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Article · October 2020

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Abiotic Stresses and Their Effects on Plant Growth, Yield and Nutritional Quality of Agricultural Produce

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How to cite this paper: Suresh Kumar. (2020) Abiotic Stresses and Their Effects on Plant Growth, Yield and Nutritional Quality of Agricultural Produce. *International Journal of the Science of Food and Agriculture*, 4(4), 367-378. DOI: 10.26855/ijfsa.2020.12.002

Received: September 3, 2020
Accepted: September 28, 2020
Published: October 14, 2020

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Abstract

Abiotic stresses, like extreme temperature, drought, flood, salinity, and heavy metals, are some of the major factors that limit crop productivity and quality. Abiotic stresses considerably affect the growth, development, and productivity of crop plants, such adverse environmental conditions may reduce the performance of the crop with reduced yield from 50% to 70%. Emission of greenhouse gases from different sources is believed to be one of the factors responsible for the gradual increase in the global ambient temperature (global warming). Global warming has also changed the precipitation pattern and contributing to erratic drought/flood stress. Abiotic stresses, particularly drought and heat stress, during the vegetative and reproductive stage of growth adversely affect biomass, grain yield, and quality of the produce. A combination of abiotic stresses, for example, drought and heat, have much greater effects on the yield and quality of the produce. However, responses of plants to these stresses may vary across the species, as well as at different developmental stages. Scarcity of water (drought) and higher temperature induces the stress-associated metabolic responses, and stomatal closure significantly decreases the uptake of CO₂. As a result, the reduction equivalents (e.g. NADPH + H⁺) for CO₂ fixation via the Calvin cycle declines considerably. Not only the photosynthetic process but also the biosynthetic processes involved in proteins, lipids, and minerals metabolism are affected by adaptive responses. As a consequence of these metabolic shifts, carbohydrate, protein, lipid, and mineral compositions are significantly affected by the abiotic stresses. Although the effects of abiotic stress on the yield of cereals and grain legumes are relatively well-understood, further research on the combined effects of abiotic stresses, abiotic and biotic stresses, and their effects on crop yield and nutritional quality of the produce needs to be undertaken. Molecular genetics of the stress responses and the tolerance mechanisms are likely to pave the way forward in developing crop plants that can withstand and give economic yield under the abiotic stresses.

Keywords

Abiotic stress, Climate change, Climate-resilient agriculture, Crop yield, Drought stress, Quality of produce

1. Introduction

One of the serious effects of global climate change has been a continuous decline in the availability and productivity of arable land [1]. A combination of abiotic stresses, such as drought and heat, salinity and heat, etc., has been known to

be even more destructive to crops than the individual stress alone [2, 3, 4, 5]. Not only these, but abiotic stresses are also known to influence the occurrence and spread of biotic stresses like insect pests, pathogens, weeds, etc. [6, 7, 8, 9, 10]. Reduced plant growth due to drought or heat stress is a frequent and common phenomenon world over. When both the stresses are combined, their effects on the yield of the crop are more severe than the effects of the individual stress [11, 12, 13]. Drought and heat stress are some of the problems for crop growth, development, yield, and sustainability of agriculture all over the world [14]. In the rainfed areas, effective rainfall and its distribution throughout the season are becoming highly variable, which has become a major cause of frequent drought stress in agricultural fields [15, 16, 17].

An increase in soil temperature, resulting from an increase in air temperature, becomes even more severe when it is accompanied by drought stress [5] [18] [19]. Under field conditions, water-deficit (drought) stress often occurs concurrently with high air temperature (heat stress), and now this has become a threat to agriculture and the sustainable food production world over [14] [20]. Severe stress(es) considerably affect(s) crop yield and quality. Under abiotic stress, plants face scarcity of essential factors and/or imbalanced nutrients that finally turn into decreased yield and loss of quality of the produce. Stresses also affect the accumulation of metabolites in plant's edible parts, sometimes positively by concentrating nutraceutical or stress-related metabolites which are appreciated as health-related compounds in human nutrition [21]. For example, the imposition of salt stress has recently been suggested as a potential stressor for enhancing the quality of fruits and vegetables [22].

Plants have evolved several strategies to cope up with the environmental stresses by prompt and harmonized changes at transcriptional and post-transcriptional levels, including the epigenetic regulation of gene expression [23, 24, 25, 26]. The plant uses a range of sensing and signaling mechanisms to provoke stress responses under the environmental stresses. Stress signaling involves several phytohormones to alert the plant quickly and efficiently to respond effectively [27]. Growing evidence indicates that epigenetic mechanisms are also involved in the regulation of gene expression at transcriptional and post-transcriptional levels [28]. Studies also indicate that heritable variations in economically important traits may also be caused by the underlying epigenetic variations [29, 30]. Several epigenetic mechanisms have been implicated to be involved in the regulation of stress-associated genes [31]. Epigenetic changes refer to the heritable variations in gene expression resulting from the modifications of DNA and its associated chromatin structure, of course without changing the underlying nucleotide sequence [32]. Among these epigenetic mechanisms, DNA methylation is currently the best understood. DNA (de)methylation plays an important role in (de)activating the specific genes in response to environmental stress or during developmental processes [33]. Genetic engineering for the development of stress-tolerant plants through epigenetic manipulation would require proper selection of the target sequence/gene. Artificial siRNA from the targeted gene can be utilized for the purpose. As methylation machinery of the host cell also plays an important role in DNA methylation, over-expression/silencing of methyltransferase genes and the other key factors like siRNAs can be combined. Although, these assumptions need to be validated. Further, understanding the epigenetic mechanisms of gene regulation will provide the basic information necessary for epigenetic engineering [34], and a valuable platform for potential applications of epigenetic engineering of plants towards enhanced tolerance to the environmental stresses. Therefore, deciphering the epigenetic mechanisms of gene regulation has become an important area of scientific investigations towards unraveling the mechanisms used by plants to tackle environmental stresses, survive under unfavorable conditions [24] [35]. Some of the plants (crop plants) have evolved to survive, reproduce, and produce edible (vegetative and/or reproductive) parts as food/feed of satisfactory quality to feed the burgeoning global animal and human populations [36]. The present review aims to emphasize the need to improve combined stress tolerance to several abiotic and biotic stresses in crop plants. For this purpose, the use of the package of practices, breeding approaches, biochemical, physiological, and/or molecular strategies are suggested to minimize the yield losses and improve the quality of products under field conditions.

2. Abiotic Stresses Affect Productivity and Quality

Most of the arable lands world over is prone to one or more of the abiotic stresses, which cause yield losses of up to 70% in many crops. According to an estimate, the ongoing climate change would enhance the intensity of the abiotic stresses which might more severely affect the productivity of crops that will have serious consequences on food security [37, 38]. Extreme temperature, water stress (drought and flood), salinity, and heavy metal stress are some of the major environmental factors that affect growth, development, and yield of crop plants [38, 39]. The concurrent and frequent occurrence of abiotic stresses is more destructive for food security. These are not only limited to abiotic environmental factors but also increase susceptibility to biotic stresses. Abiotic stress like drought enhances competition between weed and crop plants as several weeds show better water use efficiency compared to that of crops [40, 41]. The effects of combined stresses on crop plants are not always additive; it might be subtractive also, particularly when certain abiotic and biotic stress occur simultaneously, as the nature of the interaction between the stresses determines the outcome [10] [42, 43]. This involves morpho-physio-biochemical interactions between the stresses. Abiotic stresses not only affect

the productivity of the crop, but also affect the quality of the produce.

2.1 Extreme temperature

A gradual rise in the frequency and intensity of extreme temperatures are being observed [44]. Extreme temperature stresses like heat and freezing/cold/chilling stress have severe effects during critical stages of plant growth and development [45]. When the ambient temperature increases beyond a level, which causes damage to plant growth, it is known as heat stress. The deleterious effect of heat stress is a complex function of intensity, duration, and rate of increase in temperature, and a significant (5-15°C)/quick increase in temperature is more deleterious. Heat stress affects the biochemical and physiological functions of the plant by modulating molecular mechanisms [46, 47]. For example, *AtSUT2* is down-regulated under heat stress in Arabidopsis [48], and *PtaSUT4* is up-regulated under heat stress in poplar [49] which is correlated with reduced sucrose transport from leaves. Similarly, *OsSUT1* is down-regulated under heat stress in rice, and affect grain quality [50]. Higher temperature reduces germination of seeds and affects stand establishment of the crop. Moreover, the adverse effects of increased temperature vary with the duration and severity of the heat stress along with the developmental stage of the crop. Heat stress was reported to reduce the number of spikes/florets in rice [51]. Thus, high-temperature stress affects the yield of crop plants. The quality of the produce is also adversely affected by heat stress as it reduces starch and protein contents.

Low temperature/cold stress also affects biochemical and physiological activities in plants, and thus yield and quality of the produce. Lower temperature disturbs membrane structure, protoplasmic streaming, and cause electrolyte leakage/plasmolysis [52]. Freezing temperatures stress affects mineral acquisition, photosynthesis, respiration, and metabolism. Responses of plants to low-temperature stress are associated with the change in transcription of the genes associated with the production of several low molecular weight proteins.

2.2 Water Stress

Water stress includes its deficiency or excessive presence in the environment. Excessive water or flooding can be of two types, waterlogging (when water covers the root) or submergence (when water completely covers the plant, even aerial tissues). Both types interfere in oxygen availability to plant causing low-oxygen/hypoxia [53]. Flooding stress triggers significant changes in the molecular process, which help to coordinate morphological and physiological adaptations to the stress. In Arabidopsis, five *ERF* (ethylene response factor) genes were identified to be the key regulators for flooding and hypoxia tolerance [54]. *ERF-VII* TF, *SUB1A*, is known to be a master regulator of submergence tolerance. A submergence-tolerance *SUB1A* gene expresses during the submergence condition only, and its transcript disappears quickly after the withdrawal of the flooding condition [55]. Studies demonstrate the involvement of physiological, genetic, epigenetic, and molecular mechanisms in providing flooding tolerance in plants [56].

On the contrary, drought stress involves a shortage of water availability for the plant which significantly affects growth, development, and yield of the crop. Drought can also be of two types: physical drought (deficiency of water due to its unavailability) and physiological drought (failure of the plant to take up water from the soil because of various physiological reasons like salinity, freezing, etc.) [57]. Under drought stress, humidity in the atmosphere is also very low, and the increased temperature makes the problem more severe. Co-occurrence of stresses, such as drought and heat stresses, is a common incident during the summer season. Moreover, the repetitive occurrence of abiotic stress, for example, the incidence of drought stress, is becoming a common feature due to global climate change. Furthermore, the occurrence of the contrasting stresses, like drought and flood stress appearing one after another in the same area or simultaneously in different areas, is becoming frequent. Combined stresses are more detrimental to the yield and quality of the produce. Therefore, understanding the regulatory mechanisms and how they protect plants from stresses has become vital to enhance the yield and quality of the produce in the changing climatic conditions. The modern advances in “omics” technologies provide momentum to the research in this area [58, 59, 60].

