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Mitigation of Abiotic Stress in Plants

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Preface

The emergence of nanotechnology have opened up exciting opportunities for novel applications in agriculture, food, medicine, and biotechnology industries. Nanotechnology has the potential to modernize agricultural research and practice, although it has gained momentum in the agriculture sector over the last decade. Abiotic stresses are important constraints that adversely affect the production of agricultural crops. Nanobiotechnology may be a boon for the mitigation of plant abiotic stress impact.

This book provides up-to-date knowledge of the promising field of nanobiotechnology with emphasis on the mitigation approaches to combat plant abiotic stress factors including drought, salinity, waterlog, temperature extremes, mineral nutrients, and heavy metals. These factors adversely affect the growth as well as yield of crop plants worldwide especially under the global climate change. The book consists of 24 chapters discussing the status and prospects of this cutting-edge technology in relation to the mitigation of the adverse impact of the abovementioned stress factors. Moreover, it highlights contemporary knowledge of tolerance mechanisms and the role of signaling molecules and enzyme regulation as well as the applications of nanobiotechnology in agriculture.

The book is perceived as an important reference source for plant scientists and breeders interested in understanding the mechanisms of abiotic stress in pursue of developing stress-tolerant crops to support agricultural sustainability and food security. It is valuable for professional researchers as well as advance graduate students interested in nanotechnology fundamentals and utilization.

The chapters are contributed by 61 internationally reputable scientists from 10 countries and subjected to review process to assure quality presentation and scientific accuracy.The chapters start with an introduction covering related backgrounds and provide in-depth discussion of the subject supported with a total 95 of high-quality color illustrations and relevant 31 data tables. The chapters conclude with recommendations for future research directions and a comprehensive list of up-to-date pertinent references to facilitate further reading. The editors convey their appreciation to all the contributors for their delegacy and to Springer for the opportunity to publish this work.

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Lucknow, India	Mohammad Israil Ansari
Motihari, India	Akhilesh Kumar Singh

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Prof. Jameel M. Al-Khayri is Professor of plant biotechnology affiliated with the Department of Agricultural Biotechnology, King Faisal University, Saudi Arabia. He received B.S. in Biology in 1984 from the University of Toledo, M.S. in Agronomy in 1988, and Ph.D. in Plant Science in 1991 from the University of Arkansas. He is member the International Society for Horticultural Science and Society for In Vitro Biology as well as the National Correspondent of the International Association of Plant Tissue Culture and Biotechnology. For the last three decades, he dedicated his research efforts to date palm biotechnology. He has authored over seventy research articles in referred international journals, thirty chapters, and edited several journal special issues. In addition, edited twenty reference books on biotechnology, genetic resources and advances in plant breeding strategies. He has been involved in organizing international scientific conferences and contributed to numerous research presentations. In addition to teaching, students advising, and research, he held administrative responsibilities as the Assistant Director of Date Palm Research Center, Head of Department of Plant Biotechnology, and Vice Dean for Development and Quality Assurance. Dr. Al-Khayri served as Member of Majlis Ash-Shura (Saudi Legislative Council) for the 2009–2012 term. Currently, he is maintaining an active research program on date palm focusing in vitro culture, secondary metabolites production, genetic engineering and mutagenesis to enhance tolerance to abiotic and biotic stress.

Dr. Mohammad Israil Ansari is biologist with expertise in thrust areas viz. Plant Stress Physiology, Plant Molecular Biology, Nanotechnology, Post-harvest and Agricultural Biotechnology. Before joining University of Lucknow as Faculty, Dr. Ansari worked as Professor of Biotechnology at Amity Institute of Biotechnology, Amity University, Lucknow Campus, Lucknow, India (2007–2016). From 2000 to 2007 Dr. Ansari underwent international learning as Fellow of Academia Sinica and National Science Council Taiwan. Dr. Ansari has been associated with Institute of Botany, Academia Sinica, Taipei, Taiwan, Graduate Institute of Plant Biology, National Taiwan University, Taiwan, and Institute of Plant and Microbial Biology, Academia Sinica, Taipei, Taiwan. Dr. Ansari graduated and post-graduated from Department of Botany, Aligarh Muslim University, Aligarh, India, and doctoral degree from Dr. Ram Manohar Lohia Avadh University, Faizabad, India. Dr. Ansari has 75 research papers in international journals of high repute, several books (authored and edited Springer, Elsevier), book chapters, review articles, Post-doctoral, Ph.Ds. to his credit. Dr. Ansari has completed several research projects funded by Department of Science and Technology, Govt. of India. Dr. Ansari is editorial board member, reviewer of several international journals as well as member of several Academic Board/Faculty Board/Board of Studies/Research and Development bodies. Dr. Ansari has collaborated with several international groups and delivered a number of keynote, invited lecture at national, international level.

