Mirza Hasanuzzaman   *Editor*

Agronomic Crops

Volume 3: Stress Responses and Tolerance

Springer

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This book is dedicated to

*All of the Agriculturists and Farmers
of Bangladesh*

*Real heroes, who are showing the miracle
of ensuring the food production for the
increasing population*

Preface

The history of agriculture has played a major role in human development, as agricultural progress has been a crucial factor in worldwide socioeconomic change. Since the ancient civilizations, human being has been trying to explore new food crops. In the course of time, the demands for foods are increasing, and people are trying to rely on formal cropping practices. Agronomic crops fulfill most of the basic demands of human life such as food, fuel, fiber, medicine, etc. Based on the uses of crops, agronomic crops have been classified on different types such as cereals, pulses, oil crops, fodder crops, green manuring crops, sugar crops, narcotic crops, beverage crops, etc. Plant breeders have been developing many improved varieties of such crops every year to boost up the global production. However, in most of the cases, yield gaps exist in the farmers' fields due to the lack of proper agronomic management.

Crop management, therefore, becomes an integral part of food production. "Agronomy" is such a solution to make the crop field capable of securing the potential yield. Literally, it means the art of managing fields, and technically, it means the science and economics of crop production by the management of farmland. On the other hand, it is the art and science in production and improvement of field crops with the proper use of soil fertility, water, labor, and other factors related to crop production. Agronomy is the management of land for the cultivation of crop plants. The central theme of agronomy is the soil-plant-environment interrelationship. Both soil resources and climate have been changing globally, which makes crop production challenging. The basic agronomic principles can ensure the maximum yield from a crop variety, such as proper land preparation, selection of quality seeds and suitable varieties, proper water management, nutrient management, accurate pest management, proper harvesting, and postharvest operations. However, these activities should be chosen based on several factors like crop varieties, land types, agroclimate, etc. Choosing suitable cropping patterns and practicing crop rotation and multiple cropping also play an important role in enhancing land-use efficiency and crop stands.

Agricultural practices such as irrigation, crop rotation, fertilizers, and pesticides were developed long ago but have made great strides in the past century. Due to the global climate change, agronomic crops have been suffering from various abiotic and biotic stresses like salinity, drought, floods, toxic metals/metalloids, extreme temperatures, atmospheric pollutants, UV radiations, pests, etc. A substantial

portion of crop yield is being declined every year due to the adverse effect of stresses. Therefore, researchers are trying to address these problems and working to explore the stress tolerance mechanisms and manipulating adaptive features.

The knowledge of agronomic crops is essential for all agricultural graduates and scientists, not only with a view to understanding their cultivation practices but also with the objectives to know many academic and scientific details of each crop. This book covers comprehensive information on the advanced production of agronomic crops. Attempts have been made to cover all important field crops. Latest aspects about the cultivation practices, varieties, resource management, plant protection along with quality aspects, and postharvest practices are discussed in a crisp manner. The book must be immensely useful to all graduate students, faculty, and researchers in the field of agronomy and crop science.

This is the third volume (*Stress Responses and Tolerance*) of the three-volume book *Agronomic Crops*. In this volume, agronomic crops response and tolerance to stresses and the advances in research in improving agronomic crops under climate change are presented.

I would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. We are highly thankful to Dr. Mamta Kapila (Senior Editor, *Life Science*) and Ms. Raman Shukla (Senior Editorial Assistant) Springer, India for their prompt responses during the acquisition. We are also thankful to Daniel Ignatius Jagadisan, Project Coordinator of this book, and all other editorial staffs for their precious help in formatting and incorporating editorial changes in the manuscripts. Special thanks to Taufika Islam Anee, Dr. Md. Mahabub Alam, Mr. Abdul Awal Chowdhury Masud, Naznin Ahmed, and Tonusree Saha, Department of Agronomy, Sher-e-Bangla Agricultural University, Bangladesh, for their generous help in formatting the manuscripts. The editors and contributing authors hope that this book will include a practical update on our knowledge for the role of plant nutrients in abiotic stress tolerance.

Dhaka, Bangladesh   Mirza Hasanuzzaman

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Dr. Mirza Hasanuzzaman is a Professor of Agronomy at Sher-e-Bangla Agricultural University in Dhaka. He received his Ph.D. on "Plant Stress Physiology and Antioxidant Metabolism" from Ehime University, Japan. Later, he completed his postdoctoral research at the Center of Molecular Biosciences, University of the Ryukyus, Japan. He was also the Recipient of the Australian Government's Endeavour Research Fellowship for postdoctoral research as an Adjunct Senior Researcher at the University of Tasmania, Australia. His current work is focused on the physiological and molecular mechanisms of environmental stress tolerance. He has published over 100 articles in peer-reviewed journals, edited 6 books, and written 30 book chapters. According to Scopus®, his publications have received roughly 4,400 citations with an h-index of 33. He is an Editor and Reviewer for more than 50 peer-reviewed international journals and was a Recipient of the "Publons Peer Review Award 2017, 2018 and 2019." He has been honored by different authorities for his outstanding performance in different fields, like research and education, and has received The World Academy of Sciences Young Scientist Award (2014).

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Growth and Morphological Changes of Agronomic Crops Under Abiotic Stress

1

Aditi Shreeya Bali and Gagan Preet Singh Sidhu

Abstract

The escalating worldwide need for agricultural products accounts for twofold increase in crop yield by 2050. The agronomic crops especially wheat, maize, rice, barley, sugarcane, etc. contribute greatly to human food. The various environmental conditions impact the yield of agronomic crops globally. Complicating the problem, abiotic stresses especially temperature, heavy metal, drought, water, and salt stress induce toxicity in agronomic crops. Exposure to different abiotic stresses severely affects growth, morphology, productivity, and performance of crops all through the growing period. Further, increased generation of reactive oxygen species under stressful conditions might be linked to the decreased yield and development of agronomic crops. This chapter discusses an overview on the types of abiotic stress in crop plants and their effect on growth and morphological parameters. Additionally, inherent tolerance mechanisms adapted by agronomic crops to combat abiotic stress are also discussed briefly in this chapter.

Keywords

Abiotic stress · Agronomic crops · Physiology · Tolerance

Abbreviations

APX   ascorbate peroxidase
CAT   catalase
CFC   chlorofluorocarbon

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CH_4	methane
CO_2	carbon dioxide
GPX	guaiacol peroxidase
GR	glutathione reductase
H_2O_2	hydrogen peroxide
MDA	malondialdehyde
NaCl	sodium chloride
O_2	oxygen
$O_2^{\cdot-}$	superoxide radical
$OH^{\cdot}$	hydroxyl radical
ROS	reactive oxygen species
SOD	superoxide dismutase

1.1   Introduction

Climate change is a major threat to agriculture sector. Agronomic crops such as wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*), sugarcane (*Saccharum officinarum*), and barley (*Hordeum vulgare*) belong to family Poaceae or grass family which is agriculturally most important and satisfy the food demand of people worldwide. They provide a source of carbohydrates in human diet and also contribute in maintaining ecological stability. Among the different agronomic crops, maize is ranked first followed by rice and wheat in terms of production. The extremely changing environments severely affect the agriculture sector globally. Both the natural and anthropogenic activities lead to increased stress that hampers crop production. Many reports evidenced decline in yield of different agronomic crops especially wheat, rice, and maize in different parts of the world due to increased water, temperature, and salinity stress (Prasad et al. 2008a, b; Wang and Frei 2011). The global mean temperature is rising at an alarming rate of 0.3 °C, and it is predicted that it is likely to rise further to 1–3 °C by 2025 (Khan et al. 2013). Further, with elevated temperature the requirement of water for irrigation is estimated to increase by nearly 40–250% (Woznicki et al. 2015). The global yields of wheat, rice, and maize have been reported to get reduced by ~6.0%, 3.2%, and 7.4% with each °C rise in temperature (Zhao et al. 2017). Besides, high temperature, drought, salinity, floods, and cold waves cause severe economic losses worldwide. Moreover, with incrementing world population that is expected to reach to 9 billion in 2050, the major global challenge of future would be to ensure food security.

Agronomic crops are exposed to different abiotic stresses like drought, salinity, heavy metal, temperature, and waterlogging that cause huge economic loss. They negatively impact the growth and physiology of crops globally. Drought stress has been documented to cause significant reduction in growth, relative water content, and chlorophyll content in maize cultivars (Efeoğlu et al. 2009). Salinity stress has been reported to inhibit growth and physiology of different crop species such as cotton (Plaut and Federman 1991) and barley (Rawson 1986) by altering the

activities of various metabolic enzymes (Khan and Panda 2008). Further, elevated temperature is deleterious to crop yield and can reduce agricultural productivity (Schauberger et al. 2017). Asseng et al. (2015) documented that the production of wheat decreased with rising temperature. Heavy metal toxicity is also a serious problem worldwide. Excessive accumulation of metal in plant impedes crop productivity by causing detrimental effect on growth and morphological parameters such as seed germination, growth, and photosynthesis (Shahid et al. 2015). Further, waterlogging stress limits crop yield globally. It has been reported to reduce plant height, tillers, and root and shoot biomass in barley (Luan et al. 2018) and cotton (Zhang et al. 2017).

The increased incidence of abiotic stress leads to generation of reactive oxygen species (ROS) that might be responsible for adverse effect on growth and morphology of agronomic crops. Further, the reduction in yield and productivity of crops might be related to elevated amount of ROS. This chapter includes an overview on different types of abiotic stresses in agronomic crops and their effect on growth and morphological parameters in agronomic crops. Additionally, inherent tolerance mechanisms adapted by agronomic crops to combat abiotic stresses are also discussed briefly in this chapter.

1.2   Abiotic Stress and Their Effect on Growth and Morphological Parameters of Agronomic Crops

Plants are exposed to multitude of abiotic stresses such as drought, heavy metal, temperature, salinity, and waterlogging stress that adversely affect the growth and physiology of crops leading to reduction in yield. These stresses produce harmful chemical species known as reactive oxygen species (ROS) that restrict different metabolic pathways thereby limiting crop productivity. This section deals with different abiotic stresses and their impact on growth and morphology of agronomic crops.

1.2.1   Drought Stress

Drought stress causes huge loss in crop production and is an important threat to world food security. It is a major abiotic stress factor that affects the plant growth and development. Drought stress arises due to reduced available water in soil and continuous loss of water from plant through transpiration. Plants growing in regions that have low water availability face severe affect of stress on growth. Further, with changing climatic conditions and global warming, the harmful effects of drought stress are going to increase rapidly. The incrementing human population can lead to severe shortage of water in the future. Drought stress significantly harms the agriculture sector by restricting crop yield and production globally (Chaves and Oliveira 2004). It alters the growth, morphology, and physiology of many agriculturally

important plants. For example, leaf water potential and relative water content decreased in wheat in response to elevated drought stress (Siddique et al. 2000).

Drought stress has been reported to impede the growth and morphology of several agronomic crops. It is a critical factor during initial period of plant growth and development (Jaleel et al. 2009). The first effect of drought stress impeded germination (Harris et al. 2002). Under severe water stress, cell division, expansion, and elongation get damaged resulting in reduced growth and yield of crops (Hussain et al. 2008). In maize genotypes, water deficit conditions reduced the growth of the plant (Kamara et al. 2003). Water stress significantly impaired stem length in soybean (Zhang et al. 2004), rice (Mostajeran and Rahimi-Eichi 2009), and barley (Samarah 2005). Further, Alexieva et al. (2001) reported relative water content to be a major factor responsible for decreased growth in crop plants under drought conditions.

Drought stress drastically decreased number of leaves per plant and leaf size which largely depends upon water balance or turgor pressure of leaf (Anjum et al. 2011). For example, Hütsch et al. (2015) reported reduced leaf area in maize plants growing under stressed conditions. The reduction in leaf area might be due to the inhibition of leaf expansion (Rucker et al. 1995). Drought stress has been reported to induce reduction in fresh and dry weight of crop plants (Farooq et al. 2009). Efeoğlu et al. (2009) observed decreased fresh and dry biomass in three maize cultivars under water deficit conditions. Likewise, Saleem (2003) noticed decreased biomass production, plant height, ear length, grain yield in durum, and bread wheat under drought stress.

1.2.2 Temperature Stress

Temperature stress, both low (chilling stress) and high (heat stress), has been recognized as a major harm to crop plants worldwide. Temperature is an important factor governing plant growth and development (Hatfield and Prueger 2015). According to IPCC (2007) during the next 30–50 years, the temperature is expected to rise by 2–3 °C. The continuous emission of greenhouse gases like carbon dioxide (CO_2), methane (CH_4), and chlorofluorocarbons (CFCs) is one of the major reasons contributing to elevated global temperature worldwide (Shah et al. 2011). These extreme environmental conditions are likely to increase under future climatic scenarios (Barlow et al. 2015). Many reports suggested the effect of temperature stress on both the vegetative and reproductive growth stages of crop plants that severely impact the yield of the crop (Hatfield et al. 2011).

High temperature significantly affects the growth and development of agronomic crops (Wheeler et al. 2000; Prasad et al. 2008a, b). It damages the photosynthetic apparatus, reduces leaf photosynthetic yield, and affects cellular metabolism in plants (Prasad et al. 2008a, b). Long-term exposure of high-temperature (42 °C) stress inhibited the development of root and first leaves in wheat seedlings (Savicka and Škute 2010). The authors found that exposure to high-temperature stress caused increased production of $O_2^{\bullet-}$ that leads to elevated concentration of MDA which

might be responsible for reduced root growth (Savicka and Škute 2010). Similarly, Shah et al. (2011) reported that increased temperature affects emergence, ripening, and harvesting stages of rice. Further, they found that elevated night temperature is more responsible for reduced rice yield (Shah et al. 2011). Earlier, Yoshida (1978, 1981) also observed delayed emergence and poor growth of rice seedling upon exposure to high-temperature stress.

Cold stress or low-temperature stress interrupts plant's metabolic pathways and adversely affects its growth and development. It has been reported to significantly limit crop distribution and productivity (Tian et al. 2011). Low-temperature stress has been reported to affect rice seedlings due to increased concentration of stress-related proteins in response to stress (Hashimoto and Komatsu 2007). Cheng et al. (2010) investigated the effect of chilling stress on soybean seeds and found that exposure to low temperature caused poor germination, reduced seedling emergence, decreased seedling vigor, and caused severe loss of crop yield. Similarly, Aghaee et al. (2011) reported decreased stomatal conductance and dry matter accumulation in two rice genotypes in response to cold stress. Low-temperature stress has been reported to reduce growth in sorghum seedlings (Abbas 2012).

1.2.3 Salinity Stress

Salinity stress or salt stress harm one-third of the agricultural fields on Earth due to very high temperature and poor irrigation practices (Shibli et al. 2007). It has hampered 30% of irrigated and 6% of total land area (Chaves et al. 2009). Since there is scarcity of available water, saline water is therefore used for irrigation purposes. According to FAO (2005), salt stress affects 831 million hectares of agricultural land globally. It is the most common and harmful abiotic stresses that affect crop yield worldwide (Amjad et al. 2014). Salinity stress is followed by symptoms of physiological water stress similar to drought stress in plants (Chaves et al. 2009). Moreover, plants exposed to salinity stress also encounter osmotic stress (Sanchez et al. 2007). Many reports suggest the effect of salinity stress on growth, development, and physiology of plants (Hussain et al. 2013; Mustafa et al. 2014).

Amirjani (2011) exposed rice seedlings to 200mM NaCl for 14 days and observed its effect on growth and relative water content of plant. The author found that shoot length, fresh and dry weight, and relative leaf water content of rice seedlings decreased in response to salt stress (Amirjani 2011). Soil salinity significantly reduced crop yield. Accumulations of ions in higher concentration in shoot tissues cause toxic effect on plants. Tavakkoli et al. (2011) observed that high concentration of Na^+, Cl^-, and NaCl reduced growth of barley; however, the reduction was more in response to NaCl treatment compared to Na^+ and Cl^- exposure alone. Moreover, authors found reduced stomatal conductance and uptake of K^+ and Ca^{2+} in barley plants exposed to salinity stress (Tavakkoli et al. 2011). Nemati et al. (2011) reported decreased total dry weight in two genotypes of rice upon application of NaCl.

Bakht et al. (2011) conducted experiments to study the effect of NaCl on maize cultivars and found that exposure to salinity stress significantly affected

germination, emergence, plant height, shoot fresh weight, dry weight, and leaf area of plant. They observed that salt stress has negative effect on growth and development of both maize cultivars (Bakht et al. 2011). Further, Akbarimoghaddam et al. (2011) evaluated the effect of salinity stress on seed germination and seedling growth of six bread wheat cultivars and found that seed germination and dry weight decreased in all the wheat cultivars due to accumulation of toxic ions in the plant tissue. The reduction in growth caused by salinity stress might be due to the increased formation of reactive oxygen species (ROS) like singlet oxygen ($^1O_2$), H_2O_2, and hydroxyl radicals (OH^-) (Mishra et al. 2013).

1.2.4   Heavy Metal Stress

Soil contamination by heavy metals is a serious threat worldwide (Sidhu et al. 2017a, b). Rapid industrialization, harmful mining activities, and intensive agricultural practices caused accumulation of heavy metals in the environment. Natural sources such as volcanic eruptions, forest fires, and soil erosion also add heavy metals to the soil environment (Sidhu et al. 2017a). Some heavy metals such as copper, manganese, and zinc are essential micronutrients, and others like lead and cadmium are nonessential elements. Essential elements are required in small amount by plants for normal growth and activity; however, they are toxic at elevated concentrations (Wuana and Okieimen 2011). Excessive concentration of heavy metals in soil above their threshold limit poses serious concern to plants, animals, and human health. Since heavy metals are nonbiodegradable, they remain in soil for a long time, thereby causing reduction in crop yield (Sidhu et al. 2017a). An elevated amount of heavy metals in soil cause severe toxicity symptoms in plants that lead to reduced growth and photosynthesis in plants (Mahmood et al. 2007; Ghani 2010).