2.3 Salt Stress

Salinity stress appears due to increased content of salts in the soil, which mainly occurs because of a higher rate of evaporation/transpiration compared to the precipitation. Salinity stress is becoming one of the serious problems in several parts of the world, especially in the arid and semiarid regions. Salt stress is taking a serious dimension in the areas where saline-sodic water is being used for irrigation. It has been estimated that one-third of the food production of the world comes from irrigated lands, but ~20% (about 45 million hectares) of the lands are affected by salinity stress which reduces > 50% of the potential yield of annual crops [25]. The damage further intensified by the synchronized action of multiple stresses including drought, and heat stress [61]. Some of the significant impacts of salt stress on crop plants include ionic toxicity and osmotic stress. Like other abiotic stresses, salt stress causes reactive oxygen species (ROS) generation that damages several biomolecules like lipids, proteins, and nucleic acids which alters redox homeostasis [26]. Salt stress has some adverse effects on cellular growth, membrane functions, and cytosolic metabolism. Ul-

timately, it adversely affects the quantity and quality of the produce. Plants deploy different mechanisms to sense, respond, and adapt to salinity stress, including morpho-physiological, biochemical, epigenetic, and molecular mechanisms [29]. The profuse root system is important to provide salt stress tolerance to crop plants [62].

2.4 Heavy Metal Stress

Plants take up most of the nutrients from the soil for their growth and development. The increasing contamination of soil with heavy metals has become one of the important reasons for the loss in crop productivity [63]. Crops are frequently subjected to heavy metal toxicity due to irrigation with contaminated water and excessive application/use of chemical fertilizers/pesticides. Industrial waste disposal, burning of solid/liquid fuels, domestic garbage disposal, and other activities in the developing countries cause heavy metal contamination of soil and water. Some of the potentially toxic heavy metals like Zn, Fe, Cu, Co, Se, and Ni are essential microelements required for the optimal performance of crop plants. However, they become toxic when accumulated in excess in soil [64]. Certain non-essential elements like arsenate (As), cesium (Cs), lead (Pb), and cadmium (Cd) hamper the growth and productivity of crop plants when present in soil [65]. More importantly, heavy metal contamination in the soil leads to the accumulation of these toxic metals in plant parts, resulting in increased risk to animal and human health [66]. Cd toxicity adversely affects cellular molecules, thereby growth of the plant, resulting in reduced leaf area, decreased shoot/root growth, and crop yield [67].

3. Effects of Abiotic Stress on Plant Growth

Growth and development of an organism are accomplished through enlargement division and differentiation of cells and involves ecological, genetic, physiological, biochemical, and morphological events and their complex interactions. Some of the important growth parameters in the assessment of crop growth include plant height, leaf area, root growth, biomass production, etc. The plant growth depends on the environmental factors including nutrients and water supply, abiotic and biotic stresses. Cell growth is considered as one of the most stress-sensitive physiological processes because of the reduction in turgor pressure. Under severe drought, cell elongation in higher plants gets repressed due to the disruption of water movement from xylem to the surrounding elongating cells [68]. Under abiotic stress, the compromised mitotic cell division, cell elongation, and expansion result in decreased plant height, leaf area, biomass production, and finally reduced yield and quality of the produce [69, 70]. During water-deficit stress, a considerable decrease in root biomass can be seen [18]. Primary effects of abiotic stresses like drought and salinity are reduced germination of seeds and poor establishment of crop plants [69]. Drought stress combined with heat stress significantly affects nodule formation and activity; hence affects the biological nitrogen fixation and yield of the crop. Siczek and Lipiec [71] observed that mulching considerably improved soil moisture content which resulted in improved nodule formation, nitrogenase activity, symbiotic nitrogen fixation, and the crop yield.

Interestingly, some positive effects associated with water stress may also be observed. Water-deficit stress encourages secondary metabolite production, thus potentially increasing plant immunity and the level of the compounds involved in improving quality, taste, and the health benefits of certain plant products. This is also considered as one of the factors behind stress memory (in addition to epigenetic memory), and stress priming. The role of drought in the production of secondary metabolites in some fruit crops is of vital importance. ABA has been known as a key chemical stress-signal from root to shoot [72]. During abiotic stresses, ABA is produced by roots and transported through the xylem to the shoot where it affects leaf expansion and promotes stomatal closure to regulate water potential and nutrient status in leaves. ABA biosynthesis gets stimulated by a decrease in soil water and plant turgor. A study on wheat under water-deficit stress by Yang *et al.* [73] suggested that ABA and cytokinins are involved in controlling senescence and carbon remobilization in plants. Another study on wheat suggests that grain-filling in wheat gets improved due to the increased ratio of ABA to ethylene [74]. In general, stomatal regulation is considered as the first step to deal with the drought stress by retaining enough cell turgor to manage cellular metabolism in plants. However, little is known about how shoot-subjected stresses affect root growth.

3.1 Effect of Abiotic Stress on Photosynthesis

Photosynthesis is adversely affected by environmental stresses. Photosystem II (PS II) is more vulnerable to heat stress than drought stress due to exclusion of PS II in thylakoid membranes resulting in the interruption of rubisco activase [75]. The effects of the abiotic stress also vary in C₃ (e.g., wheat) and C₄ (e.g., maize) plants. C₄ plants are considered to be more sensitive to drought stress, probably due to stomatal closure and decrease in the activity of the photosynthetic enzyme [76]. However, the effect of heat stress on the photosynthetic capability is stronger in the C₃ plant compared to that in the C₄ plant due to the diverse energy distribution and actions of carbon metabolic enzymes, particularly rubisco [77]. Regardless of any change in stomatal conductance, abiotic stress reduces photosynthetic activity in the plant under stress [78]. A decrease in the photosynthetic activity under drought and heat stresses are frequently attributed to lowered internal CO₂ concentration, inhibition of enzymes involved in photosynthesis [79]. Therefore,

plants decrease their growth as an adaptive response to the stress, rather than as a consequence of resource limitation [12].

Under abiotic stresses, excessive production of ROS, such as singlet oxygen, superoxide radical, hydrogen peroxide, hydroxyl radical, cause membrane injuries [80], protein degradation [58], enzyme inactivation, and thus give rise to the oxidative stress [79]. Denaturation of proteins/enzymes, increased fluidity of membrane lipids, inactivation of enzymes, reduced production and degradation of proteins, disturbed membrane integrity, and damage to DNA are some of the cellular injuries caused by the abiotic stresses [23] [81] (Figure 1). Heat stress also affects ion flux leading to the biosynthesis of toxic compounds and ROS. Prolonged exposure to heat stress causes a decrease in chlorophyll content, increased amylolytic activity, disintegration of thylakoid, and disruption of assimilate transport. Even moderately higher temperatures for a longer period or very high temperatures for a short period may cause severe cellular injury or death of the plants [82]. To minimize the cellular damage, the affected plant produces enzymes, phenolic compounds, flavonoids, anthocyanins, lignins, and other molecules to fight against the deleterious effects and to manage the oxidative stress [79] [83]. Expression of heat shock proteins is an important strategy of plants to improve heat tolerance (thermo-tolerance) through maintaining photosynthesis, water, and nutrient use efficiency [84], and cellular membrane stability [85]. Thus, abiotic stress affects photosynthesis and partitioning of the photosynthate. This also affects the harvest index due to the disturbed transport of photosynthate to the grain.

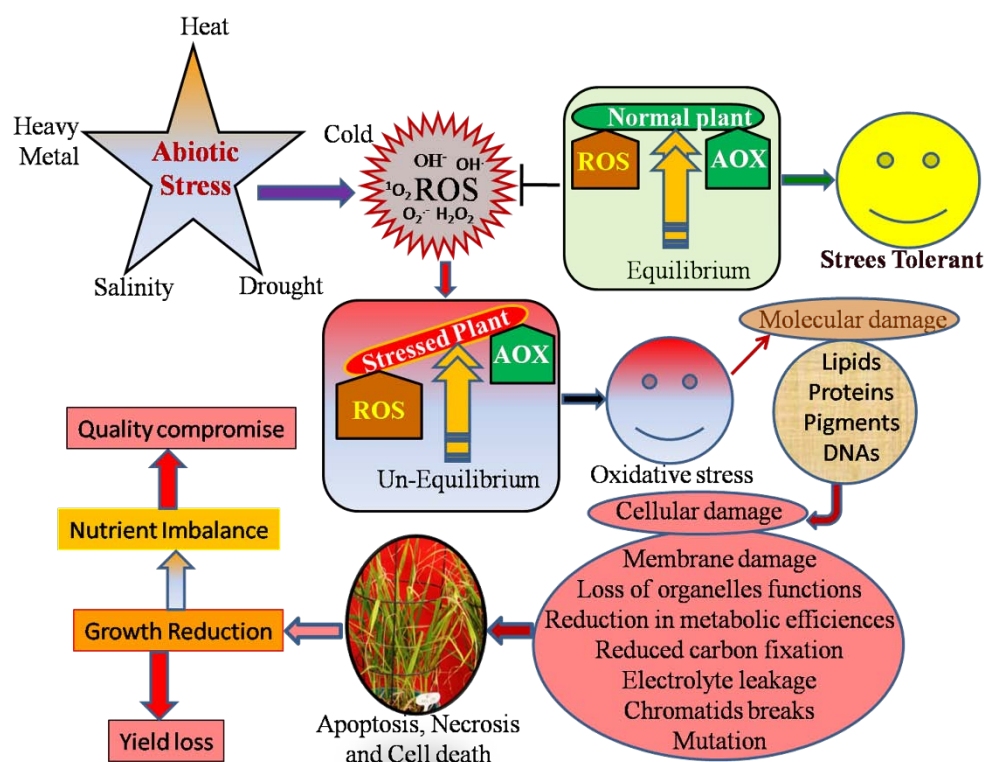


Figure 1. Effects of abiotic stresses on plants productivity, yield and quality of the produce.

Reduced activity of acid invertase can arrest the development of reproductive tissues due to improper phloem unloading. Besides, abiotic stresses, particularly drought stress, may inhibit important functions of vacuolar invertase-mediated sucrose hydrolysis and modulation of osmotic potential. In maize, low invertase activity in the young ovaries lowered the ratio of hexoses to sucrose under drought stress. This resulted in reduced cell division in the developing embryo/endosperm affecting the sink intensity and abortion of the embryo [86]. Abiotic stresses, particularly heat stress, significantly affect the plants growing in tropical and subtropical climates. The increasing temperature may alter the geographical distribution, growing duration/season of crops due to changes in the appearance of threshold temperature for proper germination of seeds (the start of the season) and that for the maturity of the crop [87].

3.2 Effects of Abiotic Stress on Productivity and Yield

Reduced shoot growth, a decline in the number of tillers in response to water-deficit is considered as a strategy of the plant to reduce the expenditure of water during the stress [88]. It has been reported that early heading in response to

heat stress is advantageous in retaining more green leaves at anthesis, leading to the minimized reduction in yield [57]. Studies on different plant species have indicated that high temperature (heat stress) is more harmful at the reproductive/gametogenesis stage of crop growth [82]. Heat stress significantly disrupts the anatomy not only at the tissue and cellular levels but also at the sub-cellular levels. At the sub-cellular level, the major disruptions include deformation of the chloroplast, swelling of stromal lamellae, lumpiness of vacuoles, which result in the altered structural organization of thylakoids and formation of antenna depleted PSII and thereby reduce photosynthetic and respiratory activities [89]. Ultimately, all these changes due to abiotic stress may lead to poor plant growth and productivity of crop plants.

