L, Arioglu H.The effects of high temperature at the growing period on yield and yield components of soybean [*Glycine max* (L.)Merr] varieties. Turkish Journal of Field Crops. 2017;22 (2):178-186.

[41] Lamichaney A, Parihar AK, Hazra KK, Dixit GP, Katiyar PK, Singh, D,et al. Untangling the Influence of Heat Stress on Crop Phenology, Seed Set, Seed Weight, Germination in Field Pea (*Pisum sativum* L.). Frontiers in Plant Science. 2021;12:437.

[42] Peterson RKD, Higley LG. Biotic Stress and Yield Loss. 1st edn. Washington: CRC Press; 2000. pp. 261. ISBN 0-8493-1145-4.

[43] Bailey-Serres J, Mittler R. The roles of reactive oxygen species in plants cells. Plant Physiology. 2006;141(2):311. DOI: 10.1104/pp.104.900191

[44] Mullineaux PM and Baker NR. Oxidative stress: antagonistic signaling for acclimation or cell death? Plant Physiology. 2010;154:521-525.

[45] Sharma I, Ahmad P. "Catalase: a versatile antioxidant in plants," in Oxidative Damage to Plants, ed P. Ahmad (Srinagar: S.P. College). Academic Press; 2014. pp. 131–148.

[46] Wahid A, Farooq M, Siddique KHM. Implications of oxidative stress for plant growth and productivity. In: Pessarakli M, editor. Handbook of Plant and Crop Physiology. 3rd edn. LLC 6000 Broken Sound Parkway, Suite 300, Boca Raton, FL 33487 USA: Taylor & Francis Group;2014. pp. 549-556. DOI: ISBN13: 978-1-4665-5328-6

[47] Caverzan A, Casassola A, PatussiBrammer S. Reactive oxygen species and antioxidant enzymes involved in plant tolerance to stress. In: Arun K. Shanker and ChitraShanker, editors. Abiotic and biotic in stress plants - recent advances future perspectives. London: InTechOpen; 2016. pp. 463-480.

[48] Carocho M, Ferreira IC.A review on antioxidants, prooxidants and related controversy: Natural and synthetic compounds, screening and analysis methodologies and future perspectives. Food and Chemical Toxicology. 2013;51: 15–25.

[49] Hasanuzzaman M, Bhuyan M, Anee TI, Parvin K, Nahar K, Mahmud JA, Fujita M. Regulation of ascorbate-glutathione pathway in mitigating oxidative damage in plants under abiotic stress. Antioxidants. 2019; 8: 384.

[50] Gratão PL, Polle A, Lea PJ, Azevedo RA. Making the life of heavy metal-stressed plants a little easier. Functional Plant Biology. 2005;32:481-494.

[51] Scandalios JG. Oxidative stress: molecular perception and transduction of signals triggering antioxidant gene

defenses. Brazalian Journal of Medical and Biological Research. 2005;38: 995-1014.

[52] Mittler R, Vanderauwera S, Gollery M, Van Breusegem F. Questions and future challenges. Trends in Plant Science. 2004;10(9):490-498.

[53] Asada K. Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiology. 2006;141:391–396.

[54] Mittler R. Oxidative stress, antioxidants and stress tolerance. Trends in Plant Science. 2002;7:405-410.

[55] Nath M, Bhatt D, Bhatt MD, Prasad R, Tuteja N. Microbe-mediated enhancement of nitrogen and phosphorus content for crop improvement. In Crop Improvement through Microbial Biotechnology; Prasad, R, Gill, S.S, Tuteja, N, Eds.; Academic Press: Cambridge, UK; 2018. pp. 291–301.

[56] Laxa M, Liebthal M, Telman W, Chibani K, Dietz KJ.The role of the plant antioxidant system in drought tolerance. Antioxidants. 2019;8:94.

[57] Hasanuzzaman M, Bhuyan MHMB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, Fujita M, Fotopoulos V. Reactive Oxygen Species and Antioxidant Defense in Plants under Abiotic Stress: Revisiting the Crucial Role of a Universal Defense Regulator. Antioxidants. 2020a;9: 681. doi:10.3390/antiox9080681

[58] Zhao Q, Zhou L, Liu J, Cao Z, Du X, Huang F, et al. Involvement of CAT in the detoxification of HT-induced ROS burst in rice anther and its relation to pollen fertility. Plant Cell Reports. 2018; 37:741–757. doi: 10.1007/s00299-018-2264-y

[59] Kawarazaki T, Kimura S, Iizuka A, Hanamata S, Nibori H, Michikawa M, et al. A low temperature-inducible protein AtSRC2 enhances the ROS producing activity of NADPH oxidase AtRbohF. Biochimica et Biophysica Acta. 2013;1833:2775-2780.doi: 10.1016/j.bbamcr.2013.06.024

[60] Lee S, Seo PJ, Lee HJ, Park CM.A NAC transcription factor NTL4 promotes reactive oxygen species production during drought-induced leaf senescence in Arabidopsis. The Plant Journal. 2012;70:831-844. doi: 10.1111/j.1365-313X. 2012.04932.x

[61] Wu Y, Yang Z, How J, Xu H, Chen L, Li K.Overexpression of a peroxidase gene (AtPrx64) of Arabidopsis thaliana in tobacco improves plant's tolerance to aluminum stress. Plant Molecular Biology. 2017;95:157-168. doi: 10.1007/s11103-017-0644-2

[62] Ahammed GJ, He BB, Qian XJ, Zhou YH, Shi K, Zhou J, et al.24-Epibrassinolide alleviates organic pollutants-retarded root elongation by promoting redox homeostasis and secondary metabolism in *Cucumi ssativus* L. Environmental Pollution. 2017;229: 922-931. doi: 10.1016/j.envpol.2017.07.076

[63] Kim DS, Hwang BK. An important role of the pepper phenylalanine ammonia-lyase gene (PAL1) in salicylic acid-dependent signalling of the defence response to microbial pathogens.Journal of Experimental Botany. 2014;65: 2295-2306. doi: 10.1093/jxb/eru109

[64] Yang C, Li W, Cao J, Meng F, Yu Y, Huang J, et al. Activation of ethylene signaling pathways enhances disease resistance by regulating ROS and phytoalexin production in rice. The Plant Journal. 2017;89:338-353. doi: 10.1111/tpj.13388

[65] Hasanuzzaman M, Nahar K, Khan MIR, Al Mahmud J, Alam MM, Fujita M. Regulation of reactive oxygen species metabolism and glyoxalase systems by exogenous osmolytes confers thermos-tolerance in *Brassica napus*. Gesunde Pflanzen. 2020b;72: 3-16.

