

Mini Review

The effect of Drought as a Stress Factor on Plant Metabolic Processes

Arystanova Sholpan Yescuatovna*

L.N. Gumilev Eurasian National University, Russia

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***Corresponding author:** Arystanova Sholpan Yescuatovna, L.N. Gumilev Eurasian National University, Russia, E-mail: Sholpan1607@mail.ru

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Abstract

This review article discusses the cellular mechanisms of the combined effects of heat and water deficit on plants. It is known that abiotic stress leads to cell dehydration and the accumulation of reactive oxygen species in the cell, which leads to the disruption of membranes and the photosynthetic system at the cellular level. In addition, new data are presented that drought and temperature stress lead to an increase in antioxidant enzymes (AO, SOD, CAT) in barley.

Plants, due to their sedentary nature and habitat, are constantly exposed to the adverse effects of not one but several environmental factors, and their ability to adapt to these changing environmental conditions directly affect their growth, development, and germination. In this regard, plants cope with abiotic stresses by activating various reactions at the molecular level, including complex gene interactions and molecular signaling pathways [1].

Over time, the world population on our planet may exceed 10 billion. In this regard, increasing food production by 60% in the next few years is important for ensuring global food security [2]. Abiotic stress factors that limit the productivity of plants and cereals include water shortage or excess, heavy metal ions, too-low or too-high temperatures, and ultraviolet radiation. According to recent data, water scarcity affects 64% of the world's land area, flooding affects 13% of the land area, salinity affects 6%, mineral deficiencies affect 9%, soil acidity affects 15%, and cold temperatures affect 57% of the world's plants [3]. Among them, temperature is an important physical component that deeply affects all stages of plant life.

Most physiological processes in plants occur in the temperature range from 0 to 40 °C. Recent studies have

shown that deviations from the optimal environmental temperature for plant growth and development cause a wide range of physiological, biochemical, and molecular-genetic changes in their cells. Among the various responses of plants to temperature increases, aspects of growth, respiration, and photosynthesis, as well as the formation of stress (shock) proteins, changes in cell membranes, and the hormonal system are well studied [4,5].

In plants, biotic and abiotic stresses, such as pathogens, drought, salinity, ultraviolet radiation, and high and low temperatures, increase the synthesis of reactive oxygen species, contributing to the development of oxidative stress. The specificity of plant responses to these abiotic stresses is directly related to the plant organ that is stressed. In addition, the level and duration of stress (acute and chronic) can significantly affect the complexity of the plant's stress response [3]. Plant adaptation to abiotic stresses occurs through stress avoidance, stress prevention, and increased tolerance (Table 1).

1. Stress avoidance is the process by which plants avoid stress before it occurs. For example, short life span, rapid growth rate, stomatal closure at night, and compact and short plant organs [6].

Table 1: Strategic responses of plants to abiotic stresses.

Abiotic stress	Plant strategic responses
Salinity	Disruption of osmotic and ionic homeostasis, membrane damage; detoxification of stress-responsive enzymes, and reduced seed yield.
High temperature	Induction of acclimatization, synthesis of heat shock proteins, increased transpiration rate, cellular water deficit.
Drought	Stomata closure, leaf curling, induction of osmolyte synthesis, reduced photosynthesis, inhibition of water transport.
Low temperature	Increased synthesis and accumulation of osmolytes, inhibition of the release of hydrophilic proteins, decreased rate of biochemical reactions, decreased carbon dioxide fixation, and formation of ice crystals.
Light	Inactivation of photosynthesis, oxidation of proteins and lipids.
Heavy metal	Generation of OBT, accumulation of metal ions in the vacuole.

2. Stress prevention is the process by which plants initiate reversible physiological processes. For example, reducing water loss (closure of stomata, reduction of light absorption by leaves), increasing root water uptake from the soil, and reducing transpiration [7].

3. Tolerance is the process by which plants initiate morphological, physiological, biochemical, and molecular processes to cope with various stresses [8].

Understanding how plants function under stress is essential for reducing stress in plants. The table below shows the biochemical responses of plants to the effects of temperature, drought, salinity, and cold temperatures.

As a result of biotic and abiotic stress factors that have an antagonistic effect on plant growth and development, crops undergo various changes. The dynamics of plant responses to abiotic stresses are either reversible or irreversible processes [3]. Due to the complexity and diversity of abiotic stress responses, comprehensive and integrative strategies are needed to study the multiple levels of stress response management. Factors such as a decrease in the relative water content of plants, an increase in the production of Reactive Oxygen Species (ROS), leakage of cellular electrolytes, a decrease in the amount of photosynthetic pigments, a reduction in the length of roots and shoots (leaves), a decrease in plant productivity, etc. lead to various changes in the plant organism. In order to withstand the effects of these abiotic factors, plants undergo many morphological, physiological, biochemical, and molecular changes.

Drought

A plant is susceptible to drought if water supply to the roots is limited or if water loss through transpiration is very high. The extent of drought damage is usually difficult to predict, so it is necessary to take into account the amount of precipitation, the water-holding capacity of the soil, and the possibility of evaporation. Drought reduces the water potential of the leaves and stomata, reduces leaf size, inhibits root development, reduces seed size, volume, and viability, delays flowering and fruiting, and limits plant growth and yield [9]. Drought negatively affects plant growth, water regime and nutrient transport, photosynthesis, and the distribution of assimilates.

Therefore, drought is one of the abiotic factors that directly affect the yield of agricultural crops [10,11].

Water scarcity is a major problem in crop production, as it activates oxidative, osmotic, and temperature stresses [12]. However, plants can counteract the effects of drought stress by switching on or off a set of genes that affect their physiology and morphology. Drought stress is currently affecting cereals and other agricultural products worldwide, leading to significant yield losses.