Dr. Akhilesh Kumar Singh is currently an Assistant Professor in the Department of Biotechnology, Mahatma Gandhi Central University (MGCU), Motihari, Bihar, India. Before joining MGCU, Dr. Singh worked as faculty at Amity Institute of Biotechnology, Amity University Uttar Pradesh, Lucknow Campus, Lucknow, India (September, 2008 to October, 2019). He has more than 12 years of teaching and multidisciplinary research experience in microbial physiology and industrial biotechnology. His research focus is on polyhydroxyalkanoate bioplastic production, metallic nanobiotechnology, nitric oxide signaling, and biofuel production. Dr. Singh holds a Ph.D. in agricultural and food engineering and an M.Tech. in agricultural biotechnology from prestigious Indian Institute of Technology (IIT), Kharagpur, India, with a master's degree in biotechnology from another prestigious institute, i.e., IIT, Roorkee, India. He has qualified Graduate Aptitude Test in Engineering (GATE) in Life Science conducted by IIT Kanpur on behalf of the Ministry of Human Resources Development, Government of India. He was awarded the prestigious Council of Scientific and Industrial Research (CSIR)-University Grants Commission (UGC) Junior Research Fellowship (CSIR-UGC JRF) by Council of Scientific and Industrial Research, India. In addition, Dr. Singh has also qualified Indian Council of Agriculture Research (ICAR)-National Eligibility Test (NET), i.e., ICAR-NET in "Agricultural Biotechnology", conducted by ICAR, India. He has been credited with 20 research papers and 10 review articles in international journals of high repute, 19 chapters in reputed books and has contributed to the book on "*Pseudomonas aeruginosa* MTCC 7925: Biofactory for Novel SCL-LCL-PHA". Dr. Singh has been on the "editorial board" as well as the "panel of reviewers" of several reputed journals of Elsevier, Springer Nature, John Wiley & Sons and so on. Dr. Singh has also supervised Ph.D., M.Tech., M.Sc. and B.Tech. students.

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Chapter 1
Abiotic Stress in Plants: Socio-Economic Consequences and Crops Responses

Mohammad Mafakheri, Mojtaba Kordrostami, and Jameel M. Al-Khayri

Abstract Evolution has long enabled plants with an adjusted response and tolerance mechanisms in the time facing drought, salinity, extreme temperatures, excessive light, and heavy metals collectively known as abiotic stress, with an accelerated incidence in climate change era owing to a rapid rise in global temperature, which has triggered a domino effect that recent studies announced its destructive influence on agricultural products. These circumstances have exposed crops to an unprecedented level of multi stress that involves a plethora of complicated morphological, physiological and molecular responses as well as survival strategies. The changes assist plants to improve water relations, regulation over oxidative stress and osmotic adjustment and induction of genes that are directly or indirectly initiate networks of signaling to organizational readiness for an arms race in plants against stress-generated harmful products. Its intertwined nature has been the subject of plenty of biological studies to reach a reliable realization of these processes, since this is the safe approach to inject this understanding into selection and breeding programs to create superior cultivars that make a human capacity to provide food to an ever-increasing population on the earth.

Keywords Adaptation · Crop productivity · Drought · High temperature · Osomolytes · Yield reduction

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1.1 Introduction

Plants as sessile organisms began their evolution in a fundamentally hostile terrestrial environment approximately 700 million ago, and gradually made the land hospitable to be colonized by other organisms (Hotton et al. 2001; Selden and Edwards 1989). Since ever, plants have successfully developed a large array of adaptation mechanisms that enable them to response properly to environmental stressors (i.e., water stress: flood and drought, high salinity, extreme temperatures: cold and heat, heavy metal toxicity) (Bray 2000; Wani et al. 2016).

Of the most prevalent type of abiotic stresses, drought will severely affect nearly 45% of arable lands in the world by 2100 (Field et al. 2014). Water is the most essential component that if water would be available, every possible ecological niche regardless of how extreme it could be colonized by organisms (Wood 2005). Drought is a prolonged period with the absence of rainfall or irrigation and mainly expected in arid and semi-arid regions. The major water consumption is in the agriculture sector which accounts for over 70% of harvesting underground water resources, chiefly in underdeveloped nations. Around 90% of arable under cultivation lands worldwide directly depend on rainfall. By the end of the twenty-first century, drought will severely affect nearly 45% of arable lands in the world. Salinity is another common place for important biotic stress known for its notorious multidimensional effects on plant performance (Burke et al. 2006; Dai 2011; Vibha 2016). Salinization of arable land has increasingly become a limiting factor in agriculture in particular with the gradual increase in global temperature by roughly 1 °C over the last century (Fig. 1.1). This increase has exacerbated the situation through intensifying the evaporation rate from soil (Nouman et al. 2018; Zhao et al. 2017), thereby disturbing the hydrological paradigms that again is a major source of stress for the agriculture sector. Salinization occurs either naturally or anthropologically through mismanagement of water resources and soil degradation with intense agricultural practice. A large portion of arable land (i.e., ~1 million hectares) is experiencing negative impacts of salinity in addition to the fact that the superiority of irrigated lands over rain-fed in terms of yield facilitates the situation in the favor of salinization (Colla et al. 2010; Munns and Gilliham 2015). By the appearance of climate change-driven impacts, the incident of abiotic stresses is on the rise particularly for high temperature and heat waves, which intensifies the severity of other stresses, in which the only 1 °C rising in global temperature causes a massive reduction in crop productivity (Iizumi et al. 2017; Zhao et al. 2017). The occurrence of cold stress as another extreme weather events similarly affected by climate change. Even though scholars have mainly zeroed on high-temperature stress, low-temperature stress is threatening plant productivity in a large scale owing to variability in climatic phenomena in the recent decades (Budhathoki and Zander 2019; Thakur and Nayyar 2013).