[66] Kar RK.Plant responses to water stress, Role of reactive oxygen species. Plant Signaling & Behavior.2011;6(11): 1741-1745.

[67] Nahar K, Hasanuzzaman M, Alam MM, Rahman A, Mahmud JA, Suzuki T, Fujita M. Insights into spermine-induced combined high temperature and drought tolerance in mung bean: Osmoregulation and roles of antioxidant and glyoxalase system. Protoplasma. 2017;254:445–460.

[68] Rady MM, Belal HE, Gadallah FM, Semida WM.Selenium application in two methods promotes drought tolerance in *Solanum lycopersicum* plant by inducing the antioxidant defense system. Scientia Horticulturae. 2020;266:109-290.

[69] Antoniou C, Chatzimichail G, Xenofontos R, Pavlou JJ, Panagiotou E, Christou A, Fotopoulos V. Melatonin systemically ameliorates drought stress-induced damage in *Medicago sativa* plants by modulating nitro-oxidative homeostasis and proline metabolism. Journal of Pineal Research. 2017;62: e12401.

[70] Munns R, Tester M. Mechanisms of salinity tolerance.Annual Review of Plant Biology. 2008;59:651-681.

[71] Rehman S, Abbas G, Shahid M, Saqib M, Farooq ABU, Hussain M, Murtaza B, Amjad M, Naeem MA, Farooq A. Effect of salinity on cadmium tolerance, ionic homeostasis and oxidative stress responses in conocarpus exposed to cadmium stress: Implications

for phytoremediation. Ecotoxicology and Environment Safety. 2019;171:146–153.

[72] Cunha JR, Neto MCL, Carvalho FE, Martins MO, Jardim-Messeder D, Margis-Pinheiro M, Silveira JA. Salinity and osmotic stress trigger different antioxidant responses related to cytosolic ascorbate peroxidase knockdown in rice roots. Environmental and Experimental Botany. 2016;131: 58-67.

[73] Li Y, Cao XL, Zhu Y, Yang XM, Zhang KN, Xiao ZY, Wang H, Zhao JH, Zhang LL, Li GB. Osa-miR398b boosts H_2O_2 production and rice blast disease-resistance via multiple superoxide dismutases. New Phytologist. 2019;222: 1507-1522.

[74] Vighi I, Benitez L, Amaral M, Moraes G, Auler P, Rodrigues G, Deuner S, Maia L, Braga E.Functional characterization of the antioxidant enzymes in rice plants exposed to salinity stress. Biologia Plantarum. 2017; 61:540–550.

[75] Alzahrani SM, Alaraidh IA, Migdadi H, Alghamdi S, Khan MA, Ahmad P. Physiological, biochemical, antioxidant properties of two genotypes of *Vicia faba* grown under salinity stress. Pakistan Journal of Botany. 2019;51: 786-798.

[76] Alsahli A, Mohamed AK, Alaraidh I, Al-Ghamdi A, Al-Watban A, El-Zaidy M, Alzahrani, SM. Salicylic acid alleviates salinity stress through the modulation of biochemical attributes and some key antioxidants in wheat seedlings. Pakistan Journal of Botany. 2019;51:1551-1559.

[77] Tanou G, Ziogas V, Belghazi M, Christou A, Filippou P, Job D, Fotopoulos V, Molassiotis A. Polyamines reprogram oxidative and nitrosative status and the proteome of citrus plants

exposed to salinity stress. Plant, Cell and Environment. 2014;37:864–885.

[78] Ali AYA, Ibrahim MEH, Zhou G, Nimir NEA, Jiao X, Zhu G, Elsiddig AMI, Suliman MSE, Elradi SBM, Yue W. Exogenous jasmonic acid and humic acid increased salinity tolerance of sorghum. Agronomy Journal.2020;112:871-884.

[79] Ding X, Jiang Y, He L, Zhou Q, Yu J, Hui D, Huang D. Exogenous glutathione improves high root-zone temperature tolerance by modulating photosynthesis, antioxidant and osmolytes systems in cucumber seedlings. Scientific Reports.2016;6:35424.

[80] Awasthi R, Gaur P, Turner NC, Vadez V, Siddique KH, Nayyar H. Effects of individual and combined heat and drought stress during seed filling on the oxidative metabolism and yield of chickpea (*Cicer arietinum*) genotypes differing in heat and drought tolerance. Crop and Pasture Science.2017;68: 823-841.

[81] Hasanuzzaman M, Hossain MA, Teixeira da Silva JA, Fujita M. Plant responses and tolerance to abiotic oxidative stress: Antioxidant defense is a key factor. In Crop Stress and its Management: Perspectives and Strategies; Bandi V, Shanker AK, Shanker C, Mandapaka M, Eds.; Springer: Berlin, Germany;2012. pp. 261-316.

[82] Liu J, Hasanuzzaman M, Wen H, Zhang J, Peng T, Sun H, Zhao Q. High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice. Protoplasma. 2019;256:1217-1227.

[83] Sarkar J, Chakraborty B, Chakraborty U. Temperature stress induced antioxidative and biochemical

changes in wheat (*Triticum aestivum* L.) cultivars. Journal of Plant Stress Physiology.2016:22-30.

[84] Zhao H, Ye L, Wang Y, Zhou X, Yang J, Wang J, Cao K,Zou Z. Melatonin increases the chilling tolerance of chloroplast in cucumber seedlings by regulating photosynthetic electron flux and the ascorbate-glutathione cycle. Frontiers in Plant Science. 2016;7: 1814.