Oxidative stress in plants

Reactive Oxygen Species (ROS), also known as Reactive Oxygen Species (ROS), are by-products of aerobic metabolism that are normally produced in all aerobic organisms [13]. ROS are produced in various cellular organelles, such as chloroplasts, plasma membranes, peroxisomes in the presence of light, and mitochondria in the dark [14]. During photosynthesis, chloroplasts produce singlet oxygen (1O_2) and superoxide anion ($O_2^{\cdot -}$) as by-products, while peroxisomes produce hydrogen peroxide (H_2O_2) [15]. ROS are mainly singlet oxygen (1O_2), superoxide anion radicals, hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^{\cdot -}$). ROS are signaling molecules that can affect a variety of stimuli, including growth, development, abiotic and biotic stress, generation of hormonal regulators, and programmed cell death. OBTs function as secondary messengers in cellular signaling pathways at low doses. However, they are toxic when accumulated in large quantities as a result of environmental stresses such as salt stress. However, plant cells can maintain a precise balance between the generation of ROS and their detoxification processes [16]. Singlet oxygen (1O_2) is produced in chloroplasts during photoinhibition and PS II electron transport processes. Table 2 below shows the occurrence of active types of oxygen in plant cells and the main antioxidant systems that neutralize them.

Among the reactive oxygen species (ROS), hydrogen peroxide (H_2O_2) has received the most attention because it plays an important role in stomatal closure, photosynthesis [17], plant senescence [18], cell cycle regulation, and tolerance [19]. Overexpression of hydrogen peroxide (H_2O_2) causes oxidation of cysteine (R-SH) and methionine (R-SCH₃) residues of protein kinases, ultimately leading to inactivation of these enzymes and oxidation of thiol groups of enzymes. The most reactive form of ROS is hydroxyl radicals ($OH^{\cdot -}$). They react with lipids, proteins, and DNA, resulting in oxidative damage [20,21]. Without proper regulation in plants, the concentration of ATO in cells increases and leads to oxidative damage to cell membranes (lipid peroxidation, oxidation of proteins, RNA, and DNA molecules). This adverse effect is called oxidative stress [22]. Oxidative stress results from an imbalance in the formation and destruction of ROS. Under optimal conditions in cells, this process is prevented by the presence of ROS-neutralizing enzymes (superoxide dismutase, ascorbate peroxidase, catalase, glutathione peroxidase, aldehyde oxidase, etc.) and antioxidants such as ascorbic acid and glutathione [23]. However, under natural conditions, ROS are also actively formed as signaling molecules. This homeostasis between ROS formation and utilization is maintained individually in all

Table 2: Mechanisms of action of reactive oxygen species and their main scavenging systems.

Reactive oxygen species (ROS)	Method of action	Cellular sources	Basic cleaning systems
Superoxide radical (O_2^-)	Interacts with compounds containing double bonds, such as iron-sulfur (Fe-S) protein clusters.	These include flavoprotein and redox cyclic reactions in photooxidation, as well as the Mehler reaction and mitochondrial electron transport chain (ETC) processes in chloroplasts. Membrane NADPH oxidase. Phosphatidylinositol peroxisomes.	superoxide dismutase (SOD)
Hydroxyl radical ($OH\cdot$)	It interacts very actively with proteins, lipids, DNA, and other macromolecules.	Reaction of H_2O_2 with $O_2^{\cdot-}$ (Haber-Weiss reaction), reactions of H_2O_2 with Fe^{2+} (Fenton reaction). Decomposition of O_3 in the apoplastic space.	Flavonoids
Hydrogen peroxide (H_2O_2)	Reduces proteins; reacts with $O_2^{\cdot-}$ in an Fe-catalyzed reaction to form $OH\cdot$.	Electron transport chains of mitochondria, chloroplasts, endoplasmic reticulum, and plasma membrane. Photorespiration, fatty acid β -oxidation, urate oxidase, and MnSOD in peroxisomes.	Peroxidases, peroxiredoxins and flavonoids
Singlet oxygen (1O_2)	Directly oxidized protein, polyunsaturated fatty acids, and DNA	Photoinhibition, electron exchange reactions of photosystem II in chloroplasts	Carotenoids and α -tocopherols

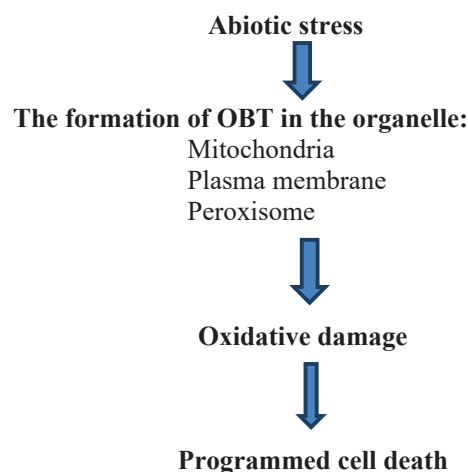
cellular compartments. Different abiotic stresses or different combinations of stresses induce the formation of different ROS patterns in plant cells [24].

Under the influence of abiotic stress, ROS are formed in two different ways: ROS formation as a result of metabolic activity disruption (metabolic ROS) and ROS formation as a signaling molecule to generate a stress response. The main sources of ROS formation during abiotic stress are the chloroplast, mitochondria, peroxisomes, and apoplast [25,26]. Abiotic stresses that limit CO_2 delivery by closing stomata induce the production of superoxide and singlet oxygen in chloroplasts [27]. Singlet oxygen in chloroplasts induces the reprogramming of gene expression in plants can lead to chlorosis and apoptosis, and can also activate a number of cellular responses to abiotic and biotic stresses. ROS in chloroplasts are eliminated by the activation of FeSOD, CuSOD, Zn-SOD, ascorbic acid, and glutathione [28]. During abiotic stress, the accumulation of reactive oxygen species in mitochondria is mainly due to electron leakage to form superoxide radicals. Hydrogen peroxide is produced in peroxisomes as a result of increased photorespiration during abiotic stress and is subsequently eliminated by catalase [29]. In contrast to the three sources of ROS formation mentioned above, ROS is intensively accumulated in the apoplast by several pathways, and the mechanism of ROS removal is not as efficient as that in the cell. This fact allows for excessive accumulation of ROS in the apoplast, which plays an important role in systemic signaling and protection against pathogens. All these types of ROS formation and accumulation mechanisms depend on the intensity of various abiotic stress factors. Free radicals are unstable, so they react with other molecules to gain stability.