Yield reduction due to drought stress has been reported in many crop species, which depends on the severity and duration of the stress. Water plays an important role in the mineral nutrition of plants since most of the nutrients from the soil are mobilized with the movement of water. Disturbance in the Na^+/K^+ ratio results in membrane damage, poor membrane stability, and disturbed ionic homeostasis [90]. Water-deficit stress may cause about a 50% decrease in the Ca^{2+} concentration which is important for in maintaining the integrity of cell membranes and other structures in shoot and root. Besides, water-deficit stress affects nutrient metabolism by inhibiting activities of nitrate reductase and glutamine synthetase involved in the intracellular assimilation of ammonia into organic compounds [91]. In barley, drought stress caused a decrease in the grain yield by reducing the number of tillers, spikes, and grains per plant as well as the grain weight. In maize, the stress decreases the yield by delayed silking, thereby increasing the anthesis to the silking period [92]. After flowering, drought stress had a lesser effect on grain filling in wheat, but it shortened the maturity (fertilization to maturity) period [93]. Drought stress during reproductive growth reduced cotton lint yield due to reduced boll formation and greater boll abortion [94].

The biological yield of plants under unfavourable environmental conditions is affected due to the inefficient physiological and biochemical activities. During grain filling in cereals and pulses, four enzymes play critical roles which include sucrose synthase, adenosine diphosphate-glucose-pyrophosphorylase, starch synthase, and starch branching enzyme. While reduced sucrose synthase activity results in a decreased rate of grain development, inactivation of adenosine diphosphate-glucose-pyrophosphorylase in wheat was reported to interrupt the growth due to drought stress [95]. Heat stress during grain filling may alter nitrogen supply/concentration in grain legumes [18], reduced starch, protein, and oil contents in wheat and maize [96, 97] which affect not only the yield but baking quality of wheat flour.

3.3 Effect of Abiotic Stress on Quality of Produce

Providing food to the burgeoning global population is a preliminary challenge today; however, a major challenge being faced is to produce safe and nutritious food under the increasingly unfavorable environmental conditions [98, 99]. Global climate change is expected to further worsen climatic conditions which will not only affect the productivity of the crops but the quality of the produces also. Therefore, we must not only bother about producing sufficient food to feed the burgeoning global population but also to produce nutritious foods to provide a healthy diet [99].

An increase in protein content at the grain formation stage has been reported by some of the workers which were explained based on an increase in the amount of starch in response to the abiotic stress. In wheat, decreased quality of gluten content, glutenin content, gliadin content, grain hardness, but increased protein content-indexes in wheat under drought and salt stress was reported [100, 101]. Hoegy *et al.* [102] reported the effect of increased soil temperature (2.5°C) causing increased protein content, particularly the content of aspartate, glycine, alanine, arginine, valine, and tryptophan in barley. The effect of heat stress on yield and grain quality of wheat was studied 18 days after anthesis, and it was found that the stress reduced grain mass by 23%. Not only this, but the stress also reduced nitrogen content by 16% in the grains. But the decrease was less than the reduction in grain yield; the net effect ultimately turned into an increase in protein content in the grains. Interestingly, a significant increase in the number of proteins in the filling grain was observed shortly after the withdrawal of the stress [103]. Dwivedi *et al.* [104] reported that mid-season drought had no effect on protein content in peanut, but the end-season drought significantly increased the total protein content. In the case of rice, high temperatures during the early grain filling stage increased the accumulation of storage proteins but decreased the accumulation of prolamins at maturity [105].

In soybean seeds, carbohydrate composition considerably changes with increasing day/night temperature (18/13°C to 33/28°C) [106]. Higher temperature (37/17°C) during flowering/grain filling caused a significant reduction in the duration for starch accumulation in wheat, this duration is generally longer in the plants grown under normal (24/17°C) temperature. Heat stress (37/28°C) was observed to shorten the starch accumulation period by 21 days compared to that in the control plant, which also increases the proportion of A-type starch granules but decreases the B-type granules [107]. The impact of abiotic stresses on non-structural carbohydrates is important in two aspects that determine the quality of the produce. Quantity, as well as quality of carbohydrates, are important in the crops which are used in food processing, fermentation, etc. The major factor contributing to the reduced starch concentration appears to be the inhibition of starch synthase enzyme in the maturing grain, resulting in the impeded conversion of sugars to starch. Increased starch concentration was observed in potato tubers under salinity and heat stress [108]. In contrast, increased sucrose

concentration, but the reduced starch formation was observed under drought stress in potato [109]. Interestingly, abiotic stresses were also found to affect the amylose/amylopectin ratio in the starch of cereal grain and tuber. Water-deficit stress during the grain filling decreased the amylose component of wheat starch, which was explained with the inhibition of granule bound starch synthase (GBSS) activity (an enzyme involved in amylose synthesis) [110]. In contrast, high temperatures led to an increase in the proportion of amylose in wheat [111], potatoes [112], and sweet potatoes [113]. These changes in heat-induced starch composition might also be attributed to the altered activity of the enzyme GBSS [113].

Oil content in soybean was found to be positively correlated with increased temperature (25°C to 36°C) [106]. Thomas *et al.* [114] investigated the effects of heat stress on the composition of soybean seeds and found the oil content to be highest at 32/22°C day/night temperature, and a decreasing pattern with further increase in the temperature. Oleic acid content increased with the increasing temperature, whereas linolenic acid content decreased. A similar result was also observed in sunflower by Izquierdo *et al.* [115]. Heat stress has a general effect on reducing the amounts of accumulated lipids, particularly non-polar lipids. Besides, unexpected qualitative changes (such as the increased apparent conversion of oleate to linoleate) were observed at higher temperatures [116]. Such alterations may significantly influence the milling properties of wheat and baking quality of the flour. Heat stress (especially when coupled with drought stress) is often associated with the production of smaller, more fibrous leaves, which usually affect nutritional quality like decreased N and increased tannins and phenols [117]. A significant decrease in the proportion of PUFA was observed under drought stress in the oil fractions of sunflower [118], groundnut [103], under salt stress in sunflower [119], and under heat stress in soybean [120]. In many of the cases, the observed decrease in PUFA (especially linoleic acid) was consistent with an increase in the proportion of oleic acid [121].

The effect of abiotic stress on the dietary fiber content of wheat and barley was reported to decrease β -glucan content. Studies on three wheat cultivars under heat, drought, and the combined effects of heat and drought were found to cause decreased β -glucan content in grains which is associated with the decrease in the ratio of short to long-chain gluco-oligosaccharides [122]. As water plays an important role in mineral mobilization in plants, drought stress reduces the uptake of Fe, Zn, and Cu from the soil, resulting in decreased concentration of these minerals in grain [123]. However, severe water-deficit stress was reported to significantly increase Ca (28%), Mg (11%), Cu (18%), and Zn (33%) content in maize [124].

4. Conclusions

Reduction in biomass production by crop plants is the most apparent and widely recognized effect of abiotic stresses, which results in quantitative and qualitative yield losses. The need of the day is not only to focus on increasing the yield but the quality of the product also, through breeding programs and agronomic practices to mitigate the effects of abiotic stresses. Reduced biomass production is often the result of reduced photosynthetic carbon assimilation; hence the concentration of many other components tends to increase, leading to higher crude protein and mineral concentrations. Stress-induced stomatal closure decreased transpiration rate, and impaired photosynthesis activity (particularly due to the effects on PS II and photosynthetic enzymes) lead to early crop maturity and poor productivity. In the case of leguminous plants, abiotic stresses decrease nodule formation and nitrogen fixation activities. Other responses include the accumulation of certain compounds of low molecular mass (like proline). While biochemical and physiological effects of abiotic stresses on crop yield are relatively understood, further research on their effects on the quality of the produce is needed. Molecular knowledge of the responses to abiotic stress is likely to pave the way for tailor making the crop plants to withstand the climatic changes and provide satisfactory economic yields. However, a multi-disciplinary research effort would be required to integrate genotypic, phenotypic, proteomic, transcriptomic, epigenetic and metabolomics data to understand the networks that lead to the quality attributes. This would help in devising better strategies to design climate-resilient crop plants to cope with the effects of global climate change.

The views expressed herein are those of the author only, and these may not necessarily be the views of the institution/organization the author is associated with.

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Chapter 2

Plant Abiotic Stress Tolerance Mechanisms



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Abstract In their life cycle, plants face a range of environmental stresses such as heat, cold, drought, salinity, etc., which greatly affects the performance of the plant and is one of the key factors in the distribution of plant species. Plants use special mechanisms to withstand these stresses. When plants are exposed to stress, the information is transmitted by the signal transduction pathway, and eventually, the response to these signals leads to physiological and biochemical changes in the plants. Usually, one type of stress is accompanied or followed by other stresses. For example, heat stress is followed by drought stress due to physical loss of water, and cold stress is followed by drought stress due to the physiological inaccessibility of water. Due to the large number of environmental hazards that the plant faces at a particular time, abiotic stress signaling is a very complex phenomenon. Plants have tools to avoid and deal with these stressors. On the one hand, they can produce inductive and appropriate responses that lead to a specific desired change for which special stress conditions are specialized. On the other hand, there is a significant overlap between the components of abiotic stress signaling and the starting points in which the pathways for stress signaling are coordinated. In this chapter summarized, how abiotic stresses in plants can be tolerated.

Keywords Adaptation · Antioxidant · Crop productivity · Drought · High temperature · Osmolytes · Transcriptome analysis

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2.1 Introduction

Growth and productive capacity of plants are adversely affected by abiotic stress worldwide. If environmental stresses did not occur, the actual yields would have to be equal to the potential yields of the plants. While in many crops the average yield of plants is 20–30% of their actual potential. Given their sessile nature and prevalence of abiotic stress, plants have evolved a plethora of tolerance mechanisms at macro and micro levels. They are often diverse from morphological to physiological and molecular changes that subjection to each abiotic stress initiates a cascade of resistance mechanisms across various levels (Grift et al. 2011; Sinclair and Muchow 2001).

This chapter deals with major abiotic stresses in plants, explores ways in which plants can cope with these stressors, and summarized how abiotic stresses in plants can be tolerated.