[85] Shi H, Ye T, Zhong B, Liu X, Chan Z. Comparative proteomic and metabolomic analyses reveal mechanisms of improved cold stress tolerance in bermudagrass (*Cynodon dactylon* (L.) Pers.)by exogenous calcium. Journal of Integrative Plant Biology.2014;56:1064-1079.

[86] Wani MA, Jan N, Qazi HA, Andrabi KI, John R. Cold stress induces biochemical changes, fatty acid profile, antioxidant system and gene expression in Capsella bursa pastoris L. Acta Physiologie Plantarum. 2018;40:167.

[87] Mohammad rezakhani S, Hajilou J, Rezanejad F, Zaare-Nahandi F. Assessment of exogenous application of proline on antioxidant compounds in three citrus species under low temperature stress. Journal of Plant Interactions.2019;14:347-358.

[88] Spano C, Bottega S, Castiglione MR, Pedranzani HE. Antioxidant response to cold stress in two oil plants of the genus Jatropha.Plant, Soil and Environment.2017;63:271-276.

[89] Cheng F, Lu J, Gao M, Shi K, Kong Q, Huang Y, Bie Z. Redox signaling and CBF-responsive pathway are involved in salicylic acid-improved photosynthesis and growth under chilling stress in watermelon. Frontiers in Plant Science. 2016;7:1519.

[90] Wang QJ, Sun H, Dong QL, Sun TY, Jin ZX, Hao YJ, Yao YX.The enhancement of tolerance to salt and cold stresses by modifying the redox state and salicylic acid content via the cytosolic malate dehydrogenase gene in transgenic apple plants.Plant Biotechnology Journal.2016;14: 1986-1997.

[91] Han QH, Huang B, Ding CB, Zhang ZW, Chen YE, Hu C,et al. Effects of melatonin on anti-oxidative systems and photosystem II in cold-stressed rice seedlings. Frontiers in Plant Science.2017;8:785.

[92] Li W, Mo W, Ashraf U, Li G, Wen T, Abrar M,et al. Evaluation of physiological indices of waterlogging tolerance of different maize varieties in South China. Applied Ecology and Environmental Research. 2018;16: 2059-2072.

[93] Anee TI, Nahar K, Rahman A, Mahmud JA, Bhuiyan TF, Alam MU, et al. Oxidative damage and antioxidant defense in *Sesamum indicum* after different waterlogging durations. Plants. 2019;8:196.

[94] Park JS, Lee EJ. Waterlogging induced oxidative stress and the mortality of the Antarctic plant, *Deschampsia antarctica*. Journal of Ecology and Environment. 2019;43:29.

[95] Mahmud JA, Bhuyan MHMB, Anee TI, Nahar K, Fujita M, Hasanuzzaman M. Reactive oxygen species metabolism and antioxidant defense in plants under metal/metalloid stress. In Plant Abiotic Stress Tolerance; Hasanuzzaman M, Hakeem K, Nahar K, Alharby H, Eds.; Springer: Cham, Switzerland;2019. pp. 221-257.

[96] Gratao PL, Alves LR, Lima LW. Heavy metal toxicity and plant

productivity: Role of metal scavengers. In Plant-Metal Interactions; Srivastava S, Srivastava AK, Suprasanna P, Eds.; Springer: Cham, Switzerland; 2019. pp. 49–60.

[97] Kumar S, Trivedi PK. Glutathione S-transferases: Role in combating abiotic stresses including arsenic detoxification in plants. Frontiers in Plant Science.2018;9:751.

[98] Chakravarthi S, Jessop CE, Bulleid NJ. The role of glutathione in disulphide bond formation and endoplasmic-reticulum-generated oxidative stress.EMBO Reports. 2006;7: 271–275.

[99] Petrussa E, Braidot E, Zancani M, Peresson C, Bertolini A, Patui S. et al. Plant flavonoids-biosynthesis, transport and involvement in stress responses. International Journal of Molecular Sciences.2013;14:14950-14973.

[100] Landi M, Tattini M, Gould KS. Multiple functional roles of anthocyanins in plant-environment interactions.Environmental and Experimental Botany.2015;119:4-17.

[101] Mori IC, Schroeder JI. Reactive oxygen species activation of plant Ca2þ channels.A signaling mechanism in polar growth, hormone transduction, stress signaling, hypothetically mechanotransduction.Plant Physiology. 2004;135(2): 702–708.

[102] Bhattacharjee S. ROS and Regulation of Photosynthesis. In: Reactive Oxygen Species in Plant Biology. Springer, New Delhi; 2019. pp. 107-125.https://doi.org/10.1007/ 978-81-322-3941-3_5.

[103] Corpas FJ, Gupta DK, Palma JM. Production sites of reactive oxygen species (ROS) in organelles from plant cells. InReactive oxygen species and oxidative damage in plants under stress. Springer, Cham; 2015. pp. 1-22. 10.1007/ 978-3-319-20421-5_1.

[104] Bhattacharjee S. ROS and oxidative stress: origin and implication. InReactive oxygen species in plant biology. Springer, New Delhi; 2019. pp. 1-31. h ttps://doi.org/10.1007/978-81-322-3941-3_1.

[105] Yamauchi T, Yoshioka M, Fukazawa A, Mori H, Nishizawa NK, Tsutsumi N, et al. An NADPH Oxidase RBOH functions in rice roots during lysigenous aerenchyma formation under oxygen-deficient conditions. The Plant Cell. 2017;29:775–790. doi: 10.1105/ tpc.16.00976.

[106] Gupta KJ, Igamberdiev AU. Compartmentalization of reactive oxygen species and nitric oxide production in plant cells: an overview. In: Gupta KJ, Igamberdiev AU (eds) Reactive oxygen and nitrogen species signaling and communications in plants. Springer International Publishing, Switzerland; 2015.pp. 1–14.

[107] del Rı´o LA, Corpas FJ, Sandalio LM, Palma JM, Gomez M, Barroso JB.Reactive oxygen species, antioxidant systems and nitric oxide in peroxisomes.Journal of Experimental Botany. 2002;53:1255–1272.