During abiotic stresses such as drought, low and high temperatures, salinity, and ultraviolet radiation, the concentration of free radicals increases, leading to an imbalance in plant homeostasis (Figure 1).

Abiotic stress

Excessive production of ROS leads to protein oxidation by oxidizing their thiol ($-SH$) groups, causing fragmentation of peptide chains and increasing the sensitivity of proteins to proteases. In addition, free radicals can react with nucleic acids and damage nitrogenous bases, deoxyribose, and ribose

**Figure 1:** Reactive oxygen species formation and programmed cell death induced by abiotic stress [20].

sugars, and in turn, such modifications lead to the disruption of hydrogen bonds between DNA strands [30]. All of the above-mentioned damages can lead to a decrease in crop yield. However, at low concentrations, ROS act as intracellular signaling molecules to activate acclimatization mechanisms [21]. For example, it has been reported that exposure of *Arabidopsis thaliana* to methyl viologen reduces the expression of genes responsible for photosynthesis, inhibits the formation of starch and sucrose, and activates catabolic pathways. These metabolic changes are reported to be directed towards the accumulation of maltose molecules, which are involved in protein structure stabilization, preventing the use of energy for non-protective activities [31]. In *Arabidopsis* mutants, photooxidative stress-induced singlet oxygen generation has been shown to cause a significant increase in lipid peroxidation [32]. Plant chloroplasts utilize carotene, tocopherol, and plastoquinones to neutralize the effects of singlet oxygen. However, if singlet oxygen is not removed or removed from the plant body sufficiently, it induces the activation of genes involved in photooxidative stress-induced defense responses [33]. Recent studies have reported that 2% of the oxygen released by plants is used to generate OBTs in various subcellular compartments [20].

Enzymatic and non-enzymatic antioxidant systems in plants. To combat free radicals, plants have developed many

strategic methods to reduce oxidative stress. Free radicals in the plant body are detoxified or eliminated by antioxidant defense mechanisms. Antioxidant defense mechanisms are divided into two groups: enzymatic and non-enzymatic antioxidants. The enzymatic group includes Superoxide Dismutase (SOD), Catalase (CAT), Peroxidase (POD), Ascorbate Peroxidase (APX), Glutathione Peroxidase (GPX), Glutathione-S-Transferase (GST), while non-enzymatic antioxidants mainly include glutathione, proline, carotenoids, vitamin C, vitamin E, vitamin B6, etc. Plants secrete low molecular weight antioxidants, including ascorbate, glutathione, and tocopherol, as well as enzymatic ones such as SOD, APX, and CAT, in response to various biotic and abiotic stresses [16,34]. These antioxidant enzymes work together to protect plant cells from oxidative damage caused by reactive oxygen species, such as peroxidation of membrane phospholipids, denaturation, and degradation of proteins [20]. Several authors have reported that under various conditions, increased levels of these antioxidants help plants eliminate ROS and increase their tolerance to a wide range of stress conditions [35]. However, in many cases, the enhanced activities of these antioxidant systems are not sufficient to increase stress tolerance in susceptible genotypes [36]. Recent studies have shown that heat stress during the developmental stages of wheat genotype C306 significantly increases the activities of SOD, APX, CAT, GR, and POD, while in wheat genotypes PBW343 significantly decreases catalase, glutathione reductase and peroxidase [37].

Superoxide dismutase (SOD, EC 1.15.1.1) is found in mitochondria and chloroplasts. SOD activates the plant's response to oxidative stress by converting superoxide radicals to hydrogen peroxide. Superoxide dismutase has a metal cofactor, which makes it a major protective metalloprotein in plants [38]. Depending on the metal ion cofactor that binds to the active site, superoxide dismutase is divided into several isoenzymes: Fe-SOD, Cu/Zn-SOD, Ni-SOD, and Mn-SOD [39]. SOD activity can vary depending on the type, intensity, and duration of stress to which the plant organism is exposed. In addition, plant species that are resistant to environmental stresses have higher SOD activity and suffer less oxidative damage than sensitive plants. Significant resistance to stress stimuli has been observed in transgenic tomato plants with increased SOD activity [40]. Recent studies have reported that increased superoxide dismutase activity helps plants adapt to environmental stress [41]. Recently, two independent studies reported that transgenic *Puccinellia tenuiflora* plants containing superoxide dismutase isomers such as Cu/Zn-SOD were more susceptible to drought and salt stress than tobacco plants [39,42]. Overexpression of the Cu/Zn-SOD isomer in plants plays an important role in preventing oxidative damage caused by abiotic stresses. Another study showed that Cu/Zn-SOD and Mn-SOD activities were significantly increased in cucumbers under low-temperature stress [43]. In conclusion, superoxide dismutase acts as a major agent that scavenges or neutralizes hydrogen peroxide from the plant body during oxidative stress caused by various environmental conditions.

Catalase (CAT, EC) is a major heme-containing antioxidant enzyme with a molecular weight of approximately 250 kDa

[44]. Catalase is mainly found in chloroplasts, peroxisomes, mitochondria, and cytoplasm. Catalase converts intracellular hydrogen peroxide to water and oxygen without the expenditure of cellular energy, thereby preventing plant peroxidation. Catalase has several isoforms, including CAT1, CAT2, and CAT3 [43]. Some studies have reported that plants lacking the CAT enzyme are more susceptible to salinity and ozone stress compared to wild-type plants [45]. In addition, it has been reported that catalase activity is reduced under drought stress in drought-sensitive rice cultivars, leading to the accumulation of hydrogen peroxide [46]. Several recent studies, including in wheat and maize, have reported increased activity of both SOD and CAT enzymes.

