

Review

Physiological Responses to Drought, Salinity, and Heat Stress in Plants: A Review

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Abstract: On the world stage, the increase in temperatures due to global warming is already a reality that has become one of the main challenges faced by the scientific community. Since agriculture is highly dependent on climatic conditions, it may suffer a great impact in the short term if no measures are taken to adapt and mitigate the agricultural system. Plant responses to abiotic stresses have been the subject of research by numerous groups worldwide. Initially, these studies were concentrated on model plants, and, later, they expanded their studies in several economically important crops such as rice, corn, soybeans, coffee, and others. However, agronomic evaluations for the launching of cultivars and the classical genetic improvement process focus, above all, on productivity, historically leaving factors such as tolerance to abiotic stresses in the background. Considering the importance of the impact that abiotic stresses can have on agriculture in the short term, new strategies are currently being sought and adopted in breeding programs to understand the physiological, biochemical, and molecular responses to environmental disturbances in plants of agronomic interest, thus ensuring the world food security. Moreover, integration of these approaches is bringing new insights on breeding. We will discuss how water deficit, high temperatures, and salinity exert effects on plants.

Keywords: climate extremes; agriculture; abiotic stress; physiological strategies; expression genes



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1. Introduction

Nowadays, the increase in temperatures as a result of global warming and other factors is already a reality. This scenario represents one of the main challenges posed to the scientific community today. Agriculture is highly dependent on climatic conditions; therefore, it may suffer a great impact if no measures are taken to adapt and mitigate agricultural systems. Among the abiotic stresses, drought, salinity, extreme temperatures, chemical pollutants, nutritional deficiency, and oxidative stress stand out as the main environmental restrictions modern agriculture faces. These are factors that compromise development and growth, in addition to influencing the morphological, physiological, biochemical, and molecular processes of plants [1]. Plant responses to abiotic stresses have been the subject of numerous studies worldwide. Initially, they were carried out on model plants and, later, on several economically important crops such as rice, corn, soybeans, coffee, and others. However, agronomic evaluations for the launching of cultivars and the classical genetic improvement process focus, above all, on productivity, historically leaving factors such as tolerance to abiotic stresses in the background. Considering the importance of the impact that abiotic stresses can have on agriculture, new strategies have been sought in breeding programs to understand the physiological, biochemical, and

molecular responses to environmental disturbances in agronomic plants. For example, we researchers are faced with the growing need to understand the genes present in important regulatory pathways that can be introgressed in breeding programs, aiming to increase and help the plant tolerate different abiotic stresses. We will discuss how water deficit, high temperatures, and salinity exert effects on plants.

2. Response Mechanism to Abiotic Stresses in Plants

Plants are often exposed to different situations of abiotic stresses. In evolutionary terms, adapted organisms are those that have managed to modulate several response mechanisms in favor of their defense in order to overcome such stresses and return to normal basal metabolism. Importantly, these environmental factors severely limit agricultural growth and productivity. As an example, the increase in atmospheric CO₂ can trigger changes in the photosynthetic rate of plants, causing changes in the growth rate, which usually impacts positively overall biomass, but decreasing nutritional quality [2,3]. Plants respond to stimuli caused by stress with distinct changes related to their development and physiology. In this context, many mechanisms like photosynthesis and gas exchange [4,5], cell death, changes in cell wall composition [6], nutrient translocation [7], transcriptional activity of genes, transposable elements [8], lipid signaling [9], metabolites, proteins [10], and antioxidant profile [11] can be changed during stresses.

The physiological response mechanism for abiotic stresses occurs from a complex pathway of responses, starting with the perception of stress, which triggers a cascade of molecular events, ending at various levels of physiological, metabolic, and developmental responses [12]. These are summarized in Figure 1.

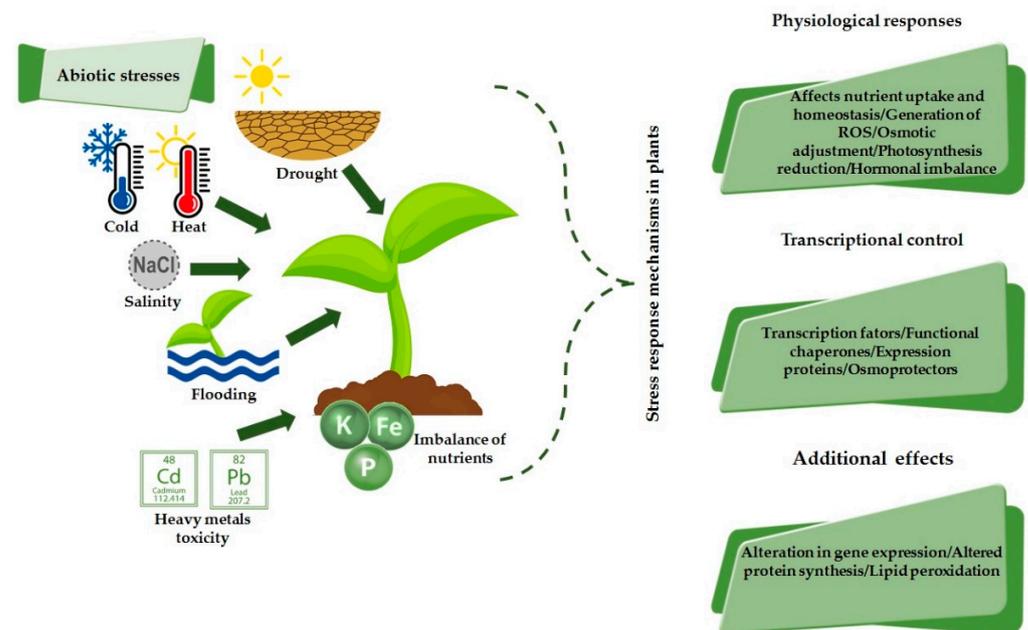


Figure 1. Plant response cascade to different abiotic stresses.

With the perception of these imbalances induced by the abiotic stresses listed above, plants redirect their energy and nutrients to reproduction and defense mechanisms, causing a decrease in the growth rate that results in lower biomass production.