Another dimension of climate change manifested itself in meteorological turmoil that causes unpredictability in terms of time and intensity with significant localization of rainfalls that have catastrophic floods in agricultural lands as aftermath

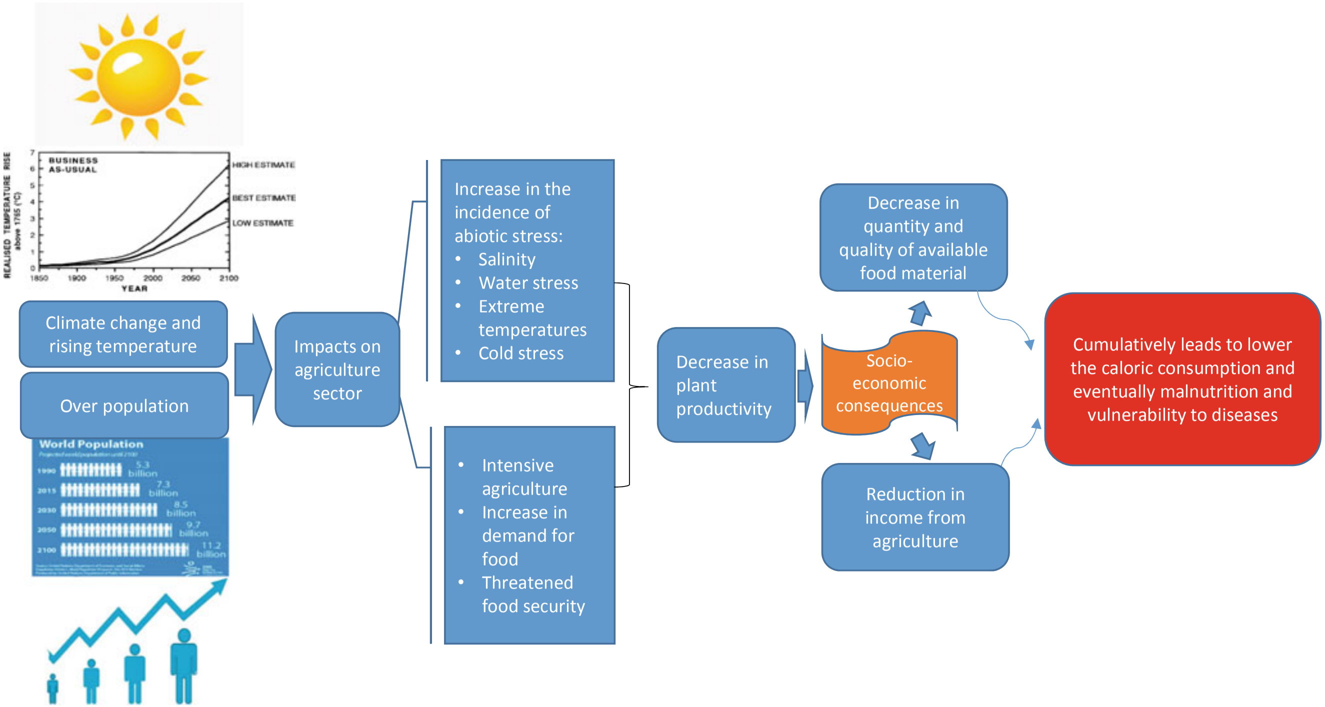

Fig. 1.1 Indirect socio-economic consequences of climate change and increasing population through negatively affecting agriculture sector

(Bailey-Serres and Voesenek 2010; Onyekachi et al. 2019). Concerning the toxicity of heavy metals in the rhizosphere, the accumulation of these elements can be attributed to various sources namely waterlogging (e.g., manganese, iron), erosion of bedrocks (e.g., nickel, cobalt, cadmium, lead), soil acidification (e.g., manganese, zinc) and anthropogenic activity (zinc, nickel, cobalt, copper, cadmium, molybdenum, chromium and lead) (Mengel et al. 2001; White et al. 2013; White and Pongrac 2017), which thanks to climate change, the sources are expanding and can considerably affect crops yield (Fageria et al. 2010). More severely, the occurrence of one stress facilitates the circumstances for other stresses, particularly high temperature and drought or salinity and drought, which often occur simultaneously (Sahin et al. 2018; Shah and Paulsen 2003). To make the matter worse, global climate change as a human-made phenomenon is dangerously jeopardizing the food production by imposing and increasing the incident of co-occurrence of the abiotic stresses at a dramatic rate.

This chapter summarizes the impacts of environmental stresses on social and economic status worldwide and give an updated perspective using most recent populations. Additionally, the morphological and physiological responses as well as tolerance mechanisms developed in plants against these stresses are discussed.