Peroxidase is a heme-containing antioxidant enzyme. Peroxidases are commonly found in chloroplasts, peroxisomes, mitochondria, vacuoles, and cell membranes. Peroxidases are proteins that catalyze the conversion of hydrogen peroxide (H_2O_2) to water, rendering it harmless. H_2O_2 is a typical byproduct of oxidative metabolism and is a strong oxidizing agent, but its accumulation in excess is harmful [47]. Under stress conditions, peroxidases serve to scavenge hydrogen peroxide from plant cells. In addition to scavenging H_2O_2 , cell wall peroxidases are also thought to catalyze the production of oxygen (O_2) and hydrogen peroxide (H_2O_2) by oxidizing substrates such as NADH and IAA [48]. They are also involved in growth, development, respiration, nitrogen metabolism, mycorrhiza formation, xenobiotic detoxification, phytoalexin production, and lignin and suberin biosynthesis [49].

Plants overexpressing antioxidant enzymes are resistant to oxidative stress, however, it has been reported that SOD and CAT levels are reduced in sunflower seedlings under water deficit conditions, leading to low ROS scavenging activity and increased oxidative damage [50]. Small and simple members of the antioxidant system include ascorbic acid, tocopherol, glutathione, carotenoids, phenols, some amino acids, and polyamines [20].

Glutathione reductase is a low molecular weight thiol molecule that is present in all cells and functions as a disulfide-reducing agent for the maintenance of the structure of tripeptide enzyme thiol groups, regeneration of ascorbate, and singlet oxygen and hydroxyl reactions. Glutathione reductase degrades herbicides either spontaneously or through glutathione-S-transferase activity and activates gene expression in response to environmental stress and pathogen attack. In addition, glutathione reductase detoxifies hydrogen peroxide (H_2O_2) in conjunction with ascorbic acid. Therefore, many studies consider glutathione reductase as an intramolecular reducing agent [29].

Another non-enzymatic antioxidant is vitamin B6 (pyridoxine). It is a vital cofactor for many enzymes and is essential for the synthesis of various biological macromolecules. It also plays a major role in the inactivation of ROS [51]. *Arabidopsis thaliana* has been reported to accumulate high levels of vitamin B (nicotinamide) under stress from ultraviolet radiation [52].

Another non-enzymatic antioxidant is vitamin C, which is an important compound in the plant defense system. Ascorbic acid is involved in the regulation of electron transport in the regeneration of chloroplasts. In addition, ascorbic acid is involved in the pH-mediated control of PSII activity associated with the production of zeaxanthin and is a potent anti-photooxidant. Vitamin C (ascorbic acid) is abundant in fruits, leaves, and flowers, while its concentration in roots and stems is low [53]. Several recent studies have shown that drought stress leads to a decrease in ascorbic acid levels in mint [54] and soybeans [55]. Ascorbic acid deficiency causes increased sensitivity to various stresses in mutant plants [14]. Ascorbic acid also helps maintain the redox potential of the cell by regenerating tocopherol and glutathione [56]. Tocopherols (vitamin E) are important components of cell membranes. The most biologically active form of tocopherols is α -tocopherol. Tocopherol molecules are located in the inner membrane of mitochondria, in the cristae. Tocopherol protects the chloroplast membranes of higher plants from photooxidative damage and maintains the structure and function of photosystem II [57]. In addition, tocopherols act as chemical scavengers of oxygen radicals, especially singlet oxygen, and as physical deactivators of these radicals [58].

In short, antioxidant enzymes are key chemical molecules that protect plants from various stresses and maintain the homeostasis of reactive oxygen species in living organisms. However, according to available evidence, the activity of antioxidant enzymes is directly dependent on the genotype of the plant and the type of stress it is exposed to.

Effects of oxidative stress on biomolecules in plants

In plants, biotic and abiotic stresses such as various infectious agents (bacteria, viruses), dehydration, salinity, ultraviolet radiation, and high and low temperatures increase the synthesis of ROS and contribute to the occurrence of oxidative stress. In turn, plants increase the activity of antioxidant enzymes to reduce and neutralize the harmful effects of reactive oxygen species to combat oxidative stress. Reactive oxygen species cause the oxidation of key biological molecules, namely proteins, lipids, and nucleic acids. Table 3 below shows several types of damage caused to biological molecules by reactive oxygen species:

When reactive oxygen species (ROS) are present in excessive amounts in plant cells, they negatively affect protein structures and inhibit the activity of important metabolic enzymes. They also lead to the oxidation of biological macromolecules such as DNA and lipids, disrupting cell integrity and ultimately leading to plant death [20].

The role of heat shock proteins in plants under stress conditions

Changes in membrane structures and cytoskeleton, chromatin remodeling, changes in protein conformation and disruption of their synthesis, increased protein degradation, changes in the rate of ion flow and various biochemical reactions, accumulation of signaling molecules of various nature, formation of ROS, activation of the antioxidant system are the cellular changes that occur when plants are exposed to high temperatures [59,36].

Heat Shock Proteins (HSPs) are one of the most widespread proteins in plant and animal cells. They are essential components of prokaryotic and eukaryotic cells that contribute to cellular homeostasis under both optimal and adverse growth conditions [60]. HSPs are responsible for protein assembly, translocation, and degradation during normal cell growth and development [39]. HSPs are also involved in protein stabilization and promote protein refolding under stress conditions [61].