3. Water Deficit in Plants

Due to the ongoing climate change scenario and the rising human population, water availability is a crucial issue for agriculture, the world's largest water user, accounting for more than 70% of global withdrawals [13]. Irrigated agriculture covers 20% of world cultivated lands and accounts for 40% of global food output. On average, irrigated agri-

culture is at least twice as productive per unit of land as rainfed agriculture [13]. Water normally represents from 50 to 90% of plants' fresh weight. The majority of water content (60–90%) is located within cells, and the rest is mainly in cell walls [14]. In this scenario, the maintenance of growth and crop productivity under adverse environmental stress conditions such as water deficit represents one of the main challenges of modern agriculture [15]. Water deficit occurs when the plant water requirement cannot be fully satisfied (e.g., through enough precipitation or irrigation), and the plant's normal functioning is affected (e.g., growth, photosynthesis rate, stomatal conductance). In other words, water deficit occurs when the transpiration rate from the leaf surface is higher than the water uptake by roots. This imbalance between water uptake and water loss is related to a lower soil water potential than the roots [16]. Several factors can cause plant water deficit, including inadequate precipitation, high evaporative demand, decreased groundwater level, and water retention by soil particles [14,17]. This period of abnormally dry weather, resulting in soil-water deficit and subsequently plant water deficit, is defined as drought, a major abiotic stress that negatively influences crop production and yield [18]. The impacts of drought on agriculture are aggravated due to the depletion of water resources, increased food demand, and climate changes [19]. These have become the most important limiting factors to crop productivity and ultimately to food security, increasing the pressure on agriculture to use water more efficiently. As such, agricultural water consumption, water use efficiency (WUE), and the development of drought-tolerant plants are crucial for improving crops. WUE is defined as the amount of carbon assimilated as biomass or grain produced per unit of water used by the crop [20]. It determines the plant's ability to cope with moderate or severe soil water deficit, representing a major factor in plant survival under drought stress [21]. Increasing the WUE of crops constitutes a major goal of breeding and genetic engineering efforts [22]. Using QTL analysis, Damerum et al. (2021) [23] identified genomic regions controlling WUE in wild and cultivated lettuce under well-watered and droughted conditions. QTL were detected for carbon isotope discrimination, transpiration, stomatal conductance, leaf temperature and yield, controlling 4–23% of the phenotypic variation. Candidate genes such as aquaporins, late embryogenesis abundant proteins, abscisic acid-responsive element binding protein and glutathione S-transferase were found in this region associated with WUE [23]. Jia et al. (2021) [24] showed that the overexpression of MdATG8i-OE (autophagy protein) gene in apple resulted in plants exhibiting higher WUE than wild-type under long-term moderate drought conditions.

Since the last century, several attempts have been made to improve and/or generate drought-tolerant plants. To achieve this goal, different techniques have been used, from plant breeding to the production of transgenic lines, as well as the use of precise genome editing methods and omics approaches.

The employment of plant breeding methods has an enormous potential to accelerate drought-tolerant plant production, and considerable progress has been made in this direction in different crops such as barley [25,26] soybean [27], popcorn [28,29], rice [30,31], wheat [32,33]. However, developing drought-tolerant plants through breeding is restricted by a narrow genetic pool, low heritability of drought tolerance/resistance, the complexity involved in tolerance, and the extent of environmental interactions [34].

In contrast, identifying and characterizing drought-related molecules by omics techniques (i.e., genomics, transcriptomics, proteomics, and metabolomics) has opened great opportunities for crop improvement. By combining molecular and physiological analysis, Chevilly et al. (2021) [35] characterized the drought response of two broccoli cultivars (drought-sensitive and drought-tolerant). The authors found increased levels of methionine and abscisic acid in drought-tolerant cultivars while urea, quinic acid, and gluconic acid lactone levels decreased. In a multi-omics and functional characterization analysis Mehari et al. (2021) [36] found that the gene Gh_A06G1257 (GhALDH7B4), belonging to the aldehyde dehydrogenase family, plays a role in drought tolerance. The authors also found that the amino acids valine, glutarate, proline, glutamate, and tryptophan were the most significant metabolites playing roles in drought stress tolerance [36]. Nevertheless,

in practical terms, generating genetically modified plants is an arduous and demanding task requiring complex and expensive laboratory methods [17]. Drought is a multidimensional stress factor, and its effects on plants are complex. As a result, there are still many gaps at the molecular and physiological levels regarding the molecular-to-physiological mechanisms underlying plant responses to drought.

3.1. Strategies to Combat the Water Deficit

As sessile organisms, plants are exposed to several adverse factors in natural environments. Water deficit, for example, can trigger a negative impact on plant growth and development, compromising its yield. Plants have evolved numerous adaptation and acclimation strategies at different levels, ranging from morphology and anatomical structures to physiological and biochemical reactions, aiming to preserve their hydric status [37]. The extension of plant responses depends on the length and severity of water deficiency and its species, age, and developmental stage. Regardless of the temporary nature of the stress, the plant's set of properties and vital functions gradually decrease according to its duration [38]. Moderate water deficit causes significant morphological and physiological alterations, while severe deficit may lead to plant death [39]. Drought resistance refers to the ability of plants to survive or grow in a harsh environment caused by drought stress conditions. This capability is a sophisticated trait related to adaptations at different levels, which allow plants to adapt to specific habitats for the benefit of their growth and development [38]. Drought resistance mechanisms in plants can be classified into four categories: avoidance, tolerance, escape, and recovery [40]. Drought avoidance is characterized by the maintenance of high plant water potentials in the presence of water limitation. It is responsible for rearrangements in plant morphology as well as in cellular metabolism (e.g., development of deeper root systems, stomatal closure, and leaf rolling, wax accumulation on the leaf surface [41,42]. Drought tolerance relies on the ability of plants to sustain physiological activities under severe drought stress conditions through the remodeling of gene regulation and metabolic pathways to reduce or repair the resulting stress damage [40,42]. Drought escape refers to the synchronization of the plant growth period, life cycle, or planting time to prevent the growing season from encountering drought [42]. Drought recovery refers to the plant capacity to regenerate metabolism after the cessation of severe drought, which causes the complete session of growth, turgor loss, and leaf desiccation [43]. Prolonged drought conditions are associated with drought escape or avoidance, whereas short but severe drought periods induce drought tolerance [42]. As mentioned above, plants have adapted to water limitation using different strategies at different levels, from anatomical to molecular changes.

3.2. Physiological Strategies for Increasing Productivity under Water Deficit Conditions

Water limitation impairs normal plant growth, disturbs water relations, and reduces water-use efficiency. To cope with this condition, plants have evolved a series of morphological, physiological, and biochemical responses, including changes in photosynthesis, respiration, ion exchange, transpiration, osmotic regulation, activation of drought-induced proteins, and antioxidant enzymes.