[108] Palma JM, Corpas FJ, del Rı´o LA. Proteome of plant peroxisomes: new perspectives on the role of these organelles in cell biology. Journal of Proteomics. 2019;9:2301–2312.

[109] Baker A, Paudyal R. The life of the peroxisome: from birth to death. Current Opinion in Plant Biology. 2014;22:39–47.

[110] Foyer CH, Noctor G. Redox sensing and signaling associated with reactive

oxygen in chloroplast, peroxysome and mitochondria. Physiologia Plantarum. 2003;119:355–364.

[111] Forman HJ, Boveris A. Free radicals in biology and medicine, vol 5. Academic Press, New York; 1982.pp. 65–90.

[112] Boveris A, Cadenas E. Mitochondrial production of superoxide anions and its relationship to the antimycin insensitive respiration. FEBS Letters. 1975;54(3):311–314.

[113] Maxwell DP, Nickels R, McIntosh L. Evidence of mitochondrial involvement in the transduction of signals required for the induction of genes associated with pathogen attack and senescence. The Plant Journal.2002; 29:269–79.

[114] Segal AW, Abo A.The biochemical basis of NADPH oxidase of phagocytes. Trends in Biochemical Sciences. 1993;18: 43–47

[115] Dvoˇrák P, Krasylenko Y, Zeiner A, Šamaj J, Takácˇ T. Signaling Toward Reactive Oxygen Species-Scavenging Enzymes in Plants. Frontiers in Plant Science. 2021;11:618-835. doi: 10.3389/fpls.2020.618835.

[116] Kliebenstein DJ, Monde RA, Last RL. Superoxide dismutase in Arabidopsis: an eclectic enzyme family with disparate regulation and protein localization. Plant Physiology. 1998;118: 637–650. doi: 10.1104/pp.118.2.637.

[117] Pilon M, Ravet K, Tapken W. The biogenesis and physiological function of chloroplast superoxide dismutases. Biochimica et Biophysica Acta. 2011; 1807:989–998. doi:10.1016/j.bbabio.2010.11.002

[118] Feng K, Yu J, Cheng Y, Ruan M, Wang R, Ye Q, et al. The SOD Gene Family in Tomato: Identification,

Phylogenetic Relationships, Expression Patterns. Frontiers in Plant Science. 2016; 7:1279. doi: 10.3389/fpls.2016.01279.

[119] Morgan MJ, Lehmann M, Schwarzländer M, Baxter CJ, Sienkiewicz-Porzucek A, Williams TC, et al. Decrease in manganese superoxide dismutase leads to reduced root growth and affects tricarboxylic acid cycle flux and mitochondrial redox homeostasis. Plant Physiology. 2008;147:101–114. doi: 10.1104/pp.107.113613.

[120] Dvoˇrák P, Krasylenko Y, Oveˇcka M, Basheer J, Zapletalová V, Šamaj J, et al. In-vivo light-sheet microscopy resolves localisation patterns of FSD1, a superoxide dismutase with function in root development and osmoprotection. Plant, Cell & Environment. 2020;44:68–87. doi: 10.1111/pce.13894

[121] Myouga F, Hosoda C, Umezawa T, Iizumi H, Kuromori T, Motohashi R, et al. A heterocomplex of iron superoxide dismutases defends chloroplast nucleoids against oxidative stress and is essential for chloroplast development in Arabidopsis. The Plant Cell. 2008;20:3148–3162. doi: 10.1105/tpc.108.061341.

[122] Shafi A, Chauhan R, Gill T, Swarnkar MK, Sreenivasulu Y, Kumar S, et al. Expression of SOD and APX genes positively regulates secondary cell wall biosynthesis and promotes plant growth and yield in Arabidopsis under salt stress. Plant Molecular Biology. 2015;87:615–631. doi: 10.1007/s11103-015- 0301-6.

[123] Xing Y, Cao Q, Zhang Q, Qin L, Jia W, Zhang J. MKK5 regulateshigh light-induced gene expression of Cu/Zn superoxide dismutase 1 and 2 in Arabidopsis. Plant and Cell Physiology.2013;54:1217–1227. doi: 10.1093/pcp/pct072

[124] Gallie DR, Chen Z. Chloroplast-localized iron superoxide dismutases FSD2 and FSD3 are functionally distinct in Arabidopsis. PLOS One. 2019;14: e0220078. doi: 10.1371/journal. pone.0220078.

[125] Rizhsky L, Liang H, Mittler R.The water-water cycle is essential for chloroplast protection in the absence of stress. Journal of Biological Chemistry. 2003;278:38921–38925. doi: 10.1074/jbc. M304987200.

[126] Tuzet A, Rahantaniaina MS, Noctor G. Analyzing the function of catalase and the ascorbate-glutathione pathway in H2O2 processing: insights from an experimentally constrained kinetic model. Antioxidants and Redox Signaling. 2019;30:1238–1268. doi: 10.1089/ars.2018.7601.

[127] Ono M, Isono K, Sakata Y, Taji T. CATALASE2 plays a crucial role in long-term heat tolerance of *Arabidopsis thaliana*. Biochemical and Biophysical Resarch Communications.2020; 534:747–751.doi: 10.1016/j.bbrc.2020.11.006

[128] Bueso, E, Alejandro, S, Carbonell, P, Perez-Amador, M.A, Fayos, J, Bellés, J. M, et al. The lithium tolerance of the Arabidopsis cat2 mutant reveals a cross-talk between oxidative stress and ethylene. The Plant Journal. 2007;52: 1052–1065. doi: 10.1111/ j.1365-313X.2007.03305.x. 40. 41.

[129] Zou JJ, Li XD, Ratnasekera D, Wang C, Liu WX, Song LF, et al. Arabidopsis Calcium-Dependent Protein Kinase8 and Catalase3 function in abscisic acid-mediated signaling and H2O2 homeostasis in stomatal guard cells under drought stress. The Plant Cell. 2015;27: 1445–1460. doi: 10.1105/tpc.15.00144.

[130] Nandi, Ankita, Liang-Jun Yan, Chandan Kumar Jana, and Nilanjana Das."Role of catalase in oxidative stress- and age-associated degenerative diseases." *Oxidative medicine and cellular longevity* 2019 .