Most members of the HSP family perform important chaperone functions in cells, such as the three-dimensional folding of newly formed and/or stress-damaged proteins. For this reason, many chaperones are considered heat shock proteins that are assembled during heat stress or denaturation. In plants, five major HSP families are conservatively recognized as molecular chaperones based on their approximate molecular weight, such as HSP100, HSP90, HSP70, HSP60, and small HSPs (sHSPs). Most of these HSPs are localized mainly in the cytoplasm and respond to abiotic and biotic stresses. Plants respond to pathogen invasion using a two-branched innate immune system, consisting of pathogen-associated molecular patterns and effector-mediated immunity. The protective role of all groups of heat shock proteins (HSPs) is described by the molecular "chaperone" model. According to this model, heat shock proteins promote the following processes by increasing the heat resistance of cells:

1. ATP-dependent stability of the native spatial structure of proteins necessary for their biological activity;
2. correct assembly of oligomeric structures under hyperthermia;
3. stabilization of mRNA and enzymes involved in the synthesis of "normal" cellular metabolic proteins under stress;
4. transport of substances through chloroplast and mitochondrial membranes;

Table 3: Damage to biological molecules caused by active types of oxygen (ATO).

Proteins	Oils	Nucleic acids
<ul style="list-style-type: none"> - inactivation of proteins and enzymes - fragmentation of peptide chains - protein folding - protein degradation by proteases - protein modification - change in electrical charges in proteins 	<ul style="list-style-type: none"> - chain rupture of polyunsaturated fatty acids - increased membrane permeability 	<ul style="list-style-type: none"> - DNA double-strand breaks and single-strand breaks - Oxidation of thymine and guanine residues - DNA base modification

5. disaggregation of incorrectly assembled macromolecular complexes;
6. "liberation" of the cell from denatured macromolecules and reuse of monomers contained in them with the help of ubiquitins.

HSPs are mainly found in the cytosol but are also involved in the transduction of cellular signals to the nucleus under stress conditions. Many cytosolic HSPs respond not only to biotic stresses such as pathogen infection and insect attack, but also to abiotic stresses such as ultraviolet radiation, warm temperatures, and salinity [62]. Among all HSP families, HSP90 is currently of considerable interest in its functions in plant immunity. HSP90 can physically interact with a wide range of co-chaperones. HSP90 is well characterized as a key component of various protein complexes that bind to co-chaperones, such as tetratricopeptide repeat co-chaperones.

HSP90 is known to be a key regulator of normal growth and development in *Nicotiana benthamiana* and *Arabidopsis*. In *Nicotiana benthamiana* plants, suppression of HSP90 is observed with symptoms such as meristem death, severe plant growth inhibition, and leaf chlorosis. In *Arabidopsis*, HSP90 deficiency resulted in multiple phenotypic changes, such as altered flowering time and the development of novel morphological traits. As a positive regulator of plant immunity, HSP90 can directly interact with R proteins. HSP90 activates cytosolic R proteins with nucleotide-binding domains and leucine-rich repeats, which confer protection against a wide range of microbial pathogens. The rice cytosolic HSP90 protein and its co-chaperone, the Hop/Sti1 complex, are known to be involved in chitin reactions and immunity against fungi [63].

Discussion

Drought and high/low temperatures are among the environmental factors that significantly damage crop yields. In recent decades, scientists have paid much attention to individual stress factors such as drought, salinity, low and high temperatures, ultraviolet radiation, etc. High and low-temperature stress and drought cause significant damage to plant development and metabolism. In addition, high and low-temperature stress is considered one of the main abiotic factors limiting crop production [36]. Plant growth and development require many metabolic, physiological, and biochemical responses that are sensitive to varying degrees of temperature [64]. The overall response of abiotic stress to plant stress varies depending on the duration of stress and the plant species. However, it is clear that plants are exposed to a combination of many abiotic and biotic factors in natural conditions. The aim of this review article was to elucidate the physiological, antioxidant, and enzymatic defense mechanisms involved in the detoxification of active types of oxygen and plant resistance to drought/temperature stresses, both separately and in combination.

Compared to drought, the pronounced effects of temperature stress are associated with severe consequences, such as protein denaturation, and changes in the composition

and structure of membranes. Drought is also known to negatively affect chlorophyll and photosynthesis under high-temperature stress. This, in turn, may explain the particularly severe symptoms of plants exposed to combined temperature and water deficit stress.

Chlorophyll is an important pigment in photosynthesis. The total amount of chlorophyll is a key indicator of the level of photosynthesis in plants.

Plants have well-developed antioxidant defense mechanisms to prevent oxidative damage caused by reactive oxygen species[65].

Adverse environmental factors activate the enzymatic and non-enzymatic defense mechanisms of plants [66]. If the level of antioxidant enzymes is high in stressed plants, the plant will be more resistant to oxidative stress. Under various stress conditions, plants produce hydrogen peroxide to protect themselves, which in turn plays an important role in cellular signal transduction [67]. Active types of oxygen such as superoxide anion, hydrogen peroxide, and singlet oxygen are considered to be highly reactive and can interact freely with cell compartments. Many studies have shown that ABA formation precedes hydrogen peroxide and that both molecules are involved in stomatal closure and stomatal opening inhibition [28]. Reactive oxygen species production and H₂O₂ accumulation are strong markers of oxidative damage.

In recent studies [68], the intensity and increase/decrease of drought tolerance enzyme activity under stress conditions were closely related to plant species. Stress-tolerant plants try to overcome stress by activating various antioxidant systems. SOD, CAT, AO, and POD are the most important natural "detoxification" enzymes produced by plants. They prevent the formation of Reactive Oxygen Species (ROS), plant membrane degradation, and oxidative damage to cells. Many studies have shown that these enzymes serve as a defense mechanism against biotic and abiotic stress factors [69].