At the morphological level, the responses of roots and leaves are crucial to reduce water loss and promote WUE. The root system plays a critical role in response to water deficit stress. Its length, weight, volume, and density are important features associated with crop drought resistance [40]. Leaf rolling is a drought-adaptive trait induced by turgor pressure that reduces water consumption under water stress. Stomata are pores allowing gas exchange between plant and environment, ensuring maximum absorption of CO₂ for photosynthesis, and meanwhile controlling the optimal transpiration [40]. Plants first recognize water deficit in the soil by root cells; then, abscisic acid (ABA) is synthesized. Subsequently, ABA triggers signals to other organs and tissues through vascular bundles, causing morphological/anatomical alterations such as leaves senescence, stomatal closure, reduction of the leaf surface, induction of root to shoot ratio, and enhancing plant water

uptake from soil by reducing the water potential contrary to the water-limiting environment through osmotic adjustments [44–46]. The ABA signaling pathway involves a cascade of receptors, phosphatases, kinases, G-proteins, proteins in the ubiquitin pathway, and transcription factors (TFs) [47]. Zhu et al. (2021) [48] found that the transcription factor *ipa1* (ideal plant architecture 1) significantly improved rice drought tolerance at seedling stage mainly through activating ABA pathway. The authors have used a pair IPA1 and *ipa1*-near isogenic lines to obtain *ipa1* plants that had a better-developed root system and smaller leaf stomatal aperture. Stomatal closure mediated by ABA can be considered a quick short-term response to water limitation. However, ROS, nitric oxide (NO), and calcium ion (Ca^{2+}) are known as secondary messengers involved in ABA-signaling, which can promote events that facilitate plants' long-term adaptation against biotic and abiotic stress (e.g., osmolyte accumulation, up-regulation of adaptive genes, hypersensitive response (HR), and programmed cell death (PCD)) [47]. Despite morpho-anatomical traits promoted by drought, physiological and biochemical limitations might have a greater impact on plant performance. Photosynthesis and respiration, the hubs of energy metabolism in plants, are negatively impacted by drought. Photosynthesis is one of the main processes affected by water stress as the photosynthetic and transpiration rates drop with the decrease of soil relative water content. Stomatal closure decreases leaf CO_2 influx, limiting carboxylation and internal CO_2 levels [49]. This lower CO_2 diffusion from the environment to the carboxylation site is considered the major reason behind decreased photosynthetic rate during mild to moderate drought stress [50]. Water limitation also alters the electron transport chain (ETC), which further enhances reactive oxygen species (ROS) (e.g., superoxide, hydrogen peroxide, and hydroxyl radicals) within cell organelles, negatively affecting PSI and PSII photosystems and causing disruption of thylakoid structures. To deal with drought-induced damage on the photosynthetic apparatus, plant responses include changes in thermal dissipation of light energy, photo destruction of the D1 protein of PSII, dissociation of the light-harvesting complexes from photosynthetic reaction centers, and others [16]. Drought tolerance is a costly phenomenon for plants, as they expend an enormous amount of energy to cope with it. The root is a major consumer of carbon fixed in photosynthesis, with is used for growth and maintenance in addition to dry matter production.

Plant growth is determined by the ratio between photosynthetic CO_2 assimilation and respiratory CO_2 release. Modulation of the carbon metabolism of plant cells depends on the balance between photosynthesis and respiration. The respiration rate is regulated by processes that use respiratory products (adenosine triphosphate—ATP, nicotinamide adenine dinucleotide—NADH) and intermediates from the tricarboxylic acid cycle (TCA), which together contribute to plant growth. Although photosynthesis can become completely impaired under severe drought, the respiration rate may increase [51] or decrease [38]. Reduced rates of photosynthesis are likely to reduce substrate supply to mitochondria, resulting in a lower rate of foliar respiration. Alternatively, drought might increase the demand for respiratory ATP to support cellular metabolism [52].

Under drought conditions, ROS are produced in plants' mitochondria and might damage cellular components [53]. The plant mitochondrial ETC includes a non-energy-conserving terminal oxidase called alternative oxidase (AOX). This pathway, as well as photorespiration, can be used by plants exposed to water deficit to maintain cell functioning by preventing ROS accumulation [54]. The TCA cycle pathway can also be modified to prevent the generation of excess reductants through the γ -aminobutyric acid (GABA) synthesis. Its accumulation occurs during stress conditions and may constitute a stress adaptive response [55,56]. The TCA cycle pathway can also be modified to prevent the generation of excess reductants through the γ -aminobutyric acid (GABA) synthesis. Its accumulation occurs during stress conditions and may constitute a stress adaptive response [55,56]. Xu et al. (2021) [57] found that GABA does not initiate changes in stomatal pore aperture, rather it antagonizes changes in pore size and, the authors proposed that cytosolic GABA signals modulate stomatal opening, WUE and drought resilience transduced through negative regulation of the ALMT9 (aluminum-activated malate transporter 9) activity.

Plant hormones, secondary metabolites, inorganic acids, carbohydrates, amino acids, and polyamines play crucial roles in stress tolerance mechanisms. The accumulation of these compounds in plants reduces the osmotic potential and improves cell water retention in response to water stress. Their increased levels represent the plant biochemical responses to water limitation by altering membrane stabilization, osmoregulation, and ROS scavenging, reducing leaf area and ion leakage, and promoting root development [58]. An example is the amino acid proline, a key signaling moiety against drought stress, which acts as an osmoprotectant [59]. Its accumulation helps plants maintain membrane integrity through decreased lipid peroxidation by defending cell redox potential and declining ROS levels. Other amino acids have been found to have a role in drought tolerance. [35] found that drought tolerant broccoli plants presented higher levels of methionine [35]. In cotton, valine, glutarate, glutamate, tryptophan and proline accumulated under drought stress [36]. Recently, studies have indicated that exogenous application of various plant growth regulator (PGRs), such as hormones, polyamines, organic acids, antioxidants, osmoprotectants, and others improved drought resistance in crops [60–62]. These studies reported that the application of PGRs enhance parameters such as photosynthetic capacity, relative water content (RWC), gas exchange attributes and accumulation of osmolytes and antioxidants. Such priming treatment is a very promising strategy in modern crops for the development of drought resistance plants. As an example, Xie et al. 2021 [63] identified that exogenous application of citric acid in tobacco plants resulted in higher chlorophyll content, net photosynthesis, relative water content, abscisic acid content and lower stomatal conductance, transpiration, and water loss under drought conditions.

3.3. Difficulties and Advances in the Development of Drought-Tolerant Cultivars

Drought tolerance is not a qualitative trait, but a complex quantitative polygenic trait controlled by a large number of genes, each contributing to a small effect [64]. Furthermore, drought-tolerant cultivars suffer from high interactions between genotype and environment ($G \times E$), low heritability, and difficulty in mass screening of plant traits and genes [64,65]. This complexity explains the difficulty of understanding the molecular mechanisms triggered by drought as well as the slow progress in yield improvement in drought-prone environments. Conventional plant breeding has achieved genetically improved drought-tolerant lines/cultivars of some selected crops [66]. However, this approach is highly time-consuming and labor- and cost-intensive [67]. In recent decades, crop physiology, marker-assisted breeding, and omics have led to insights into drought tolerance mechanisms providing new knowledge and tools for plant improvement. Some of the new technologies rely on marker-assisted selection (MAS), genome-wide selection (GWAS), gene editing strategies, and omics approaches (genomics, transcriptomics, proteomics, metabolomics). Phenomics is another important strategy that has been used to improve the detection of drought-related traits by linking plant physiology with genomics through image analysis, machine vision, robotics, and computing to widen the scope of plant biology [68].