Heavy metals strongly influence growth and development of agronomic crops (Mahmood et al. 2007). A study was conducted by Mahmood et al. (2007) to find out the effect of different heavy metals on growth of cereal crops. The authors observed that application of copper (Cu), zinc (Zn), lead (Pb), magnesium (Mg), and sodium (Na) exerted negative effect on the seed germination, total root numbers, root length, shoot length, and root-shoot ratio of barley, rice, and wheat (Mahmood et al. 2007). This might be due to the heavy metal-induced oxidative stress that causes reduction in enzyme activities that leads to lowering of seed metabolic processes involved in seed germination (Ayaz and Kadioglu 1997). Similarly, Ghani (2010) reported decreased growth and protein content in maize seedlings in response to exposure of Mn (manganese), Pb, Cd (cadmium), Cr (chromium), and Co (cobalt).

Excessive accumulation of heavy metals causes adverse effect on growth of crops. For example, Thounaojam et al. (2012) observed gradual decrease in root and shoot growth of rice seedlings with increasing concentration of Cu. This might be attributed to increased amount of H_2O_2 and lipid peroxidation that cause oxidative

stress in plant tissues in response to elevated accumulation of Cu (Thounaojam et al. 2012). Further, Ahmad et al. (2012) reported effect of Cd toxicity on growth of four wheat cultivars and found that exposure to high concentration of Cd decreased root length, shoot length, percent germination, and germination index in all the cultivars.

1.2.5 Waterlogging Stress

Soil structure has a huge impact on waterlogging of soils. Excessive rainfall causes waterlogging stress in soil that severely affects the gaseous exchange between soil and water. It hampers the crop production and yield worldwide. Insufficient oxygen supply to roots for respiration is the main reason for lowered yield under water-logged environment (Linkemer et al. 1998). Sallam and Scott (1987) reported reduced root growth and nodulation in soybean and attributed this to the inadequate amount of O_2 which inhibits nitrogen and mineral uptake.

Waterlogging stress restricted growth of winter wheat that resulted in decreased shoot dry weight and grain yield (Dickin and Wright 2008). Studies have shown that waterlogging stress increased leaf senescence, damaged photosynthetic pigments, and inhibited photosynthetic rate of plants (Smethurst et al. 2005). Winter wheat was found to be most sensitive to waterlogging stress after germination and affected the shoot numbers in plant (Cannell et al. 1980). Further, Grzesiak et al. (1999) found that waterlogging stress caused small number and reduced dry matter of lateral branching as compared to control in maize plants. The root and shoot growth and chlorophyll content of six barley genotypes were negatively affected by water-logging stress (Pang et al. 2004). It also affected growth and development and decreased the plant morphology (plant height, ear height, and leaf area index) and ear characteristics of maize (Ren et al. 2014).

1.3 Tolerance Mechanisms

Exposure of crops to unfavorable conditions such as drought, temperature, salin-ity, heavy metal, and waterlogging caused severe harm to both growth and mor-phology of agronomic crops. Further, these abiotic stresses lead to reduction in crop production and yield. This might be attributed to increased concentration of toxic reactive oxygen species, i.e., H_2O_2, $O_2^{\cdot-}$, $OH^{\cdot}$, etc. These ROS produced in response to abiotic stresses might be responsible for reduced growth and mor-phology of plants. They target proteins, lipids, RNA, and DNA and cause irrepa-rable damage to plant metabolic pathways (Petrov et al. 2015). Plants adopt various tolerance mechanisms to combat abiotic stress-induced decrease in mor-phology. They have systematic antioxidant machinery with different enzymatic [superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidize (APX),

guaiacol peroxidize (GPX), and glutathione reductase (GR)] and nonenzymatic [ascorbic acid (AsA), reduced glutathione (GSH), carotenoids, and flavonoids] antioxidants. The antioxidant machinery helps in scavenging ROS generated under different stressful conditions. Various researchers have reported increased activity of antioxidant enzymes to tolerate increased production of ROS generated in response to abiotic stresses (Sidhu et al. 2016, 2017b).

1.4   Conclusion

The increased incidence of abiotic stresses harms the growth and development of agronomic crops worldwide. These abiotic stresses, viz., temperature, salinity, drought, heavy metal, and waterlogging, reduce the yield of crops and cause huge economic losses globally. Plants have also adopted various strategies to combat these stresses and to mitigate increased ROS generation. However, future research is needed to find out the effect of these abiotic stresses on genes that are responsible for growth of crops.

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Impact of Climate Variability on Phenology of Rice

2

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Abstract

Rice (*Oryza sativa* L.) is an important staple food for nearly half of the world population. It is extremely variable in phenology which depends strongly on cultivars and prevailing environmental conditions. During the last three decades, rice production is showing a declining trend, and it is expected to continue because of anthropogenic practices involving emission of greenhouse gases (GHGs) that contribute to the global climate change. The weather and climate variability directly influence the phenological development of rice such as canopy radiation capture, biomass production, seed germination, crop duration and maturation, and grain yield that lead to food insecurity. The warnings in weather episodes modify rice cultivars to grow in vulnerable situations and even changes in agronomic management practices. In rice, plant developmental responses to elevated temperature vary significantly at all vegetative and reproductive stages. Due to high temperature, vapor pressure deficit increased and enhances evaporation from the anthers which results in anther dehiscence, reduced pollination, pollen germination, and pollen tube growth. Increase in CO_2 concentration in the atmosphere increases the grain yield in rice to an extent, but further CO_2 elevation shows negative result. In addition, high temperature contradicts the positive effects of CO_2 fertilization on plant. However, rice is relatively more tolerant to weather variability during germination and active tillering and toward maturity but sensitive during early vegetative and reproductive stages. Reproductive processes in rice especially flowering stage show greater sensitivity to drought than do vegetative processes. Hence, appropriate mitigation strategies need to be adopted on sustainable basis to combat the menaces in crop cultivation and to feed the population explosion.

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Abbreviations

$(NH_4)_2 SO_4$	Ammonium sulfate
AWD	alternate wetting and drying
CH_4	methane
$CO(NH)_2$	urea
CO_2	carbon dioxide
FAO	Food and Agricultural Organization
GHGs	greenhouse gases
HNT	high night temperature
IPCC	Intergovermental Panel on Climate Change
IRRI	International Rice Research Institute
LAI	leaf area index
N_2O	nitrous oxide
RH	relative humidity

2.1 Introduction

Rice (*Oryza sativa* L.) has been a staple food for nearly half of the world population. It is one of the three most important staple crops in the world as it provides 35–80% of total calorie intake (providing 27% of dietary energy and 20% of dietary carbohydrate) to around 3 billion people (Wassmann et al. 2009; FAO 2004). More than 90% of global rice is produced and consumed in Asia where China and India account for more than half of the world's rice area and along with Indonesia consume more than three-fourths of the global rice production (FAOSTAT 2010). Rice is grown under wide range of geographical locations in tropical, subtropical, and temperate regions at latitudes ranging from 35 ^{0}S to 53 ^{0}N and at elevations of 0–2000 m (Yoshida 1981) and hence is extremely variable in phenology (duration from germination to flowering) which also depends strongly on cultivars and the prevailing environmental conditions (Tripathi et al. 2016). Based on the different agroecological zones and the production system used, productivity of rice varies among countries as well as within the same country (Ntanos and Koutroubas 2002).

Globally, intensive farming methods are now being followed in rice which depends heavily on high-yielding varieties, chemical fertilizer application, and irrigation. During the last three decades, rice production is showing a waning tendency and is expected to continue as these anthropogenic practices have given birth to emission of GHGs like the CO_2, CH_4, and N_2O emissions (IPCC 2014);

deforestation in upland rice production under slash-and-burn shifting cultivation is also considered contributors to global climate changes (Nguyen and Ferrero 2006). Carbon dioxide is released largely from microbial decay or burning of plant litter and soil organic matter (Janzen 2004; Smith 2004). Since 2000, anthropogenic CO_2 emissions have risen by more than 3% annually where as methane is the major end product of anaerobic fermentation from submerged soils to the atmosphere having >20 times more heat absorption capacity than CO_2 (Stigter and Winarto 2013). On the other hand, N_2O emissions have global warming potential of about 300 times higher than CO_2 which is the most important threat to the ozone layer in this twenty-first century (Ravishankara et al. 2009). These short-term weather warming components like CO_2, temperature, and unpredictable rainfall affect plants at the level of molecular function, developmental processes, and morphological and physiological traits that bring about a gradual shift in the fruiting and flowering season of rice (Tripathi and Singh 2013) distressing the food security aspects of the world (Poudel and Kotani 2013).

In this chapter, we will discuss the factors and intensity of the climatic variables and their consequences on rice production, productivity, and yield. Appropriate strategies need to be developed to combat the menaces in crop cultivation and to feed the population explosion.

2.2 Weather and Climate Variability

Weather and climate variability have great influences on the rice cropping season. Weather anomalies like increase in global mean maximum and minimum temperature can accelerate the phenological development (Lansigan et al. 2000; Tao et al. 2006; Shimono et al. 2010) leading to earlier senescence, decrease in canopy radiation capture and biomass (Ishii et al. 2011), crop duration, and maturity. Such increases in temperature also have substantial consequences on precipitation and its intensity (Sun and Huang 2011) affecting the sequences of dry or wet days especially drought and flood episodes in both the tropics and the subtropics during all crop growth stages of rice (Vadez et al. 2013). Delay in the onset of rain affects timing of initiation of the cropping season, particularly in rainfed areas of the world. The regions with year-round distribution of rainfall may exhibit overlaps in rice planting and harvesting operations, shattering of grains, on-field germination, and reduction in grain yield of rice. Precipitation fluctuation has significant long- and short-term impacts and affects the region's rice production that leads to food insecurity (Koudahe et al. 2018). These warnings in weather episodes modify rice cultivars to grow in vulnerable situations and even changes in agronomic management practices including fertilizer use, irrigation, and control of pests and diseases leading to serious social and economic implications (Geng and Cady 1991; Hossain 1997). Farming system response is more critical with regard to sudden fluctuations in weather rather than gradual, long-term climatic shifts, and adaptation is geared up more by occurrence of climate extremes (Murdiyarso 1998).

2.2.1 Effect of Elevated CO_2

The global atmospheric CO_2 concentration has been increasing day by day, and it has noteworthy impacts on physiology and quality of plants such as photosynthesis, nutrient uptake along with translocation, enzymatic activity, nutritive value, etc. (Ainsworth et al. 2007). Increase in CO_2 concentration increases the grain yield in rice to an extent, but excess CO_2 elevation reduces the yield (Bugbee et al. 1994). Hence, higher CO_2 have undesirable impacts on rice production and quality.

The effects of elevated CO_2 change the density and size of stomata as well as leaf morphology (Pedersen et al. 2009). The alterations in plant development also occur for elevated CO_2 due to increase in flux of carbohydrates and related metabolites and by the action of glucose which acts as signaling molecule (Gray and Brady 2016). Taub et al. (2008) reported that the protein concentrations in rice may be affected by elevated CO_2 (540–958 mmol/mol^{-1}). During reproductive stage, rate and duration of grain filling are also reduced due to CO_2 enrichment (Hu et al. 2007) which causes poor grain filling and grain chalkiness. Besides this, elevated CO_2 decreases brown rice percentage and head rice percentage and induces the ratio of amylose to amylopectin in grain (Jing Li-quan et al. 2016). The yield augmentation in rice under higher CO_2 concentration is due to CO_2 fertilization, increased tiller numbers, LAI, photosynthesis, and enhanced water use efficiency (Saseendran et al. 1999). Goufo et al. (2014) found that concentration of α-linolenic acid increased, but linoleic and γ-linolenic acids decreased due to elevated CO_2. However, high temperature can result in the rise of leaf surface temperature which affects photosynthesis and root growth of plant; hence, it is expected to contradict the positive effects of CO_2 fertilization in rice (Gu et al. 2010; Poudel and Kotani 2013).

2.2.2 Effect of Temperature Variability

The phenology of rice is influenced by the environment conditions in a certain range; the optimum temperature for maximum photosynthesis in rice is 25–30 °C for daytime and 20 °C for night time (IRRI 1997). Yano et al. (2007) reported that an increase in temperature leads to a decrease in vegetative phase. Baker et al. (1992) and Sun and Huang (2011) confirmed that in tropical regions, the effect of the temperature rise due to climate change is probably less compared to temperate region as it increases near or above the optimum temperature range for the physiological activities of rice. Such warming reduces crop duration, alters photosynthate partitioning to economic products, and increases respiration and evapotranspiration by disrupting water, ion, and organic solute movement across plant membranes.

In rice, plant developmental responses to elevated temperature vary significantly at all vegetative and reproductive stages – seedling, booting, and heading to flowering stages (Nishiyama 1976). At vegetative stage, peak biomass development takes place at 33 °C, while grain formation and yield are adversely affected by temperatures above 25 °C (Matsushima et al. 1964; Baker et al. 1995). Elevated air and soil

temperature imbalances leaf function by change in gas exchange properties, electrolytic leakage from leaves (Halford 2009), reduced heat dissipation from leaf surface (Zhang et al. 2015), reduced root development, and critical root functions including respiration and nutrient uptake by roots (Atkin et al. 2000).

During panicle emergence, higher temperature causes spikelet sterility owing to heat injury. Flowering to anthesis for a duration of 5–7 days is extremely sensitive to high-temperature stress (Jagadish et al. 2007). Rice flowers open for approximately 45 mins; fertilization completes within 1.5–4 h after anthesis (Cho 1956) during which a series of heat stress-sensitive processes such as anther dehiscence, pollination, pollen germination, and pollen tube growth occur (Jagadish et al. 2010; Matsui et al. 1999, 2001; Yoshida 1981). High temperature during this period results in increased vapor pressure deficit, enhancing evaporation from the anthers, thereby depriving the crucial moisture needed for pollen grain swelling which results in anther dehiscence. Pollen viability decreases to zero at midday temperatures of 40 °C (Kim et al. 1996) and ultimately leads to floral bud abortion (Guilioni et al. 1997), hence lowering seed-set.

At grain filling stage, high temperature also affects the accumulation of dry matter, carbon, and nitrogen (Kim et al. 2013) in the kernel (Kobayashi et al. 2007). Elevated temperatures have been found to cause lower amylose content which determines the grain quality in rice (Terao et al. 2005). Variation in amylase content leads to decreased hardiness or increased stickiness of rice grains at warmer temperatures (Counce et al. 2005).

Increased heat tolerance is most needed in *O. sativa* compared to *O. glaberrima*, which exhibits peak anthesis during late morning till mid-afternoon (Yoshida et al. 1981) exposing the heat-sensitive reproductive organs to high temperatures invariably leading to increased spikelet sterility (Jagadish et al. 2008; Prasad et al. 2006). The japonica varieties require lower temperature for ripening than indica varieties (Krishnan et al. 2011).

In temperate regions, increased air temperatures hasten rice development, thereby shortening the time from transplanting (or direct seeding) to harvesting and reducing the total time for photosynthesis and grain development (Neue and Sass 1994).

An increase in high night temperature from 27 °C to 32 °C causes the crop production to decrease due to lower translocation efficiency of assimilates as a result of higher respiration rate of up to 40% in rice leaves and drop in photosynthesis (Mohammed and Tarpley 2009b) with decrease in leaf chlorophyll and leaf nitrogen content in rice. This affects the grain filling phase, seed-set, milling quality, grain dimensions, and starch branching in rice (Counce et al. 2005; Mohammed and Tarpley 2009a, 2010). Night temperature is predicted to increase at a faster rate than day temperatures due to less radiant heat loss because of increased cloudiness (Alward et al. 1999).

Rice is a low-temperature-sensitive crop; thus, low temperatures below 15 °C restrict seed germination and delay transplanting date; large day and night temperature difference of 1–3 °C induces rice blast, specially in upland rice (Luo et al. 1995), interrupts plant growth (Baker et al. 1990), and reduces yield (Shimono 2011).

2.2.3   Effect of Relative Humidity (RH)

Humidity also plays an important role in rice yield. Optimum RH for rice cultivation lies between 60% and 80% (Nguyen 2003). Physiological influences of RH include water relations of plant and indirectly affect leaf growth, photosynthesis, pollination, occurrence of diseases, and finally economic yield (Yan et al. 2010). During vegetative phase, RH had little effect on root-shoot dry matter ratio (Hirai et al. 1992). When RH is low, the duration from transplanting to panicle initiation reduces (Sunil 2000) and transpiration increases causing water deficits due to partial or full closure of stomata. Besides, mesophyll resistance also increases blocking entry of CO_2 which indirectly affects photosynthesis. The effects of temperature on rice may be intermingled with those of RH and solar radiation. The mean RH during rice cultivation is generally negatively associated with solar radiation. At reproductive stage, RH below 40% inhibits flowering (Vijayakumar 1996), but spikelet sterility at high air temperatures increases with increased humidity (Nishiyama and Satake 1981; Matsui et al. 1997). High humidity of 88% at 35 °C decreases fertility percentages, and the degree of decline differs among the cultivars. Under high humidity at 31 °C, pollination is cultivar dependent but not fertility percentage. Matsui et al. (1997) showed that fertility of spikelets at 37.5 °C was highest at 45% RH followed by that at 60% RH and lowest at 80% RH. So, high humidity increases the percentage of spikelet with only a few pollen grains on the stigmas and lowers the fertility. Similarly, low humidity can promote spikelet sterility under high temperature (Matsushima et al. 1982).