2.1.1 *Morphological Flexibility Conferring Abiotic Stress Tolerance*

2.1.1.1 Water Stress

Ample of survival strategies enable the plant to complete their life cycle by escape or avoid the harsh environment, which the former strategy encourages the plant to shorten the vegetative growth and enter the reproduction stage to yield seeds to take advantage of the current water resources that would not available by the onset of the drought period. Therefore, by producing progenies as primary goals before the arrival of fatal drought several plant species mostly early maturing inhibited in desert environment opt to escape while having complete reproduction (Fahad et al. 2017; Farooq et al. 2012). Whereas some other species choose to develop more sophisticated techniques to avoid dehydration with structural modification in favor of drought tolerability. These changes either minimize the rate of water loss from aerial parts or maximize the capability of the root system to uptake water that in both scenarios the main motive is to maintain a high water status so the growth and development can continue (Blum 2005). Reduction in biomass production under drought stress has been observed in various species with significant variation between aboveground and underground parts; also, decrease in the biomass of vegetative parts does not necessarily mean the absence of change or increase in root system biomass. As Xu et al. (2015) observed in rice that increases in root/shoot ratio was because of higher reduction rate in shoots not increasing the biomass of roots. The correlation between the root and shoot biomass was positive in drought-tolerant chickpea cultivars as higher biomass in aboveground was accompanied by high biomass production in root system which is a successful adaptation strategy to absorb water and nutrient through an extensive root system (Rahbarian et al. 2011). Changes in root architecture

are essential to tackle the crisis caused by drought, which is normally involved in increasing the number of main roots and fine roots, the rapid expansion of root system to the upper layer of soil and enhancing root diameter and tissue density. Most importantly, deep roots greatly contribute to improving the water relation on drought-affected plants as their positive contribution in various crop plants exposed to drought have been observed such as rice (Manschadi et al. 2010; Wasson et al. 2012), maize (Hussain et al. 2019), and wheat (Krishnamurthy et al. 1999). Improvement in root length density up to 30 cm in the function area of root resulted in increased water and mineral nutrient absorption in chickpea subjected to drought stress (Sadok and Sinclair 2011). On the other hand, an extensive root system should not be considered advantageous constantly because a larger a root is the greater portion of allocated assimilated material for its maintenance will be, which can partially responsible for a decrease in aboveground biomass (Bramley et al. 2009; Li et al. 2010). Significant structural modification in leaves to avoid water deficit takes place in drought-stressed crop plants including reduction in volume of leaf as a prominent source of losing water. This modification has been known as an effective approach to resist water deficit by minimalizing water loss through transpiration; however, it penalize the productivity with low carbon assimilation efficiency (Lei et al. 2006; Sinclair and Muchow 2001). Additionally, enhancement in cuticle thickness, stomatal resistance, stomatal size and the last but not the least inclination of leaves toward vertical angles or rolling are other ways to lower the light interception and water consumption under drought stress (Sinclair and Muchow 2001).

A range of morpho-anatomical adaptation in plants to survive under flood stress have been developed to mitigate limitations caused by flood in particular reduction in CO₂ and exchange of gases overall. Several effective strategies exist that among them formation of novel roots with gas-filled spaces (aerenchyma) as result of cell separation or programmed cell death, is a characteristic common in numerous plant species provide oxygen for organs in plants submerged underwater as rice that creation of aerenchyma is by the termination of specific cells. Such adaptation enhanced the oxygen transport in rice effectively where submerging underwater prevents oxygen transfer (Cardoso et al. 2013; Colmer 2002; Drew et al. 1979). The capability of the root system to leakage oxygen to the anaerobic soil oxidizing the rhizosphere, therefore, reducing possible damages from reduced toxins like Fe²⁺ (Colmer 2002). In some crops such as maize, creation of aerenchyma can be induced with a reduction in oxygen and increase of ethylene which leads to initiating programmed cell death for cells in root cortex (Drew et al. 1979). Additionally, root architecture that confers adaptability to flooded plants exhibits less-branched main roots, large root diameter and deep roots (Aguilar et al. 2003, 2008; Visser et al. 1997). While in woody species the adaptations are to some extent different and it seems there is a positive correlation between drought tolerant with flood-tolerant as Sena Gomes and Kozlowski (1980) observed in *Eucalyptus* spp. In maize, if the shoot base submerged in water, the formation of aerenchyma in outer leaves may occur (Matsukura et al. 2000). The number of aerenchyma formed in flood stressed wheat affected by the level of tolerance in genotypes in which resistance genotypes had a higher number of aerenchyma (Johnson and Huang 1996). Obviously, owing to the organizational interconnection

between the root system and aerial parts, the flood also affects the photosynthesis apparatus through depleting root area from oxygen and limiting the function of roots to uptake water, thus creates a drought-like condition, wilting leaves and consequently damages carbon assimilation. Further, N deficiency is common under flood stress but to tackle this problem, at least for a short-term, plants attempt to relocate N from older leaves to young leaves in order to continue growth (Drew and Sisworo 1977). Sometimes changes in leaves to resist water loss in crops under flood involve downward movement of leaves (epinasty) to lower the interception with light, this behaviour has been observed in tomato (Ellsworth and Freebairn 1969).

2.1.1.2 Extreme Temperature

A simple definition of thermos-tolerability of crops plant is the potential to endure heat stress, grow, develop and provide an economically reasonable yield, which candidate crop plants possibly morphologically enabled to stabilize its internal temperature just below the irreversible point where damages are terminal under heat stress. Such mechanism is achievable through changes similar to adaptation detailed earlier for drought stress as leaf rolling, change in leaf orientation to reduce the light absorption, reflecting solar radiation and regulating stomatal behavior as well as a promoted cuticle and wax layer on the surface of leaves to enhance stomatal resistance (Grift et al. 2011). Additionally, the capability to maintain photosynthesis activity, distribution of the fixed carbon and absorption of necessary minerals are also characteristics of tolerant crop cultivars (Cui et al. 2006; Grift et al. 2011). In wheat crops, rolling of flag leaf is to lower the temperature and consequently transpiration to improve the yield of photosynthetic activity (Perkons et al. 2014). The implication of escape-like strategies in plants inhabited areas with extreme fluctuation in temperature has been observed, these species commonly tend to early maturation and seed production before the arrival of heat stress period which is unavoidably has a drought in the company as well (Trachsel et al. 2009). To enhance the radiation use efficiency as well as saving the limited water resource some plants incline to form thinner blade leaves with reduced weight and prostrate growth habit (Richards 1996). A usual procedure in the plant to reduce the temperature and prevent heat stress damage is to promote transpiration. Employ this strategy requires deep root system to support the water use lowering the temperature in the canopy by transpiration proven to be effective as Chauhan et al. (2009) stated that tolerance of heat stress in wheat genotypes observed in those with lower temperature canopies when compared to genotypes with higher temperature canopies. Likewise, the positive features reported in tetraploid wheat had a higher yield (Bahar et al. 2008). A potent root system with branched yet deep main roots can uptake water and mineral nutrient that are highly in demand when the plant is challenged by heat or drought stress. On the adaptation strategy in crop plants against cold stress, we did not find any relevant information or published research indicating specific morphological adaptation in crop plant under low temperature possibly because cold stress resistance

mechanisms in crops chiefly rely on physiological and molecular approaches as a quick relief to survive the suboptimal temperature.

2.1.1.3 Salinity

Salinity exerts multiple negative impacts on plants fitness. Plants have evolved with numerous morpho-anatomical adaptation strategies in their root system and aerial parts. The changes regarding morphological features in this section mainly concerns salt tolerance plant species that are not considered crop plants since these adaptations at this level mostly but not always have been seen in plant species inhabited in saline waters or areas with high salt content and dry soils. Halophytes (salt-tolerant plants) and glycophyte (e.g., are halophytes that only tolerate a low level of salinity) are mainly monocotyledon families and in some cases belong to dicotyledonous (Rozema 1991; Sharma et al. 2016). Since salinity is accompanied by extreme water deficit in soil root system architecture is more similar to the species adapted to drought stress and are deep, extensive, high length density and diameter as well as higher root weight. Enhanced root weight was recorded in grasses subjected to salinity (Seregin and Ivanov 2001). Maintaining biomass biosynthesis rate is associated with salt resistance, comparing salt-tolerant plant species *Leptochloa fusca* L. and *Puccinellia distans* with *Pennisetum divisum* L. as salt intolerant indicated a significant reduction in biomass of the latter species (Ashraf and Yasmin 1997). More, increasing, or maintaining the mesophyll area per leaf area in the tolerant species such as *Atriplex patula* L. provide the possible capability to protect photosynthesis apparatus against salt-induced terminal effects, unlike two glycophyte species *P. vulgaris* and *Gossypium hirsutum* that the ratio of mesophyll area significantly reduced. Longstreth and Nobel (1979) developing salt glands to secrete salt ions is probably the most common approach in halophytes which as an adaptive mechanism their density intensified in *Zoysia* spp. that improved salt tolerance and continued with the removal of those glands (Marcum et al. 1998). Another approach that some plant species enabled themselves to tolerate salinity under drought conditions is to collect water from the scarce resources into thick halo-succulent leaves to sustain the water status. Densely covered leaves with pubescence are specific to xerophytes and can help halophytes to lower the water loss and sustain growth and development in drylands with high salinity (Marcum et al. 1998).

2.1.1.4 Heavy Metal

The extensive array of adaptation mechanisms either avoidance or tolerant heavy metals have evolved, the studied survival mechanisms implemented by plants to protect the leaves or roots from lethal effects of heavy metals are mainly biochemical and molecular, and to this day a little attention has been paid to morpho-anatomical adaptations in plants against heavy metals (Shahid et al. 2017). However, the importance of some modification and organs in plants explored that found to be associated

with heavy metal tolerance, for instance, leaf cuticular structure where heavy metal ion can penetrate and accumulate (Vu et al. 2013). Or symbiosis relationship with mycorrhizal fungi which as frequently has been observed serves the roots of hosts with limiting the mobility of metal ions while assisting the host with the uptake of essential nutrients to form soil matrix (Jentschke and Godbold 2000), in inoculated maize roots with a strain of *Glomus* sp. The concentration of heavy metal ions was significantly reduced by comparison to non-inoculated seedlings (Kaldorf et al. 1999). The preventative effect of fungi strains reported to vary from one species to another and several mechanisms have been suggested on the influence of symbiotic relationship with mycorrhiza with a reduction in transportation of heavy metal ions to aerial parts (Hall 2002), perhaps a combination of different mechanisms are involved.

2.2 Positive Physiological Modification to Tackle Abiotic Stress

Continuum of growth and development to reach productive stage is the prime intention of plants experiencing abiotic stresses. In addition to morphological changes, they resort to physiological modification enable them to maintain the vital water status by implicating osmotic regulation besides controlling and detoxifying the consequences of ROS-generated oxidative damage (Fig. 2.1) (Hasanuzzaman et al. 2013).