Despite the relevance of quantitative trait loci (QTL) and GWAS analysis in the identification of genomic regions for selecting drought-related alleles and identifying genetic variants associated with drought-related traits, the candidate genes through which the identified genetic variants exert their effects on traits are remained largely unknown [69]. In this respect, integrating a suite of modern breeding techniques with multi-omics platforms and high-throughput phenotyping can greatly improve the current knowledge about drought stress response in crops.

4. Salinity

In agriculture, land salinization has been shown to be a limiting factor in the last half-century [70]. Currently, about one-third of the world's arable area is suffering from salinization, significantly reducing crop production and yield [71]. Soil salinization is further aggravated at the global level due to poor irrigation practices, inappropriate agro-

chemical usage, and industrial pollution [72]. In the meantime, salt concentrations, in general, can cause changes in physiological and biochemical functions, restricting the growth and development of both the aerial part and the root system of the plants. Salt causes two types of stress in plants: osmotic and ionic. High salt concentrations in the soil reduce the soil water potential, leading to reduced water uptake by plant roots [73]. On the other hand, an excessive accumulation of ions as Na^+ and Cl^- in cells results in toxicity on the plant or nutritional disorders [74]. In this sense, it is necessary to improve management techniques to reduce the damage caused by this phenomenon and intensify studies and plant improvement programs aimed at increasing tolerance to salt stress. Agricultural land salinization poses a significant challenge for the future, given the predictions of climate change and population growth.

4.1. Response Mechanisms to Saline Stress

In plants subjected to salinity, an osmotic adjustment mechanism is initiated to maintain the turbidity of the cells, resulting in the slow growth of stressed plants. In the meantime, when plants are induced by salt stress, the changes triggered by it may vary according to management and genotype, developmental stage, intensity, and duration of stress [75]. Plants can trigger different physiological and biochemical mechanisms to deal with the resulting stress (Figure 2), which include: changes in morphology, anatomy, water relations, photosynthesis, hormones, ion distribution, and biochemical adaptation [76].

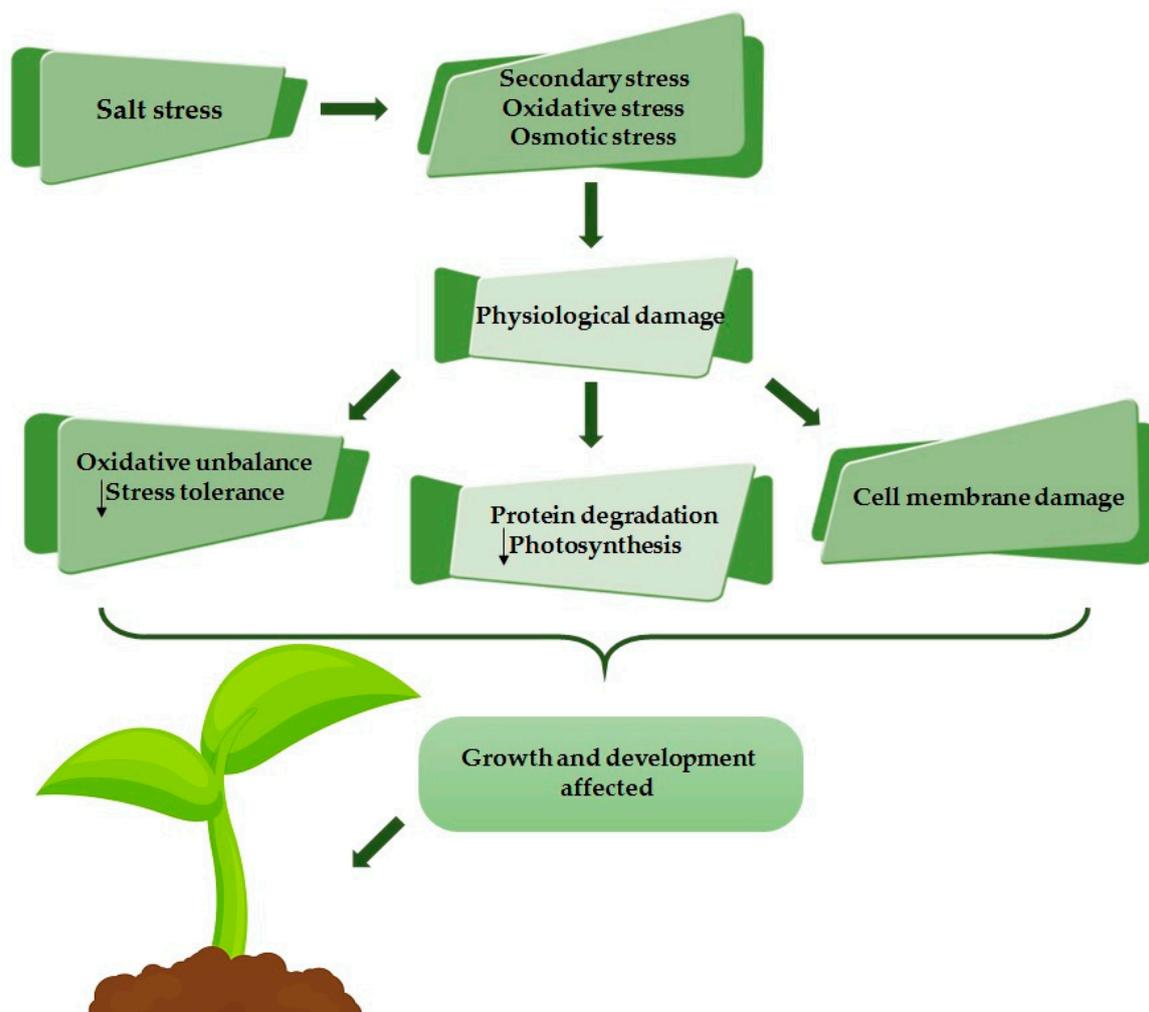


Figure 2. Some of the effects triggered by salt stress on plants.