Lower RH of 60% at 38 °C leads to a higher vapor pressure deficit of 2.65 facilitating the plant to exploit its transpiration cooling ability (Jagadish 2007; Jagadish et al. 2007). A combination of high temperatures (32–36 °C) with low RH (55–60%) and high RH (85–90%) recorded a 1.5 °C increase in spikelet temperature and high spikelet sterility (Weerakoon et al. 2008; Abeysiriwardena et al. 2002). The increased humidity and wind velocity due to climate change have immense impacts on the viability of pollens in rice (Matsui et al. 2005; Jablonski et al. 2007).

2.2.4   Effect of Rainfall

The initiation of a cropping season is determined largely by the start of the rainy season particularly in rainfed areas. An increase in the level, timing, and variability of precipitation may benefit the semiarid and other water-scarce areas due to increase of soil moisture but can aggravate the problem of waterlogging in rainfed areas (Schlenker and Lobell 2010). A positive relation is observed between water supply and plant water need from seedling to heading stage in rice, but flowering to dough stage and maturity to harvesting experience a negative relation between rainfall and fertile grain formation. Consequences like formation of unfilled grains, loss in quality of grain (Baker et al. 1990), delay in harvesting for waterlogged or wet field conditions, and reduction of crop yield (Sreenivasan and Banerjee 1973) are noticed.

2.2.5   Effect of Salinity

Rice is a glycophytic plant. Rice is relatively more tolerant during germination and active tillering and toward maturity but sensitive during early vegetative and reproductive stages. Presently, the increasing threat of salinity is an important issue. As a result of sea level rise, large areas of coastal wetlands may be affected by flooding and salinity in the next 50 to 100 years. Sea level rise will increase salinity encroachment in coastal and deltaic areas that have previously been favorable for rice production.

At vegetative stage, salinity stress affects seed germination, seedling growth, leaf size, shoot growth, shoot and root length, shoot dry weight, shoot fresh weight, and number of tillers per plant (Gupta and Huang 2014). Stress during reproductive stages delays heading in rice and decreases spikelet number, percent of sterile florets, and pollen viability which negatively affects a number of yield components that determine the grain yield (Khatun and Flowers 1995; Grattan et al. 2002; Singh et al. 2004).

2.2.6   Effect of Drought

Drought stress is the largest constraint to rice production in the rainfed systems (Datta et al. 1975) affecting 10 million ha of upland rice and over 13 million ha of rainfed lowland rice in Asia alone. Drought is a water stress or water-limited condition related to insufficient soil moisture available to support average crop production (Pandey et al. 2007). The response of rice to water stress depends on the duration and severity of the stress (Araus et al. 2002; Bartels and Souer 2004) and the developmental stage (Zhu et al. 2005).

Water stress is characterized by reduction of water content, diminished leaf water potential, turgor pressure, and stomatal activity, reduced rate of cell enlargement which leads to stomatal closure and limitation of gas exchange (Singh et al. 2012). Reproductive processes in rice especially flowering stage show greater sensitivity to drought than do vegetative processes, and male reproductive development is more drought sensitive than female reproductive development (Gray and Brady 2016). Water stress during vegetative stage affects morphological characters in rice like tiller number, LAI, apparent canopy photosynthetic rate, and leaf nitrogen and increases ratio of root to shoot biomass (Poorter and Nagel 2000) and root length density (Cruz et al. 1986), while mild water stress at reproductive stage will delay panicle initiation, exertion, and development by 10 days which slow downs the rate of development of inflorescence, or lead to partial or complete inhibition of flowering (Saini and Westgate 1999). Water stress during flowering is more serious and devastating because the anther size is reduced and shriveled, and the pollen loses its viability (Sheoran and Saini 1996) causing flower abortion, grain abscission, and increased percentage of unfilled grains.

2.3   Adaptation and Mitigation Strategies

2.3.1 CO_2 Emission

Agriculture is expected to help slow down the CO_2 increase in the atmosphere by sequestering part of it in soil organic matter and by producing suitable biomass as a substitute for fossil fuel.

(a) The sustainable-biochar concept: Biochar is a recalcitrant form of carbon and suitable as a soil amendment, biofuel through pyrolysis of biomass/feedstock, and straw and husk in case of rice. This means that there is more carbon being removed from the atmosphere than would have been released to heat the atmosphere. Slow decay of biochar in soils returns a small amount of CO_2 to the atmosphere directly through combustion of bio-oil and syngas use in transport activities and domestic purposes (Woolf et al. 2010). The conversion to biochar locks the carbon in a stable form that will not react with oxygen to produce CO_2.

(b) Land use management: Soil organic matter of cropland can be increased either by the addition of biomass or feedstock or when the decomposition rates of biomass are reduced. Conversion from plow till to no-till with residue mulch or crop residue input to the soil and other conservation tillage practices is a viable option for SOC sequestration (Lal 2004); as it does away with drastic soil disturbance and improves soil organic matter in the surface layers, higher cropping intensity through intercropping especially in bare fallows increases the photosynthetic input, thereby "sequestering" C or building C "sinks."

(c) Agronomic practices: Carbon emissions decreased substantially in the production system where less synthetic fertilizer or chemical pesticides is used. Pulse-based cropping systems reduce the loss of soil organic carbon and nitrogen compared with cereal-based cropping systems (Gan et al. 2014). Also practicing relay cropping to use residual moisture, integrated cropping systems over monoculture systems through early seeding, optimum plant establishment, and proper crop sequencing can increase rice productivity without increasing production inputs due to the improved diversity of the microbial populations (Yang et al. 2014) and the function of microbial communities in the soil (Cruz et al. 2012), thus decaying the biomass slowly and depositing more carbon to the soil sink.

2.3.2 CH_4 Emission

The production and release of CH_4 gas can best be reduced by:

(a) Practice of midseason drainage instead of continuous flooding: The effect of midseason drainage is in controlling nitrogen absorption, keeping oxidative soil condition, increasing productivity and quality of rice, and decreasing methane emissions (Nagata 2010). Flooded rice culture with puddling and transplanting

is considered one of the major sources of emission and accounts for 10–20% of total global annual CH_4 emissions (Humpreys et al. 2006). Water drained mainly during reproductive period for 7–10 days can reduce methane production and emission (Nagata 2010). Wassmann et al. (2009) reported that midseason drainage and intermittent irrigation through alternate wetting and drying (AWD) method reduce methane emission by over 40%.

(b) Crop establishment methods: It is done by growing rice under nonflooded conditions like adoption of SRI method of rice cultivation or with aeration like dry-seeded rice like "aerobic rice" or upland rice cultivation (Chauhan and Mahajan 2013).

(c) Fertilizer management: Inhibitory effect of sulfate in CH_4 formation causes 10–67% reduction in methane emission when ammonium sulfate is used instead of urea (EEAA 1999; Wassmann et al. 2000).

2.3.3 N_2O Emission

Paddy fields are a major source of N_2O emission accounting for about 13–24% of annual global N_2O emission (Olivier et al. 1998; Kroeze et al. 1999; Mosier et al. 1998). N_2O from rice fields is associated with soil water content and nitrogen status (Wang et al. 2011; Skinner et al. 2014).

(a) Nitrogenous fertilizers: Application of nitrate (NO_3–N) fertilizers, e.g., calcium ammonium nitrate (CAN), in crops with aerobic conditions and ammonium (NH_4–N) fertilizers, e.g., ammonium sulfate, and urea in wetland crops helps reduce the nitrous oxide emission (Pathak and Nedwell 2001).

(b) Use of low C:N organic manure and biogas slurry: The decomposition of straw with high C/N ratio causes immobilization of fertilizer N that is required by soil microbes for nitrification and denitrification processes in which N_2O is produced (Bronson et al. 1997). Direct-seeded rice crop with conservation practice of brown manuring must be avoided because the addition of organic matter to soil increased the decomposition rate which resulted in higher emission of N_2O.

2.3.4 Water Management

Rice consumes almost 50% of irrigation water used for all crops, and the water stress or drought condition needs to be combat by increasing water use efficiency and rainwater harvesting in irrigated agriculture to extend the cropping period.

(a) It can be achieved through reducing the losses caused by seepage, percolation, and evaporation. Laser land leveling and crack plowing help to reduce bypass flow along with bund maintenance (Chauhan et al. 2012).

(b) Cai et al. (1997) reported comparatively low N_2O fluxes in continuously flooded fields, but high N_2O fluxes just after the water table are lowered or drained as

aeration of continuously flooded rice fields releases the trapped N_2O in the soil solution and provides favorable conditions for N_2O production. Thus, there is a need to develop water management practices in such a way that soil redox potential can be kept at an intermediate range (-100 to $+200$ mV) to minimize emissions of both CH_4 and N_2O (Hou et al. 2000).

2.3.5 Crop Management

O'Toole and Chang (1978) recommended the use of early maturing rice varieties as a strategy in unstable production areas, by shifting planting dates (Lansigan et al. 2000); ratooning for shorter growing periods due to unpredictable rainfall and proper seed and seedbed establishment; planting lodging-resistant, non-shattering, and waterlogged-resistant varieties for flood-prone areas; and establishing windbreaks in dry land areas (Pantastico and Cardenas 1980).

2.3.6 Genetic Aspects

(a) Gene resources that can benefit from rising CO_2 concentration have been reportedly found in rice varieties, such as IR8, Dular, etc.
(b) Induction of the early morning flowering gene from *Oryza officinalis* into *O. sativa* has positive effect on reducing the spikelet sterility under high-temperature areas (Sheehy et al. 2007; Ishimaru et al. 2010; Hirabayashi et al. 2015).
(c) Approximately 15–20 million ha of rice-growing areas are submergence-prone because of sea level rise and salinity stress in coastal areas (Nicholls and Cazenave 2010). Submergence-tolerant varieties such as Swarna-Sub1 and IR64-Sub1 and salinity-tolerant genotypes for flood-prone areas, maintenance of whole plant and shoot water status, and mechanisms like Na^+ exclusion or maintenance of potassium in developing tissues and rapidly growing leaves contribute to salt tolerance in rice varieties (Yeo et al. 1990).
(d) Inclusion of characteristics like deep root system, leaf rolling, cuticle wax, position of stomata, and rapid recovering ability will help rice plants to survive under water stress condition and to sustain productivity (Singh et al. 2012).

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Abiotic Stress Responses and Tolerance Mechanisms for Sustaining Crop Productivity in Sugarcane

3

Sangeeta Srivastava and Pavan Kumar

Abstract

Sugarcane (*Saccharum* species hybrids) is a long duration, high-water-requiring agroeconomic crop cultivated in various climatic conditions. Being a long duration crop, it faces vagaries of climate all the year-round affecting plant growth and development, synthesis of sugar, its accumulation and recovery, and ratooning ability. Climate change brings an increase in greenhouse gases (GHGs), temperature, extreme events, drought, heavy rainfall, western disturbance, changes in the level of the sea, etc. and culminates into multiple abiotic stresses affecting soil health, growth, and development of cane and its chemical composition, ripening, and availability of the seed cane. Besides, it aggravates some other abiotic and biotic stresses augmenting the losses further. But, sugarcane is relatively more resilient to abiotic stresses probably due to some natural endowments like a good deal of compensatory ability, C4 photosynthesis, higher-temperature optima for most of the growth processes except sugar accumulation, higher water-use efficiency, and genetic components from *Saccharum spontaneum*. All these characteristics impart tolerance in sugarcane to various abiotic stresses and carbon sequestration as phytoliths, etc. which helps reduce the damaging impact of various abiotic stresses. Further, the development of climate-resilient sugarcane varieties and technological interventions for stress management may mitigate the impact of climate change-induced multiple abiotic stresses and sustain sugarcane and sugar productivity. Physiological interventions like inducing drought hardiness, deeper root system, reduction of heat load by trash mulching, increasing the age of the crop at the advent of moisture stress, organic matter

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amendment in the soil, nutrient management, managing rhizospheric salinity/alkalinity, etc. also contribute to elevate its stress tolerance. A number of genes, molecular markers, and miRNAs related with abiotic stress response also contribute to the resilience of sugarcane to abiotic stresses.

Keywords

Climate change · Abiotic Stress · miRNA · Stress tolerance

Abbreviations

ABA	abscisic acid
ABF	ABRE binding factor
ABRE	ABA-responsive element
Adh1	alcohol dehydrogenase
ALDH5F1	aldehyde dehydrogenase
ANPs	anaerobic proteins
APX	ascorbate peroxidase
AREB	ABRE-binding protein
AS	asparagine synthase
bZIP	basic leucine zipper
cAPX	cytosolic ascorbate peroxidase
CAT	catalase
CDPK	calcium-dependent protein kinase
DHAR	dehydroascorbate reductase
DHNs	dehydrins
DRE	dehydration-responsive cis-acting element
DREB	DRE-binding protein
ERF	ethylene-responsive element-binding factor
GB	glycine betaine
GBF1	G-box-binding factor-1
GPOX	guaiacol peroxidase
GR	glutathione reductase
GSHS1	glutathione synthase
GST1	glutathione-*S*-transferase
IGS	indole 3-glycerol phosphate synthase
LEA	late embryogenesis abundant
MAPK	mitogen-activated protein kinase
MDA	malondialdehyde
miRNA	microRNA
MYB	myeloblastosis
MYC	myelocytomatosis
NADP-ME	NADP malic enzyme
NIPs	NOD 26-like intrinsic proteins
OAT	ornithine aminotransferase

P5CS	Δ^1-pyrroline-5-carboxylate synthase
PCK	phosphoenolpyruvate carboxykinase
PEPcase	phosphoenolpyruvate carboxylase
PIN1	polar auxin transport gene
PIPs	plasma membrane-intrinsic proteins
PLD	phospholipase D
POD	peroxidase
POX	proline oxidase
PPDK	pyruvate phosphate dikinase
ROS	reactive oxygen species
Rubisco	ribulose- 1, 5-biphosphate carboxylase
SAM	S-adenosyl methionine
ScMYB2	sugarcane R2R3-Myb gene
SIPs	small basic intrinsic proteins
SOD	superoxide dismutase
SOS	salt overly sensitive
TAPX	thylakoid ascorbate peroxidases
TFs	transcription factors
TIPs	tonoplast intrinsic proteins
TSase	*Grifola frondosa* trehalose synthase

3.1 Introduction

Sugarcane is derived from hybridization of *Saccharum* species and is extensively grown in over 120 countries across the world not only for sugar but also to obtain other sugar by-products. It is estimated that approximately 70% of the world sugar production is derived from sugarcane, while the rest is derived from sugar beet cultivated in temperate regions. Because of the limited amount of fossil fuel and increasing world population, there is an agreement among scientists and government ministerial officials to incorporate lignocellulosic biomass as a feedstock for biofuel production and amplify the production. Right now, the sugarcane yield is capable in providing the largest amount of lignocellulosic biomass than any other crop species together with potential bioenergy feedstock crops named as *Miscanthus* and switch grass. Due to all the superior traits of sugarcane as a lignocellulosic biomass feedstock crop, commercial sugarcane hybrids have been adopted for biofuel production along with sugar production. However, their cultivation is affected by abiotic stresses in sugarcane-growing countries. Abiotic stresses such as drought, salinity, flood, and high and low temperature including nutrient stress affect sugarcane and result in a major loss in terms of productivity, lignocellulosic biomass, as well as downstream products of the sugar industry (Table 3.1). Most research findings suggest osmotic stresses like drought, salinity, and low-temperature stress are often interconnected to each other and impose an osmotic stress that can lead to turgor loss. For instance, both drought and salinity are manifested by formerly

Table 3.1 Drought stress responses in sugarcane

S.N.	Physiological responses	Biochemical responses	Molecular responses
1	Root signal recognition at the shoot	Reduced photochemical activity	Drought responsive gene expression
2	Turgor loss	Reduced activity of RuBisco, PEP carboxylase, NADP malic enzyme (NADP-ME), pyruvate phosphate dikinase (PPDK)	Increased expression of ABA biosynthetic genes
3	Impairment of osmotic adjustment	Accumulation of compatible solutes such as proline, trehalose, polyamines	Increased gene expression of ABA-responsive genes
4	Decreased transpiration rate due to closure of stomata (low stomatal conductance)	Increase in antioxidative enzymes such as SOD, CAT, and APX	Synthesis of specific proteins such as LEA, etc.
5	Decreased CO_2/O_2 ratio	Decease in accumulation of ROS	
6	Reduced photosynthetic rate		
7	Reduced growth		

osmotic stress, resulting in the disruption of homeostasis and ion distribution in the cell (Serrano et al. 1999; Zhu 2001a), and low temperature may immediately give rise to mechanical constraints, alterations in actions of macromolecules, and reduced osmotic potential in the cellular environment. Two major strategies can be distinguished: stress avoidance and stress tolerance (Levitt 1980). Stress avoidance includes a variety of protective mechanisms that delay or prevent the negative impact of a stress factor on a plant. In contrast, stress tolerance is the potential of a plant to acclimatize a stressful situation. Drought avoidance in sugarcane includes decreased stomatal conductance, rolling of leaf and senescence, and impairment of growth, while drought tolerance is characterized by a higher content of chlorophyll, higher stomatal conductance, photosynthesis, and maintenance of growth and osmotic adjustment. Plants recover soil water potential by the accumulation of compatible solutes and antioxidant system during osmotic stress (Moussa and Abdel-Aziz 2008).