References

1. Bhatta M, Sandro P, Smith MR, Delaney O, Voss-Fels KP, Gutierrez L, et al. Need for speed: manipulating plant growth to accelerate breeding cycles. *Curr Opin Plant Biol.* 2021;60:101986. Available from: <https://doi.org/10.1016/j.pbi.2020.101986>
2. Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K. Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol.* 2011;11:163. Available from: <https://bmcpplantbiol.biomedcentral.com/articles/10.1186/1471-2229-11-163>
3. Hatfield J, Prueger JH. Temperature extremes: Effect on plant growth and development. *Weather Clim Extrem.* 2015;10:WACED1400046. Available from: <http://dx.doi.org/10.1016/j.wace.2015.08.001>
4. Niu Y, Xiang Y. An Overview of Biomembrane Functions in Plant Responses to High-Temperature Stress. *Front Plant Sci.* 2018;9:915. Available from: <https://doi.org/10.3389/fpls.2018.00915>
5. Liu B, Cheng L, Ma F, Zou Y, Liang D. Growth, biomass allocation, and water use efficiency of 31 apple cultivars grown under two water regimes. *Agrofor Syst.* 2012;84(2):117–29. Available from: <https://link.springer.com/article/10.1007/s10457-011-9427-y>

6. Chaves MM, Maroco JP, Pereira JS. Understanding plant responses to drought - from genes to the whole plant. *Funct Plant Biol.* 2003;30(3):239–64. Available from: <http://dx.doi.org/10.1071/FP02076>
7. Ingram J, Bartels D. The molecular basis of dehydration tolerance in plants. *Annu Rev Plant Physiol Plant Mol Biol.* 1996;47:377–403. Available from: <https://www.scirp.org/reference/referencespapers?referenceid=2728147>
8. Porter JR, Semenov MA. Crop responses to climatic variation. *Philos Trans R Soc B Biol Sci.* 2005;360:2021–35. Available from: <https://doi.org/10.1098/rstb.2005.1752>
9. Osakabe Y, Osakabe K, Shinokaki K, Tran LP. Response of plants to water stress. *Front Plant Sci.* 2014;5:86. Available from: <https://doi.org/10.3389/fpls.2014.00086>
10. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra S. Plant drought stress: effects, mechanisms and management. *Agron Sustain Dev.* 2009. Available from: <https://research-repository.uwa.edu.au/en/publications/plant-drought-stress-effects-mechanisms-and-management>
11. Praba ML, Cairns JE, Babu RC, Lafitte HR. Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. *J Agron Crop Sci.* 2009;195:30–46. Available from: <https://doi.org/10.1111/j.1439-037X.2008.00341.x>
12. Reynolds M, Tuberosa R. Translational research impacting on crop productivity in drought-prone environments. *Curr Opin Plant Biol.* 2008;11:171–9. Available from: <https://doi.org/10.1016/j.pbi.2008.02.005>
13. Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu Rev Plant Biol.* 2004;55:373–99. Available from: <https://doi.org/10.1146/annurev.arplant.55.031903.141701>
14. Bose J, Rodrigo-Moreno A, Shabala S. ROS homeostasis in halophytes in the context of salinity stress tolerance. *J Exp Bot.* 2014;65(5):1241–57. Available from: <https://doi.org/10.1093/jxb/ert430>
15. Asada K. Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiol.* 2006;141(2):391–6. Available from: <https://doi.org/10.1104/pp.106.082040>
16. Mittler R, Vanderauwera S, Gollery M, Van Breusegem F. Reactive oxygen gene network of plants. *Trends Plant Sci.* 2004;9(10):490–8. Available from: <https://doi.org/10.1016/j.tplants.2004.08.009>
17. Exposito-Rodriguez M, Laissue PP, Yvon-Durocher G, Smirnov N, Mullineaux PM. Photosynthesis-dependent H₂O₂ transfer from chloroplasts to nuclei provides a high-light signalling mechanism. *Nat Commun.* 2017;8(1):49. Available from: <https://www.nature.com/articles/s41467-017-00074-w>
18. Jajic I, Sarna T, Strzalka K. Senescence, stress, and reactive oxygen species. *Plants (Basel, Switzerland).* 2015;4(3):393–411. Available from: <https://doi.org/10.3390/plants4030393>
19. Lv X, Li H, Chen X, Xiang X, Guo Z, Yu J, et al. The role of calcium-dependent protein kinase in hydrogen peroxide, nitric oxide and ABA-dependent cold acclimation. *J Exp Bot.* 2018;69:4127–39. Available from: <https://doi.org/10.1093/jxb/ery212>
20. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol Biochem (PPB).* 2010;48(12):909–30. Available from: <https://doi.org/10.1016/j.plaphy.2010.08.016>
21. Mittler R, Vanderauwera S, Suzuki N, Miller G, Tognetti VB, Vandepoele K, et al. ROS signaling: the new wave? *Trends Plant Sci.* 2011;16(6):300–9. Available from: <https://doi.org/10.1016/j.tplants.2011.03.007>
22. Mittler R. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* 2002;7(9):405–10. Available from: [https://doi.org/10.1016/s1360-1385\(02\)02312-9](https://doi.org/10.1016/s1360-1385(02)02312-9)
23. Mittler R, Vanderauwera S, Gollery M, Van Breusegem F. Reactive oxygen gene network of plants. *Trends Plant Sci.* 2004;9:490–8. Available from: <http://dx.doi.org/10.1016/j.tplants.2004.08.009>
24. Huang S, Van Aken O, Schwarzländer M, Belt K, Millar AH. Roles of mitochondrial reactive oxygen species in cellular signalling and stress response in plants. *Plant Physiol.* 2016;171:1551–9. Available from: <https://doi.org/10.1104/pp.16.00166>
25. Gilroy S, Bialasek M, Suzuki N, Górecka M, Devireddy AR, Karpiński S, et al. ROS, Calcium and Electric Signals: Key Mediators of Rapid Systemic Signaling in Plants. *Plant Physiol.* 2016;171:00434. Available from: <https://doi.org/10.1104/pp.16.00434>
26. Takagi D, Takumi S, Hashiguchi M, Sejima T, Miyake C. Superoxide and singlet oxygen produced within the thylakoid membranes both cause photosystem I photoinhibition. *Plant Physiol.* 2016;171(3):1626–34. Available from: <https://doi.org/10.1104/pp.16.00246>
27. Asada K. Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiol.* 2006;141(2):391–6. Available from: <https://doi.org/10.1104/pp.106.082040>
28. Mittler R, Blumwald E. The roles of ROS and ABA in systemic acquired acclimation. *Plant Cell.* 2015;27(1):64–70. Available from: <https://doi.org/10.1105/tpc.114.133090>
29. Foyer CH, Noctor G. Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. *Antioxid Redox Signal.* 2009;11(4):861–905. Available from: <https://doi.org/10.1089/ars.2008.2177>
30. Sarker U, Oba S. Catalase, superoxide dismutase and ascorbate-glutathione cycle enzymes confer drought tolerance of *Amaranthus tricolor*. *Sci Rep.* 2018;8(1):16496. Available from: <https://www.nature.com/articles/s41598-018-34944-0>
31. Scarpeci TE, Valle EM. Rearrangement of carbon metabolism in *Arabidopsis thaliana* subjected to oxidative stress condition: an emergency survival strategy. *Plant Growth Regul.* 2008;54(2):133–42. Available from: <https://link.springer.com/article/10.1007/s10725-007-9236-5>
32. Triantaphylidès C, Kriskche M, Hoebrechts FA, Ksas B, Gresser G, Havaux M, et al. Singlet oxygen is the major reactive oxygen species involved in photooxidative damage to plants. *Plant Physiol.* 2008;148(2):960–8. Available from: <https://doi.org/10.1104/pp.108.125690>
33. Krieger-Liszakay A, Fufezan C, Trebst A. Singlet oxygen production in photosystem II and related protection mechanism. *Photosynth Res.* 2008;98(1–3):551–64. Available from: <https://link.springer.com/article/10.1007/s11120-008-9349-3>
34. Turkan I, Demiral T. Recent developments in understanding salinity tolerance. *Environ Exp Bot.* 2009;67:2–9. Available from: <https://doi.org/10.1016/j.envexpbot.2009.05.008>
35. Sharma P, Dubey RS. Drought induces oxidative stress and enhances the activities of antioxidant enzymes in growing rice seedlings. *Plant Growth Regul.* 2005;46:209–21. Available from: <https://link.springer.com/article/10.1007/s10725-005-0002-2>
36. Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *Int J Mol Sci.* 2013;14(5):9643–84. Available from: <https://doi.org/10.3390/ijms14059643>
37. Almeselmani M, Deshmukh P, Sairam RK. High temperature stress tolerance in wheat genotypes: Role of antioxidant defence enzymes. *Acta Agron Hungarica.* 2009;57:1–14. Available from: <https://akjournals.com/view/journals/014/57/1/article-p1.xml>
38. Davies KJ. Oxidative stress, antioxidant defenses, and damage removal, repair, and replacement systems. *IUBMB Life.* 2000;50(4–5):279–89. Available from: <https://doi.org/10.1080/713803728>