[131] Hackenberg T, Juul T, Auzina A, Gwizdz S, Malolepszy A, Van Der Kelen K, et al. Catalase and No Catalase Activity1 promote autophagy-dependent cell death in Arabidopsis. The Plant Cell. 2013;25: 4616–4626. doi: 10.1105/tpc.113.117192

[132] Teh OK, Hofius D. Membrane trafficking and autophagy in pathogen-triggered cell death and immunity. Journal of Experimental Botany.2014;65: 1297–1312. doi: 10.1093/jxb/ert441.

[133] Yang Z, Mhamdi A, Noctor G. Analysis of catalase mutants underscores the essential role of CATALASE2 for plant growth and day length-dependent oxidative signalling. Plant Cell& Environment. 2019;42:688–700. doi: 10.1111/pce.13453.

[134] Zhang Y, Ji TT, Li TT, Tian YY, Wang LF, Liu WC. Jasmonic acid promotes leaf senescence through MYC2-mediated repression of Catalase2 expression in Arabidopsis. Plant Science. 2020;299:110-604. doi: 10.1016/j. plantsci.2020.110604.

[135] Palma, J. M, Mateos, R. M, López-Jaramillo, J, Rodríguez-Ruiz, M, González- Gordo, S, Lechuga-Sancho, A. M, et al. Plant catalases as NO and H_2S targets. Redox Biology.2020;34:101525. doi: 10.1016/j.redox.2020.101525

[136] Campa, A. Biological roles of plant peroxidases: Known and potential function. In: Peroxidases in Chemistry and Biology, eds. J. Everse KE, Everse MB, Grisham Boca Raton, FL: CRC Press; 1991. pp. 25–50.

[137] Bunkelmann JR, Trelease, RN. Ascorbate peroxidase: A prominent

membrane protein in oilseed glyoxysomes. Plant Physiology. 1996; 110: 589–598.

[138] Maruta T, Inoue T, Noshi M, Tamoi M, Yabuta Y, Yoshimura K, et al. Cytosolic ascorbate peroxidase 1 protects organelles against oxidative stress by wounding- and jasmonate-induced H_2O_2 in Arabidopsis plants. Biochimica et Biophysica Acta.2012;1820:1901–1907. doi: 10.1016/j.bbagen.2012.08.003.

[139] Maruta T, Sawa Y, Shigeoka S, Ishikawa T. Diversity and evolution of ascorbate peroxidase functions in chloroplasts: more than just a classical antioxidant enzyme? Plant and Cell Physiology.2016;57:1377–1386. doi: 10.1093/pcp/pcv203.

[140] Chew O, Whelan J, Millar AH. Molecular definition of the ascorbate-glutathione cycle in Arabidopsis mitochondria reveals dual targeting of antioxidant defenses in plants. Journal of Biological Chemistry.2003;278:46869–46877. doi: 10.1074/jbc.M307525200.

[141] Foyer CH. Noctor G. Ascorbate and glutathione: the heart of the redox hub. Plant Physiology. 2011;155:2–18. doi: 10.1104/pp.110.167569.

[142] Eltayeb AE, Kawano N, Badawi GH, Kaminaka H, Sanekata T, Shibahara T, et al. Overexpression of monodehydroascorbate reductase in transgenic tobacco confers enhanced tolerance to ozone, salt and polyethylene glycol stresses. Planta.2007;225:1255–1264. doi: 10.1007/s00425-006-0417-7

[143] Sultana S, Khew CY, Morshed MM, Namasivayam P, Napis S, Ho CL. Overexpression of monodehydroascorbate reductase from a mangrove plant (AeMDHAR) confers salt tolerance on rice. Journal of Plant Physiology. 2012;169:311–318. doi: 10.1016/j.jplph.2011.09.004.

[144] Rahantaniaina MS, Li S, Chatel-Innocenti G, Tuzet A, Issakidis-Bourguet E, Mhamdi A, et al. Cytosolic and chloroplastic DHARs cooperate in oxidative stress-driven activation of the salicylic acid pathway. Plant Physiology.2017;174:956–971. doi: 10.1104/pp.17.00317

[145] Yoshida S, Tamaoki M, Shikano T, Nakajima N, Ogawa D, IokiM, et al. Cytosolic dehydroascorbate reductase is important for ozone tolerance in *Arabidopsis thaliana*. Plant and Cell Physiology.2006;47:304–308. doi: 10.1093/pcp/pci246.

[146] Noshi M, Hatanaka R, Tanabe N, Terai Y, Maruta T, Shigeoka S. Redox regulation of ascorbate and glutathione by a chloroplastic dehydroascorbate reductase is required for high-light stress tolerance in Arabidopsis. Bioscience, Biotechnology, and Biochemistry.2016; 80:870–877. doi: 10.1080/09168451.2015.1135042.

[147] Foyer CHH, Lopez-Delgardo H, DatJF, Scott IM.Hydrogen peroxide and glutathioneassociated mechanisms of acclimatory stress tolerance and signaling. Physiologia Plantarum.1997; 100: 241–254.

[148] Akram NA, Shafiq F, Ashraf M. Ascorbic Acid-A Potential Oxidant Scavenger and Its Role in Plant Development and Abiotic Stress Tolerance. Frontiers in Plant Science.2017;8:613. doi: 10.3389/fpls.2017.00613.

[149] IgamberdievAU, Seregelyes C, Manac N,Hill RD.NADH-dependent metabolism of nitric oxide in alfalfa root cultures expressing barley hemoglobin. Planta.2004;219:95–102.doi:10.1007/s00425-003-1192-3.

[150] Agati G, AzzarelloE,PollastriS, TattiniM. Flavonoids as antioxidants in plants: location and functional significance. PlantScience.2012;196: 67–76.doi: 10.1016/j.plantsci.2012.07.014.

[151] You J,Chan Z. ROS regulation during abiotic stress responses in crop plants.Frontiers in Plant Science. 2015;6: 1092.