A number of abiotic stress tolerance genes and proteins have been identified in plants. These genes are divided into three groups: (1) genes encoding products that instantly protect plant cells against stresses such as heat stress proteins (HSPs) or chaperones, aquaporins (water channel proteins), LEA protein, osmolytes, anti-freezing proteins, detoxification enzymes, and free-radical scavengers (Bray et al. 2000); (2) those that are involved in regulation of gene expression such as protein kinases MAPK, MAPKKK, CDPK (Ludwig et al. 2004), SOS kinase (Zhu 2001b), and phospholipases (Frank et al. 2000) and transcriptional factors such as MYB, MYC, NAC, and bZIP (Choi et al. 2000; Shinozaki and Yamaguchi-Shinozaki 2000; Shinozaki and Yamaguchi-Shinozaki. 2007); and (3) those that are involved in water and ion uptake and transport (Blumwald 2000).

The dehydrin proteins (DHNs) classified as a group of LEA proteins typically accumulate in embryogenesis or in vegetative part in response to dehydrative forces like drought, salinity, and freezing (Close 1997). Osmolytes, that is, organic solutes and inorganic ions, play a key role in osmotic adjustment. Organic solutes known as compatible solutes include sugars, proline, polyols, quaternary ammonium compounds like glycine betaine, and other low molecular weight metabolites that lower or balance the osmotic potential of intracellular and extracellular ions to tolerate osmotic stresses. Inorganic ions mainly Na^+, Ca^+, K^+, and Cl^- also make a great contribution in osmotic adjustment (OA) (Chen and Jiang 2010). The organic compatible solutes besides OA play a role in stabilization of enzymes/proteins and in protection of membrane integrity (Yancey et al. 1982; Bohnert and Jensen 1996; Yeo 1998). However, its synthesis occurs at an energy cost (Raven 1985) and may be one of the causes of a decrease in plant growth. A study from phylogenetic analysis (Johanson and Gustavsson 2002) suggested plant aquaporins widely distributed in higher plants are classified into four main subfamilies, PIPs, TIPs, SIPs, and NIPs. The MIPs are extensively studied since their significance ranges from animal physiology to osmoadaptation of microbes and plants (Ayadi et al. 2011). The aquaporins or major intrinsic proteins (MIPs) are proteins assembling water channels in the cell membrane and facilitate the bidirectional water transport. Along with this function, these proteins are also concerned with many plant metabolic processes, together with the acquisition of nutrients, cell growth, carbon fixation, cell signaling, and variety of stress responses (Maurel 2007; Besse et al. 2011). The aquaporins also permit infiltration of small molecules such as glycerol (Gerbeau et al. 1999), urea (Liu et al. 2003), CO_2 (Uehleln et al. 2003), ammonia (Loqu'e et al. 2005), boric acid (Dordas et al. 2000), H_2O_2 (Henzler and Steudle 2000), and even arsenic (Bienert et al. 2008). The role of miRNA is considerably studied in the regulation of abiotic stress in sugarcane (Patade and Suprasanna 2010; Thiebut et al. 2012; Gentile et al. 2015; Yang et al. 2017).

3.2 Morphological and Physiological Responses to Drought

Sugarcane development is divided into four development stages: germination, the development of buds and shoot (30–35 days); tillering, the formation of secondary and tertiary tillers (initiating approximately on 48th day after planting and lasting up to 120 days); grand growth, the development and growth of tillers with height gain (stem elongation) and basal sugar accumulation (taking up to 9 month from planting); and maturity, C4 photo assimilation and increased sugar synthesis, ending until the harvesting period. Sugarcane tillering and grand growth phases are recognized as drought sensitive due to high requirement of water for growth (Ramesh 2000; Machado et al. 2009; Lakshmanan and Robinson 2014). At tillering and grand growth phase, the relationship of water content, and the respective physiological responses can be used to identify and distinguish between sugarcane genotypes that is either tolerant or drought sensitive (Endres et al. 2010). On the other hand, as compared to stem growth phase, moderate water stress at the maturity

phase has positive effects on sucrose accumulation, since photosynthesis is less sensitive to water stress in the maturity phase, and channeling the assimilation of CO_2 to sucrose is accumulated in the stalk (Inman-Bamber 2004). Severe drought stress affects the whole sugarcane morphology and physiology, albeit both responses, in turn, vary according to the genotype, duration (rapid or gradual), and intensity (severe or mild) of stress as well as the type of the tissue affected (Bartels and Sunkar 2005; Smit and Singels 2006; Da Graça et al. 2010; Inman-Bamber et al. 2012). Physiological responses in sugarcane are recognized as interruption of cell division and cell elongation (Machado et al. 2009), rolling of leaf, closing of stomata, inhibition of stalk and leaf growth, leaf senescence, and reduced leaf area (Inman-Bamber and Smith 2005; Inman-Bamber et al. 2012); stem and leaf elongations are also affected by growth processes (Inman-Bamber 2004; Inman-Bamber et al. 2008). Drought stress is firstly sensed by the root, and the development of the root is affected but relatively less than the above ground biomass. During moderate water deficit stress response, stomatal limitations occur in sugarcane which cause a reduction in stomatal conductance (gs), transpiration rate (E), internal CO_2 concentration (Ci), and C4 photosynthesis (Du et al. 1996; Inman-Bamber and Smith 2005; Silva et al. 2007; Da Graça et al. 2010; Endres et al. 2010; Medeiros et al. 2013; Basnayake et al. 2015). However, including the above responses, stalk and leaf growth inhibition is the foremost common early adaptation when sugarcane plants are exposed to mild to moderate dehydration (Inman-Bamber and Smith 2005). Additionally, water stress responsible for both nonstomatal and stomatal limitations has been reported due to impairment of photosynthesis in sugarcane (Ribeiro et al. 2013). These kinds of effects occur when the experience of drought stress is severe (Basnayake et al. 2015). Drought causes a reduction in photosynthetic rate principally due to decreased activity of PEPcase and Rubisco enzymes (Du et al. 1996; Inman-Bamber and Smith 2005; Lakshmanan and Robinson 2014). In unstressed state, low content of sugar in the leaf is helpful to photosynthetic activity, whereas high sugar content shows moderate effect on CO_2 fixation (Goldschmidt and Huber 1992). This is important that the rate of photosynthesis is also influenced by sugar accumulation in the sugarcane leaves (McCormick et al. 2008).

3.3 Biochemical Drought Responses in Sugarcane

In C4 plants, some facts suggested that photosynthesis is very susceptible to water deficit stress (Ghannoum 2009). Du et al. (1998) revealed the activities of different C4 photosynthetic enzymes, viz., PEPcase, NADP-ME, Rubisco, and fructose 1,6 bisphosphate, and observed the 2 to 4 times decreased activity under drought conditions, whereas the activity of PPDK declined 9.1 times in C4 plant, sugarcane. The efficiency of CO_2 fixation in C4 plants may have three forms of decarboxylation metabolism identified by three enzymes, while in sugarcane facts suggest the presence of two enzymes, NADP-ME and PCK, where PCK forms decarboxylation that appeared to prevail over NADP-ME (Ghannoum 2009). The C4 metabolism plants such as sugarcane can probably face a hot and dry environment by dropping the

photorespiration rate and losing water. Despite the process that assists CO_2 fixation in sugarcane, other plant species are also susceptible to water deficit. Plants under drought lower carbon assimilation rate which facilitates an insufficient sink for electrons generated in the electron transport chain and therefore oxidative stress due to overproduction of reactive oxygen species (ROS) (Edreva 2005). Antioxidant system imparts the drought tolerance through scavenging free radicals by the accumulation of compatible solutes and antioxidant molecules (Vilela et al. 2017). In plants, both enzymatic and nonenzymatic antioxidant systems have been found. The non-enzymatic antioxidant system includes compounds such as ascorbate (AsA), gluta-thione (GSH), alkaloids, phenols, tocopherols, and carotenoids (Grat˜ao et al. 2005). The enzymes are comprised of superoxide dismutase (SOD), catalase (CAT), ascor-bate peroxidase (APX), guaiacol peroxidase (GPOX), and glutathione reductase (GR) (Martins et al. 2011). The enzyme CAT is responsible for the reduction of H_2O_2 to H_2O and O_2, and a decline in peroxidase activity is considered a limiting step to ROS neutralization in sugarcane (Chagas et al. 2008). Activities of SOD, CAT, APX, GPOX, and GR were changed according to variety and stress intensity in sugarcane (Cia et al. 2012). Madhav et al. (2017) reported the increased enzy-matic activity of peroxidases and SOD during water stress in sugarcane. The accu-mulation of the osmolytes, trehalose, and proline also contributes to the reduction of the damage caused by the accumulation of ROS and is associated with drought tol-erance in sugarcane (Zhang et al. 2006; Molinari et al. 2007; Guimarães et al. 2008). Sales et al. (2012) reported an increase in starch hydrolysis, leading to higher levels of soluble sugars that helped sustain carbon supply even in a reduced CO_2 fixation condition, facilitating growth recovery after stress.

3.4 Drought-Responsive Genes in Sugarcane

Drought stress affects morphological and functional characters in plants, eventually becoming one of the main hindrances to sustainable agricultural production glob-ally. In a plant cell, the scarcity of water content provokes a complex phenomenon of molecular responses, involving stress perception and initiation of signal trans-duction cascade as a consequence of physiological, cellular, and morphological changes (Bray 1993), including closing of stomata, reduced cell growth and photo-synthesis, and activation of cellular respiration. Transcription factors expressed by SP83–2847 moderately resistant variety indicate that abscisic acid (ABA)-dependent and ABA-independent pathways are presented for drought-responsive gene expres-sion. In ABA-dependent pathways, genes have an ABA-responsive element (ABRE) with an affinity for myeloblastosis (MYB) and basic leucine zipper (bZIP) domain transcription factors that signal for expression of specific genes involved in plant stress response. In ABA-independent pathway, the transcription factor dehydration-responsive cis-acting element (DRE) binds to DRE-binding protein (DREB) and triggers gene expression (Shinozaki and Yamaguchi-Shinozaki 2007; Yoshida et al. 2014). The drought-responsive gene expression has also been reported in the regula-tion of auxin (Swapna and Hemaprabha 2012) and salicylic acid (Almeida et al.

2013). The ABA-responsive element (AREB) and ABRE binding factor (ABF) are members of the bZIP superfamily of transcription factor (TFs), and the DREBs are members of APETALA2 (AP2)/ERF, which are known to be involved in abiotic stress responses in *Arabidopsis* and grasses (Nakashima et al. 2009; Mizoi et al. 2012). According to Schlögl et al. (2008), ABA regulates six bZIPs, with two genes being upregulated (ScbZIP29 and ScbZIP31) and four genes downregulated (ScbZIP21, ScbZIP24, ScbZIP70, and ScbZIP79) in sugarcane plants exposed to ABA in vitro. The expressed genes in sugarcane included those that respond to drought through auxin-dependent manner using IGS and PIN1 and ABA-independent manner. Abscisic acid-independent pathway DREB genes regulate plant defense mechanism via SOD, DHAR, cAPX, GST1, GSHS1 (glutathione synthase), and encoding different drought protein kinase (Prokin) genes and ABA-dependent group of proteins, viz., LEA 3 (Swapna and Hemaprabha 2012). Rodrigues et al. (2009) demonstrated increased expression of a gene encoding a peroxidase in a drought-tolerant sugarcane cultivar. Wang et al. (2015) suggested that TAPX gene expressed in roots, stems, and leaves of sugarcane, but the most in leaves, plays a role in sugarcane response to drought, salt, and other stresses. Swapna Simon and Hemaprabha (2010) reported SOD and IGS genes expressed under drought-tolerant sugarcane variety Co 740 and clones of CoC 671. The genes encoding for polyamine oxidase, cytochrome-c-oxidase, SAM-decarboxylase, and thioredoxins have been found upregulated in sugarcane under drought environment which are involved in the regulation of the intracellular redox status (Prabu et al. 2011). In response to foliar application of salicylic acid, expression of genes responsible for synthesis/expression of trehalose 5-phosphate and sucrose phosphate was involved under drought stress in sugarcane (Almeida et al. 2013). The role of SoSnRk2.1 gene of sugarcane is subject for more research and upregulated under drought stress (Qin-Liang et al. 2013; Phan et al. 2016). Proline synthesis is catalyzed by rate-limiting enzyme P5CS. In sugarcane, P5CS (SoP5CS) gene was isolated and plays a role in water deficit stress noticed in transgenic sugarcane (Li et al. 2018). It was noticed that under drought state, sugarcane is connected to elevated levels of N and K in the leaves and stems, and greater accumulations of K and P in the shoot (da Silva et al. 2017). Several gene expression studies have been carried out in sugarcane. Gene like *Grifola frondosa* trehalose synthase (*TSase*) expressed in drought-tolerant genotypes in sugarcane was reported (Zhang et al. 2006).

There are numerous expressed sequence Tags (EST) related to stress-responsive gene sequences that have been submitted to the SUCEST and SASRI databases. Gupta et al. (2010) identified 25 clusters of the gene in sugarcane associated with water deficit stress using real-time reverse transcription-PCR profiling of selected EST clusters. The most recent report was carried out by Iskandar et al. (2011) that investigated that the expression of eight stress-related genes – P5CS, OAT, AS, PST5 (sugar transport gene), TF1, LEA, POX, and dehydrins – was correlated with the sucrose content in the sugarcane culm and whether such genes were also responsive to water deficit stress. Microarray-based expression profile study of 15,593 sugarcane genes describes that 1501 genes were differentially expressed of which 821 genes were upregulated and 680 genes were downregulated in different

water level condition in sugarcane variety (GT21) (Li et al. 2016). Microarray and RNAseq analysis in sugarcane genotype suggested that 10 genes were differentially expressed using the qPCR analysis, of which three genes' transcript profile was found to correlate with drought tolerance. These genes were lipoxygenase (ScLOX) (plays a role as a precursor of biosynthesis of jasmonic acid, and current study describes their role in drought resistance), dehydrin (related to water deficit stress as well as maintenance of turgor cells) and dirigent-jacalin (which correlated to biotic and abiotic stresses along with jasmonic acid) (Andrade et al. 2014). The role of aquaporins in roots of sugarcane is noticed under drought (da Silva et al. 2013). The transcripts encoding sugarcane aquaporins have only slightly been illustrated, in spite of their important physiological influence and contribution in numerous biological processes in the course of plant growth and acclimation in response to biotic and abiotic stresses (Maure et al. 2008; Lembke et al. 2012). Such genes may be very useful in transgenic studies linked to sugarcane (Andrade et al. 2014). The Scdr1 gene of sugarcane conferring tolerance under drought is also useful in providing salt and drought tolerance in tobacco (Begcy et al. 2012). Sugarcane *R2R3-MYB* (*ScMYB2*) gene plays an important role during drought (Guo et al. 2017). *SoDip22* gene in sugarcane leaves is identified as drought-responsive gene. The identification of genes encoding structural proteins directly related to the establishment of drought tolerance could be useful in developing genetic markers to select tolerant and/or sensitive genotypes. This helps to obtain improved cultivars by direct manipulation (transgenic) or classical breeding. Drought tolerance would also contribute to reduce irrigation and water use (Rocha et al. 2007).

3.4.1 Lipid Peroxidation

A correlation between water stress tolerance and lower levels of lipid peroxidation was suggested (Cia et al. 2012; Sales et al. 2015). High levels of H_2O_2 generated due to an increase in lipid peroxidation were observed during the initial growth phase in young sugarcane plants under severe water stress (Boaretto et al. 2014). Lipid peroxidation may meet important criteria to recognize water-tolerant cultivars of sugarcane (Abbas et al. 2014).

3.5 Salt Stress in Sugarcane

Salinity affects the productivity of various crops by exerting the greatest effects on agriculture across the world and imposes morphological, physiological, biochemical, and molecular changes (Munns 2005). Physiological process is hindered by salinity chiefly photosynthesis via a reduction in leaf area, chlorophyll content, and stomatal conductance and to a lesser extent through a decrease in photosystem II efficiency. The adverse effects of salinity on plant development are more profound during the reproductive phase. *Saccharum* species differ in their response to soil

salinity and acidity, and, the germination and early growth stages are more sensitive to these stresses than later stages of crop growth; moreover, ratoon crop is more sensitive to salinity than plant crop. According to Zhu (2001a), tolerance to salinity depends on the interrelations among the biochemical pathways involved in detoxification, homeostasis, and growth regulation. First, accumulated ROS are removed via synthesis of important compounds, such as osmolytes and various proteins that reduce the intracellular concentration of ROS. Concurrently, ionic homeostasis is pulled off via the compartmentalization of ions in vacuoles. Finally, the expression of important genes is regulated to efficiently maintain plant growth and high productivity. Although sugarcane is sturdily affected due to salt stress, the fact concerning the cellular, biochemical, and molecular mechanisms in response to salt stress lacks in sugarcane. In current existence, the available information concerning the mechanism essential to tolerance of sugarcane to salt stress has increased. These current studies might be important in response to salt stress; in particular, proteins associated with carbohydrate metabolism and energy might be involved in the response of sugarcane to salt stress (Patade et al. 2012; Pacheco et al. 2013). Passamani et al. (2017) reported that by proteome analysis, proteins, such as CDPK, photosystem I, PLD, and glyceraldehyde-3-phosphate dehydrogenase, were plentiful in the sugarcane micropropagated shoot RB855536 cultivar under salt stress. Thus, proteomic-based study will be supportive to the identification and understanding of the salt stress-induced response mechanisms in sugarcane. In addition, the information obtained through differential protein analysis might be used in modern breeding programs for the production of new cultivars (Agrawal et al. 2012). A β1,3-glucanase D family gene *ScGluD2* is noticed in induced form against salt, H_2O_2, and heavy metal stress (Su et al. 2016a).