The response of plants to salinity comprises two main steps: (i) the first is considered rapid and is described as the osmotic phase, as the salt reaches the roots decreasing the osmotic potential of the soil–plant relationship, triggering a reduction in shoot growth due to reduced water potential.; (ii) the second is described as slow, and consists of absorption and signaling of toxic ions, such as Na^+ [77]. The main ions involved in salt stress signaling are cations, such as Na^+ , Ca_2^+ , Mg_2^+ , and K^+ , and anions, such as Cl^- , SO_4^- , HCO_3^- , CO_3^{2-} and NO_3^- , as it is through the interaction of these ions that cell homeostasis occurs. Plants under extreme salinization conditions limit the entry of Na^+ or accumulate this ion in their older tissues, providing the formation of a “stock” environment, which will later be eliminated. Plants that, throughout evolution, have shown characteristics and mechanisms adaptable to the saline environment are described as halophyte plants. Several comprehensive reviews have been published on various aspects of halophyte physiology [78,79]. Halophyte plants have developed three main strategies to adapt to saline soils stress: uptake of high-concentration ions and store in vacuoles, removal of absorbed salts by special cells, and restriction of salt uptake by stem cells [80]. Salinity-sensitive plants (glycophytes) can accumulate minimal amounts of Na^+ and Cl^- . Glycophytes are more sensitive to the accumulation of these ions in their tissues due to improper salt compartmentation, harming development and productivity [60]. The roots are usually the first organ to sense the salt signal after plants are exposed to saline conditions [81]. The root architecture modifications in response to salinity are mediated by the suppression of cell division, initiation, elongation, or growth redirection away from salt [82]. In addition, to adapt to stressful conditions, plants can acquire tolerance by modifying root developmental processes that require metabolic alterations. In this sense, Chun et al. (2019) [83] showed that in callus suspension, salt-adapted cell cultures from *Arabidopsis* roots accumulated higher levels of sugars, amino acids, and intermediary metabolites in the shikimate pathway, such as coniferin. Moreover, adapted cells acquired thicker cell walls with higher lignin contents, suggesting the importance of adjusting physical properties during adaptation to high-saline conditions. Another typical response to salt stress is an increase in the root–shoot ratio, associated with water stress, rather than a specific effect of salt [80]. A greater root proportion under salt stress can favor the retention of toxic ions in this organ, controlling their translocation to the aerial parts [84]. Furthermore, a high spatial distribution of roots under salt stress can favor water absorption due to plants’ increased soil exploration [81]. These responses may constitute a typical plant resistance mechanism in saline conditions.

The increase in the concentration of soluble organic compounds in the cytoplasm of cultivated plants subjected to salt stress is a mechanism used by plants to balance the osmotic potential between the cytosol, vacuole, and external environment [85]. In addition, these compounds prevent damage to the enzymatic systems and stabilize the structures of the enzyme [86]. The osmotic adjustment can be performed by some compounds that plants often produce and/or accumulate in stress situations, including quaternary derived from amino acids such as proline, glycine, glycine betaine, β -alanine, and complex sugars such as raffinose [87]. For example, in kiwi plants (glycophyte species) subjected to 0.3% and 0.6% sodium chloride (NaCl), an increase in proline levels was observed in all genotypes [88]. In salt stress conditions, there was also an increase in the proline content and growth rate in *Zea mays* [89]. The accumulation of proline in the cell wall can reduce the effects of external disturbances on plants and increase the salt tolerance in *Glycine max* L. [90]. Plazek et al. (2013) [91] describe that, in halophytes, this osmolyte can act directly on the osmotic pressure, while in glycophytes, proline can play two roles, playing both an osmotic function and acting in the stabilization of the tertiary structure of proteins. In addition to this osmoprotective function, these osmolytes help in the redox balance within the cell and maintain the provision of energy, carbon, and nitrogen in plants [92]. Analyses performed on *C. arabica* leaves under salt stress (150 mM NaCl) showed changes in cell wall polysaccharides and increased monolignol content, which confers a barrier for salt entrance [93].

The photosynthetic process is involved in productivity and nutrient flows in plants. Salinity affects the physiological activity of the leaf, particularly photosynthesis, which is the main cause of reduced plant productivity [94]. Exposure to salinity leads to stomatal closure, which reduces the photosynthesis ratio due to a decrease in stomatal conductance, which restricts the access of CO₂ for the Calvin-Benson cycle [95]. In addition, the effects of salinity on photosynthesis may involve inhibition of electron transport and inactivation of the photosystem II (PSII) reaction centers [96], destroying the oxygen-evolving complex (OEC), and impairing the electron transfer capacity on the donor side of PSII [97]. The salinity led to a decrease in photosynthetic rate, leaf osmotic potential, electron transport rate, and CO₂ concentrations in the chloroplasts of rice leaves [98]. PSII is damaged by salinity. This was observed in cultivars of wheat, in which the total chlorophyll contents and quantum yield of PSII significantly decreased due to salt stress (150 mM) [99]. Exposure to 300 mM NaCl caused a decrease in stomatal conductance from day three and a reduction in water potential, CO₂ assimilation, and in the maximum quantum yield of photosystem II (Fv/Fm) from day nine in leaves of *Portulaca oleracea* L. [100]. In addition, a decrease in chlorophyll content is a commonly reported phenomenon under salt stress. Some studies propose that chlorophyll concentration can be used as a possible indicator of the cellular metabolic state [101]. In rice leaves, the reduction of the chlorophyll a and b content of the leaves was observed after treatment with NaCl (200 mM NaCl, 14 days), where the chlorophyll b content of the leaves (41%) was affected more than the content of chlorophyll a (33%) [102].

Salinity induces oxidative stress in plants at the subcellular level [80,103]. ROS are formed due to the reduction of oxygen by reducing molecules. Their concentration increases due to environmental stress, and the stomata close to reduce water losses. The CO₂ in the leaves is reduced so that the reducing power of NADPH, or reduced ferredoxin, is conveyed to oxygen, which is, therefore, reduced in its radical forms, superoxide (O₂ •−), hydrogen peroxide (H₂O₂), and hydroxyl radical (HO•) [104]. This increase in ROS level in plant tissues results in oxidative damage of membrane lipids, proteins, and nucleic acids [105]. To scavenge high ROS levels, plants develop an efficient system of non-enzymatic and enzymatic antioxidants [106]. Non-enzymatic antioxidants include reduced ascorbate (ASC), glutathione (GSH), phenolics, flavonoids, and tocopherols [107]. Enzymatic antioxidants responsible for detoxifying ROS accumulation include superoxide dismutase (SOD; EC 1.15.1.1), peroxidase (POX; EC 1.11.1.7), catalase (CAT; EC 1.11.1.6), and the enzymes of the ascorbate (ASC)–glutathione (GSH) cycle: GSH reductase (GR), ASC peroxidase (APX; EC 1.11.1.11), monodehydroascorbate dehydrogenase (MDHAR; EC 1.6.5.4), and dehydroascorbate reductase (DHAR; EC 1.15.1.1) [105,108].

Up-regulation of antioxidants was observed in different cultivated plants like rice, wheat, maize, soybean, and tomato [98,99,105,109,110]. Salt-tolerant cultivars demonstrated that the increased resistance to salinity is associated with the alleviation of oxidative damage is often correlated with an efficient antioxidative system. In addition, many studies have demonstrated the role of enzymatic and non-enzymatic antioxidants in medicinal plants as *Lonicera japonica* L., *Hyssopus officinalis* L., *Melissa officinalis* L., and *Curcuma longa* L. [111–114]. This evidences the role of antioxidants in alleviating salt stress-induced oxidative damage.