[152] Zhang H, Ni L, Liu Y, Wang Y, Zhang A, Tan M, et al. The C2H2-type Zinc Finger Protein ZFP182 is involved in Abscisic Acid-Induced Antioxidant Defense in Rice F. Journal of Integrative Plant Biology. 2012;54(7): 500-510.

[153] Li F, Li M, Wang P, Cox Jr KL, Duan L, Dever JK,et al. Regulation of cotton (*Gossypium hirsutum*) drought responses by mitogen-activated protein (MAP) kinase cascade-mediated phosphorylation of Gh WRKY 59. New Phytologist.2017;215(4):1462-1475.

[154] Ning J, Li X, Hicks LM, Xiong L. A Raf-like MAPKKK gene DSM1 mediates drought resistance through reactive oxygen species scavenging in rice. Plant Physiology.2010;152(2):876-890.

[155] Asano T, Hayashi N, Kobayashi M, Aoki N, Miyao A, Mitsuhara I, et al. A rice calcium-dependent protein kinase OsCPK12 oppositely modulates salt-stress tolerance and blast disease resistance. The Plant Journal. 2012;69: 26–36.

[156] Deng X, Hu W, Wei S, Zhou S, Zhang F, Han J, et al. TaCIPK29, a CBL-interacting protein kinase gene from wheat, confers salt stress tolerance in transgenic tobacco. PLOS One.2013;8: e69881.

[157] Hu DG, Ma Q J, Sun CH, Sun MH, You CX, Hao YJ. Overexpression of

MdSOS2L1, a CIPK protein kinase, increases the antioxidant metabolites to enhance salt tolerance in apple and tomato. Physiologia Plantarum.2015;156 (2):201-214.

[158] You J, Zong W, Hu H, Li X, Xiao J, Xiong L. A Stress-responsive NaC1-regulated protein phosphatase gene rice protein phosphatase18 modulates drought and oxidative stress tolerance through abscisic acid-independent reactive oxygen species scavenging in rice. Plant Physiology.2014;166(4): 2100-2114.

[159] Schmidt R, Mieulet D, Hubberten HM, Obata T, Hoefgen R, Fernie AR, et al. Salt-Responsive ERF1 regulates reactive oxygen species–dependent signaling during the initial response to salt stress in rice. The Plant Cell.2013;25(6):2115-2131.

[160] Fukao T, Yeung E, Bailey-Serres J. The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. The Plant Cell. 2011;23(1):412-427.

[161] Wu L, Zhang Z, Zhang H, Wang XC, Huang R. Transcriptional modulation of ethylene response factor protein JERF3 in the oxidative stress response enhances tolerance of tobacco seedlings to salt, drought, freezing. Plant Physiology.2008;148(4):1953-1963.

[162] Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX. A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. Genes & Development.2009;23(15):1805-1817.

[163] Zhang H, Liu Y, Wen F, Yao D, Wang L, Guo J, et al. A novel rice C2H2-type zinc finger protein, ZFP36, is a key player involved in abscisic acid-induced antioxidant defence and oxidative stress

tolerance in rice. Journal of Experimental Botany.2014;65(20):5795-5809.

[164] Jan A, Maruyama K, Todaka D, Kidokoro S, Abo M, Yoshimura E, et al. OsTZF1, a CCCH-tandem zinc finger protein, confers delayed senescence and stress tolerance in rice by regulating stress-related genes. Plant Physiology.2013;161(3):1202-1216.

[165] Wang F, Chen HW, Li QT, Wei W, Li W, Zhang WK, et al. Gm WRKY 27 interacts with Gm MYB 174 to reduce expression of Gm NAC 29 for stress tolerance in soybean plants. The Plant Journal.2015;83(2):224-236.

[166] Fang Y, Liao K, Du H, Xu Y, Song H, Li X, et al.A stress-responsive NAC transcription factor SNAC3 confers heat and drought tolerance through modulation of reactive oxygen species in rice. Journal of Experimental Botany.2015;66(21):6803-6817.

[167] Yan Y, Jia H, Wang F, Wang C, Liu S, Guo X. Overexpression of GhWRKY27a reduces tolerance to drought stress and resistance to *Rhizoctonia solani* infection in transgenic *Nicotiana benthamiana*. Frontiers in Physiology. 2015;6:265.

[168] You J, Hu H, Xiong L.An ornithine δ-aminotransferase gene OsOAT confers drought and oxidative stress tolerance in rice. Plant Science. 2012;197:59-69.

[169] Du H, Wang N, Cui F, Li X, Xiao J, Xiong L. Characterization of the β-carotene hydroxylase gene DSM2 conferring drought and oxidative stress resistance by increasing xanthophylls and abscisic acid synthesis in rice.Plant Physiology.2010;154(3):1304-1318.

[170] Zhang Y, Tan J, Guo Z, Lu S, He S, Shu W, et al. Increased abscisic acid levels in transgenic tobacco over-expressing 9

cis-epoxycarotenoiddioxygenase influence H_2O_2 and NO production and antioxidant defences.Plant, Cell & Environment. 2009; 32(5), 509-519.

[171] McKersie BD, Bowley SR, Harjanto E, Leprince O. Water-deficit tolerance and field performance of transgenic alfalfa overexpressing superoxide dismutase. Plant Physiology.1996;111(4):1177-1181.

[172] Zhang Z, Zhang Q, Wu J, Zheng X, Zheng S, Sun X, et al. Gene knockout study reveals that cytosolic ascorbate peroxidase 2 (OsAPX2) plays a critical role in growth and reproduction in rice under drought, salt and cold stresses. PLOS One.2013;8(2): e57472.

[173] Huda KM, Banu MS, Garg B, Tula S, Tuteja R, Tuteja N. OsACA6, a P-type IIB Ca2+ ATPase promotes salinity and drought stress tolerance in tobacco by ROS scavenging and enhancing the expression of stress-responsive genes. The Plant Journal. 2013;76:997–1015

[174] Kalaivani N, Hasidah MS.The green MAPKs. Asian Journal of Plant Sciences. 2010;9(1):1-10.

[175] Lu W, Chu X, Li Y, Wang C, Guo X. Cotton GhMKK1 induces the tolerance of salt and drought stress, mediates defence responses to pathogen infection in transgenic *Nicotiana benthamiana*. PLoS One.2013;8(7):e68503.