2.2.1 Antioxidants

The imbalanced water status leads to a reduction in photosynthesis activity owing to stomatal closure. An approach to prevent water loss through transpiration which by limiting carbon influx carbon reduction is in Calvin cycle declines that as result the electron acceptor in the photosynthesis process, oxidized NADP⁺ is decreased (Blokhina et al. 2003; Wilson et al. 2014b). By excessive decline in iron-sulfur proteins in the course of electron transfer through a reaction process known as Water-Water Cycle or Mehler reaction harmful ROS are created such as O₂^{•-} and H₂O₂ in the chloroplast, peroxisome, and mitochondria. This process starts a detrimental knock-on-effect leads to oxidative stress and peroxidation of lipids in the membrane, structural damage to proteins and large molecules, also more potent ROS like single oxygen (¹O₂) and •OH. Despite the detrimentally of ROS and their overproduction under stress condition, plant armed with effective enzymatic and non-enzymatic antioxidants to quench these lethal ROS, antioxidant defense system suggested as the main mechanism in plant tolerance to abiotic stress (Blokhina et al. 2003; Sairam et al. 2009; Wilson et al. 2014b; Xie et al. 2019; Zhang et al. 2007). Commonly, antioxidants experience an elevation in plant cells not only for

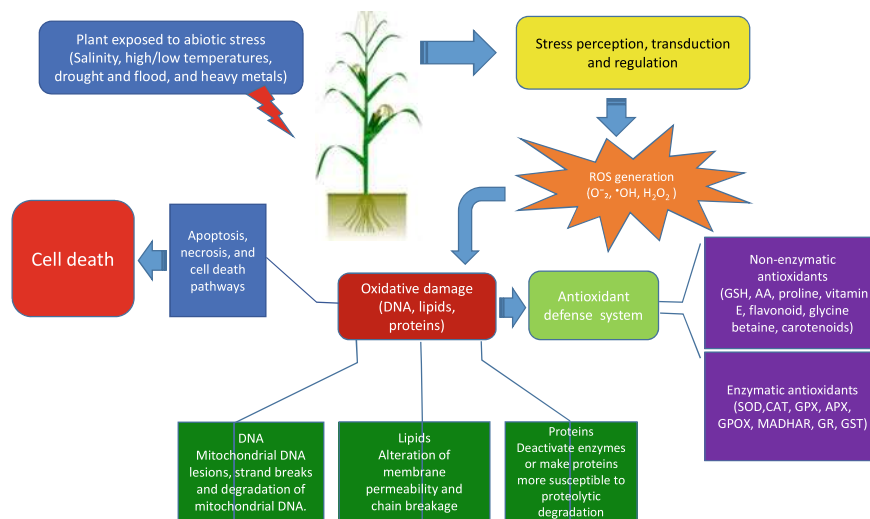


Fig. 2.1 Imposed oxidative stress as a result of abiotic stress (ROS, single oxygens; $O_2^{\cdot-}$, superoxide anion; H_2O_2 , hydrogen peroxide; $\cdot OH$, hydroxyl radical). Oxidative damage leads to either cell death eventually or with involvement of antioxidant defense system (enzymatic or non-enzymatic) the ROS detoxified. GSH, glutathione; AA, ascorbic acid; SOD, superoxide dismutases; CAT, catalase; GPX, glutathione peroxidase; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; GR, glutathione reductase; GST, glutathione S-transferase

drought stress but in most stresses are superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione reductase (GR), and ascorbate peroxidase (APX) and glutathione peroxidase (GPX) as enzymatic and, ascorbic acid (ASC), α -tocopherol, reduced glutathione (GSH), β -carotene, compatible solutes such as proline as non-enzymatic show increased concentration in crop plants in general (Polidoros et al. 2005; Xie et al. 2019).

The ability of antioxidants to alleviate the ROS and range of activity in terms of an organ is well-documented. Of the antioxidants that almost has no organizational limitations, SOD that is known to be the forefront of defense against radicals and can be found in all subcellular sections majorly catalyzing $O_2^{\cdot-}$ reduction to H_2O_2 and finally to water possibly by GR and APX (Almeselmani et al. 2006; Lu et al. 2010). Moreover, ROS signaling-mediated by POD in various cellular organs leads to the accumulation of SOD, CAT, and APX (Mittler and Blumwald 2010; Mittler et al. 2011). Probably the highest efficiency to convert oxygen species into the water and/or oxygen is CAT with an estimated transformation rate of 6,000,000 H_2O_2 per molecule of CAT per min particularly in peroxisome where photorespiration takes place owing to the existence of tetra-ham in its chemical structure (Garg and Manchanda 2009). An essential combination of antioxidants with a high detoxification rate is the GR-AsA cycle that is greatly influenced by GR which is mainly chloroplast-located. Another H_2O_2 potent scavenger is APX with various isoforms each one specific to

a cellular organ or GPX that converts H_2O_2 into the water using glutathione (Noctor et al. 2002; Xie et al. 2019).

In the case of non-enzymatic antioxidant AsA with high water solubility and potency against ROS, is an important participant of the cyclic pathway of enzymatic detoxification of ROS that can be found in high concentration in photosynthetically active cells and leaves with high chlorophyll content (Almeselmani et al. 2006; Foyer and Noctor 2011). This molecule, along with other components of the antioxidant system, protects plant cells against oxidative damage caused by aerobic respiratory metabolism, respiration, and even pollutions also are essential for alpha-tocopherol reproduction. It also acts as a secondary antioxidant in the recycling of alpha-tocopherol and other lipophilic antioxidants, similarly, alpha-tocopherol is a capable antioxidant owing to possessing methyl which makes it superior in comparison to its other three isoforms (Blokhina et al. 2003; Hasanuzzaman et al. 2013). Among photosynthetic pigments carotenoids play a key role as they are preserving photosynthetic apparatus, PS I in particular, against damaging surplus light radiation, scavenging ROS affecting thylakoid membranes and photoreceptors (Niyogi et al. 2001). Effect of essential versatile metabolites such as GSH is also important due to its role in detoxifying ROS and participate in various pivotal processes like signal transmission throughout the plant (Foyer and Noctor 2011; Wojciechowska et al. 2013). As an expected osmolyte in most of the abiotic stresses, proline also is capable of providing ROS scavenging to lessen the damage imposed by oxygen species (de Campos et al. 2011). Plant secondary metabolites especially phenolic compounds and flavonoids can be detected inclusively in cellular organs with a major concentration in vacuoles, possess a high antioxidant activity that their increment in plants under abiotic stress is common (Blokhina et al. 2003).

2.2.1.1 Water Stress

Water deficit with inhibiting the stomatal conductance and consequently photosynthesis activity prepares the ground for oxidative damage as a result accumulation of ROS which in turn cellular mechanisms provoke the production of an array of anti-radicals (Fig. 2.1). Ample of factors can influence the quality and quantity of antioxidants in water-stressed affected plants, Lin et al. (2006) in a comparative study subjected three cultivars of *Ipomoea batatas* L. plants to waterlogging and drought stress. The outcome indicated a high variation in SOD, phenol, flavonoid, and carotenoid content, but in general, reduction in these biochemical compounds were higher in flooded plants except for carotenoids that remained unaffected by both stressors. The content of nutrients in drought-stressed and growth stage observed to influence the concentration of antioxidants aim to improve the tolerance of crops. Case in point, canola seedlings at early stages subjected to water shortage and N deficiency had the highest CAT content while an increase in N application increased polyphenol oxidase and PO. However, the latter reduced in the following stage, or proline content that enhanced the most in the moderately water-stressed seedlings and incremented indiscriminately across at stages (Ahmadi et al. 2015). Reduction in

antioxidants as a substantial contributor to plant adaptation by ontological advancement has been observed in maize (Zhang et al. 2007) which is possibly owing to their replacement with other mechanisms such as morphological adaptations to prevent the generation of ROS in the first place. Acquiring a reliable level of tolerance to water deficit is possible by having a proper level of antioxidant induction (Wang et al. 2009). Recent studies on detecting responsible genes for antioxidants yielded several important breakthroughs such as OsLG3 in rice which its overexpression associated with induction of numerous ROS scavenger-linked genes confer tolerance to drought-stressed rice (Lu et al. 2010). Similarly, rice plants expressing MnSOD (originally transferred from *Pisum sativum* L.) exhibited a lower level of peroxidation of lipids when compared with wild type, which implies the enhancement in antioxidants controlling ROS. Induced expression of APX and Cu/ZnSOD in *I. batatas* led to an improvement in drought adaptation with incremented photosynthetic activity (Lu et al. 2010). Accumulation of antioxidant in oxygen-deprived plant exposed to flood stress in the studied species is highly inconsistent which partially can be explained by the effect of species and experimental conditions (Blokhina et al. 2003). However, is one of the comprehensive assessments on eleven species composed of anoxia-sensitive and tolerance, the evaluation of the functionality of monodehydroascorbate (MDHAR) dehydroascorbate (DHAR) and quantity of AsA and GSH unveiled a notable increase in MDHAR and DHAR whereas the sensitive species the indices did not change or decreased. The content of AsA after GSH after anoxia treatments were incremented and decremented, respectively (Wollenweber-Ratzer and Crawford 1994). Studies also suggested a lower aggregation of ROS ($O_2^{\bullet-}$ and H_2O_2) in flood stressed plants, for instance, stressed *V. radiata* L. the content of $O_2^{\bullet-}$ and H_2O_2 reduced in sensitive genotypes while the ROS status did not change in the tolerant genotypes but APX and GR experienced an increase (Sairam et al. 2011). The exact similar pattern reported in *Cajanus cajan* L. treated with the flood (Sairam et al. 2009). The fluctuation in content and activity of antioxidants in hypoxia or anoxia treated plants as mentioned earlier is extremely circumstantial with significant dependency on duration possibly due to exacerbation of oxidative stress and the change in need for specific antioxidants.

2.2.1.2 Extreme Temperature

Plant responses and adaptation to abiotic stress mainly share a great deal of similarity specifically in respect of physiological and biochemical approaches to mitigate the terminal effects of oxidative stress caused by limiting CO_2 conductance and assimilation and photorespiration. Analogs to other abiotic stress, extreme temperatures (heat or cold) impose the generation of ROS in which antioxidants have been reported to have a key role in their regulation in plants under high/low temperatures. The best-case scenario to understand the behavioral paradigm in the effect of high/low temperature on specific antioxidants is to subject a given plant species to high/low temperature and evaluate the quality and quantity of antioxidants of interest. Soengas et al. (2018) conducted the similar study on two cold-season vegetable crop,

Kale (*Brassica oleracea acephala* group) and Cabbage (*B. oleracea capitata* group) which a general enhancement in CAT, SOD, GR and glutathione in crops of both groups exposed to high/low observed with no significant species effect. Contrasting reaction to high/low-temperature stress was observed in canola seedlings, under chilling stress, the activity of SOD reduced while CAT was unaffected but in heat-stressed seedlings, CAT indicated an increment and SOD decremented (Alscher et al. 1997; Blokhina et al. 2003; de Campos et al. 2011; Soengas et al. 2018). It's well-documented that accumulation of ROS generates damage to all cellular organs chloroplasts in particular. In a study screening the induction of antioxidants in five heat-stressed wheat genotypes, the stressed late-planted seedlings across the entire vegetative and reproductive stages experienced elevated content of SOD, CAT, and APX plus reduction in GR and POX. However, two genotypes showed proportionately higher values for all the evaluated antioxidants and also degradation in photosynthetic pigments and membrane was the least which is a vivid manifestation of essentiality of antioxidants in conferring heat stress tolerance (Almeselmani et al. 2006). Similarly, the heat-tolerance Kentucky bluegrass cultivar 'Eagleton' under high temperature exhibited an increase in chlorophyll content and enhanced level of antioxidants CAT, SOD and APX (He and Huang 2010). Moreover, in heat tolerance citrus cultivar, Carrizo, a significant elevation in antioxidants (GR, CAT, APX, and SOD) discovered to be responsible for its tolerability to high temperature while in the heat-sensitive cultivar, Cleopatra the reduction of antioxidant or lack of response observed, but proline content remained statistically unaffected in both cultivars (Zandalinas et al. 2017). The overexpression of AtGRXS17 in tomato seedlings enabled the genetically modified tomato to resist low-temperature stress with experiencing no growth-related negative effects most likely due to the reduced ion leakage and efficient photosynthetic activity under low temperature when compared with wild-type (Foyer and Noctor 2011). The accumulation of phenols, flavonoids, and glutathione in cold/heat-stressed have been reported as well (Raseetha et al. 2013; Wilson et al. 2014b; Wojciechowska et al. 2013).