However, understanding the plant's response to salt stress is difficult because the morphological characteristics of plants, which present differences among species, particularly among the root systems of different species, represent an important aspect of the tolerance mechanisms. Thus, the combination of molecular and morphological differences between sensitive and tolerant cultivars makes it difficult to determine the specific role of each tolerance factor.

3.6   Low-Temperature Stress

Sugarcane is cultivated in tropical and subtropical regions where cold stress is not very common, but lower yields and reduced industrial quality of the plants are observed when it occurs. Under cold stress, the root length and root volume were significantly lowered, and with the prolongation of cold stress, the root activity of sugarcane varieties decreased significantly (Sun et al. 2016). Chilling and freezing stresses differ from each other according to effect. First has a direct effect of low temperature on cells, whereas freezing often acts indirectly via damaging cells due to dehydration. Sugarcane susceptibility to cold injury, either by chilling or freezing, is the primary factor limiting the distribution of the crop to within 30 °C of the equator. The optimum temperature for growth is about 35 °C. The development of

cold stress tolerance in sugarcane is of great importance for improving production, but it is hindered by the lack of more precise physiological knowledge. Cold-induced genes can also be induced by drought stress, and these genes are also regulated by the ABA (Nogueira et al. 2003) and sometimes not sensitive to ABA treatment. This indicates the existence of both dependent and independent ABA regulatory pathways with respect to the transcriptional control of the response to drought and cold (Shinozaki and Yamaguchi-Shinozaki 1996). Exogenous abscisic acid plays a major role during low-temperature stress in sugarcane (Huang et al. 2015). Nogueira et al. (2003) identified 34 cold-responsive ESTs, of which 20 were novel cold-responsive genes (COR) including cellulose synthase, ABI3-interacting protein 2, a negative transcription regulator, phosphate transporter, and others identified as unknown genes in *Saccharum* species (cv SP80–3280) using EST profiling studies (Nogueira et al. 2003). The expression of SsNAC23 (member of NAC transcription factor) was induced in sugarcane plants when exposed to low temperatures (4 °C), and thioredoxin acts as an interacting protein (Ditt et al. 2011). The expression of MIPs such as SspNIC2 was observed more during cold stress in cold-resistant cultivar (TUS05–05) of *Saccharum spontaneum* (Park et al. 2015). Under cold stress, the contents of malondialdehyde (MDA), proline, soluble sugar, and soluble protein and the activities of SOD and peroxidase (POD) were initially increased and then decreased, especially in the cold-susceptible sugarcane variety (Sun et al. 2016). Therefore, these parameters were closely related to the cold resistance of different sugarcane varieties.

3.7 Heat Stress Tolerance

Heat stress gravely diminishes the germination and early seedling development in various plants together with sugarcane crop (Wahid et al. 2008, 2010). Even though a tropical plant needs comparatively higher temperatures for growth, sugarcane shows heat sensitivity above 36 °C as manifested from its reduced growth and water relations (Wahid et al. 2010). High-temperature stress is a widely occurring problem in many sugarcane-growing countries and affects the growth and development of sugarcane. Plant age and intensity of heat play an important role during heat stress (Wahid et al. 2007). The noticeable sign of heat injury includes rolling of leaf, dehydration, chlorosis, tip burning, photosynthesis, respiration, and other metabolic activities. Heat stress applied to sugarcane abridged the Hill reaction, chlorophyll fluorescence, and electron flow at PSII (Ebrahim et al. 1998). Plants gradually exposed to heat stress indicated an accumulation of several heat-stable proteins. Most common molecular response of plants submitted to heat stress is the expression of HSPs, which have a fairly wide range of molecular masses (10–250 kDa). The DHNs are water-soluble proteins, rich in glycine and charged polar amino acids, and free of cysteine, and tryptophan is also observed during heat stress. Wahid et al. (2007) reported heat stress-induced expression of three DHNs in sugarcane with apparent molecular masses of 21, 23, and 27 kDa, appearing between 48 and 72 h. The former one matched with the molecular mass of DHN4 of barley cv.

Morex. The latter two matched with DHN11 and DHN8 of cv. Dicktoo, which were expressed during freezing stress (Zhu et al. 2000). There is also increasing evidence for considerable interlinking between the responses to heat stress and oxidative stress. Enzymatic antioxidants as well overcome heat stress-induced oxidative damage in sugarcane (Jain et al. 2007). Srivastava et al. (2012) reported that higher expression of CAT and APX enzymes under high temperature in the leaves of heat-tolerant sugarcane genotypes might protect them from ROS such as hydrogen peroxide (H_2O_2), superoxide ($O_2^{\cdot-}$), and hydroxyl radicals ($OH^{\cdot}$) produced after exposure to high temperature. Wahid and Close (2007) reported that, despite ample water supply to roots, water potential and its components were severely affected in sugarcane leaves under heat stress. As a heat tolerance strategy, sugarcane showed the synthesis of primary and secondary metabolites. A study showed that soaking with GB and proline had an indirect function in the improvement of bud growth under heat treatment (Rasheed et al. 2011). However, Heat tolerance mechanism is rather less unspoken in sugarcane.

3.8   Waterlogging Stress in Sugarcane

Waterlogging or excess water is one of the abiotic stresses responsible for a loss in potential productivity of crop plants. Sugarcane is moderately tolerant to flooding and waterlogging. It was experienced that sugarcane crop is very susceptible in the first 3 to 4 months to waterlogging, while comparatively tolerant at 5–9 months to waterlogging stress. Some physiological changes in sugarcane observed during waterlogging stress are (1) transpiration rates decreased due to stomatal closure, (2) rate of photosynthesis is considerably reduced presumably due to the lessening of effective leaf area, (3) crop growth rates are significantly shortened in waterlogging stress, and (4) higher respiration rate of submerged organs compared to leaves. The flood stress on crops is divided into two situations (Van Toai et al. 2001). The first situation is flooding or waterlogging in which only the root of crop is flooded, and the second situation is the complete submergence or submergence, in which whole plant or part of the plant is completely flooded. Some destructive situations that can be sensed by flooding plants are owing to the turn-down of gaseous interchange between the soil environment and air, subsequently hypoxia condition for roots and reduction in the rate of air diffusion. Moreover, the flooding stress has an influence on the physiological process such as photosynthesis, root permeability, and the absorption of water and nutrition. Varieties that can grow in the flooding land also adapt to develop some adjustment in morphology (Winkel et al. 2014). To overcome hypoxia and anoxia under flood, the expression of various candidate genes such as zinc finger protein (Mo17), aldehyde dehydrogenase 5F1 (ALDH5F1), alcohol dehydrogenase (Adh1), ACC oxidase, submergence-induced anaerobic proteins (ANPs), and G-box binding factor-1 (GBF1) (Gomathi et al. 2014) have also been reported in sugarcane along with other plants. The ANPs significantly impart their function under flood and are associated with the following activities: pH regulation,

starch breakdown, aerenchyma tissue formation, free radical scavenging enzymes, signal perception (ethylene receptor) and transduction, and other unidentified function.

3.9   Role of miRNA in Abiotic Stress in Sugarcane

Several miRNAs which are also part of gene regulation during environmental stress in plant species have been studied (Sunkar and Zhu 2004). The role of miRNA observed during abiotic stress (Patade and Suprasanna 2010; Thiebut et al. 2012; Gentile et al. 2015; Yang et al. 2017) and the expression profile of miRNA were also studied in sugarcane. Numbers of drought-responsive miRNA transcripts have been noticed in sugarcane via high-throughput small RNA deep sequencing. A report suggested that in most of the situation, miR396 and miR171 were observed as expressed (Gentile et al. 2015). The expression of miR159 at transcript level is observed as regulated under short-term osmotic stress induced by NaCl or PEG in sugarcane. It has also been suggested that the MYB, one of the expected targets of miR159, was concurrently up- or downregulated with the down- or upregulation of the miRNA, respectively, and MYB act as the target of miR159 (Patade and Suprasanna 2010). Thiebut et al. (2012), using stem loop RT-PCR, found that miR319 was upregulated in sugarcane plants exposed to 4 °C for 24 h. The expression profile of miR319 was more during cold stress in both roots and shoots. The expressions of miRNA transcripts were also regulated under ABA treatment. Bottino et al. (2013) suggested that miRNA can also play an important role in the response to salinity in sugarcane cultivar. The five transcripts of miR5671, miR5054, miR5783, miR5221, and miR6478 have target gene sites and thereby play roles in regulation of the mitogen-activated protein kinase (MAPK) signaling pathway and plant hormone signal transduction in smut-resistant and susceptible sugarcane variety (Su et al. 2016b). The expression level of miRNA 156 was found to have increased in cold, salt, and drought stress in sugarcane (Yang et al. 2017). These studies suggested that miRNA potentially plays a major role during abiotic stresses.

3.10   Conclusion

Sugarcane is an agroeconomic crop resilient to climatic changes in nature by abiotic stressful conditions like temperature stress (cold and heat), mineral stress (salinity), and water availability stress (waterlogging and drought). Due to its resilient nature, it has mechanism to counteract weather imposed stresses to sustain productivity. Various stress-responsive hormones, enzymes, and genes are involved in signaling cascade in sugarcane. From physiological viewpoint, components involved in the photosynthetic process are primarily affected by water availability stress, temperature stress, and salinity stress in sugarcane crop like other crops. Hormonal molecules such as ethylene, jasmonic acid, salicylic acid, and ABA have been considerably studied in drought stress in sugarcane. It has been suggested that proline

accumulation in sugarcane under drought situation appears as an important biochemical marker of drought susceptibility than the activities of antioxidant enzymes. The role of ABA is also observed in cold stress in sugarcane. Participation of candidate genes like zinc finger protein (Mo17), aldehyde dehydrogenase 5F1 (ALDH5F1), alcohol dehydrogenase (Adh1), ACC oxidase, submergence-induced ANPs, and GBF1 are also studied in flood stress in sugarcane. Briefly, a numbers of genes, enzymes, transcription factors, and cellular miRNA transcripts have been identified in sugarcane to actively respond to abiotic stress. The mechanism of how these genes exactly respond to abiotic stress is unclear till date in sugarcane. A proposed mechanism may be early cell perception to environmental stimulus and induction of kinases or proteins which will stimulate the upregulation of genes involved in the stress response. This will lead to the function of second messenger and induction of physiological stimuli like stomatal closure and ion homeostasis, and then this signal will induce TFs in a hormonal-dependent manner like the drought in ABA-dependent and ABA-independent manner or auxin/salicylic acid. This induces the antioxidant system to reduce abiotic stress. Recently, the high-throughput techniques have provided an anticipated approach for improving abiotic stress tolerance in sugarcane, but it is undoubtedly clear that this attempt will require close connection among the scientists of different plant fields with "omics" approach, particularly in the field of proteomics and metabolomics.

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Sugar Beet: A Sustainable Crop for Saline Environment

4

Varucha Misra, A. K. Mall, and A. D. Pathak

Abstract

Salt stress is an abiotic stress wherein high concentrations of sodium and chloride ions present in the soil affect sugar beet productivity. About 13% of the land in the world is affected by such soils. Growth of mesophyll cells under such a situation is affected as there is decrease in uptake of water and nutrients along with toxicity of either sodium or chloride ions or both. Sugar beet (*Beta vulgaris* L.), a short-duration crop, besides being tolerant to salt stress, also reclaims saline soil in which it is grown. Under salt stress condition, yield of sugar beet is hampered when electrical conductivity is >7 dsm^{-1}. In sugar beet, several morphological, physiological as well as biochemical changes have been observed under response to salt stress. Nutritional imbalance, alteration in leaf characteristics, less water potential in plant, decline in fresh weight of shoots, etc., are some of its responses under salt stress conditions. Furthermore, this crop possesses adaptive properties such as osmotic adjustment, accumulation of proline, glycine betaine and lipid peroxidation, etc., which helps the crop in surviving under such a situation for giving better productivity. Management practices have also been suggested for minimizing the effect of salt stress making it a sustainable crop under salt stress conditions.

Keywords

Physiobiochemical resultants · Proline · Salinity · Salt stress · Sugar beet

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Abbreviations

APOX	ascorbate peroxidase
BADH	betaine aldehyde dehydrogenase
CAT	catalase
EC	electrical conductivity
GPX	glutathione peroxidase
POX	peroxidase
PS II	photosystem II
RuBP	ribulose biphosphate
SOD	superoxide dismutase

4.1 Introduction

Salinity or salt stress in soil is one of the well-known and important constrains in agricultural crops all over the world (Wang et al. 2019). It is one of the important abiotic stresses wherein the concentration of the salt in soil is increased naturally and precipitation of salt content can be insufficient for leaching (Zhao et al. 2007). Soils of hot and dry regions in the world possess saline soils having low agricultural prospective (Glick et al. 2007). Munns (2002) had revealed that 13% of world's land has been affected by salt stress. Different people had defined salinity in different ways. According to Ponnamperuma (1984), a saline soil is defined as the one possessing rich content of salt in root zone of the plant and plant's growth under such a condition is compelled. Also, USDA salinity laboratory has defined it as one having an electrical conductivity (EC) of 4 dsm^{-1} or greater. According to Epstein and Rains (1987), salinity in soil is associated with high concentration of dissolved ions such as sodium ions, calcium ions, etc. However, the most acceptable definition of salinity has been given by FAO in 1996 according to which saline soils are the ones possessing EC of 4 dSm^{-1} or greater while strong saline soils are the one which have EC greater than 15 dSm^{-1}. Natural and/or human induced are two types of salt stress which are being generally observed. The former one occurs basically due to longer period of accumulation of salts in soil by the two natural processes, *viz.*, weathering of rocks containing salts and deposition of oceanic salt due to winds and rains, while the latter one is due to action of humans wherein the balance of water applied in soil and water which is uptaken by the crops gets disturbed (Garg and Manchanda 2008). Many reasons could be behind this type of salt stress like cleaning up of lands and planting of annual crops in place of perennial plants, insufficient drainage system and usage of water rich in salts for irrigating crops. Salt stress is a global problem covering larger areas in the world and crops grown under such a condition is a major challenge for the farmers as cultivation of crops leads to excessive intake of salts which results in causing injury to crop (Frazen 2007; Rengasamy 2010). Crops grown under salt stress condition vary not only in showing different response toward such condition but even in coping up with it. This variation differs not only from one species to another but also from one genotype to another (Munns 2002). It is well known that

salt stress condition affects the physiological and metabolic activities of crops leading to hampering of growth, yield and productivity (Ashraf and Harris 2004).

Sugar beet is one among the three sources used for the production of sugar worldwide. Around 21.5% of the sugar produced from the cultivation in fifty-seven countries in the world is obtained from this crop. It is a rich source for alcohol production having a capacity of 4400 lha^{-1} against a production of 3900 lha^{-1} from cane (Shrivastava et al. 2013). Sugar beet (*Beta vulgaris* L.), belonging to Chenopodiaceae family, is a well-known salt-tolerant crop (Yang et al. 2012; Wedeking et al. 2017) having a tolerance power of 9.5 m mhos/cm toward salt stress (Shrivastava et al. 2013). In comparison to other crops such as 6.0 for paddy, 4.4 for sugarcane and 2.4 for wheat, this salt-tolerant ability is very high. It is a halophyte that acts as a scavenger for sodium salts by removing about 500 kg of sodium salts per hectare per season in saline soils (Shrivastava et al. 2013). Yield of this crop declines only when the salt concentration in soil exceeds an EC of >7 dSm^{-1} (Maas 1990). Due to its salt-tolerant capability, it is well known to be economically grown in reclaimed soils (Khandil et al. 2017).

4.2   Mechanism of Salt Tolerance in Sugar Beet

Several studies have revealed the tolerance mechanism in salt stress condition (Lindhauer et al. 1990; Marschner 1995; Koyro and Huchzermeyer 1997; Eisa and Ali 2005). In general, for salt tolerance, plant adopts three mechanism, *viz.*, osmotic tolerance, tissue tolerance and ion exclusion. Lindhauer et al. (1990) and Marschner (1995) illustrated that this crop has natural endowment for tolerating salt stress where the plant intakes the salty water from the soil and transports it to its shoots assisting in maintaining the osmotic balance, but this in turn may lead to either toxicity in crop or disturbance in nutritional balance, while Koyro and Huchzermeyer (1997) revealed that it is the capability of the sugar beet crop to accumulate soluble sugars in its root that helps in regulating the osmotic potential under salt stress condition. This is the reason why exposure to salt stress during germination and early stages of growth show pronounced effect on the crop as the photosynthesis activity is very low which in turn causes low amount of sugar production in roots (Eisa and Ali 2005). Another reason for salt tolerance in sugar beet is the building up of sodium and potassium ions in vacuolar and cytoplasmic region of the cells which plays a role in osmotic regulation under such situation in this crop (Subaarao et al. 2001; Ghoulam et al. 2002). As per Flowers (1988), it is the sodium ions that get absorbed and accumulated in the leaf tissues of sugar beet where the former play roles in regulating and adapting its osmotic potential with soil. Wang et al. (2019) had also found another reason for sugar beet tolerance towards salt stress by identifying 47 differentially expressed proteins in sugar beet roots and 56 in its leaves under such situation that play important role in tolerant cultivars.