1.2 Socio-Economic Consequences of Abiotic Stress on Crop Production

A dramatic increase in average temperature over the last century has been enormously effective in orchestrating the circumstances for salinizing the arable land through increasing evaporation rate, instability in soil water content by floods or drought, and fluctuation in precipitation paradigms, which entirely severely affecting global food security. Human-caused increase in the global temperature reached 1 °C in 2017, which given the recent estimation that temperature will continue to rise ~0.2 °C per decade (Allen et al. 2018). So, conclusion that can be made is the exacerbation of the abiotic stress effects of crops and jeopardize the food security livelihood of a significant portion of the people on the earth. However, increasing the yield of some crops such as maize estimated to benefit from the rising global temperature in some areas, since a higher CO_2 concentration in the atmosphere as well as a higher temperature accelerates growth and development and biomass production. By 2025, complete water shortage will affect over 1.8 billion of the world population (Fig. 1.1), additionally, 65% of the population may face water stress (Lal 2018). Extreme fluctuation in climatic events generating socio-economic burdens worldwide specifically in developing nations, where agricultural products serve as an important source of financial income for families besides its role in providing food directly (Fig. 1.1). Among abiotic stresses, drought is probably the most economically disasters one, in a combination of drought and extreme high temperature stress during a 3-decade timeframe (1980–2010), a crop loss of worth about US $2 billion projected. Over half of rice cultivated farms as substantial food commodity in Asia is estimated to negatively influenced by water deficit stress (Bouman et al. 2005; Singh et al. 2018), whereas 95% of the world rice production is consumed in Asia, which indicates the scale of the threat that two-third world population will be faced (Dey et al. 2018). Lately, Ray et al. (2019) conducted a comprehensive assessment on climate change impact on the production of top ten crops (i.e., barley, cassava, maize, oil palm, rapeseed, rice, sorghum, soybean, sugarcane, and wheat: composing 85% of global consumable calories). Further, with a data collection from 1974 to 2013 at approximately 20,000 political units, it was discovered that roughly 1% decrease in crop production in these main crops accounted for abiotic stresses imposed by climate change worldwide, which means that effects of global warming are already in place. Of the three major cereal crops, rice, a major production loss was observed in India and Vietnam with approximately 2.2 million tons (Aggarwal and Mall 2002) and 1 million mt (Peng et al. 2004), respectively, wheat production similarly affected especially in Turkey with 0.8 million mt. Analogously, in South and North America changes in climate negatively influenced the production of three top kinds of cereal, whereas the changes seemed to be in favor of maize, sugarcane, oil palm and soybean production (Mourtzinis et al. 2015; Tack et al. 2015). During the abovementioned period, 3% reduction in consumable calories from the top ten crops of Australian people observed (Hochman et al. 2017). In the case of sub-Saharan Africa, this decrease was up to 1.8% despite the increase in Cassava production or some country-specific increases in the crops of interest. European country suffered the most with the highest production loss in top ten consumable calories owing to climate change generated negative effects in France 24%, Germany 11%, Hungary 10%, Romania 7%, Italy 7%, Spain 4% and Ireland 3% (Ray et al. 2019). The production losses worth billions of dollar, which renders vulnerable financial capability and food security; thus, putting a large portion of the world population in a greater risk. Additionally, half of the countries that have ongoing food insecurity issues, to make the matter worse, experience significant production losses.

Health-associated impacts of climate change on society can be reflected in the malnourishment in children that is projected to rise from 8.5 to 10.5% in a base case scenario. Interestingly, climate change-driven effects may be positive in temperate zones, however reduces the yield in tropical regions. Due to an increase in inputs required in the production process of agricultural products, the price in the favor of producers will rise, but affect the net consumers of agricultural products reside in urban or rural areas (Al et al. 2008; Budhathoki and Zander 2019).

Besides the substantial socio-economic impact of abiotic stress, these stresses cumulatively impose deleterious impacts on crop productivity through generating osmotic pressure, ionic toxicity, oxidative damage, and finally inadequacy in nutrient elements. As mentioned earlier, plants have evolved a countless number of adaptive tolerance mechanisms that can greatly contribute to stress tolerance (Bohnert et al. 2006; Waqas et al. 2019). Obtaining a profound understanding of how crops respond, develop, and employ tolerance mechanisms under stress is critical in having a clear picture to address the increasing impact of abiotic stress in the climate-changing era.

1.3 Crops Response to Abiotic Stress

Unlike animals, plants are immobile and cannot escape detrimental conditions that directly aim their overall function, hence crop plant responses to these situations enable them to cope with new changes. The abiotic stresses imposed are interlinked and may multidimensionally depress growth and yield formation of the crops through osmotic stress, oxidative stress and disruption of ion distribution, water relations, and plant cell homeostasis. These conditions can provoke the tolerance mechanisms that counteract the abiotic stress by a long list of morphological, physiological, and molecular modifications to exercise damage control (Bray 2000; Wani et al. 2016).

Responses to abiotic stresses involve changes that morphologically includes: leaf area reduction, increase in wax content and decrease in stem size, damage the productivity and reproduction processes under water stress and salinity, physiologically: disrupting water relations, stomatal conductivity, and transpiration, biochemically: increase in antioxidant and non-enzymes and osmoprotectants and finally molecularly: increase in biosynthesis of phytohormones in particular abscisic acid (ABA), specific proteins and transcription factors (DREB, ZIP, and WRKY) (Conesa et al. 2016; Ding et al. 2016; Lim et al. 2013; Singh et al. 2015). The abiotic stress trigger complex processes in crop plants that the precise interpretation and deciphering the network are rather difficult. Here we attempted to provide the responses and tolerance mechanisms in crop plants to cope with abiotic stresses.

1.3.1 Growth and Productivity

A determinative factor in the profitability of farming crops is a specific level of density that affects every agricultural practice up to harvest. Taking into consideration that intensity of abiotic stress on plant growth has a significant growth stage-dependency, the responses of crops could be specific. For example, if crops are in germination stage the consequences of abiotic stress would be detrimental by killing off a large percentage of seedlings that reduces the profitability of the whole farm (Okçu et al. 2005; Wang et al. 2009).