39. Wu J, Zhang J, Li X, Xu J, Wang L. Identification and characterization of a PutCu/Zn-SOD gene from *Puccinellia tenuiflora* (Turcz.) Scribn. et Merr. *Plant Growth Regul.* 2015;79:55–64. Available from: <https://link.springer.com/article/10.1007/s10725-015-0110-6>
40. Shen C, Que Z, Xia Y, Tang N, Li D, He R, et al. Knock out of the annexin gene OsAnn3 via CRISPR/Cas9-mediated genome editing decreased cold tolerance in rice. *J Plant Biol.* 2017;60:539–47. Available from: <https://link.springer.com/article/10.1007/s12374-016-0400-1>
41. Singh S, Khan NA, Nazar R, Anjum NA. Photosynthetic traits and activities of antioxidant enzymes in blackgram (*Vigna mungo* L. Hepper) under cadmium stress. *Am J Plant Physiol.* 2008;5:31–8. Available from: <https://doi.org/10.3923/ajpp.2008.25.32>
42. Negi NP, Shrivastava DC, Sharma V, Sarin NB. Overexpression of CuZnSOD from *Arachis hypogaea* alleviates salinity and drought stress in tobacco. *Plant Cell Rep.* 2015;34(7):1109–26. Available from: <https://doi.org/10.1007/s00299-015-1770-4>
43. Lee DH, Lee CB. Chilling stress-induced changes of antioxidant enzymes in the leaves of cucumber: in gel enzyme activity assays. *Plant Sci.* 2000;159(1):75–85. Available from: [https://doi.org/10.1016/S0168-9452\(00\)00326-5](https://doi.org/10.1016/S0168-9452(00)00326-5)
44. Mhamdi A, Noctor G, Baker A. Plant catalases: peroxisomal redox guardians. *Arch Biochem Biophys.* 2012;525(2):181–94. Available from: <https://doi.org/10.1016/j.abb.2012.04.015>
45. Sharma I, Ahmad P. Catalase: A versatile antioxidant in plants. In: *Oxidative Damage to Plants: Antioxidant Networks and Signaling.* 2014;131–48. Available from: <https://doi.org/10.1016/B978-0-12-799963-0.00004-6>
46. Abid M, Ali S, Qi LK, Zahoor R, Tian Z, Jiang D, et al. Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). *Sci Rep.* 2018;8(1):4615. Available from: <https://doi.org/10.1038/s41598-018-21441-7>
47. Bania I, Mahanta R. Evaluation of peroxidases from various plant sources. *Int J Sci Res Publ.* 2012;2:1–5. Available from: https://www.researchgate.net/publication/235348418_Evaluation_of_peroxidases_from_various_plant_sources
48. Blokhina O, Virolainen E, Fagerstedt KV. Antioxidants, oxidative damage and oxygen deprivation stress: a review. *Ann Bot.* 2003;91 Spec No(2):179–94. Available from: <https://doi.org/10.1093/aob/mcf118>
49. Passardi F, Longet D, Penel C, Dunand C. The class III peroxidase multigenic family in rice and its evolution in land plants. *Phytochemistry.* 2004;65(13):1879–93. Available from: <https://doi.org/10.1016/j.phytochem.2004.06.023>
50. Quartacci MF, Navari-Izzo F. Water stress and free radical mediated changes in sunflower seedlings. *J Plant Physiol.* 1992;139:621–5. Available from: [https://doi.org/10.1016/S0176-1617\(11\)80381-0](https://doi.org/10.1016/S0176-1617(11)80381-0)
51. Czégény G, Wu M, Dér A, Eriksson LA, Strid Å, Hideg É. Hydrogen peroxide contributes to the ultraviolet-B (280–315 nm) induced oxidative stress of plant leaves through multiple pathways. *FEBS Lett.* 2014;588(14):2255–61. Available from: <https://doi.org/10.1016/j.febslet.2014.05.005>
52. Ristilä M, Strid H, Eriksson LA, Strid A, Savenstrand H. The role of the pyridoxine (vitamin B6) biosynthesis enzyme PDX1 in ultraviolet-B radiation responses in plants. *Plant Physiol Biochem (PPB).* 2011;49(3):284–92. Available from: <https://doi.org/10.1016/j.plaphy.2011.01.003>
53. Smirnoff N. Ascorbic acid metabolism and functions: A comparison of plants and mammals. *Free Radic Biol Med.* 2018;122:116–29. Available from: <https://doi.org/10.1016/j.freeradbiomed.2018.03.033>
54. Munné-Bosch S, Alegre L. Drought-Induced Changes in the Redox State of α -Tocopherol, Ascorbate, and the Diterpene Carnosic Acid in Chloroplasts of Labiatae Species Differing in Carnosic Acid Contents. *Plant Physiol.* 2003;131:1816–25. Available from: <https://doi.org/10.1104/pp.102.019265>
55. Seminario A, Song L, Zulet A, Nguyen HT, González EM, Larrainzar E. Drought Stress Causes a Reduction in the Biosynthesis of Ascorbic Acid in Soybean Plants. *Front Plant Sci.* 2017;8:1042. Available from: <https://doi.org/10.3389/fpls.2017.01042>
56. Khan TA, Mazid MA, Mohammad F. Role of ascorbic acid against pathogenesis in plants. *J Stress Physiol Biochem.* 2011;7:222–34. Available from: https://www.researchgate.net/publication/309283911_Role_of_ascorbic_acid_against_pathogenesis_in_plants
57. Fryer MJ. The antioxidant effects of thylakoid Vitamin E (α -tocopherol). *Plant Cell Environ.* 1992;15:381–92. Available from: <https://doi.org/10.1111/j.1365-3040.1992.tb00988.x>
58. Anjum SA, Wang L, Farooq MA, Khan I, Xue L. Methyl Jasmonate-Induced Alteration in Lipid Peroxidation, Antioxidative Defence System and Yield in Soybean Under Drought. *J Agron Crop Sci.* 2011;197:296–301. Available from: <https://doi.org/10.1111/j.1439-037X.2011.00468.x>
59. Grover A, Mittal D, Negi M, Lavania D. Generating high temperature tolerant transgenic plants: Achievements and challenges. *Plant Sci.* 2013;205–206:38–47. Available from: <https://doi.org/10.1016/j.plantsci.2013.01.005>
60. Wang D, Weaver ND, Kesarwani M, Dong X. Induction of protein secretory pathway is required for systemic acquired resistance. *Science.* 2005;308(5724):1036–40. Available from: <https://doi.org/10.1126/science.1108791>
61. Hüttner S, Strasser R. Endoplasmic reticulum-associated degradation of glycoproteins in plants. *Front Plant Sci.* 2012;3:67. Available from: <https://doi.org/10.3389/fpls.2012.00067>
62. Breiman A. Plant Hsp90 and its co-chaperones. *Curr Protein Pept Sci.* 2014;15(3):232–44. Available from: <https://doi.org/10.2174/1389203715666140331115603>
63. Chen Z, Zhou T, Wu X, Hong Y, Fan Z, Li H. Influence of cytoplasmic heat shock protein 70 on viral infection of *Nicotiana benthamiana*. *Mol Plant Pathol.* 2008;9(6):809–17. Available from: <https://doi.org/10.1111/j.1364-3703.2008.00505.x>
64. Żróbek-Sokolnik A. Temperature stress and responses of plants. In: Ahmad P, Prasad MNV, editors. *Environmental adaptations and stress tolerance of plants in the era of climate change.* New York, NY: Springer New York; 2012:113–34. Available from: http://dx.doi.org/10.1007/978-1-4614-0815-4_5
65. Hussain HA, Men S, Hussain S, Chen Y, Ali S, Zhang S, et al. Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. *Sci Rep.* 2019;9. Available from: <https://www.nature.com/articles/s41598-019-40362-7>
66. Ashraf M, Harris P. Abiotic stresses: Plant resistance through breeding and molecular approaches. 2005. Available from: <https://doi.org/10.1201/9781482293609>
67. Berwal MK, Ram C. Superoxide dismutase: A stable biochemical marker for abiotic stress tolerance in higher plants. In: *Abiotic and Biotic Stress in Plants.* 2019. Available from: <https://www.intechopen.com/chapters/64689>
68. Zhanasova K, Kurmanbaeva A, Gadilgerayeva B, Yermukhambetova R. ROS status and antioxidant enzyme activities in response to combined temperature and drought stresses in barley. *Acta Physiologiae Plantarum.* 2021;43(8):114. Available from: <https://doi.org/10.1007/s11738-021-03281-7>
69. Wang W, Zhang X, Deng F, Yuan R, Shen F. Genome-wide characterization and expression analyses of superoxide dismutase (SOD) genes in *Gossypium hirsutum*. *BMC Genomics.* 2017;18(1):376. Available from: <https://doi.org/10.1186/s12864-017-3768-5>