Among the changes arising from the excess of these ions, one of great importance is the decrease in water absorption by the plant, which ion toxicity can cause a reduction in nutrient absorption. In this way, salt stress induces a potassium (K) deficiency with an increase in salinity. In salt, stress incurs the accumulation of Na⁺, which is accompanied by a sharp decrease in K⁺ content [105,110,115]. This inverse relationship is due to the competition between Na⁺ and K⁺ uptake in the roots. For example, in wheat cultivars under salt stress (150 mM), the growth and yield were reduced due to a decline in plant water status, limited uptake of macronutrients (N, P, and K), and reduced K⁺/Na⁺ ratio [99]. In addition, salinity can interfere with the acquisition and use of nitrogen (N) by plants, influencing the different steps of N metabolism: absorption, assimilation, and synthesis

of proteins. Li et al. (2019) [116] showed that salt stress significantly inhibited the N assimilation process in cucumber leaves. In this sense, the nutrient imbalance contributes to reducing growth rate under stressful salinity conditions.

4.2. Molecular Approaches to Salt Stress

The decoding of genome sequences of diverse major food crops provides useful genomic information related to structural, functional, and comparative genomics for novel trait discovery and genetic enhancement of cultivated crops [117]. For example, to increase crop production in saline soils, identifying quantitative trait loci (QTLs) associated with salt tolerance is an essential step for improving varieties of salt-tolerant plants [118]. In this way, different QTLs associated with salt tolerance have been identified in cultivated crops: soybean [119,120]; maize [121] and rice [122,123] (Supplementary Table S1). The QTLs were mainly identified for various agronomic traits, including physiological and agronomic traits involved in salinity tolerance, yield and yield contributing factors, and root architecture (Supplementary Table S1).

By integrating diverse omics approaches, it is possible to understand what changes occur in the gene expression, proteins, and metabolites, in response to salt stress. Studies from genomics, transcriptomics, proteomics, metabolomics, and epigenomics have been developed to understand the salt stress tolerance process and its possible use to increase salinity tolerance in plants. With the development of several advanced technologies, including CRISPR/Cas9, which can be used for target-site genome editing to gain salt-tolerant cultivars. Some recent examples were developed for rice [124,125] and tomato [126]. Other examples of molecular approaches used to understand and to develop salt-tolerant plants are also reported in Supplementary Table S1.

Salinity tolerance can trigger and alter the expression of numerous genes, divided into different functional groups, responsible for minimizing the effects of excess salt [61]. These genes are involved with photosynthetic proteins, proteins linked to transport the vacuole, synthesis of osmolytes, membrane channels, and activation of protectors against ROS, and signaling/regulatory elements, including TFs. According to a study carried out by Roy et al. (2014) [127], overexpression of genes involved in ROS removal resulted in decreased cell damage, maintenance of photosynthetic energy, and an improvement in root growth under saline conditions. The same also occurs in the overexpression of H⁺ and potassium antiport channels, which allow the greatest accumulation of biomass associated with greater tolerance to salinity [128].

Among TF, the major TFs are bZIP, DREB, MYC, MYB, NAC, and WRKY, which strongly correlate with salinity and are identified with great potential in promoting crop tolerance against salt stress. Wang et al. (2021) [99] showed that overexpression of ThNAC12 TF enhanced salt tolerance through modulation of ROS scavenging via direct regulation of *ThPIP2;5* expression in *Tamarix hispida*. In transgenic rice, the *SiMYB19* overexpression promotes abscisic acid (ABA) accumulation and upregulates the ABA synthesis gene *OsNCED3* and the ABA signal transduction pathway-related genes *OsPK1* and *OsABF2* [129]. Under salt stress, the overexpression technology combined with the CRISPR-Cas9 system shows that *GmNAC06* TF could cause the accumulation of proline and glycine betaine to alleviate or avoid the negative effects of ROS; similarly, it could control the Na⁺/K⁺ ratios in hairy roots to maintain ionic homeostasis in *G. max*. In this way, *GmNAC06* plays a role in response to salt stress and could be useful in generating salt-tolerant transgenic crops [130]. The development of these new methodologies will generate new avenues for harnessing and exploring these tools to improve agriculture traits.

5. Heat Stress

In the near future, global warming will provide a challenge for crops in maintaining their development, growth, reproduction, and yield [131]. To minimize the effects of heat stress, plants have evolved a series of mechanisms, including molecular responses and changes in their physiology and biochemistry, to try to defend against the damage

caused by temperature elevation [132,133]. These changes have damaged agricultural production [134]. Plants are subject to heat stress when: (i) the air temperature is high, and plants receive energy through sensible heat transfer; (ii) solar radiation incident on the soil surface raises the temperature above the air temperature; and (iii) in leaves, substantial heating caused by solar radiation and inability to dissipate heat can result in leaves heating very quickly (up to 15 °C above air temperature), so leaves with low transpiration rates are often subjected to high temperatures [135].

The exposition to thermal stress can cause enormous damage to the cell membrane and the protein conformation, leading to ROS production, triggering oxidative stress. In addition, heat stress decreased protein synthesis, transcription, and translation of heat shock proteins (HSPs), production of phytohormones and antioxidants, and changes in the organization of cell structures leading to alterations in hormonal homeostasis [136,137].

5.1. Response Mechanisms to Heat Stress

To bear heat stress, plants change their morphology by increasing the root system, reducing the stomatal number and conductance while the leaf curls, folds, and decreases its area, becoming thinned to avoid water loss by evapotranspiration [138,139]. Previously, Lima et al. (2013) [140] studied the cell wall structure of coffee plants subjected to heat stress (37 °C), which showed changes related to cell wall stiffening, as well as an increase in the structural size of the wall polysaccharides and in the lignin content. Regarding structure, the period of thermal stress led to a decrease in the content of starch granules, changes in the organization of internal membranes, and a decrease in the general size of the mesophyll cells, especially in the palisade parenchyma [140].

Abiotic factors such as high temperatures combined with water shortage affect the growth and development of many plants, decreasing crop productivity. Heat stress causes numerous disturbances to plants, altering the stability of membranes and proteins, disorganizing the metabolism of nucleic acids and proteins, degenerating membrane structure, inhibiting photosynthesis, among other adverse effects (Figure 3).