1.3.2 Germination and Early Seedling Stages

The occurrence of drought at early phases of germination can be harmful to the germination percentage owing to a deficiency in water uptake (Jain et al. 2019), reduction in water potential then improper enzymatic functions (Ahmad et al. 2009). Analogously high salinity in this stage prevents seed germination and emergence, since not only increases the necessity of water uptake due to high osmotic pressure but also limits the cell expansion and emergence of primary roots by a decline in water availability round the seed and in-between (Panuccio et al. 2014; Rauf et al. 2007). The crops responses to drought as well as salinity at early stages have been studied extensively, where recent observation on soybean showed the transferability of the drought stress effects from parents who experienced stress to progenies, which in this case manifested low germination rate and vigor (Wijewardana et al. 2019). The study conducted by Jovović et al. (2018) indicated a considerable variation in responses of various wheat cultivars to salinity during germination, which beside decline in germination rate and related features, delay in germination was observed. As mentioned earlier the accumulation of salt and decrease in osmotic potential could be responsible in deceleration or inhibition of water absorption vital for mobilizing nutrient components in the course of germination and/or sodicity damaged to the embryo. Similar results on crop plant responses to drought and salinity such as maize, soybean, barley, and sorghum have been reported. Germination of seeds additionally highly depended on optimum soil temperature and is vary from one crop to another. Whereas proper germination can start in wheat, as for temperate crops, around 4 °C with optimal temperature from 12 to 37 °C, the threshold in chilling sensitive crops such as rice is 20–35 °C, which similarly maize and rice have the same minimum critical temperature, 10 °C (Hasanuzzaman et al. 2013). Cold stress often defined under two terms: chilling (less than 20 °C) and freezing (less than 0 °C). Considering fluctuation in temperature pattern due to climate change, extreme temperatures also can be significantly destructive in particular in tropical and temperate regions, where the main part of grain crops (e.g., maize, wheat, rice and soybean) are produced (Beck et al. 2004; Savitch et al. 2011; Srinivasan et al. 1999; Yan et al. 2019). Cold stress can hamper the germination and root development mainly through simulating physiological effect similar to drought, for instance, in *Brassica napus* L. seeds exposed to chilling stress of 2 °C, only 50% germination was observed after almost two weeks, while in 3 days period under 8 °C the same germination rate recorded. In a recent study so as to monitor the responses of rice cultivars as germination index, coleoptile length, and radicle length to two weeks chilling stress (13 °C), Cong Dien and Yamakawa (2019) reported germination index of zero or no germination in 55 of 181 cultivars and germination index of 50% in solely 13 cultivars. The length of coleoptile under chilling stress downed by averagely 97.72% (2.7 mm), in the same manner, radicle length declined by 96.73% with 12.7 mm as the longest. Mainly, the reduction in water conductivity under chilling stress observed to be responsible for postponing the germination and emergence. Imbibition is considered to be the most sensitive phase of seed germination to abiotic stress, which cold stress specifically has the highest negative impact on germination rate in this phase. Mostly, because cold stress damages plasma membrane, which facilitates the situation of solutes (e.g., amino acids and carbohydrates) to leave the seeds, the condition is so-called ‘chilling imbibition’ (Lyons 1973). In a study where tomato seeds exposed to 4 °C symptoms of electrolyte leakage was observed (Bae et al. 2016). Further, undesirable effects of extremely high temperatures on the germination rate of crops have been investigated extensively, the germination rate of wheat seeds dramatically decreased in 45 °C, obviously owing to eventual drying up the water content of embryo and cell death in the course of early stages of germination. The combined effect of high (30 °C) and low (10 °C) temperatures, and salt-induced osmotic stress (−0.3 MPa) on *Triticum aestivum* seeds led to delay and inhibition of germination (Hampson and Simpson 1990).

Another major source of soil abiotic stress is the toxic level of heavy metals, which affects germination potential through reducing generating plenty of anomalies in seeds through toxicity and oxidative damage to vital biological membranes that disrupt the biosynthesis of carbohydrate and proteins. Among them, the toxic influence of Cd on seed germination has been investigated frequently, where effects are dose-dependent. However delayed germination, membrane leakage (Bae et al. 2016; Smiri et al. 2011), impediment of the process to mobilize the stored resources in seed by dysfunctioning the essential enzymes such as alpha-amylase and invertases (Sfaxi-Bousbih et al. 2010), hampering the production of amino acids and ultimately uncontrollable peroxidation of lipids have been frequently reported (Ahsan et al. 2007), analogously, Cu aims alpha-amylase and invertases, which inhibits the mobilization and finally production of energy to start the germination (Pena et al. 2011; Sfaxi-Bousbih et al. 2010). Similar responses in crop seeds during germination to some extend apply to other known heavy metal ions, for example, Ni in addition to the above-described reaction also impairs the activity of amylase, protease, and ribonuclease which again leads to arresting the digestion of reserved food in albedo (Ahmad and Ashraf 2012; Ashraf et al. 2011). Also, Pb majorly targets the energy production process in the cell by disrupting the absorption of nutrient elements (Fe and Mg) required for the function of enzymes participate in Calvin cycle, consequently inhibiting the germination process or root elongation (Mohamed 2011; Sethy and Ghosh 2013), (for review see Sethy and Ghosh (2013); Bae et al. (2016)).