Belonging to halophyte group, sugar beet is also known to use the controlled mechanism for the uptake of sodium and chloride ions into the vacuolar space of the cells for intake of water by the plant (Glenn and Brown 1999). The study of Flowers and Colmer (2008) revealed that the tolerance power bestowed in halophytes is due

to controlled mechanism of uptake of ions, cellular compartmentalization of ions, and production of organic solutes.

Also, association of salt stress and potassium ions has been revealed under such a condition. There is a decrease in the amount of potassium ions due to the osmotic regulation mechanism adopted by sugar beet under such condition (Lindhaeur et al. 1990). Ghoulam et al. (2002) had revealed its high capability pertaining to osmotic adjustment by production of inorganic ions like Na^+, K^+ (Mari et al. 2018) and Cl^- ions as a response mechanism to salt stress condition. This makes sugar beet crop the most suitable one for uncultivated lands, especially the barren ones. In saline tracts of Sunderbans, studies had revealed that this crop may be used as a remunerative one after cultivation of paddy giving a yield of 50 t ha^{-1} (Shrivastava et al. 2013).

4.3   Response of Salt Stress in Sugar Beet

Salt stress is a limiting factor for production of any crop. This results in retarding the growth and yield of crop. When excess amount of salt is consumed/uptaken by the plant, it hampers the uptake process of water and nutrients through roots from the soil (Frazen 2007). Khan et al. (1995) have shown various reasons behind the inhibitory effect caused by salt stress condition like ion toxicity, disturbance in the nutritional balance, reduction in efficiency of processes of photosynthesis and enzymatic action as well as other associated processes (Fig. 4.1). During flowering, beets showed early flowering which is associated with reduction in dry matter, increase in ratio between root and shoot, and increase in size of leaf, thereby contributing to decrease in beet yield under salt stress condition (Maghsoudi and Maghsoudi 2008).
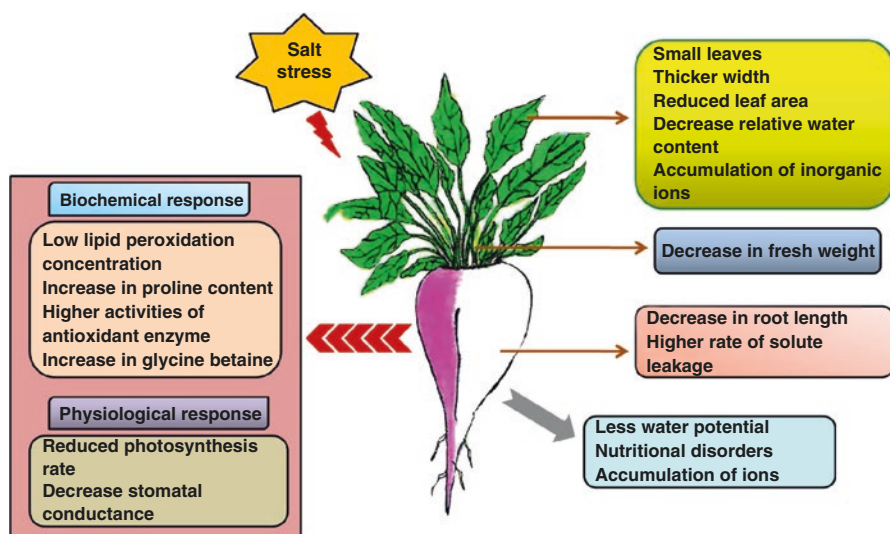
Fig. 4.1 Morphological, biochemical, and physiological response in sugar beet under salt stress condition

Under salt stress conditions, a number of alterations in biochemical and morphological attributes have been observed in this crop like in nutrient level, proline content, leaf area, leaf number, etc., which in turn affect the yield and productivity of this crop (El-Wakeel 1993; Kaffka et al. 1999; Taghizadegan et al. 2019).

4.3.1   Germination Response on Sugar Beet Grown Under Salt Stress Condition

Several studies indicate that sugar beet grows well under salt stress conditions (Yang and Houng 2012). But Jamil et al. (2006) have shown that this crop is also sensitive to salt stress at germination, shoot emergence and seedling stage as a result of toxicity of ions in spite of the general known reason of osmotic alteration (Ghoulam and Fares 2001). Variation in the concentration of sodium chloride levels causes a negative effect on germination of seeds as water-absorbing capability is hampered in seeds (Mostafavi 2012; Dodd and Donovan 1999). Growth response in shoots and roots of sugar beet under such condition, with respect to germination, is the first response to be looked at as it establishes the base of good crop production, root length and yield (Bhattacharjee 2008). Inhibition in cell division process and increase in the growing point are the two reasons behind it (Maghsoudi and Maghsoudi 2008).

4.3.2   Nutrient Status

Water quality and nutrient status are mainly concerned for good production of sugar beet in most of the soils. In salt stress condition, it is known that growth of sugar beet is hampered due to the imbalance of nutrients in their tissues (El-Etriby 2000). Even if calcareous soils possess rich salt content, low nutrient availability, especially in N, P, K, Zn, Fe, and Mn in plants grown in such soils, has been reported (Armin and Asgharipour 2011). Under salt stress condition, when sodium and chloride ion concentrations were increased, a decrease in potassium ions was observed (Shehbata et al. 2000; Ghoulam et al. 2002) as there is decrease in uptake of potassium ions from soil (Reda et al. 1980). Also, level of N ions in shoots, roots, and leaves of this crop under such condition has been reported to be significantly reduced (Flowers 1985; Warne et al. 1990). The reason behind such effect is that under such condition, when the sodium ion level increases, it causes efflux of K ions which results in lowering of the ratio between K^+ and Na^+. When Cl^- ions increased, it competes with the nitrous ions leading to a reduction in the absorption of these ions (Chinnusamy et al. 2005). On the other hand, an increase in P content in leaves in such condition in sugar beet has been seen which contributes to the delay in growth of the crop. On general basis under salt stress condition, plant stimulates to absorb P ions which may cause P toxicity when absorbed by the plants in excessive amounts (Alam et al. 2016; Ren et al. 2012; Zhou et al. 2008).

4.3.3 Growth and Productivity Response of Sugar Beet Under Salt Stress Condition

4.3.3.1 Response of Root

The most important parameter in such a condition to be looked for is the response of sugar beet root under salt stress condition. This is because roots come in direct contact with soil and any disturbance in the soil concentration will affect either the root's length or diameter or its survival to some or great extent. Zhu (2002) had shown that when salt concentration is increased in root zone, then it affects the growth of the plant due to lack of water in cells. This happens so because there is less water potential, nutritional disorders, and buildup of toxic ions under such condition (Zhu 2002). It is known that under salt stress condition generally, root length was decreased. The performance of H30917 genotype showed the longest root length, whereas H30973 genotype showed the shortest among the cultivars tested. Another way in which the roots respond in such a situation is when the concentration of NaCl is high and then the solutes leak out from the roots at a higher rate by affecting membrane permeability (Ghanoum et al. 2002).

4.3.3.2 Response of Shoot

Shoots of sugar beet plant also respond to an increase or decrease in salt concentration in the soils. A decrease in fresh weight of shoots by 36% was observed when there is a moderate salt stress condition (less than 125 mM). Wakeel et al. (2010) had shown that large amount of sodium ion accumulation in beet shoots (about 75%) is only seen when it is supplied with fertilizer possessing sodium ions.

4.3.3.3 Response of Leaf

Salt stress condition in sugar beet crop also causes alterations in leaf morphological parameters. Leaf number was relatively lesser affected under such conditions compared to leaf area (Ghoulam and Fares 2001) as decrease in leaf area is due to inhibition of expansion of leaves under salt stress condition and reduction in size of cells and cell number (De-Herralde et al. 1998; Dadkhah and Grrifiths 2006). Studies have also shown that the reason behind reduction in leaf area is lesser loss in water in the process of transpiration resulting in small leaves and thicker width under such conditions (Witkwski and Lamont 1991). It has also been reported that the amount leaf area is reduced at a certain amount of salt stress condition and the same amount is increased in leaf sodium chloride concentration (Munns and Termaat 1986). Hajiboland et al. (2009) had revealed that leaf area under such condition in plants increases transitionally at initial phases of growth; however at later ones, this gets decreased. Ghoulam et al. (2002) have also illustrated that under salt stress condition, sugar beet leaf shows a decrease in relative water content. Reports suggested that the effect of salt stress was clearly evident on leaf area than on dry weight as under such a situation higher accumulation of Na and Cl ions occurs in shoots through transpiration flow that results in the highest accumulation of oldest leaf leading to death (Greenway and Munns 1980). An increase in leaf thickness was also seen when salt concentrations were increased which is correlated to enhancement in the amount of sodium and chloride ions in leaf blades, petioles and also roots of sugar beet (Geng

et al. 2011). Under salt stress conditions, leaves accumulate more inorganic ions in many sugar beet varieties like Zwaanpoly, Kawemegapoly, Top, Desprezpoly, and Nejma which are known to be includers (Ghoulam et al. 2002).

4.3.3.4 Physiological Response

Photosynthesis is an important physiological process for any crop and also for sugar beet. Crop grown in salt stress conditions alters the photosynthetic process. Sugar beet grown in salt stress condition shows a decrease in area of photosynthesis due to less leaf area and biomass weight as mentioned earlier (Yang et al. 2008). The rate of photosynthesis was increased at initial stages of growth in two sugar beet cultivars, *viz*., Monirac and Kawemegapoly, when grown under such condition, but when the time duration increases, there was no change in carbon fixation process in Monirac, whereas in Kawemegapoly, it decreased significantly (Zviplaut 1989). Association between photosynthesis and shoot growth has also been observed as decrease in photosynthesis area will hamper the shoot growth as well as its development (Campbell and Nishio 2000). Everard et al. (1994) had illustrated that a decrease in photosynthesis rate also affects the stomatal conductance which results in limiting the availability of carbon dioxide to the plant for the process of carboxylation. It has been also known that under salt conditions chlorophyll content may also be affected. Studies have shown that in sugar beet cultivars, under salt stress conditions, significant differences were observed in fluorescence measurement of chlorophyll content indicating that energy translocation rate may be restricted to some extent (Long and Hallgern 1993). Furthermore, reduction in level of Fv/Fm was also seen indicating that there might be hindrance in RuBP regeneration as ample amount of electron translocates from PS II under saline condition (Abbas et al. 2014).

4.3.3.5 Biochemical Response

For adaptation of plants in salt stress conditions, osmotic adjustment is a crucial regulatory mechanism (Volkmar et al. 1998). Under such a situation, plants accumulate several organic solutes like glycine betaine, proline, free amino acids, organic acids and soluble sugars or their derivatives so as to sustain the turgidity of the cells (Flowers and Colmer 2008). These organic solutes play crucial roles in physiological processing of any crop (Fig. 4.1). For instance, the soluble sugars are known for their functioning in maintaining the cell membrane integrity when saline conditions are high. Soluble sugars are even recognized as a sensitive aspect under salt stress condition (Tuteja 2007).

4.3.3.5.1 Lipid Peroxidation and Enzyme Activity

Lipid peroxidation is an active antioxidant enzyme that uses oxygen ion for the production of superoxide radical (Fridovic, 1986). In salt stress condition, sugar beet (*B. vulgaris*) and wild beet (*B. maritime*) showed lower lipid peroxidation concentration as compared to beet grown in normal condition. This may be due to higher activities of antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT) that help in the prevention of damage to cells (Scandalios 1993). It has been illustrated that wild species of sugar beet had hereditary character as well as tolerating power for salt stress due to enhancement in the leakage of solutes that

helps in improving protection from oxidative damage (Bor et al. 2003). In such a case, wild sugar beet leaves possess higher constitutive activities of SOD and induced activities of antioxidants like peroxidase (POX), ascorbate peroxidase (APOX) and CAT. Superoxide dismutase is a well-known metalloenzyme used for protecting against cellular damage (Feng et al. 2016). The antioxidant enzymes found in the leaves under salt stress show effectiveness in preventing the cellular damage especially SOD and CAT (Scandalios 1993). But it is not true in case of *B. maritima* as under salt stress condition, there is an increase in lipid peroxidation particularly when the concentration was 500 mM for 12 days. This in turn causes enhancement in permeability of membrane; as a result of which, there is an increase in solute concentration. This, on overall basis, decreases the resistivity of sugar beet under such a situation. Higher activity of SOD was also seen in *B. maritima* in spite of lower ratio of salt-induced SOD activity. This indicated that wild sugar beet had higher potential to resist the oxidative damage without increasing its SOD activity. Peroxidase is another enzyme that play a role in scavenging hydrogen peroxide present in chloroplast. This is produced by dismutation of oxygen molecule catalyzed by SOD (Asada et al. 1987). No difference in response of POX activity was reported in the wild and commercial cultivated beet as in both cases increase in POX activity was observed when concentration of salt lies under 150 mM and 500 mM. But variation in the induction of activity of this enzyme under salt stress was seen in both the cultivars; in wild ones, it was higher, while in commercial ones, it was not so high. Ascorbate peroxidase enzyme is important for detoxification of hydrogen peroxide (H_2O_2) as it uses ascorbate for reducing H_2O_2 (Asada et al. 1987). Generally, overexpression of this gene leads to higher protection against oxidative damage. In wild types of sugar beet, both SOD and APOX activities were increased. Even the CAT activities were higher in wild beet cultivars as compared to commercial ones. Catalase is also known for playing an important part in protection against cellular damage. Similarly, glutathione peroxidase (GPX) enzyme too plays a role in the same pathway (Mitler et al. 2004).

4.3.3.5.2 Proline

Proline plays an important role in protection of cytomembrane system and even retains the structure of intracellular enzymes (Hong et al. 2000). At 6000 mg NaCl per kg in soil, proline content increases significantly in this crop. Grzik (1996) had shown that when salt stress levels increase, this soluble organic solute level also increased that might result in tolerance to plants cultivated in such a condition. Delauney and Verma (1993) revealed two pathways for the formation of proline content in plants, i.e., one is *via* glutamate, while the other is *via* ornithine.

4.3.3.5.3 Glycine Betaine

It is well known that members of the Chenopodiaceae family (sugar beet, spinach, etc.) produce large amounts of glycine betaine (Catusse et al. 2008) as a response to salt stress condition. Zheng et al. (2015) had revealed the production of betaine in many salt-tolerant crops. Sugar beet plant (in roots and leaves) showed relatively higher increase in betaine aldehyde dehydrogenase (BADH) by two–four folds with

the increase in salt levels (from 0 to 500 mM) in water supply for irrigation (McCue and Hanson 1991). Hanson and Rhodes (1983) revealed the synthesis pathway of glycine betaine in leaves of sugar beet crop under salt stress condition. Studies suggested that under such a situation, glycine betaine concentration was increased indicating their role in coping up the problem of osmotic disturbance. This even may suppress the functioning of nitrogenous compounds formed other than it (McCue and Hanson 1992; Colmer et al. 1996).

4.4 Approaches for Overcoming the Effect of Salt Stress in Sugar Beet

Approaches have been tried for enhancing the tolerance capability in sugar beet for salt stress conditions. Application of potassium as a fertilizer in sugar beet is one such approach (Sarkar and Ghosh 1989). Also, external intake of potassium ions by sugar beet plants in salt stress condition also enhances the tolerance power. The role of potassium ions in sugar beet plants has been clearly illustrated in many studies and has shown the association of potassium ions with sucrose, total soluble solids and purity coefficient of juice of sugar beet (El-Maghraby et al. 1998; Khalil et al. 2001). Photosynthesis rate, sucrose translocation, and sucrose accumulation in roots were enhanced after application of K fertilizer which may be due to the role of K in enhancing metabolic activity of beet (metabolic activity of carbohydrate and nitrogen, transpiration, and water-absorbing capacity) (El-Hawary 1994a, b; Bondok 1996; El-Etreiby 2000). El-Harriri and Gobarh (2001) had also shown that with the usage of K fertilizer in sugar beet grown under salt stress condition, quality and quantity of sugar in beet roots were improved significantly. Dry weight of leaves and top of sugar beet was revealed to increase after application of potassium fertilizer. Application of phosphorus also showed increase in fresh weight of root and shoot (Hussain et al. 2014). In addition, application of gibberellic acid (GA$_3$) in such a condition also helped in minimizing the effect on sugar beet.

4.5 Conclusion

Sugar beet is a secondary crop used for production of about 20% of sugar from 45 countries (four continents) of the world majorly where sugarcane cultivation is not possible. Sugar beet is largely grown in temperate climates, but now it is being moved to subtropical parts of the world for fulfilling the further enhanced needs of sugar and ethanol production and minimizing the burden on sugarcane crop. Salt stress is a crucial problem for most of the areas of the world which has hampered the agricultural productivity. Sugar beet is the one used for sustainable growth and production under salt stress condition due to the natural ability possessed by it for tolerating the osmotic potential by having a tolerance power of 9.5 m mhos/cm towards salt stress. The mechanism involved is the absorption of sodium ions from soil to leaves where it gets accumulated in their tissues mainly in the vacuolar

spaces. Besides, it also reclaims the saline soil by removing 500 kg of sodium salts per hectare per season from salt-affected marginal lands, thereby making it suitable for other crop cultivation. Furthermore, this crop will act as boon to agriculture in salt-affected marginal lands.