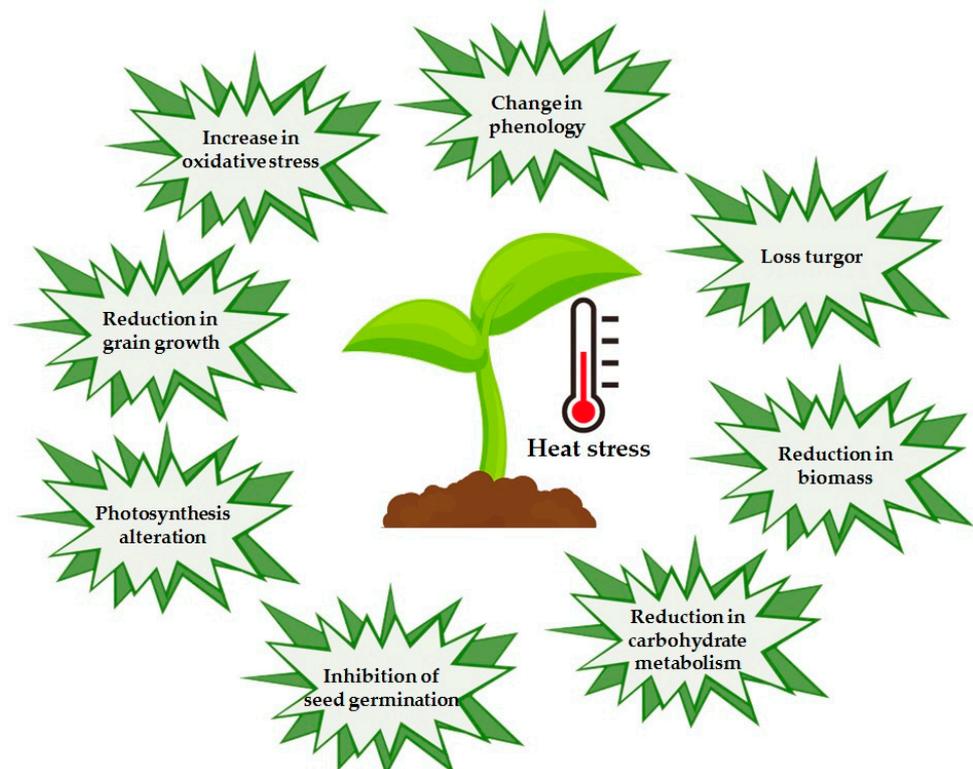


Figure 3. Some of the effects triggered by heat stress on plants.

Heat stress causes physiological adjustments in plants. The photosynthetic apparatus is usually damaged, decreasing transpiration due to stomatal closure and CO₂ content, inhibiting photosynthetic enzymes and ATP synthases rates, reducing leaf expansion, and accelerating senescence; as a consequence, plant development is hampered [141–143]. To mitigate the effects of heat stress, the metabolism of carbon assimilation is altered, remobilizing plants' starch reserve in chloroplasts by releasing energy, sugars, and derived metabolites to survive stress periods and prevent further damage [144,145].

The ribulose 1,5 bisphosphate carboxylase/oxygenase (Rubisco) enzyme, central to carbon fixation, usually works efficiently between temperatures of 20 and 30 °C. Above these conditions, photosynthetic rates tend to be reduced [146]. Throughout evolution, plants have developed different metabolic strategies that have allowed them to react to adverse conditions. The C₄ and CAM photosynthetic mechanisms present structures for concentrating CO₂ that provide the Rubisco with greater photosynthetic efficiency, even under extreme high-temperature conditions, except in C₃ plants [146]. However, most crops have a C₃ metabolism, comprising species which usually fix less carbon under high temperatures, as they do not have optimized mechanisms for CO₂ concentration [147].

Heat stress interferes with redox homeostasis, leading to ROS production, harming the elimination mechanisms of these toxic forms of O₂ in different cell compartments, causing oxidative stress. The increase in ROS produces molecule oxidation, membrane decomposition, enzyme inactivation, and changes in gene expression [133]. ROS-scavenging enzymes such as SOD, CAT, APX, monodehydroascorbate reductase (MDHAR), DHAR, and glutathione reductase (GR) play a role in detoxifying the excess of ROS produced by cells under stress conditions [148], as well as non-enzymatic mechanisms (ascorbate—ASA, glutathione—GSH, α -tocopherol, and flavonols). Oxidative stress also leads to epigenetics, including histone modifications regulating the gene expression [149,150]. Manipulation of photosynthesis through rubisco activase and enzymes functioning in the detoxification of reactive oxygen species is a suitable approach for generating heat-tolerant crop plants [151].

Plants can perceive changes in temperature through sensors in different cellular compartments. Chloroplasts that house the photosynthetic apparatus, the most damaged by heat, are considered sensors of heat stress because they change the dynamics in response to ROS/redox changes at the cellular level [152]. The signals generated by these different sensors rapidly trigger a specific signal transduction network that involves calcium fluxes, calmodulin, CDPKs, mitogen-activated protein kinases (MAPKs), phosphatases, and transcriptional regulators [149].

One of the best-known means of responding to potential damage caused by high temperatures is through the synthesis of HSPs, a group of protective proteins including Hsp100, Hsp90, Hsp70, Hsp60, small Hsps, and some MAPKs [149,153,154]. Heat stress-responsive genes are regulated by a series of TFs, including heat stress TFs (HSFs), NAC, MYB, WRKY, RAV, bZIP, AP2/ERF, and ZAT that regulate the expression of stress-responsive genes. The transcription is activated by binding the *cis*-elements (ARE, CORE, W-box, GCC box, as-1 like) in the promoters of such stress-inducible genes [133]. Genes responsive to heat stress such as NADPH oxidases (Rboh), dehydration-responsive element-binding protein 2A (DREB2A), heat shock (HsfA2, HsfA7a, HsfBs), multiprotein bridging factor 1C (MBF1C), and MAPK are regulated by such HSFs. Additionally, TFs, epigenetic regulators, and small RNAs also regulate heat stress-responsive genes [149].

Plants under heat stress also increase the biosynthesis of several hormones to regulate their response to stress. Temperature elevation stimulates the biosynthetic pathways of hormones such as auxins, salicylic acid (SA), ABA, brassinosteroids (BRs), cytokinin (CK), jasmonate (JA), and ethylene (ET), resulting in higher accumulation in plant cells as a manner to tolerate heat stress [137]. The overexpression *TaNAC2L* transcription factor activated the expression of heat-related genes in the transgenic *Arabidopsis* plants, suggesting that *TaNAC2L* may improve heat tolerance by regulating the expression of stress-responsive genes [155]. However, the overexpression of NAC transcription factor (SIJA2) reduced the accumulation of SA in transgenic tobacco, resulting in increased susceptibility

to heat stress [156]. In this way, the transcription factors binding genes from hormone biosynthesis pathway should be analyzed whether they work as positive or negative regulators to genetic engineering plants to improve heat stress tolerance.

5.2. Approaches to Generate Heat-Tolerant Plants

Conventional breeding to develop heat stress tolerance genotypes is very difficult, since this trait is usually complex, being controlled by several genes present at multiple QTL. Moreover, germoplasm evaluation is time-consuming and costly [157]. Although it is challenging, QTLs associated with heat tolerance have been identified in recent years, for example, in the wheat [128,158–163], barley [164], chickpea [165], cotton [165,166], tomato [167,168], and rice [169], among other crops (Supplementary Table S1).