1.3.3 Vegetative and Reproductive Stages

Overall, abiotic stress affect crops from early stages of growth up to the maturation, however germination and its quality is the key pillar of crop production with high vulnerability to abiotic stress. Abiotic stress aim at disrupting the energy production through imposing low turgor pressure, inhibiting enzymatic activity, which means even if the incidence of stress is after early stages of establishment, is will arrest the growth and development to production phases. The negative effects of drought stress with respect to growth and productivity can be properly observed in the study conducted by Colla et al. (2010) in which responses of hybrid lines of maize under drought resulted in a tremendous reduction in dry matter produced in shoot and root. Consequently, the yield reduced by 2–3-fold in comparison with control under normal condition. Reduction in growth vary within the plant organs, increasing the root:shoot ratio has been reported in maize lines responses to water deficit stress (Rahul et al. 2019), which is possibly due to lower sensitivity in roots toward low water potential (Wu and Cosgrove 2000). A ubiquitous response to drought stress is decreasing the leaf surface by folding, which is adaptation mechanisms leads to a reduction in light absorption and lessening the necessary component to maintain the ongoing biological processes, of course, such changes decreases the photosynthetic pigments as well that reflects in reducing the yield (Flagella et al. 2002; Hajibabaee et al. 2012). The important part is the involvement of the additive effects of other biotic stress in particular high temperature. Water shortage in soil and plants leads to rising temperature in the plant that triggers decreasing the leaf area in response or structural and functional modification in leaves such as minimizing the stomatal conductivity to improve water use efficiency (WUE), which ends up with a reduction in net photosynthesis. The concomitant of drought, heat, and salinity has been observed more often than not, however, owing to the difficulty in its assessments scholars tend to individual evaluation. Salinity responses of crops often compose of diminishing in shoot development and stunting by preventing the formation of internodes, as well as acceleration leaf shedding (Kozlowski and Pallardy 2002; Lacerda et al. 2003). Arresting growth and development can be attributed to aggregation of toxic ions leads to the removal of leaves (Hatfield and Prueger 2015; Lacerda et al. 2003). In pistachio rootstocks subjected to salinity necrosis symptoms in leaf were exhibited that had a high correlation with Na^+ and Cl^- accumulation (Rahneshan et al. 2018). In general, either low carbon fixation rate owing to the reduction in stomatal function as a result of decreased water potential (Hajiboland et al. 2014) and damage to photosynthetic pigments (Ashraf 2003), or direct preventative influence of accumulation of toxic ions (and unbalancing uptake of an essential ion such as K^+) (Munns 2002; Rahneshan et al. 2018) on cell division and elongation can be accountable for a decline in growth and biomass production under salinity. The incidence of chilling stress during growth may cause, as often have been reported, in damaging photosynthetic activity. Of course, mainly chilling is transient, and the intensity of its damage depends on the moment of occurrence whether the stomata are open or close. In watermelon plants subjected to 2 °C reduction in the activity of photosynthesis apparatus (Korkmaz and Dufault 2001) possibly owing to damage to oxidation production chain bridging two photosystems (I and II) in opened stomata that could not have a successful recovery after the course of stress was reported (Markhart III 1986). The arid and semi-arid region is prone to stimulate the combined effect of abiotic stress such as high light intensity and high temperature, or the latter one vs. salinity. In some case, combined effects of strictly regional with a superb instance is water deficit accompanied by low temperature stress in vineyards of north of China that happened to negatively influence the productivity considerably (Su et al. 2015). In another example, Mediterranean areas that environmental conditions facilitates the occurrence of combined effect of low temperature vs. high light stress (Loreto and Bongi 1989). Seasonal variation in atmospheric gases also sometimes contribute in make crops more sensitive to abiotic stress (Xu et al. 2007), in case of the point elevated O_3 concentration in winter increases the damage of low temperature stress in winter wheat (Barnes and Davison 1988) and/or O_3 vs. salinity exacerbated the reduction in productivity of *Oryza sativa* and *Cicer arietinum* (Welfare et al. 2002).

Productive phases of crops are susceptible to abiotic stress the most, the level of economic damage that stresses can cause is even much higher, since maintaining a farm in a region capable of severing abiotic stress requires a great deal of capital. Thus damages in critical stages of flowering, fertilization or filling in grain crops can be financially catastrophic. The responses of grain crops to abiotic stress during reproduction phases have been well-documented. Pollen formation and development as Achilles' heel of crop productivity in wheat is highly vulnerable to water deficit stress (Ashtox 1948; Ji et al. 2010), encourages out-crossing as often found linked to low grain set rate (Bingham 1966). Likewise, between the pollen mother cell and leptonema in sorghum showed the highest vulnerability to low-temperature stress (Brooking 1976). Extreme temperatures singly or in combination with drought and salinity can be terminal in pollen germination as heat stress in cereals overall led to a dramatic reduction in grain-filling time (Jagadish et al. 2007; Wardlaw and Wrigley 1994). This unfavorable conditions affecting the functionality of starch production enzymes subsequently incomplete grain-filling and low yield in cereals (Zahedi et al. 2003). However, the main vulnerability accountable for the reduction in grain number is before the appearance of ear and panicle out of leaf sheath. Even after meiosis as the most sensitive stage toward stress in rice and wheat, water deficiency and low-temperature stress caused a significant degree of infertility (Ji et al. 2010; Oliver et al. 2005). Male sterility additionally enhanced under drought stress (Saini 1997). The influence of temperature could be sometimes very specific, as the low temperature in rice enhances the number of grains but notably reduces the fertility of pollens (Dolferus et al. 2011; Okada et al. 2018). From an evolutionary perspective, the size of grain in undomesticated plants is more important since the fecundity of larger seeds is higher, while in grain crops this is actually number of grain that is determining the yield, a component of productivity which affects by biotic stress the most (Bingham 1966). Interestingly, while ovary is relatively stress-tolerant and reported to still be fertile, stress-simulated pollen sterility can be occurred in early stages of microspore (Hayashi et al. 2000).

Of the physiological responses linked to an increase in sterility is induction and concentration of ABA under stress conditions. The evidence such as a decrease in ABA content of anther of transgenic rice lines and their higher tolerance to low-temperature stress indicates the key role of ABA in the sterility of crops under stress. Similarly, a high level of male sterility in tomato under high-temperature stress and increased ABA is providing proof of its effects. The flowering and milk grain stages are observed to be the most vulnerable to drought in Chenopodium quinoa Willd (Blum 2011) which is coincidence with increasing the concentration of ABA in plant organs (Jacobsen et al. 2009; Razzaghi et al. 2011; Yang et al. 2016). Even the transient cold stress depressed the pollen germination in chickpea (Srinivasan et al. 1999). That is possibly owing to low energy that's frequently linked to inhibition influence of ABA on sugar and amino acid synthesis and supply through lessening the turgor pressure as an essential part of energy production that ultimately leads to hindering the growth of pollen tube, fertilization, and formation of seed (Clarke and Siddique 2004; Shivanna 1985; Thakur et al. 2010). Involvement of ABA in regulating anther sink strength recently attracted the attention of scholars as an important marker in screening germplasms for potential lines (Dolferus et al. 2011). Also using distinguishing phenotypic features such as fertility or sterility of pollen can provide remarkable breakthroughs that end up in exploring underlying molecular mechanisms.