2.2.1.3 Salinity

The main source of adverse impacts in salinity-stressed plants is oxidative stress induced by limitation in stomatal conductance, uptake and accumulation of toxic ions and deficiency in mineral nutrients (Shah et al. 2017). Plants evolved a potent capability to turn the cellular milieu into a battlefield to scavenge ROS and alleviate the resulting damage by enhancing the quantity of enzymatic and non-enzymatic antioxidants efficiently collaborate to tackle the matter (Aziz and Khan 2001; Azizian and Sepaskhah 2014; Parida and Das 2005). In date, palm seedlings resistance to salinity ('Umsila') the uptake of Na⁺ reduced and notable increment in SOD, CAT, and APX in addition to proline, glutathione and polyphenolic substances in leaves was observed as compared to sensitive one 'Zabad' (Al Kharusi et al. 2019). Similarly in two soybean cultivars with contrasting tolerance to salinity exposed to various level of salt, the biomass production and healthiness in the tolerant cultivar was affected

non-significantly with a dramatic induction in SOD, CAT, APX, and GR, whereas the otherwise observed in the sensitive one (Khan et al. 2009). More, in osmotic stress tolerance wheat genotypes treated with salt, an accumulation in CAT, PO, and APX recorded while its absence observed in the sensitive genotype (Siddiqui et al. 2017). Sometimes antioxidants exhibit organ-specificity, for instance CAT and DHAR showed increase universally in the plant under salt stress while SOD, APX, GST, and GR enhanced particularly in the root system (AbdElgawad et al. 2016). Given the presence of physiological evidence as a difficult to reject data supporting the essentiality of an antioxidant system for salt tolerance, several genes associated with induction of antioxidants aiming tolerance to oxidative stress have been reported (Guan et al. 2015). For example, a putative gene (PutAPX) in *Puccinellia tenuiflora* L. detected and its induction under oxidative stress conferred tolerance to salinity stress, following its transformation to *Arabidopsis* exhibited decrement in lipid peroxidation and terminal effect of salinity in general (Blokhina et al. 2003).

2.2.1.4 Heavy Metals

Impairing the photosynthetic apparatus, automation, and Fenton reaction and ion disequilibrium resulting in the formation of ROS beyond a controllable level (Schutzendubel and Polle 2002). We should keep that in mind that not all heavy metals are toxic for plants since elements as Fe, Mn, Cu, Zn, and Ni are essential for the very fundamental processes, required in small amounts and increasing their concentration after a certain point lead them to be juxtaposed with non-essential highly detrimental ions such as Cd, Cr, Pb, Co, Hg and Ar (Salt et al. 1995). Heavy metal ion classified into two groups with and without redox ability, the former composed of essential heavy metal ions except for Ni, also Cr considered in the first group that by participation in cycling reactions generate an excessive level of $\cdot\text{OH}$ with high damaging potential to biological cellular organs, while the latter group includes the non-essential elements plus Ni (Emamverdian et al. 2015; Pandey 2018). An important dimension in heavy metal stress is the exhibition of antagonistic and/or synergistic behavior in the absorption of essential elements that tremendously contribute to the negative effects of heavy metal stress. Accelerated antioxidant defense system has been referred to as a viable mechanism against heavy metal-induced oxidative stress (Mousavi et al. 2013), which its diversity and concentration vary considerably depending on growth stage, type of metal ion, species, cultivar and even organs of the plant (Mediouni et al. 2006). Significant enhancement in CAT, SOD, POD, GR, GSH, PO, APX, phenolic compounds, osmolytes have been reported in plants subjected to heavy metal ions. Also, the intensity of oxidative stress vary between heavy metals. For instance, the seedlings of *Ocimum basilicum* L. received treatments of Ni, Cu, and Zn, which the order of the oxidative damage the seedlings experienced from high to low was in this order $\text{Cu} > \text{Zn} > \text{Ni}$, which indicated the difference in toxicity of heavy metals (Georgiadou et al. 2018). In some cases, the absence of responsiveness from antioxidants in heavy metal-treated plants as Milone et al. (2003) reported that SOD was ineffective in the root system of two contrasting Cd-treated wheat cultivars

while APX and CAT exhibited a reduction in the sensitive one. In another study on maize seedlings affected by Cr, increase in SOD, CAT, and POD in early stages and followed by a dramatic reduction in the content of SOD and POD in leaves (Zou et al. 2009). The results projected in literature are overwhelmingly diverse and contradictory which reflects the complexness of antioxidant defense machinery and underlying mechanisms in plants against heavy metal stress.

2.2.2 Osmotic Adjustment

Of course, the adaptation of various strategies in plants to mitigate the negative changes caused by abiotic stress is in many cases are specific but if there is one biologically universal reaction exists against abiotic stress that could be osmotic adjustment which is a simple term is the accumulation of osmolytes. This mechanism aims to further reduce or tranquilize the water potentially affected by the interference of abiotic stress simulate water deficit, on water relations. Under abiotic stress-prone environments, water deficit, in particular, plants with the physiological potential to accumulate osmolytes to adjust the water relations have tremendous survival superiority. Since there is a misuse of terms in this area, some clarification would help to convey scientifically correct information; the term ‘osmotic adjustment’ is correctly applied to the aggregation of novel solutes occurred not when the reduction in water potential caused by the current solutes owing to water loss (Babu et al. 1999). Another one is the misapplication of ‘osmoregulatory’ and ‘osmoprotectants,’ it’s safe to say that all osmolytes contribute in improving cell turgor pressure, which is imperative for efficient carbon fixation. While not all these osmolytes possess the antioxidative capability and lightweight molecules such as proline, glycine betaine (GB) and polyamines are both osmoregulators and osmoprotectants. Whereas sugars, polyols and mineral ions including K^+ , Na^+ , and Cl^- are solely osmoregulators, also these compounds collectively known as compatible solutes mainly accumulate in vacuoles. Additionally, a difference might appear between the osmotic adjustment of leaves vs. roots, where most believe that osmotic adjustment is higher in roots OA could be greater in roots than in leaves. Plenty of studies have revealed the critical role of osmolytes involves in osmotic adjustment in plants exposed to abiotic stress, a summary on each abiotic stress given as follows (Sharp and Davies 1979; Westgate and Boyer 1985; Hsiao and Xu 2000).

2.2.2.1 Water Stress

The first deadly impact of water deficit is unbalancing the water status of the plant which initiate a series of damaging changes specifically in cellular water potential that threatens the carbon assimilation. Therefore crop plants mainly aim to increase the accumulation of new compounds to lessen the water potential without a reduction

in existing water content which often found to be an effective remedy as osmoregulation. It's a wonderful achievement for plant and unlike many other adaptations, the accumulation of osmolytes is not a bitter pill to swallow since the energy consumption is significantly low and has no tangible negative consequences (Cechin et al. 2006; Kiani et al. 2007). When it comes to crop plants survival does not properly apply and owing to the economic importance of crops, survival for crop plants means the production of an economically reasonable yield for which scientific discussion of scholars in this case majorly considered the osmotic adjustment as a mechanism that only serves the survival purposes rather than productivity, an issue that addressed by Blum (2017) using the current data on the effect of osmotic adjustment on yield in twelve main crops from cereals, legumes and oil crops who found that high yield of the crops under water deficit condition significantly associated with greater osmotic adjustment (for review see Turner [2018]). Osmotic adjustment assist plant in two main approaches, I. enhancing the cell turgor, makes a proper carbon fixation possible, II. enables the root system for correctly operate and absorb water from soil matrix which otherwise would be impossible or at least difficult, a third (III) approach can be provided by the antioxidant function of osmoprotectants (Kiani et al. 2007). Similar to other adaptation mechanisms, the concentration and type osmolytes changed in different growth stages of drought-stressed Bentgrass cultivars, is that an improved water relation was observed. Mainly due to the accumulation of sugars by the beginning of drought stress which replaced by proline as the stress continued, moreover, the non-organic ions remained almost unaffected (DaCosta and Huang 2006). As earlier explained, possible improvement in water uptake and stomatal behavior contributed to osmotic stress tolerance. Likewise, an enhanced yield in drought-stressed wheat found in association with the accumulation of compatible solutes through improving CO₂ conductance and consequently higher carbon fixation (Živcák et al. 2009). Irrespective of contrary reports, vacuole localized K⁺ accumulation is a prerequisite to have an electrochemical gradient required for stomatal movements (Zhu 2001). The positive impact of increased accumulation of polyamines, putrescine, spermidine, and spermine in plants under drought stress has been reported (Singh et al. 2015; Yamaguchi et al. 2007). The protective role of GB on components of the photosynthetic system also has been suggested (Xing and Rajashekar 1999). Considering the damage to the root system in flooded plants, therefore the collapse of transpiration and carbon fixation, flood simulates a water deficit which similar to drought in flooded plants. Accumulation of osmolytes in an attempt to prevent or restore the situation has been studied in several plants species. In two wheat genotypes exposed to hypoxia during waterlogging, tolerance and recovery from the stress observed to be strongly associated with accumulation carbohydrates in root in the virtue of balancing water relations (Huang and Johnson 1995), while in another study on alfalfa, absence of a positive relationship between accumulation of osmolytes and flood stress was discovered (Barta 1988). In waterlogged young seedlings of Caisin (*Brassica rapa* subsp. *parachinensis*) a higher RWC and thus CO₂ conductance was accompanied by an improved osmotic adjustment (Issarakraisila et al. 2007). The versatility of osmolytes in dealing with two main stress-generated effects, osmotic- and oxidative-stress through reducing water

potential and antioxidative function is a unique capability which so far a little attention has been paid from breeders possibly owing to the difficulty in using osmotic adjustment as a biochemical marker.

2.2.2.2 Extreme Temperatures

In plants subjected to high/cold temperature stress depress of photosynthetic apparatus by stimulate water deficit and lowering the transpiration rate leading to a reduction in the assimilation of carbon. Therefore, unleashing ROS as well as osmotic stress, for which, similar to water stress plants resort to adjustment of osmose through the accumulation of solutes (Argentel-Martínez et al. 2019). The behavior sometimes may be contradictory, however similarity in accumulation of compatible solutes have been observed. The prime example is high/cold stressed ecotypes of Iranian tall fescue ecotypes (*Festuca arundinacea* L.) exhibited that intensity of high/cold stress tolerance linked to the accumulation of carbohydrate and proline and the order to the tolerance of ecotypes was to some extent the same. Nevertheless, except for FA 1 and FA 2, the content of compatible cytosolutes dramatically reduced after 24 days, in those two ecotypes the osmolytes remained constantly high (Sheikh-Mohamadi et al. 2018). Acclimation of strawberry seedlings to overwintering indicated the importance of osmolytes in an immediate reduction in water potential, and prioritized reallocation of the solutes to younger leaves in which only young leaves survived. Also, the conversion of stored starch into soluble sugars is pivotal for reducing water potential in particular under cold stress (O'Neill 1983). The major contribution of a balanced water status is regular transpiration which accumulation of GB and decrementing water potential in the root system, as well as aerial parts. This reaction enabled heat-stressed plants of *Triticum durum* L. to have high transpiration and an efficient carbon fixation throughout the growth and reproduction stages, however, it was not with no cost as delaying in phenophases observed (Argentel-Martínez et al. 2019). Enhancement of GB content in crop plants under high-temperature stress has been observed by other scholars such as Rienth et al. (2014) who found a strong correlation between GB and proline accumulation (66 and 58%, respectively) with heat tolerance in vines. An increase in compatible solutes in heat-stressed crops also have been reported (Tian et al. 2017; Wilson et al. 2014a). Commonly proline has been known to greatly contribute to stress tolerance through osmotic adjustment (Zandalinas et al. 2017), on the other hand, plant secondary metabolites particularly flavonoids reported to confer tolerance to heat stress in citrus plants (Zandalinas et al. 2016). For a review see Lamaoui et al. (2018).