Whenever these characteristics are found in commercial or wild relatives, conventional breeding, mainly assisted by molecular tools, can be used to improve heat tolerance in commercial genotypes [170]. However, it is necessary to keep in mind that an undesirable portion of the genome, mainly from wild relatives, could be transferred to the target genotype by crosses [168,171].

Metabolome has been a valuable tool for understanding how plants behave under heat stress. In response to high temperatures, plants change their metabolism to accumulate assimilates, mainly sugars, amino acids, and carbohydrates [145,172–178] (Supplementary Table S1).

Transgenic approaches have also been of great interest for generating abiotic stress-tolerant plants in recent years. Heat stress factors and DREB2A genes have been identified to engineer transgenic plants tolerant to heat [148,179]. Genes coding to molecular chaperons (HSP, EF-Tu), osmolytes (glycine betaine), sugars (trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP), antioxidant enzymes (peroxisome-located ascorbate peroxidase (APX), glutathione peroxidase gene, Cu/Zn superoxide dismutase) and transcriptions factors (AP2/EREBP, WRKY, NAC, MYB and basic leucine zipper (bZIP)) have been proved to increase tolerance to heat stress by transgenic approaches [180]. In addition to such genes, plant nucleoside diphosphate kinase 2 (NDPK2), CBF3, antioxidative enzyme 2-cysteine peroxiredoxin (2-Cys Prx), have been assayed in *Solanum tuberosum* to increase heat tolerance [181]. The overexpression of heat shock protein 70 (AsHSP70) and 101 (AtHSP101), pyrophosphate-energized vacuolar membrane proton pump 1 (AVP1), and *Arabidopsis* SUMO E3 ligase (OsSIZ1) genes in cotton proved to increase heat tolerance of this plant [182].

However, the overexpression of HSFs could affect developmental and stress responses in an undesirable way [183]. For the overexpression of such genes, tissue-specific and stress-inducible promoters should be preferable to decrease the impact on plant growth [181,184]. Manipulation of photosynthesis through Rubisco activase and enzymes functioning in ROS detoxification are also candidate genes to generate heat-tolerant crop plants.

Modification of the cell wall structure in plants, leading, for example, to increased levels of expansin, can help to increase tolerance to high temperatures through the loosening and relaxation of the cell wall. In this sense, the overexpression of the expansin gene *PpEXP1* in the grass *Poa pratensis* improved heat tolerance (35 °C), with less structural damage to the cells [185]. In the thale cress *Arabidopsis thaliana*, it was shown that the production of enzymes involved in the biosynthesis of oligosaccharides of the raffinose family, as well as the accumulation of these carbohydrates, play crucial roles in tolerance during heat stress, possibly acting as an osmoprotectant [186].

Although transgenic approaches are suitable for engineering heat-stress-tolerant plants, public concern and regulatory issues regarding the release of such GMO cultivars present difficulties to the process [182]. On the other hand, the genome edition (GE) approach has become the most used system to modify plants by disrupting genes (knockout) or inserting fragments (knock-in) or regulatory elements to genes' promoters to modulate gene expression [187,188]. The most recent technique used to edit plant genomes is clustered regularly interspaced short palindromic repeats (CRISPR) associated with protein9

nuclease (Cas9). To obtain heat-tolerant plants, CRISPR-Cas can be used to either activate or repress genes in a very specific way. For example, positive gene regulators associated with HSPs and stress-related TFs can be activated, or negative regulators can be silenced by the CRISPR-Cas system [189]. The advantage of GEd is that in cases of gene disruption or silencing, the plants could be considered transgene-free in some countries, facilitating the development of new varieties.

Similarly, plant microRNAs (miRNAs) function as positive or negative regulators, which have been studied as targets for genetic engineering tolerance to heat stress [190,191] by transgenesis or genome editing approaches [192]. For instance, the overexpression of miR156 in *Arabidopsis* increased tolerance to heat stress [149]. Several miRNAs were differentially regulated in two contrasting rice genotypes under different heat stress treatments, suggesting that the tolerant cultivar was more efficient in its use of molecular and physiological machinery at the reproductive stage than the susceptible one after heat stress, making it a candidate for genetic engineering [155] Supplementary Table S1.

6. Conclusions and Future Outlook

The scientific community emphasizes the importance of increasing yield crop farming due to food demand and population increase. However, there is a certain neglect regarding how to correctly use biotechnological tools to minimize the adverse effects caused by abiotic stresses in morphological, physiological, biochemical, and molecular processes. Given such a problem with which our agriculture has been confronted, the big questions are what and how to correctly apply the information generated by these techniques to really mitigate these adversities?

Bearing this in mind, we aggregated the main mechanisms involved in the stresses of greatest impact in recent decades for agriculture. With this approach, we want to improve and increase the understanding of these processes. Advances in molecular genomic tools including MAS, QTL mapping, high-throughput DNA sequencing (including long read technologies), RNA sequencing (RNA-seq), chromatin immunoprecipitation sequencing (ChIP-seq), genome-wide association study (GWA study), genomic selection (GS), proteomics and metabolomics approaches, and CRISPR technologies are of fundamental relevance to understanding the complex mechanisms of abiotic stresses in plants and developing new resilient cultivars [136,145,157,193,194]. Although a myriad of new approaches have emerged in the last 20 years, it is probable that the integration of such analyses, rather than new techniques, will deliver the best approaches for plant breeding for abiotic stresses throughout this decade.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/stresses2010009/s1>, Table S1: Molecular approaches to develop resilient plants to abiotic stresses (drought, heat, and salinity).

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Abbreviations

WUE	water use efficiency
ABA	abscisic acid
ETC	electron transport chain
ROS	reactive oxygen species
ATP	adenosine triphosphate
NADH	nicotinamide adenine dinucleotide
TCA	tricarboxylic acid cycle
AOX	alternative oxidase
GABA	γ -aminobutyric acid
NO	nitric oxide
HR	hypersensitive response
PCD	programmed cell death
MAS	marker-assisted selection
GWAS	genome-wide selection
QTL	quantitative trait loci
PSII	photosystem II
RWC	relative water content
PGRs	plant growth regulator
OEC	oxygen-evolving complex
ASC	ascorbate
GSH	glutathione
SOD	superoxide dismutase
POX	peroxidase
CAT	catalase
GSH	glutathione
APX	ascorbate peroxidase
MDHAR	monodehydroascorbate dehydrogenase
DHAR	dehydroascorbate reductase
K	potassium
N	nitrogen
HSPs	heat shock proteins
GR	glutathione reductase
SA	salicylic acid
BRs	brassinosteroids
CK	cytokinin
JA	jasmonate
ET	ethylene
CuZn-SOD	copper-zinc superoxide dismutase
Ged	genome edition
RNA-seq	RNA sequencing
ChIP-seq	chromatin immunoprecipitation sequencing
GWA	genome-wide association
GS	genomic selection

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