1.4 Crop Water Relations

Understanding how crop plants behave regarding water relationships in critical periods of dealing with continuous or transient abiotic stress requires having reliable indices that truly convey the ongoing responses of the plant to the conditions (Passioura 2010). Abiotic stress often targets disturbing water relations in the aboveground and underground organs of the plant since growth and development to a large degree linked to a stable water relation. The most cited useful indicators of water relation in plants under stress are relative water contents (RWC), leaf water potential, osmotic potential, pressure potential, and transpiration rate (Kirkham 2005; Lazar et al. 2003; Okçu et al. 2005). Additionally, canopy temperature reported that can appropriately reflect the plant water potential status under heat, salinity, and drought stress because increasing in water potential means enhancement of photosynthetic activity which automatically lessens the canopy temperature (Ehrler et al. 1978; Siddique et al. 2000). Water relations is a delicate matter that defines the faith of plants dealing with long-term or short-term consequences of transient or permanent abiotic stress numerous processes involved in responses of plants to the stress-driven impacts on water status, nonetheless, they are mainly similar among various abiotic stresses. Owing to its predominant effect on productivity, tolerant genotypes and the application of comprehensive programs for their screening in germplasms can boost breeding programs (Chavarria and dos Santos 2012; Kirkham 2005).

1.4.1 Water Stress

Although each abiotic stress follows a specific damage mechanism their effects on water relation related-characteristics are similar to a large extend. Similar to extreme temperature stress responses of plant, imposing water deficit stress on soybean genotypes changed water relation through decreasing water potential in leaves, RWC, intensified exudation and expectedly enhanced temperature in the canopy, reduction in such features was delayed or not occurred in tolerance genotypes (Ouvrard et al. 1996). Likewise, sunflower manifested reduction in water relation associated features as RWC, leaf water potential when exposed to drought (Tezara et al. 2002). Stomatal closure, reduction in transpiration rate, and osmotic stress can be responsible for changing water relations in roots and shoots of crops under drought stress. A hydraulic gradient created by transpiration in plants that enables a constant flow of water from roots to leaves (Chavarria and dos Santos 2012). This connection depends on the availability of water in rhizosphere which by the increasing resistance in plant-soil relation transpiration leads to depletion of water content if stomata don't close down consequently reduction in water leaf potential and dehydration. The latter one is vary based on numerous factors such growth stage, atmosphere condition, the microclimate of aerial parts and water regime (Acosta-Motos et al. 2017). Commonly, response to the duration of drought stress is various, however, RWC, water potential, and osmotic pressure rise as the intensity of drought continues (de Campos et al. 2011). To save water content plants often tend to close the stomata which improved WUE while the rate of net photosynthesis decreased. WUE of genotypes and crops varies under drought (Abebe et al. 2003; Subramanian et al. 2006). Growth stage-dependency in WUE also has been reported in sunflower under water deficit stress, which is during reproduction phases, WUE markedly reduced in comparison to vegetative stages (Hussain et al. 2009). The absence of transpiration is accompanied by increase in respiration which means wasting stored resources that eventually recovery would be highly difficult or unlikely after irrigation (Franco et al. 2011; Sánchez-Blanco et al. 2004).

1.4.2 Extreme Temperatures

The influence of temperature on the water status of crop plants can be at multiple levels. That means changes in temperature beyond the optimal affects the enzymatic function directly through increased temperature or indirectly by imposing oxidative stresses that damage the activity of vital enzymes or causing osmotic stress which all lead to disruption the water relations (Bloom et al. 2004; Chavarria and dos Santos 2012; Ehrler et al. 1978; Kirkham 2005). Aerial parts of tomato (*Lycopersicon esculentum* L. cv. T5) that the roots exposed to low-temperature stress (5 °C) indicated the signs of low water potential and wilting. While another species of *Lycopersicon* (*L. hirsutum* LA 1778) known for its cold stress tolerance showed a higher level of water potential under the similar condition. Assessing the hydraulic conductance in either species proven to be similar, whereas stomatal behavior was a distinguishable difference. Further, stomatal closure in cold-tolerant species occurred in contrary to the sensitive one which stomata kept open until the temperature in root system dropped to 5 °C that resulted in sever wilt and injury. Interestingly, using grafting technique, the aerial part of one grafted to the roots of another, the response of stomata changed (Bloom et al. 2004). The stomatal behavior is a significant cold tolerance strategy in crops, which similar to the above-detailed study maize as tropical species vulnerable to cold failed to maintain water pressure that caused excessive transpiration under the cold condition of the soil. However, not due to reduction in root water hydraulic movement (de Juan Javier et al. 1997; Enders et al. 2019). Mainly, cold stress effects on crops are either individually through changing turgor or by formation ice that intracellularly stimulates a drought stress-like condition and drains water from cell to reach balance (Beck et al. 2004; Hansen and Beck 1988). Heat stress responses of crops are species-specific and duration of high-temperature stress is important, for instance, affecting water status in crops has extensively been reported, but heatwave in olive trees mainly lowered the CO_2 assimilation by damaging the photosystems and stomatal closure (Fahad et al. 2017; Haworth et al. 2018). The coincidence of high temperature and drought stress under field condition is common (Machado and Paulsen 2001; Velikova et al. 2009), water shortage in aerial part, leaves in particular during heat stress majorly attributed to intensification of transpiration rate (i.e., in the day time) and absence of equal response form roots. That all lead to depletion of water in leaves and drought stress while water is available in the soil. The unbalanced water potential in crops under high-temperature stress has been recorded in tomato (Morales et al. 2003), sugarcane (Wahid and Close 2007), and potato (Naz et al. 2018).