2.2.2.3 Salinity

Salinity stress in short leads to imbalanced water relation and osmotic stress through reduce the availability of water in the soil for the root system and ion toxicity which all result in a wilting and radical decrease in the amount of assimilated carbon (Ashraf 2003; Azizian and Sepaskhah 2014; Rahnesan et al. 2018; Sahin et al. 2018). Analogous to other abiotic stresses plants forced to seek adaptation by accumulating osmolytes in roots and leaves to lessen the water potential in the virtue of avoiding disrupt of cellular membranes and detoxify ROS with the aim of antioxidant activity in some of the compatible solutes. Despite the effectiveness of this approach the required energy is rather high and suggested as possible causes of growth reduction (Greenway and Gibbs 2003). The excessive uptake of Na^+ and Cl^- is the major source of nutritional deficiency in particular crucial mineral nutrients such as K^+ which affected by the antagonistic effect of Na^+ absorption and lack of discriminability from transporter channels against Na^+ that uses K^+ channels (Hmidi et al. 2018; Lacerda et al. 2003). Given the multidimensionality of salt effect, a combination of different mechanisms may trigger to address the situation but surely osmotic regulation is the main one. The linear increase in amino acids, proline, and GB have been frequently reported in salinity stressed plants (Bohnert et al. 1995). Accumulation of solutes in salt-treated *Cakile maritima* L. plants was varied in respect to either type and organ, is that osmotic adjustment in the stem was mainly (60%) attributed to Na^+ accumulation while this feature for proline was 36% in roots. Interestingly, the activity of ornithine- δ -aminotransferase which involved in N distribution under non-stress condition found to be highly correlated with proline synthesis which it can be implied that ornithine pathway significantly engaged in the production of proline (Hmidi et al. 2018), previous studies confirmed the involvement of ornithine pathway in proline biosynthesis which have accompanied symptoms of nitrogen deficiency (Öztürk et al. 2006; Roosens et al. 2002).

2.2.2.4 Heavy Metals

The exposure of plants to heavy metals stress have known to generate intense ROS accumulation that interferes with vital biological processes at the cellular level. The toxicity of heavy metals in soil targets root system by causing necrosis which depends on the level of tolerance and dose leads to reduction in water uptake from soil in addition to disables the photosynthesis apparatus thus carbon fixation through decrementing cell turgor. That leads the reduction in accumulation of cytosolutes to decline the cell turgor and preventing further water loss as well as imbalanced ionic condition. Moreover, the antioxidant capability of solutes such proline, GB, and glutathione can serve as dual-purpose compounds (Emamverdian et al. 2015; Georgiadou et al. 2018; Schat et al. 1997; Schutzendubel and Polle 2002). Therefore, the increased content of solutes is a significant mechanism to detoxify heavy metals and improve heavy metal stress tolerance. In heavy metal stressed *Salvinia natans* seedlings with Cd, Cu, Ni, Zn, Pb, Fe, Mn, and Cr treatments an increased level of GB, carbohydrates, and

polyols observed (Schutzendubel and Polle 2002). Exogenous enhancement in the concentration of GB likewise has been reported in wheat subjected to heavy metal stress to provide a decrease in oxidative stress and improving osmotic adjustment (Alscher et al. 1997). Despite some paradoxical behavior in proline accumulation under heavy metal stress, often increase in proline content has been reported for example in *Lactuca sativa* (Costa and Morel 1994) and soybean (Balestrasse et al. 2005). However, proline accumulation and its association with osmotic adjustment have been questioned by Saradhi (1991) who observed enhanced water potential in Pb-treated wheat seedlings regardless of proline accumulation to a high level whereas in control seedlings the osmotic potential was significantly lower. The increase in accumulation of proline as key element in osmotic adjustment and oxidative stress is rather controversial, observed increased proline tied to water deficit since proline increased in transpiration suppressed discs of leaf as mu as or even higher in heavy metal stressed plants (Schat et al. 1997), following (Kastori et al. 1992) challenged their result by arguing that leaf discs exposed to heavy metal ions under full turgor experienced a dramatic increase in proline, however, there was a possibility of disruption in cellular membranes owing to a high level of toxic metal used (Ric de Vos et al. 1993). Observation made on Cu-stressed segments of rice leave raised the possibility of ABA involvement (Chen et al. 2001). Soluble sugars in plants under Co stress conferred adaptation by reducing cell turgor (Yu et al. 2019). Ultimately, Sharma and Dietz (2006) suggested that accumulation of amino acids and soluble sugars in heavy metal-stressed plants are not owing to disruption of biosynthetic process but rather tolerance mechanisms provide protection against heavy metal stress.

2.2.3 Molecular Strategies

Alongside various adaptation strategies that provide the plant with survival capability or more precisely enable the crop plant to have an economically reasonable yield under abiotic stress, the molecular level that plant as a response to abiotic stress many genes are triggered and make the occurrence of tolerance at the higher level possible, therefore the quantity of the expressed genes initiates a series of processes that acquiring an in-depth understanding is a necessity to reliably go forward on developing stress-tolerant crop cultivars which thanks to genomics and proteomics technologies an appreciable body of knowledge on model plants in particular and in many cases on crop plants exist that can be exploited for this purpose (Hossain et al. 2012; Shi et al. 2018; Yang et al. 2005).

2.2.3.1 Water Stress

Investigations regarding the identification of underlying genes responsible for conferring tolerance to high/low temperatures mainly in model plants and some crops using transcriptome and proteome analysis have enlightened our perspective toward the evolution of adaptive mechanisms. Notable experiments majorly those studied contrasting genotypes have yielded critical findings. In general, the flood- and drought-induced responsive genes by causing aggregation of specific proteins or hormones play their roles (Kavar et al. 2007). In most cases, the interplay of hormones and gene expression determines the tolerance to water stress as ABA a key hormone that its enhanced biosynthesis in drought-stressed plants leads to tolerance-related regulation specifically the expression of associated genes (Yamaguchi-Shinozaki and Shinozaki 2006) which transferring of ABA-related *GhCBF3* from cotton to *Arabidopsis* conferred tolerance to water deficit through improving water relations and osmotic adjustment, and carbon assimilation (Ma et al. 2016). The expression of some genes can occur under different stresses, case in point SUB1A gene responsible for waterlogging tolerance in rice observed to bestow water-deficit resistance by enhancing antioxidants and improving the responsiveness of ABA (Fukao et al. 2011). Considering the importance of circadian clock that induces the expression of a larger number of genes to obtain a level of tranquility in energy consumption and production in plants subjected to drought or flood stress. Two related genes, PRR7 (water deficit) and TOC1 (flood stress), which the latter provoked an increase in ABA content and linked with fluctuation in sugars during the day which manifests the dominant regulatory role of ABA in determining the energy homeostasis in drought and flood stressed-soybean plants (Syed et al. 2015). Water channels (aquaporins) are integral membrane proteins that are essential in the transformation of water across the membrane passively. That can amplify the water transfer by 10 to 20 times across membranes (Tyerman et al. 2002). Further, several transcription factors controlling the expression of drought-related genes have been identified including myeloblastosis protein (MYB), myelocytomatosis (MYC), DREB/CBF (drought-responsive *cis*-element binding protein/C-repeat-binding factor), ABF/AREB, NAC (NAM, ATAF, and CUC), and WRKY (Ishida et al. 2012; Nakashima et al. 2009; Sakuma et al. 2006; Tran et al. 2007). In *TaWRKY2*-transgenic wheat seedlings with limited water loss, enhanced content compatible solutes and higher survival rate proven to be drought resistance (Gao et al. 2018). Expression of *AtMYB60* and *AtMYB61* in rice localized in guard cells and found to be critical in controlling stomatal behavior under water deficit (Liou et al. 2005). Expression of genes involved in the induction of GB and proline biosynthesis evoked in under drought stress in several species including a number dicotyledons (Weretilnyk et al. 1989), *Amaranthus hypochondriacus* L. (Vojtěchová et al. 1997), barley (Jagendorf and Takabe 2001), cotton (Parida et al. 2008) and maize (Zenda et al. 2019). The significant up-regulation of xyloglucan endotransglycosylase (XET) gene family encoding enzymes involved in cell elongation observed in waterlogging-resistance maize genotype, HKI 1105, whereas its down-regulation occurred in flood-intolerant line, V 372

(van Veen et al. 2013). More, the resistant rice line indicated a higher induction level of IAA3, IAA14, and IAA16 genes (Wang et al. 2017). The interplay between ethylene and IAA in flood-tolerant maize is possibly linked to development of adventitious roots. Two of the regulatory energy-sensing protein kinases in carbon use under oxygen deprivation in *Arabidopsis*, KIN10 and KIN11, the former one encoding genes actively engage in carbohydrate and protein breakdown (Baena-González et al. 2007; Cho et al. 2012), additionally one of the two protein, KIN10/11, is responsible for EXORDIUM-LIKE1, an HUP critical for managing carbon in hypoxia circumstances (Schröder et al. 2011). The flood-stressed soybean seedlings the proteomics analysis revealed an enhanced activity of ADH and delta-1-pyrroline-5-carboxylate synthase as well as presentation of seventeen various proteins such as β -glucosidase 31 and β -amylase 5 in both roots and leaves, which probably β -amylase 5 expression may have been linked to reallocation of carbohydrates to aerial part specially leaves (Wang et al. 2017).

2.2.3.2 Extreme Temperature

The main determinate of plant growth and productivity is temperature due to the substantial influence of temperature on biological processes which evidenced that high/low-temperature stress can severely affect crop plants. Plants are capable of triggering organizational tolerance response to extreme temperatures. These responses often leads to the expression of numerous genes initiating osmotic adjustment, antioxidants or regulating water status of under stress plants by modifying in the transcriptome, proteome, and metabolome or even in some cases by evoking programmed cell death to detach a specific organ or eliminating the whole plant (Lamaoui et al. 2018; Qi et al. 2011; Shi et al. 2018). Of the critical commonplace proteins such as heat shock proteins (HSPs) and heat stress transcription factors (HSFs) reported that their expression genotypes are associated with thermos-tolerance (Cheng et al. 2016; Sanghera et al. 2011), of course, a large array of metabolites as osmolytes and antioxidants involved in tolerance mechanisms which primarily influenced by the nature of genotype (Challinor et al. 2007; Kaya et al. 2001). Studies covering the molecular mechanisms conferring heat tolerance are often conducted on model plant species and a small portion have dedicated to crop plants which we try to mainly focus on the latter. The effects of HSPs majorly concern their role as molecular chaperones prevent misfolding and enhancing and stabilizing the structure of the protein so they function properly under heat stress, however knocking out this protein had a marginal negative influence of thermos-tolerance (Schramm et al. 2008; Yoshida et al. 2011). The association of heat stress tolerance with the superfamily of HSP70 has been discovered in several crop plants including, rice (Sarkar et al. 2013), maize (Rochester et al. 1986), and wheat (Duan et al. 2011). Isolated HSP proteins (HSP70 and HPS90) from *Sitodiplosis mosellana* as a harmful pest insect of wheat has obligatory diapause to avoid extreme temperatures in larval stages, and their transformation to wheat plants indicated contrasting capability in these two