[176] Zhang L, Li Y, Lu W, Meng F, Wu CA, Guo X. Cotton GhMKK5 affects disease resistance, induces HR-like cell death, reduces the tolerance to salt and drought stress in transgenic *Nicotiana benthamiana*. Journal of Experimental Botany. 2012a;63(10):3935-3951.

[177] Wang C, Lu W, He X, Wang F, Zhou Y, Guo X,Guo X. The cotton

mitogen-activated protein kinase kinase 3 functions in drought tolerance by regulating stomatal responses and root growth. Plant and Cell Physiology.2016; 57(8):1629-1642.

[178] Danquah A, de Zélicourt A, Boudsocq M, Neubauer J, Freidit Frey N, Leonhardt N, et al.Identification and characterization of an ABA-activated MAP kinase cascade in Arabidopsis thaliana. The Plant Journal.2015;82(2): 232-244.

[179] Ashraf MA, Akbar A, Parveen A, Rasheed R, Hussain I, Iqbal M. Phenological application of selenium differentially improves growth, oxidative defense and ion homeostasis in maize under salinity stress. Plant Physiology and Biochemistry. 2018;123: 268-280.

[180] Porcel R, Redondo-Gómez S, Mateos-Naranjo E, Aroca R, Garcia R, Ruiz-Lozano JM. Arbuscular mycorrhizal symbiosis ameliorates the optimum quantum yield of photosystem II and reduces non-photochemical quenching in rice plants subjected to salt stress. Journal of Plant Physiology. 2015;185: 75-83.

[181] Orhan F. Alleviation of salt stress by halotolerant and halophilic plant growth-promoting bacteria in wheat (*Triticum aestivum*). Brazilian Journal of Microbiology. 2016;47(3): 621-627.

[182] Sajyan TK, Naim L, Sebaaly Z, Rizkallah J, Shaban N, Sassine YN. Alleviating the adverse effects of salinity stress on tomato crop (*Solanum lycopersicum*) using nano-fertilizer as foliar application. In XXX International Horticultural Congress IHC2018: International Symposium on Water and Nutrient Relations and Management of 1253; 2018. pp. 33-40.

[183] Asrar AWA, Elhindi KM. Alleviation of drought stress of marigold (*Tagetes erecta*) plants by using arbuscular mycorrhizal fungi. Saudi Journal of Biological Sciences. 2011;18 (1):93-98.

[184] Kour D, Rana, KL, Kaur, T, Sheikh, I, Yadav, AN, Kumar, et al. Microbe-mediated alleviation of drought stress and acquisition of phosphorus in great millet (*Sorghum bicolour* L.) by drought-adaptive and phosphorus-solubilizing microbes. Biocatalysis and Agricultural Biotechnology. 2020;23:101501.

[185] Gagné-Bourque F, Bertrand A, Claessens A, Aliferis KA,Jabaji S. Alleviation of drought stress and metabolic changes in timothy (*Phleum pratense* L.) colonized with *Bacillus subtilis* B26. Frontiers in Plant Science. 2016;7:584.

[186] Ouzounidou G, Giannakoula A, Ilias I, Zamanidis P. Alleviation of drought and salinity stresses on growth, physiology, biochemistry and quality of two *Cucumis sativus* L. cultivars by Si application. Brazilian Journal of Botany. 2016;39(2):531-539.

[187] Barnawal D, Bharti N, Maji D, Chanotiya CS, Kalra A. 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase-containing rhizobacteria protect *Ocimum sanctum* plants during waterlogging stress via reduced ethylene generation. Plant Physiology and Biochemistry. 2012;58: 227-235.

[188] Iqbal Z, Sarkhosh A, Balal RM, Gómez C, Zubair M, Ilyas N, et al. Silicon alleviate hypoxia stress by improving enzymatic and non-enzymatic antioxidants and regulating nutrient uptake in muscadine grape (*Muscadinia rotundifolia* Michx.). Frontiers in Plant Science. 2020;11.

[189] Ali MM, Waleed Shafique M, Gull S, Afzal Naveed W, Javed T, Yousef AF et al. Alleviation of Heat Stress in Tomato by Exogenous Application of Sulfur. Horticulturae. 2021;7(2):21.

[190] Sarwar M, Saleem MF, Ullah N, Ali S, Rizwan M, Shahid MR, et al. Role of mineral nutrition in alleviation of heat stress in cotton plants grown in glasshouse and field conditions. Scientific Reports. 2019;9(1):1-17.

[191] Khan MA, Asaf S, Khan AL, Jan R, Kang SM, Kim KM, et al. Thermotolerance effect of plant growth-promoting Bacillus cereus SA1 on soybean during heat stress. BMC Microbiology. 2020;20(1):1-14.

[192] Da Jeong Shin SJY, Hong JK, Weon HY, Song J, Sang MK. Effect of *Bacillus aryabhattai* H26-2 and *B. siamensis* H30-3 on Growth Promotion and Alleviation of Heat and Drought Stresses in Chinese Cabbage. The Plant Pathology Journal. 2019;35(2):178.

[193] Abass, S. M. and Mohamed, H. I. (2011).Alleviation of adverse effects of drought stress on common bean (Phaseolus vulgaris L.) by exogenous application of hydrogen peroxide. Bangladesh Journal of Botany, 40(1), 75-83.

[194] Saikia J, Sarma RK, Dhandia R, Yadav A, Bharali R, Gupta VK,et al. Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. Scientific reports. 2018; 8(1):1-16.

[195] Mishra PK, Bisht SC, Ruwari P, Selvakumar G, Joshi GK, Bisht J.K, et al. Alleviation of cold stress in inoculated wheat (*Triticum aestivum* L.) seedlings with psychrotolerant Pseudomonads

from NW Himalayas. Archives of microbiology. 2011;193(7):497-513.

[196] Ma J, Janouskova M, Ye L, BaiLQ, He CX.Role of arbuscular mycorrhiza in alleviating the effect of cold on the photosynthesis of cucumber seedlings. Photosynthetica. 2019;57(1):86-95.