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Agronomic Crop Responses and Tolerance to Drought Stress

5

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Abstract

Drought (water stress) is one of the most important stresses that occurs widely in agricultural fields and can affect different aspects of crop growth, development, and metabolism. There are several reasons of drought stress in agriculture fields, including low rainfall or irrigation, high and low temperature, high intensity of light, high EC (electrical conductivity) due to salinity and fertilizer misapplication, etc. Plant water potential and turgor decline in dehydration condition; therefore, plant cells could not do normal functions and inducing all drought stress aspects in plants. In addition, it can negatively affect quantity and quality of growth and yield in crops. Plants are sessile organisms and must tolerate environmental stresses; hence, they have developed various mechanisms for resistance to stresses such as drought stress. Moreover, as plants are multicellular organisms, their responses to environmental stresses such as drought are complex. Generally, plant resistance to environmental stress is divided into two main strategies: stress avoidance and stress tolerance. Besides tolerance, avoidance is one of the common drought resistance mechanisms in annual plants. Escape from stress conditions is the strategy for plant growth under drought condition that is less important in agronomic plants. The alteration in resistance capacity of crops' seeds and young seedlings by priming methods, production of tolerant crops by traditional breeding methods, and the generation of transgenic plants by gene manipulation are useful procedures to minimize the negative effects of drought on agronomic products. In addition, several strategies for drought management in agricultural fields on multiple levels can be effective.

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Abbreviation

5-HTP	5-hydroxy-L-tryptophan
ABA	abscisic acid
AFLP	amplified fragment length polymorphism
ALA	5-aminolevulinic acid
AM	arbuscular mycorhizal fungi
APX	ascorbate peroxidase
BABA	β-aminobutyric acid
BR	brassinosteroid
CAT	catalase
CPK	Ca^{2+}-dependent protein kinase
EC	electrical conductivity
ERF	ethylene response factors
GABA	γ- aminobutyric acid
Gas	Gibberellins
GB	glycine betaine
GR	glutathione reductase
GSH	glutathione
H_2O_2	hydrogen peroxide
IAA	indole-3- acetic acid
JA	jasmonic acid
L-DOPA	L-3,4-dihydroxyphenylalanine
LEA	late embryogenesis abundant
LMW	low molecular weight
MGDG	monogalactosyldiacylglycerol
$O_2{}^{\bullet-}$	superoxide radical
OH	hydroxyl radical
P5CR	pyrroline-5-carboxylate reductase
PEG	polyethylene glycol
PM-ATPase	plasma membrane ATPase
POD	peroxidase
PP2Cs	protein phosphatase 2Cs
QTL	quantitative trait loci
RAPDs	random amplified polymorphic DNA
RCS	reactive carbonyl species
RFLPs	restriction fragment length polymorphisms
RNS	reactive nitrogen species
RO	alkoxy radicals
ROS	reactive oxygen species
RSS	reactive sulfur species
RuBisCO	ribulose bisphosphate carboxylase/oxygenase
RWC	relative water content
SA	salicylic acid
SCARs	sequence characteristic amplified regions

SnRK2s	SNF1-related protein kinase 2s
SOD	superoxide dismutase
SSRs	simple sequence repeats
TF	transcription factors
VOCs	volatile organic compounds

5.1   Introduction

Under agricultural conditions, plants are often exposed to various environmental stresses such as drought stress. Drought is one of the most important and common abiotic stress factors for agronomic plants in many parts of the world, especially in arid and semiarid areas (Madhava et al. 2006). "Drought" is a general term usually used to describe a relatively long period without rainfall and derives from an agricultural context (Salehi-lisar et al. 2012). There are several reasons for a water-deficit condition in agronomic plants, such as low irrigation, high electrical conductivity (EC) due to salinity, fertilizer misapplication, high temperature, high intensity of light, dry wind, and so on (Dai 2012; Mafakheri et al. 2010; Shao et al. 2008a; Trujillo et al. 2008). Water accounts for between 80% and 95% of the fresh biomass of nonwoody plants and plays an important role in many aspects of plant growth, development, metabolism, and so on (Hirt and Shinozaki 2004; Salehi-lisar et al. 2012). In many conditions there is enough water in the soil, but plants cannot uptake it. This type of water stress is called a pseudo-drought or physiological drought (Arbona et al. 2013; Ashraf et al. 2009). Drought stress is a multidimensional stress and generally leads to changes in the physiological, morphological, ecological, biochemical, and molecular traits of plants (Bhargava and Sawant 2013; Farooq et al. 2009; Shao et al. 2008a). In addition, it can negatively affect the quantity and quality of plant growth and yield (Jaleel et al. 2009; Nezhadahmadi et al. 2013; Zlatev and Lidon 2012). Plant responses to a water deficit depend on the length and severity of the water deficiency as well as the plant species, age, and developmental stage (Madhava et al. 2006). Many plants have developed resistance mechanisms to tolerate drought stress, but these mechanisms are varied and depend on the plant species. In addition to drought tolerance, drought avoidance is another common drought escaping mechanism in annual crops (Ashraf et al. 2009; Madhava et al. 2006; Salehi-lisar et al. 2012). Scientists have tested different methods for improving plants' capacity for drought resistance such as traditional breeding methods (Nezhadahmadi et al. 2013; Rana et al. 2013), transgenic technology (Khan et al. 2011; Nakashima et al. 2014; Xoconostle-Cazares et al. 2010), priming methods (Mondal and Bose 2014; Paparella et al. 2015), and so on. However, each method has some problems and limitations because of the complexity of drought effects on plants and the plants' responses to the drought. In addition, several strategies for drought management in agricultural fields could be useful in order to minimize the effects of drought on plants, especially on crops. Although the terms "drought,"

"water deficit," "dehydration," and "water stress" can address different issues, in this text we will use these terms to mean an inadequate water supply for plants.

5.2 Concept of Drought

5.2.1 General Aspects

Global warming influences air temperature as well as amount and distribution of precipitation and is one of the most important reasons of drought expansion. The climatic variability and more frequent periods of extreme conditions for water availability result in drought for the organisms, particularly plants (Dai 2012; Trenberth et al. 2014). Drought (water stress) is one of the most important stresses that occurs widely in agricultural fields (Keyvan 2010; Rahdari and Hoseini 2012; Rana et al. 2013; Zlatev and Lidon 2012) and can affect different aspects of crop growth, development, and metabolism (Rahdari and Hoseini 2012; Rana et al. 2013; Zlatev and Lidon 2012). "Drought" is a general term for the description of atmospheric or weather phenomena and is commonly explained as a relatively long period without rainfall (Bray 2001; Dai 2012; Jaleel et al. 2009; Shao et al. 2008a). Drought is difficult to define; it can be described from several viewpoints, such as meteorological, agricultural, hydrological, and socioeconomic (Barriopedro et al. 2012; Dai 2012; Jaleel et al. 2009; Rahdari and Hoseini 2012). However, from agricultural viewpoint it has special importance due to effects on agronomic productions. Drought stress in agronomic conditions occurs when the soil moisture is decreasing at a certain time leading to a decline in the available water for plants (Dai 2012; Keyvan 2010). Basically, when the water potential of the soil is lower than the water potential of plants, drought stress occurs. Mostly, the atmospheric conditions cause a continuous water deficit by transpiration or evaporation in agricultural fields (Dai 2012; Mafakheri et al. 2010; Shao et al. 2008a; Trenberth et al. 2014). Therefore, an agricultural drought comes after a meteorological drought (Barriopedro et al. 2012; Dai 2012; Jaleel et al. 2009). Usually, under normal conditions, drought is not a disaster in many regions, but it could be an important problem when humans' feeding is water-dependent (Kheradmand et al. 2014). In addition, in some regions rainfall is adequate, but nonuniform precipitation leads to water stress in plants.

5.2.2 Drought Stress in Agronomic Crops

Drought occurs worldwide every year; therefore, it has become important in the agronomic plants especially under arid and semiarid climates. The effects of drought on the crop yields are well known; however, the water-deficit effects at the biochemical and molecular levels are not considerably understood yet. All plants have some degree of tolerance to water stress, but the extent varies from species to species (Nezhadahmadi et al. 2013; Salehi-lisar and Bakhshayeshan-Agdam 2016).

Agronomic plants are more susceptible to water stress than wild-type species. Studies show that crop plants have lost its resistance to environmental stresses such as drought during traditional plant breeding and desirable trait selection (Bhargava and Sawant 2013; Ding et al. 2013; Farooq et al. 2009; Nakashima et al. 2014; Nezhadahmadi et al. 2013; Rana et al. 2013; Xoconostle-Cazares et al. 2010). On the other hand, crop and medicinal plants supply feed and health of human beings, respectively. Hence, drought stress effects on crops and its management in agricultural fields have become more important today than in the past.

5.3   Drought Stress Causes in Agricultural Fields

Generally, the alterations in rainfall patterns due to global climate changes lead to increases in drought condition worldwide (Arbona et al. 2013; Dai 2012; Mishra and Singh 2011; Nezhadahmadi et al. 2013). Although global climate alterations are the main factor triggering drought stress (Mishra and Singh 2011; Rana et al. 2013), there are many other reasons for drought, such as low irrigation, high EC due to salinity, fertilizer misapplication, high temperature, high intensity of light, dry wind, and so on. In addition, these factors increase water losses from plants and subsequently facilitate plant exposure to water stress (Dai 2012; Mafakheri et al. 2010; Salehi-lisar et al. 2012; Shao et al. 2008a; Trenberth et al. 2014). Sometimes drought does not occur truly because of a water deficit in the environment. In some cases, there is enough water in the soil, but several soil factors, such as salinity, low soil temperatures, and flooding, prevent or decrease water uptake by roots and subsequently lead to water stress in plants. This type of drought is called pseudo-drought or physiological drought, and the atmospheric conditions are not determining factors in this type of drought (Arbona et al. 2013).

5.4   Effects of Drought Stress in Crops

5.4.1   Crop Growth and Yield

Drought severely reduces plant growth and development by influencing different physiological and biochemical aspect (Bhargava and Sawant 2013; Farooq et al. 2009; Rahdari and Hoseini 2012; Shao et al. 2008a). In addition, drought can negatively affect the quantity and quality of growth and yield of plants, especially crops (Jaleel et al. 2009; Nezhadahmadi et al. 2013; Zlatev and Lidon 2012). Plant growth and development are dependent to cell division-, elongation-, and differentiation. All of these phases are affected under drought conditions by loss of turgor and subsequently disordered enzyme activities and decreased energy supply from photosynthesis (Bhargava and Sawant 2013; Ding et al. 2013; Jaleel et al. 2009; Keyvan 2010; Osakabe et al. 2014; Shao et al. 2008a). Plant water potential and turgor are reduced in dehydration conditions; therefore, plant cells cannot perform their normal functions (Keyvan 2010; Rahdari and Hoseini 2012). Turgor reduction leads to

suppressed cell expansion and growth. Cell expansion and growth are necessary phenomena for the initial phase of plant growth and establishment (Barriopedro et al. 2012; Keyvan 2010). Growth decline in vegetative phase of crops leads to negative effects on reproductive phase and finally reduced the quantity and quality of crop yield (Farooq et al. 2009; Rahdari and Hoseini 2012; Shao et al. 2008a).

5.4.2 Morphological and Anatomical Characteristics

Morphological changes are consequence of a wide spectrum of physiological effects of drought stress on plants (Chernyad'ev 2005; Jaleel et al. 2009; Keyvan 2010; Mafakheri et al. 2010; Nezhadahmadi et al. 2013). The morphological acclimation strategy usually includes smaller leaf area to decrease the transpiration and larger root system to enhance the water uptake capacity (Chernyad'ev 2005; Jaleel et al. 2009; Mafakheri et al. 2010; Salehi-lisar et al. 2012; Shao et al. 2008a). The anatomy of a leaf and its ultrastructure are altered by water stress (Hirt and Shinozaki 2004; Madhava et al. 2006; Salehi-lisar et al. 2012). A decrease in leaves' size, a lower aperture and a decrease in the number of stomata, cell wall thickening, cutinization of the leaf surface and developed conductive system (increase in the number of large vessels), submersion of stomata in succulent and xerophyte plants, and the formation of tube leaves in cereals are some alterations that occur in plants exposed to drought (Chernyad'ev 2005; Jaleel et al. 2009; Keyvan 2010; Mafakheri et al. 2010; Nezhadahmadi et al. 2013; Shao et al. 2008a). Leaf senescence is a key developmental process which occurs naturally during plant maturation, but premature leaf senescence was observed in water-deficit situations. In leaf-forage crops, premature leaf senescence is a main reason of yield loss of these crops (Farooq et al. 2009; Shao et al. 2008a). Optimal leaf area development before leaf senescence and optimum stomatal density and opening are essential factors for optimal photosynthesis in plants (Jaleel et al. 2009). Therefore, net photosynthesis under drought stress is reduced due to a low leaf area and an increase in leaf senescence (Ding et al. 2013; Mishra and Singh 2011; Shao et al. 2008a; Zare et al. 2011). The main effect of drought stress on plant morphology is size reduction. A low photosynthesis rate is one of the most important factors involving in the reduction of plant size and biomass production (Farooq et al. 2009; Franco 2011; Shao et al. 2008a; Zare et al. 2011). In order to increase water uptake under dehydration conditions, plants expand their roots and produce a ramified root system (Akhtar and Nazir 2013; Bhargava and Sawant 2013; Farooq et al. 2009; Franco 2011; Jaleel et al. 2009; Rahdari and Hoseini 2012). An increased biomass allocation to roots under drought situations and an expansion of the plant's root system generally lead to a higher capacity for water uptake (Bhargava and Sawant 2013; Farooq et al. 2009; Franco 2011; Shao et al. 2008a). Accordingly, despite reducing the shoot growth, the root growth is not significantly reduced under a mild water deficit. Therefore, under dehydration conditions, the root-to-shoot ratios of plants usually increase; however,

the total biomasses of plants are reduced considerably (Akhtar and Nazir 2013; Jaleel et al. 2009; Salehi-lisar et al. 2012; Shao et al. 2008a; Zare et al. 2011).

5.4.3   Plant-Water Relationships and Ion Uptake

The relative water content (RWC), leaf water potential, stomatal resistance, transpiration rate, leaf temperature, and canopy temperature are important factors in plant-water relationships (Bhargava and Sawant 2013; Farooq et al. 2009; Keyvan 2010; Shao et al. 2008a; Zlatev and Lidon 2012). Relative water content reduction is the earliest effect of drought on crop plants (Farooq et al. 2009). A decrease in the leaf water potential due to low RWC leads to stomatal closing. A higher stomatal resistance decreases the transpiration rate and finally leads to increases in the leaf temperature, because transpiration is the main factor controlling the leaf temperature (Arbona et al. 2013; Farooq et al. 2009; Mafakheri et al. 2010; Sapeta et al. 2013). Higher temperatures of leaves can lead to denaturation of proteins especially enzymes and changes in membrane permeability which can influence different aspects of metabolism such as the synthesis of important macromolecules including amino acids and proteins, photosynthesis, respiration, ion uptake, and mineral nutrition (Bhargava and Sawant 2013; Rana et al. 2013; Salehi-lisar et al. 2012; Sapeta et al. 2013; Zlatev and Lidon 2012). Water stress affects plant mineral nutrition and disrupts ion homeostasis in crops due to increasing leaf temperature and stomatal resistance and changes cell metabolism (Akhtar and Nazir 2013; Bray 2001; Kheradmand et al. 2014). Generally, decreasing water availability under water stress conditions limits the total nutrient availability in soil, decreases the nutrient uptake by roots, and finally reduces their tissue concentrations in crops (Farooq et al. 2009; Kheradmand et al. 2014). Changing nutrient uptake by the root and their transport to the shoots is an important effect of water deficit on plants. Generally, drought stress leads to an increase in N and causes a reduction in the P and PO_4^{3-} contents in the plant tissue because of lowered PO_4^{3-} mobility as a result of lower water availability, and has no definitive effects on the K concentration in plants (Akhtar and Nazir 2013; Farooq et al. 2009; Shao et al. 2008a). A decrease in the Ca content of plants has been reported by many researchers as well (Akhtar and Nazir 2013; Bhargava and Sawant 2013). The cell membrane is one of the earliest targets of many stresses such as drought. Membrane stability in the roots plays an essential role in the appropriate mineral nutrition of plants. Therefore, preservation of the membrane stability is a very important factor in plant resistance to drought. Damage of cell membranes under water-deficit conditions is an important factor leading to disruption of ion homeostasis in plants (Farooq et al. 2009; Kheradmand et al. 2014; Rahdari and Hoseini 2012; Salehi-lisar et al. 2012).