genes in which HSP70 and HSP90 conferred thermo-tolerance and cold-stress resistance, respectively (Cheng et al. 2016). 32 HSP70 has been identified in rice and the involvement of HSP70 also has been proven (Sarkar et al. 2013). A high level of accumulation of HSP70 in heat-stress tolerance grape genotypes also reported (Zhang et al. 2005). Whereas HSP101 observed to not be inducible by heat stress but is essential for growth in root in maize, nevertheless, the heat-stressed maize experienced amount in the transcript of HSP101 in developing tassel, ear, silks, endosperm, and embryo but it was without an increment in HSP101 protein (Nieto-Sotelo et al. 2002; Young et al. 2001). The otherwise was identified for HSP101 in *Arabidopsis* which was critical in expression of antioxidants to lessen the damage caused by heat stress (Queitsch et al. 2000). More, HSP100 aim at the chloroplast intermembrane space and stroma to facilitate protein import of nuclear-encoded proteins (Nielsen et al. 1997). Comparing contrasting genotypes in rice using proteomic analysis revealed that high-temperature tolerance genotype had a significantly higher accumulation of HSPs a direct correlation between thermos-tolerability in rice genotypes and level of HSPs observed (Jagadish et al. 2009). Of the important most studied transcription factors responsive to cold stress, dehydration-responsive element-binding (DREB) protein/C-repeat binding factors (CBFs) or DREBs/CBFs bind to promoter cis-element CRT/DRE to regulate the expression of these cold-responsive genes. The overexpressed CBF1/DREB1b and CBF3/DREB1a observed to induce cold regulated genes (Gilmour et al. 2000; Kasuga et al. 1999), additionally, overexpression of DREB1A conferred tolerance to low temperature and water deficit in wheat and peanut (Kasuga et al. 2004; Pellegrineschi et al. 2004). Using comparative transcriptome Cai et al. (2019) discovered low-temperature sensitive genes, CBF4, ICE2, and several other ABA-associated ones. Successive gene silencing indicated the effective role of CBF4, ICE2 in the reduction of lipid oxidation in membranes as well as increasing SOD and proline to assist the adaptation to cold stress in *Gossypium thurberi* L. CBFs similarly identified and isolated in several crop plants such as rice, tomato, wheat, barley and maize (Shi et al. 2018). The expression of CBFs negatively affected by MYB15 by direct binding to conserved MYB motif in their promoters (Agarwal et al. 2006), moreover, Su et al. (2010) observed the inhibition of the expression of cold-sensitive OsDREB1B by OsMYBS3 in rice.

2.2.3.3 Salinity

Similar to other abiotic stresses addressed above, plants molecular mechanism to tackle the negative influence of salinity which majorly is osmotic- and oxidative-stress includes a vast range salinity-specific gene families and general stress-sensitive genes that express upon the occurrence of abiotic stress. In both cases transcriptomic analysis provided a comprehensive image of underlying genes conferring tolerance to plants by triggering the biosynthesis of antioxidants or ABA production that each one initiates sets of modification (Fujita et al. 2013; Johnson et al. 2002). Wu et al. (2019) in salt-stressed flax plants identified several TFs namely bZIP, HD-ZIP, NAC, MYB, GATA, CAMTA, and B3 which are renowned as stress-responsive TFs for

expression of compatible solutes, hormones and signal transduction, in particular bZIPs that regulates effective tolerance mechanisms in plants under salinity. Moreover, salt specific molecular mechanisms are expressed in salinity-affected plants. Salt Overly Sensitive (SOS) signaling pathway is a classical signal pathway involved in salinity stress resistance, SOS composed of three proteins regulating vital processes such as Na^+/H^+ antiporter in the plasma membrane, transport of Na^+ from the root system to aerial organs, activating Ca^+ signals under salinity and signaling stress (Liu et al. 2000; Ma et al. 2019; Shi et al. 2000). Similar to SOS especially SOS3, the function of SNF1-related protein kinases (SnRKs) is long-distance signaling and regulation of ion translocation from roots to shoots. By its engagement with SnRK2.4 and SnRK2.10 in regulating numerous antioxidants to balance the ROS production in salt-stressed *Arabidopsis* has been reported (Szymańska et al. 2019). Limited ion toxicity and ROS aggregation in salt-treated *Arabidopsis* seedlings associated with Ca^{2+} -dependent protein kinases (CDPKs), since its silencing led to a significant salt-stress vulnerability (Zhang et al. 2018). In respect of ionic stress and related tolerance mechanisms, high-affinity potassium-type transporter 1 (HKT1) is crucial to maintain cytoplasmic K^+/Na^+ homeostasis under salinity stress which is utmost essential for salinity tolerance (Ali et al. 2019). Regarding transcription factors, the inner ability of cultivars can sometimes affect their level of expression, as an example, upregulation of bZIP in salt-intolerant wheat genotypes occurred while in salt-tolerant genotype down-regulated (Johnson et al. 2002). Overexpressed OsNAC6, a member of NAC TFs, in rice, regulated multiple stress tolerance including drought, salinity, and blast disease. Additionally, using microarray analysis it was discovered that OsNAC6 induced two other genes associated with stress tolerance (Nakashima et al. 2007). From other TFs, regulation of salt-tolerance in rice found be strongly controlled by DREB1/CBF, DREB2, and AREB/ABF (Fujita et al. 2013; RoyChoudhury et al. 2008). One of the latest discovered salt-stress related TFs in rice was SALT-RESPONSIVE ERF1 (SERF1) with root-localized induction under salinity stress which its silencing defected the upregulation of salt-induced mitogen-activated protein kinase (MAPK) related genes, following studies indicated the H_2O_2 responsiveness of SERF1-dependent genes with specific promoters (Schmidt et al. 2013).

2.2.3.4 Heavy Metals

A vast range of molecular mechanisms involves heavy metal tolerance which possibly indicates the evolution of tolerance to the edaphic limitation in these heavy metals before other abiotic stressors. Similar to the previously discussed general TFs expressed under abiotic stresses, in heavy metal stressed plants the expression of TFs has been reported frequently. For instance, HSPs, molecular chaperones responsible for repairment of damaged proteins and protecting the proteins from denaturation. The inducibility of HSPs have been shown in plants stressed with heavy metal ions (Zn, Cu, Cd, Hg, Al and Cr) (Gupta 2010; Sarry et al. 2006; Zhen et al. 2007), from which HSP70 a potent protein and known for conferring significant

tolerance to plants under high temperature, it's the accumulation in Cd-treated plants was reported (Neumann et al. 1994; Sarry et al. 2006). Similarly, the aggregation of HSP70 in seaweed and several other freshwater plants under Cd-stress have been observed (Ireland et al. 2004). The sea thrift (*Armeria maritima* L.) grown in Cu-contaminated soils experienced the induction of small HSP (sHSP) in the root system (Neumann et al. 1995). Likewise, HSP25 accumulated in soybean as a reaction to Al toxicity (Zhen et al. 2007). Interestingly, a transit heat-stress exposure in the plant caused Cd-tolerance which can be suggested the heat-responsive HSPs such as HSP70/90 induced by the heat stress that led to tolerance against Cd. Considering the destructive effect of heavy metal toxicity, HSPs' preservation of proteins could be a viable reason for the induction of HPS under heavy metal stress, nonetheless, the actual influence of HPSs in heavy metal stressed plants yet to be clarified (Hossain et al. 2012). The metal responsive TFs known as MTF-1 has a significant effect on heavy metal tolerance through initiating the expression of genes account for absorption, transport, and detoxification (Fusco et al. 2005; van de Mortel et al. 2008). Several MTF-1 have been reported for instance WRKY, bZIP, ethylene-responsive factor (ERF), and MYB, which regulate the induction of Cd-tolerance genes (Yang et al. 2005). For the bZIP TFs family, an important OsbZIP39 was identified which its induction led to the endoplasmic reticulum responds to the aggregation of unfolded proteins (Takahashi et al. 2012). The very specific metal stress proteins are metallothioneins (MTs), a family of small, conserved metal-binding proteins critical for the toxicity of heavy metals, which induced by phytohormones, cytotoxic agents, and heavy metals such as Cd, Zn, Hg, Cu, Au, Ag, Co, Ni, and bismuth (Bi) (Kägi 1991; Yang et al. 2005). The tissue specificity in MT genes regarding the growth stage and the effect of different heavy metal ions (Castiglione et al. 2007). (Ahn et al. 2012) reported the dependent-expression of 3 MT genes (BrMT1, BrMT2, and BrMT3) to heavy metal ions Mn, Zn, Fe, and Cu. Upregulation of related genes to MTs by TFs such as heat shock transcription factor A4a (HsfA4a), have been reported to improve the Cu-resistance in rice (Shim et al. 2009). Al tolerance incremented in rice seedlings with the induction of ASR5 that suggested acting as a TF which express genes protect cells against Al toxicity. Similarly, another TF, C2H2, induce ART1 protein localized in root that expresses genes associated with Al-tolerance (Arenhart et al. 2013). Nakashima and Yamaguchi-Shinozaki (2006) detected the DREB TFs down-regulated in heavy metal-stressed rice seedlings, which they introduced the possibility of DREB assistance in osmotic adjustment to decrement the uptake of heavy metals.

2.3 Conclusion and Future Perspective

Along with the pace of change in edaphic and atmospheric properties on earth the evolution enabled the primary forms of plants to survive and propagate. In the modern era, the definition of surviving in domesticated plants changed to the capability of the plants of interest to yield agricultural products under various conditions, a potential

that is now jeopardized more than ever by a dramatic increase in the incidence of abiotic stresses. This resulted from the accelerated rhythm of negative changes caused by climate change majorly driven from exacerbating anthropological activity. During the last half-century, statistically speaking, the probability of severe water deficit, salinization of soil and water resources, and extreme temperatures has dramatically incremented in addition to the risk of simultaneous occurrence of these stressors. This all comes down to the fact that from the few limited choices to improve the food security of a world that population is increasing, improving the knowledge and understanding of crop plants response and tolerance mechanisms as a critical input for breeding programs can be perhaps the most viable approach if not only. Using phenotypic screening of germplasm responses to abiotic stresses under open-field conditions since lab trials may not be realistic. Probing for a pattern in response to abiotic stresses could be significantly helpful, of course, abiotic stress tolerance in crops controlled by multiple genes. However, commonality of dehydration due to damage to root system or unavailability of water as well as failure in proper stomatal reaction to the stress needs be considered together with the physiological level, where the general response is the disruption of water relations and/or reduction in carbon assimilation. Generating osmotic stress and oxidative stress is the lethal approach of abiotic stresses that force the plant to compulsorily initiate universal and sometimes small scale costly (i.e., from both the percentage of energy budget and the prospective reduction in ultimate yield) approaches as decreasing the carbon fixation. This often happens by the obligatory morphological changes in leaves to lower the light interception and biosynthesis of compatible solutes (i.e., GB, proline, and glutathione) and antioxidants (i.e., SOD, POD, CAT, APX, GR, GSH, and PO, etc.) by expression of stress-inducible TFs (DREB, bZIP, CBFs, NAC and BrMT1, etc.). A body of knowledge that's a compilation of traditional and modern approaches is a valuable possession that can broaden our perspective to develop crop plants resilient for the climate-changing era.

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