[197] Ahmad P, Nabi G, Ashraf M. Cadmium-induced oxidative damage in mustard [*Brassica juncea* (L.)Czern.& Coss. plants can be alleviated by salicylic acid. South African Journal of Botany. 2011;77(1):36-44.

[198] Ali S, Chaudhary A, Rizwan M, Anwar HT, Adrees M, Farid M, et al. Alleviation of chromium toxicity by glycinebetaine is related to elevated antioxidant enzymes and suppressed chromium uptake and oxidative stress in wheat (*Triticum aestivum* L.). Environmental Science and Pollution Research. 2015;22(14):10669-10678.

[199] Chen Z, Zhang L, Zhu C. Exogenous nitric oxide mediates alleviation of mercury toxicity by promoting auxin transport in roots or preventing oxidative stress in leaves of rice seedlings. Acta Physiologiae Plantarum. 2105;37(9):1-9.

[200] 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. Advances in Bioscience and Biotechnology. 2014;5: 777.

[201] Yang X, Li H, Yang Y, Wang Y, Mo Y, Zhang R, et al. Identification and expression analyses of WRKY genes reveal their involvement in growth and abiotic stress response in watermelon (*Citrullus lanatus*). PlOS One. 2018;13 (1):e0191308.

[202] Khan N, Fatima F, Haider MS, Shazadee H, Liu Z, Zheng, et al.Genome-wide identification and expression profiling of the polygalacturonase (PG) and pectin methylesterase (PME) genes in grapevine (*Vitis vinifera* L.). International Journal of Molecular Sciences. 2019;20(13):3180.

[203] Xue T, Wang D, Zhang S, Ehlting J, Ni F, Jakab S, et al. Genome-wide and expression analysis of protein phosphatase 2C in rice and Arabidopsis. BMC Genomics.2008;9(1):1-21.

[204] Singh A, Giri J, Kapoor S, Tyagi AK, Pandey GK. Protein phosphatase complement in rice: genome-wide identification and transcriptional analysis under abiotic stress conditions and reproductive development. BMC Genomics.2010;11(1):1-18.

[205] Fuchs S, Grill E, Meskiene I, Schweighofer A. Type 2C protein phosphatases in plants. The FEBS Journal.2013;280(2):681-693.

[206] Joshi R, Wani SH, Singh B, Bohra A, Dar ZA, Lone AA, et al. Transcription factors and plants response to drought stress: current understanding and future directions. Frontiers in Plant Science. 2016;7:1029.

[207] Kimotho RN, Baillo EH, and Zhang Z. Transcription factors involved in abiotic stress responses in Maize (*Zea mays* L.) and their roles in enhanced productivity in the post genomics era. Peer J. 2019;7:e7211.

[208] Nadarajah KK.ROS homeostasis in abiotic stress tolerance in plants. International Journal of Molecular Sciences.2020;21(15):5208.

[209] Yu S, Zhang L, Chen C, Li J, Ye S, Liu G, et al. Isolation and characterization of BnMKK1 responsive

to multiple stresses and affecting plant architecture in tobacco. Acta Physiologiae Plantarum.2014a;36(6): 1313-1324.

[210] Ariel FD, Manavella PA, Dezar CA, Chan RL.The true story of the HD-Zip family.Trends in Plant Science.2007;12 (9):419-426.

[211] Fang Y, You J, Xie K, Xie W, Xiong L. Systematic sequence analysis and identification of tissue-specific or stress-responsive genes of NAC transcription factor family in rice. Molecular Genetics and Genomics.2008; 280(6):547-563.

[212] Ciftci-Yilmaz S, and Mittler R.The zinc finger network of plants.Cellular and Molecular Life Sciences.2008;65(7): 1150-1160.

[213] Fukao T, Xiong L. Genetic mechanisms conferring adaptation to submergence and drought in rice: simple or complex?.Current Opinion in Plant Biology.2013;16(2):196-204.

[214] Yeung E, van Veen H, Vashisht D, Paiva ALS, Hummel M, Rankenberg T, et al. A stress recovery signaling network for enhanced flooding tolerance in *Arabidopsis thaliana*.Proceedings of the National Academy of Sciences.2018;115 (26):E6085-E6094.

[215] Mittler R, Kim Y, Song L, Coutu J, Coutu A, Ciftci-Yilmaz S, et al. Gain-and loss-of-function mutations in Zat10 enhance the tolerance of plants to abiotic stress. FEBS Letters. 2006;580:6537–6542.

[216] Sun SJ, Guo SQ, Yang X, Bao YM, Tang HJ, Sun H, et al. Functional analysis of a novel Cys2/His2-type zinc finger protein involved in salt tolerance in rice. Journal of Experimental Botany.2010;61 (10):2807-2818.

[217] Riechmann JL,Ratcliffe OJ.A genomic perspective on plant transcription factors.Current Opinion in Plant Biology.2000;3(5):423-434.

[218] Nuruzzaman M, Manimekalai R, Sharoni AM, Satoh K, Kondoh H, Ooka H et al. Genome-wide analysis of NAC transcription factor family in rice. Gene.2010;465(1-2): 30-44.

[219] Jin H, Huang F, Cheng H, Song H, Yu D. Overexpression of the GmNAC2 gene, an NAC transcription factor, reduces abiotic stress tolerance in tobacco. Plant Molecular Biology Reporter.2013;31(2):435-442.

[220] Wu KL, Guo ZJ, Wang HH, Li J.The WRKY family of transcription factors in rice and Arabidopsis and their origins. DNA Research.2015;12(1):9-26.

[221] Ning P, Liu C, Kang J, LvJ. Genome-wide analysis of WRKY transcription factors in wheat (*Triticum aestivum* L.) and differential expression under water deficit condition. PeerJ.2017;5:e3232.

[222] Shukla D, Huda KMK, Banu MSA, Gill SS, Tuteja R, Tuteja N. OsACA6, a P-type 2B Ca^{2+} ATPase functions in cadmium stress tolerance in tobacco by reducing the oxidative stress load. Planta.2014;240(4):809-824.