1.4.3 Salinity

Plant–water relations explain the behavior is a true reflection of plant responses to dehydration and ion toxicity caused by salinity (Passioura 2010). The salinity of soil and water resources, especially in arid and semi-arid regions can drastically reduce crop growth and yield. The level of intensity in effect on plant vary depending on species, season, tolerance threshold, duration of exposure to salinity stress, rainfall pattern during the growing season, intensity and type of salinity and soil physical and chemical properties. The salinity caused by sodium chloride is significantly higher than other salts and affects plant tissues in a higher rate, salts have a negative on water potential, water uptake, transpiration rate, stem water potential, osmotic potential and stomatal conductivity (Kirkham 2005; Munns and Gilliham 2015; Razzaghi et al. 2011). Salinity disturbs a plant's water relations owing to reduced availability of water from the soil solution as a result of negative water potential initiated by the toxic effects of the sodium and chloride ions (Munns 2005). This response has been observed in several species such as *Euonymus japonica* L., *Phlomis purpurea* L., and *Rosmarinus officinalis* L. (Alarcón et al. 2006; Álvarez et al. 2012; Gómez-Bellot et al. 2013).

The short-term responses of crops to salinity are highly analogs to water deficit specifically concerning osmotic stress (Navarro et al. 2008). Significant reduction in RWC, turgor pressure, and stomatal conductance of wheat genotypes subjected to a 4-week salinity (150 mM) during vegetative stages observed. However, while RWC affected by salt stress with no further modification during the experiment, the stomatal function considerably changed (Rivelli et al. 2002) which indicates the influence of hormonal regulation emerging from root system (Kaur et al. 2016; Passioura 1988). In general, crops (wheat and maize) responses related to water relations to high salt concentration in soil is either osmotic or aggregation of toxic ions in aerial parts (Azevedo Neto et al. 2004; Azizian and Sepaskhah 2014; Fortmeier and Schubert 1995). As mentioned earlier, responses often are highly situation-specific and depend on growth stage reaction might be different (Alarcón et al. 1999; Sánchez-Blanco et al. 2004). Fall in the number of water channels (or aquaporins) is probably responsible for the reduction of turgor and water conductivity (Kaldenhoff et al. 2008). Salt-treated *E. angustifolia* as a salt intolerance *and L. barbarum* with a higher ability to tolerate salinity showed a distinct difference in WUE as the former WUE decreased dramatically, whereas in latter one the water status was more stable (Acosta-Motos et al. 2017).

1.4.4 Heavy Metal

The negative effects of heavy metal stress on water relation frequently found to be linked with a change in aquaporins as the primary pass for water flow from roots that caused a reduction in hydraulic conductivity of water. This diminishment of aquaporins by heavy metal has been supported by experimental studies on *Alium cepa* L. and *Lupinus luteus* L. subjected to Pb (Przedpelska-Wasowicz and Wierzbicka 2011). The literature suggests that heavy metal stress mainly aim at the flow of water internally, which in this case notable reduction in transfer of water by xylem in *Ace saccharinum* L. under Cd stress was reported. A possible explanation can be justified with the decrease in xylem tissues capable of transferring water as well as shrinking in the size of vessels and clogging of xylem by fractions of gums or cell remnants (Lamoreaux and Chaney 1977). Disruption of water relations in heavy metal-treated plants sometimes caused by the accumulation of metal ions to a lethal level in root cells that led to cell death and limiting functional cells to uptake water, which simulating drought in aerial parts was the aftermath. Further, RWC is a sensitive indicator of changing in the water status of crops, however, its value under heavy metal stress reported to be stable, that is possibly due to the specific phenomenon known as vacuolization in various growth points in the plant (Gzyl et al. 1997; Przymusiński and Woźny 1985). This as a normal tolerance response in root cells helps to maintain RWC under heavy metal stress and mitigate water fluctuation in root cells subjected toxic ions. This development has been observed in meristematic cells of *Festuca rubra* (Davies and Zhang 1991) and maize (Doncheva 1998) exposed to a high level of Zn and Cu, respectively in addition to root epidermis and cortex cells of Ni-stressed *Psidium guajava* (Bazihizina et al. 2015). Induction of vacuolization in *L. luteus* received concentrations of Pb was similarly observed (Przedpelska-Wasowicz and Wierzbicka 2011). Increase in the number of stomata and reduction in their size clearly due to turgor pressure decrease in the heavy metal-treated plant also have been reported including *H. annuus* exposed to various levels of Pb, Cd, Cu and Zn (Kastori et al. 1992) and Cd-treated *Beta vulgaris* (Greger and Johansson 1992). However, contrary results on *S. bicolor* and *B. vulgaris* subjected to concentrations of Cd and Cu (Kasim 2006), and Zn (Sagardoy et al. 2010), respectively, indicated reduction in the number of stomata. Seemingly, responses have dose-and-species-dependency may to some extend explain the variation in results (Bazihizina et al. 2015; Doncheva 1998).

1.5 The Effect of Abiotic Stressors on Photosynthesis Pigments and Apparatus

An incredible ability of plants is to transform light energy into chemical energy through a delicate complicated chain of chemical reaction with H_2O_2 and CO_2. The process initiated by light breaking down water molecules into O_2 and hydrogen, the