5.4.4 Plant Metabolism

Carbon metabolism is one of the most important metabolism pathways in plants. A reduction and/or inhibition of photosynthesis is one of the main effects of drought on plant metabolism (Bhargava and Sawant 2013; Bray 2001; Keyvan 2010; Nezhadahmadi et al. 2013). The reasons of these effects are decrease in the leaf expansion rate and a low leaf surface, an increase in leaf temperature, impaired photosynthetic machinery, and premature leaf senescence (Bhargava and Sawant 2013; Farooq et al. 2009; Zare et al. 2011). Stomatal and nonstomatal factors can be effective in reducing and/or inhibiting photosynthesis under water-deficit situations (Bray 2001; Sapeta et al. 2013; Zlatev and Lidon 2012). Carbon dioxide limitations due to prolonged stomatal closure, especially under light saturation conditions, lead to the accumulation of reduced photosynthetic electron transport components. The accumulation of these compounds can reduce molecular oxygen and give rise to the production of reactive oxygen species (ROS), resulting in oxidative damage in chloroplasts (Arbona et al. 2013; Bhargava and Sawant 2013; Osakabe et al. 2014; Shao et al. 2008a; Xoconostle-Cazares et al. 2010; Zlatev and Lidon 2012). Low CO_2 uptake due to stomatal closure decreased the photosynthesis rate due to reduced activity of enzymes involved in CO_2 reduction (Calvin cycle, dark reactions). The lower activity of dark reactions could lead to imbalances between the light and dark reactions of photosynthesis and ROS accumulation in chloroplasts (Bhargava and Sawant 2013; Farooq et al. 2009; Nezhadahmadi et al. 2013). Besides, the ROS can damage the photosynthetic apparatus, including thylakoid membranes, photosynthetic pigments, and enzymes (Bhargava and Sawant 2013; Farooq et al. 2009; Salehi-lisar et al. 2012). A decrease in the chlorophyll content of leaves under water stress is another factor involved in the reduction of the photosynthesis rate (Keyvan 2010; Rahdari and Hoseini 2012; Sapeta et al. 2013). Despite inhibiting photosynthesis under water-deficit, carbon-rich molecules such as soluble carbohydrates (hexose, sucrose, trehalose, mannitol), amino acids (proline), organic acids (malate, fumarate, citrate), and structural compounds (cellulose and lignin) increase within plant tissues during drought stress. Many of these compounds act as compatible solutes and protect subcellular structures against effects of water deficit (Muller et al. 2011). According to the literature reports, carotenoids are less sensitive to water stress than chlorophylls. However, unlike chlorophylls, an increase in xanthophyll pigments such as zeaxanthin and antheraxanthin in plants under water stress has been reported. Carotenoids as low molecular weight (LMW) antioxidant metabolites play a protective role in plants under stress, and some of these pigments are involved in the xanthophyll cycle, which is involved in ROS detoxification (Chernyad'ev 2005; Farooq et al. 2009; Jaleel et al. 2009; Nezhadahmadi et al. 2013). The key enzyme for carbon metabolism in the Calvin cycle is ribulose bisphosphate carboxylase/oxygenase (RuBisCO) (Farooq et al. 2009; Salehi-lisar et al. 2012). The amount and activity of RuBisCO decrease rapidly under water-deficit conditions. This effect is evident in all studied crops, but the severity of the decrease is species-dependent (Chernyad'ev 2005; Farooq et al. 2009; Salehi-lisar et al. 2012). A decline in RuBisCO activity is caused by the acidification of

chloroplast stroma, a lack of the substrate for carboxylation (CO_2 and ribulose bisphosphate), a reduction in the amount and/or activity of the coupling factor (ATPase, ATP synthase), structural alterations of chloroplasts and RuBisCO, and release of RuBisCO from damaged plastids (Akhtar and Nazir 2013; Bhargava and Sawant 2013; Chernyad'ev 2005; Farooq et al. 2009; Zlatev and Lidon 2012). In addition to RuBisCO, activities of some other enzymes involved in carbon metabolism, such as phosphoenolpyruvate carboxylase, NADP-malic enzyme, fructose-1,6-bisphosphatase, NADP-glyceraldehyde phosphate dehydrogenase, phosphoribulokinase, sucrose phosphate synthase, and pyruvate orthophosphate dikinase, decrease linearly with lowered leaf water potential under drought conditions (Chernyad'ev 2005; Farooq et al. 2009; Salehi-lisar et al. 2012). Drought stress also disrupts the cyclic and noncyclic types of electron transport in the light reactions of photosynthesis (Bhargava and Sawant 2013). A lower electron transport rate negatively affects the photophosphorylation process (ATP biosynthesis) (Akhtar and Nazir 2013; Bhargava and Sawant 2013; Chernyad'ev 2005) as well as the $NADPH/H^+$ reduction (Chernyad'ev 2005; Farooq et al. 2009; Salehi-lisar et al. 2012). These alterations cumulatively disrupt the photosynthetic apparatus under water stress conditions (Bhargava and Sawant 2013; Chernyad'ev 2005). Both photosystems, PSI and PSII in chloroplasts, are affected by water-deficit conditions mainly due to a lower electron transport rate and the accumulation of ROS (Bhargava and Sawant 2013; Chernyad'ev 2005). Drought stress leads to a disturbance in the association between membrane lipids and proteins as well as decreases the membrane-bound enzyme activity and transport capacity of the bilayer (Farooq et al. 2009; Kheradmand et al. 2014). Monogalactosyldiacylglycerol (MGDG) is a major leaf glycolipid and that content decreases after plant exposure to drought. The MGDG is the most important component of the chloroplast membrane; accordingly, its lower content leads to destruction of the chloroplast membrane and negatively affects photosynthesis (Farooq et al. 2009; Mafakheri et al. 2010; Rahdari and Hoseini 2012; Salehi-lisar et al. 2012). Plant growth and development, as well as environmental conditions influence the respiration rate. Under water-deficit conditions, a change can occur in carbon metabolism as a result of diminished photosynthesis and active respiration. A plant's growth rate is determined precisely by photosynthetic CO_2 assimilation and the respiration ratio (Bhargava and Sawant 2013; Ding et al. 2013; Farooq et al. 2009; Keyvan 2010). Under drought stress, the tricarboxylic acid (TCA) cycle and ATP biosynthesis in the mitochondria are negatively affected and lead to a decrease in the respiration rate (Arbona et al. 2013; Bhargava and Sawant 2013; Farooq et al. 2009). There are two mitochondrial electron transport pathways from ubiquinone to oxygen in plants. The alternative pathway branches from the cytochrome pathway and transfers electrons to oxygen directly by alternative oxidase (Bhargava and Sawant 2013; Farooq et al. 2009). When plants are exposed to the drought stress, they produce ROS in the mitochondria. These free radicals could damage cellular components (Arbona et al. 2013; Labudda and Safiul Azam 2014). Alternative oxidase activity could be useful in maintaining normal levels of metabolites and reducing ROS production by transferring electrons to O_2 and production of H_2O_2 (Akhtar and Nazir 2013; Bhargava and

Sawant 2013; Farooq et al. 2009). Functional changes in photosynthesis and respiration spread to all parts of the cell and finally cause a change in the metabolism of the whole plant, and drought stress was induced in physiological level.

5.4.5 Osmotic Adjustment

Plants synthesize compounds such as proteins and amino acids and accumulate some minerals in response to water-deficit situation (Nezhadahmadi et al. 2013; Rahdari and Hoseini 2012). Drought conditions change the quantity and quality of plant proteins (Chernyad'ev 2005; Farooq et al. 2009; Rahdari and Hoseini 2012). Typically, the protein content decreases under a water deficit due to suppression of their synthesis (Bernacchia and Furini 2004; Chernyad'ev 2005; Nezhadahmadi et al. 2013; Salehi-lisar et al. 2012). However, the synthesis of some proteins and enzymes such as late embryogenesis abundant proteins or LEA proteins; proteases; enzymes required for the biosynthesis of various osmotic compatible compounds (osmoprotectants); enzymes involved in the detoxification of ROS including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR); and protein factors involved in the regulation of signal transduction and gene expression increases under drought stress (Ding et al. 2013; Farooq et al. 2009; Labudda and SafiulAzam 2014; Nezhadahmadi et al. 2013; Rahdari and Hoseini 2012; Xoconostle-Cazares et al. 2010; Zlatev and Lidon 2012). The accumulation of compatible solutes (osmoprotectants in some texts) in order to provide osmotic adaptation (osmotic regulation and osmotic adjustment) is a well-known mechanism for plant resistance to drought and some other stress such as salinity (Ashraf et al. 2009; Hirt and Shinozaki 2004; Madhava et al. 2006; Salehi-lisar et al. 2012). Compatible solutes have a low molecular weight and can accumulate at high concentrations without having damaging effects on the cell components and metabolism (Rahdari and Hoseini 2012; Xoconostle-Cazares et al. 2010). The accumulation of compatible solutes increases the cellular osmotic pressure and triggers water uptake from soil. In addition, compatible solutes regulate the osmotic balance between the vacuole and the cytosol, maintain the turgor pressure and water content of cells, and protect against water loss from plants because of their high lipophilicity. Also, they might replace water molecules around nucleic acids, proteins (like enzymes), and membranes during water shortages. Compatible solutes might prevent interactions between ions (at a high concentration) with cellular components by replacing the water molecules around these components and protecting against the destabilization of important macromolecules (Ashraf et al. 2009; Hirt and Shinozaki 2004; Madhava et al. 2006; Salehi-lisar et al. 2012). Some compatible solutes have antioxidative activity (Salehi-lisar and Bakhshayeshan-Agdam 2016). Compatible solutes are divided into five major groups (Arbona et al. 2013; Bray 2001; Ding et al. 2013; Farooq et al. 2009; Rangan et al. 2014; Xoconostle-Cazares et al. 2010).

5.4.5.1 Sugars

Sugars, including monosaccharides (e.g., fructose and glucose) and di- and oligosaccharides (e.g., sucrose, trehalose, and raffinose), are accumulated in the leaves of different crops under drought stress. Sugars may represent a major part of all compatible solutes in the plant cells; for example, the osmotic potential of sorghum tissues is containing over 40–50% sugar (Jones et al. 1981). Sugars provide the carbon and energy required for normal functions of plant metabolism as well as plant growth and development after water-deficit elimination. Sugars especially accumulated when the utilization of carbohydrates by metabolism is reduced. For example, fructans are a reserve source of carbohydrates and can protect plants against severe drought stress. These carbohydrates accumulate especially in the vacuoles (Munns and Weir 1981). Similarly, trehalose is important for drought resistance in dehydration-tolerant plants (Vinocur and Altman 2005).

5.4.5.2 Amino Acids

Some amino acids such as proline and citrulline are important organic compounds involved in osmotic adaptation. The proline accumulation as an amino acid is a typical response in plants, eubacteria, protozoa, and marine invertebrates exposed to the various stresses. Proline accumulation was frequently reported under water-deficit situation in plants. Proline level under drought stress can increase over 100 times greater than that in the control, but the accumulation capacity differs from species to species (Verbruggen and Hermans 2008). Drought increases cell proline levels in two ways: by increasing proline synthesis and by decreasing the activity of enzymes involved in its degradation. Low turgor pressure is the first reason for proline accumulation under drought stress. There are close relationships between proline accumulation and plant resistance to drought stress (Keyvan 2010; Rahdari and Hoseini 2012). Many researchers have reported that proline has an important role in osmotic regulation. Proline accumulation and that of other osmoprotectants lead to a lower water potential of cells and hence help water uptake from soil under drought conditions (Bray 2001; Farooq et al. 2009). In addition, proline protects cell components from oxidative stress, and its biosynthesis and degradation process play important roles in balancing the energy and reducing equivalent between chloroplasts and mitochondria (Salehi-lisar et al. 2012). During proline generation and destruction pathways, $NADPH/H^+$ oxidizes to $NADP^+$ in chloroplasts and NAD^+ reduces to $NADH/H$ in mitochondria, respectively. The $NADPH/H^+$ oxidation in chloroplasts reduces the ROS generation because of the consumption of excess electrons. In addition, $NADH/H^+$ oxidation in mitochondria is necessary for energy supply for cells as well as for recovery processes after stress (Mafakheri et al. 2010; Rahdari and Hoseini 2012; Salehi-lisar et al. 2012). The upregulation of proline biosynthesis depends on the activity of enzymes such as pyrroline-5-carboxylate reductase (P5CR) and pyrroline-5-carboxylate synthetase (Nounjana et al. 2012). Moreover, the level of proline in plants is controlled by proline dehydrogenase activity, which is inhibited under stress conditions, and therefore the content of proline increases (Peng et al. 1996). Proline is not the only compatible solute or osmoprotectant whose production and accumulation are induced under water-deficit conditions.

5.4.5.3 Onium Compounds

Onium compounds are including tertiary and quaternary ammonium (such as glycine-betaine), as well as sulfonium compounds (such as 3-dimethylsulfoniopropionate). Betaines, a well-known onium compounds, are quaternary ammonium compounds from which glycine betaine (GB) is accumulated in the largest quantities and has important physiological functions in the plant cells (Singh et al. 2015). Glycine betaine has multiple functions in the plant cells under drought stress such as stabilizing the enzyme's quaternary structure and maintaining the membrane integrity (Sakamoto and Murata 2000). It contributes to osmoregulation directly as well as indirectly by protecting the membrane stability, which is necessary for normal functions of channels and ion carriers and consequently maintaining cell homeostasis (Ashraf and Foolad 2007). The protective role against reactive oxygen species has also been proven (Einset et al. 2007).

5.4.5.4 Polyols and Sugar Alcohols

Polyols (e.g., mannitol, pinitol, glycerol, and sorbitol), sometimes also called sugar alcohols, generally have one of two following structures: (1) a cyclic structure, such as myoinositol and pinitol, or (2) a linear structure, which matches sorbitol, xylitol, mannitol, and ribitol (Tari et al. 2010). Polyols play key role in the regulation of osmotic balance in the plant cells. They provide significant protection of plant structures against indirect effects during drought stresses. The recent studies have revealed that polyol molecules improve plant growth and development under water-deficit condition (Li et al. 2011). For example, sorbitol as a polyol is produced in parallel with sucrose during photosynthesis and serves as carbon and energy translocation compound between sources and sinks (Jain et al. 2010).

5.4.5.5 Polyamines

Polyamines (e.g., putrescine, spermidine, and spermine) are small aliphatic organic molecules that contain two or more amino groups. They are involving in different physiological processes such as cell division, growth, and differentiation (Minguet et al. 2008). Polyamines in plant cells were found free or conjugated with phenolic compounds or with proteins and nucleic acids (Gill and Tuteja 2010). The metabolism of polyamines is associated with ethylene generation, which can be important in responses to drought stress. Polyamine accumulation under drought stress conditions has been reported in many crop species (Hussain et al. 2011). Besides, polyamines are components of the antioxidant system and play key role in ROS scavenging (Kuznetsov et al. 2007).

In addition to compatible compounds, in some cases plants accumulate specific inorganic ions such as K^+, Na^+, and Cl^- in order to maintain the intracellular water potential (Rauf et al. 2014; Salehi-lisar et al. 2012).

5.4.6 Molecular Effects

A complex set of genes are involving in plant responses to drought stress (Bernacchia and Furini 2004; Bhargava and Sawant 2013; Farooq et al. 2009). Many gene expression patterns change when plants are exposed to drought stress (Bernacchia and Furini 2004; Bhargava and Sawant 2013). First, the expression of genes involved in early responses such as signal transduction, transcription, and translation factors has been changed. Next, changes in the expression of genes involved in late responses such as water transport, osmotic balance, oxidative stress, and the damage-repair process have occurred (Bhargava and Sawant 2013; Osakabe et al. 2014; Xoconostle-Cazares et al. 2010). Drought sensing and signal transduction are still not clearly known. Generally, drought signaling is closely joined with abscisic acid (ABA) signal transduction. Plant gene expression is controlled at different levels, including the transcriptional, posttranscriptional, translational, and posttranslational phases (Bhargava and Sawant 2013; Bray 2001; Osakabe et al. 2014). Apparently, the regulation of plant response mechanisms to abiotic stresses including drought stress is controlled at two levels: the transcriptional and translational levels (Bhargava and Sawant 2013; Farooq et al. 2009; Xoconostle-Cazares et al. 2010). Bioinformatic analyses have identified several transcription factors (TFs) induced under drought stress. Transcription factors are classified into several families, including MYB/MYC, zinc-finger protein, and NAC (Bray 2001; Ding et al. 2013; Nakashima et al. 2014; Nezhadahmadi et al. 2013; Osakabe et al. 2014; Xoconostle-Cazares et al. 2010). Molecular biology researches has shown that plants respond to stress not only at the cells, mRNA, or protein level but also at the posttranscriptional phase (Bhargava and Sawant 2013; Nezhadahmadi et al. 2013). MicroRNAs (miRNAs) are a class of small RNAs that are recognized as important modulators of gene expression at the posttranscriptional level (Bej and Basak 2014; Bhargava and Sawant 2013). Previously, many RNA molecules were counted, such as miR474, miR528, miR167, miR160, miR390, miR166, miR397, miR398, miR393, miR159, miR169, miR172, miR395, NAT-siRNA$_s$, and tasiRNA$_s$, which are involved in plant response and resistance to drought (Bej and Basak 2014; Ding et al. 2013). Studies have shown that these miRNA molecules are involved in responses mediating with ABA, auxin signaling, cell growth, antioxidant defense, osmotic adjustment, photosynthesis, and respiration under drought (Bej and Basak 2014; Ding et al. 2013; Farooq et al. 2009). Epigenetic mechanisms play a critical role in regulating gene expression through small RNAs, histone modifications, and DNA methylation (Bhargava and Sawant 2013; Bray 2001; Nezhadahmadi et al. 2013). However, hormones are now known to play key roles in the regulation of plant processes and triggering molecular effects and response of plants exposed to various stress. Some hormones are involved in plant interactions with environmental stresses such as drought, and the other are produced as plant response to drought (Bernacchia and Furini 2004; Kheradmand et al. 2014).

5.4.6.1 Abscisic Acid

Abscisic acid is one of the most important hormones in plant response to drought stress (Akhtar and Nazir 2013; Bernacchia and Furini 2004; Bhargava and Sawant 2013). After plants are exposed to drought, ABA is synthesized in roots and translocated to shoots, especially leaves. Furthermore, water stress induces ABA synthesis in chloroplasts. In addition, the plasma membrane ATPase (PM-ATPase) activity decreases under water-deficit conditions due to a lower ATP supply by photosynthesis and respiration. Low PM-ATPase increases the apoplastic (cell wall) pH and leads to the conversion of ABA to its anionic form (ABA). ABA cannot cross the plasma membrane of the leaf cells and translocates toward the gourd cells of stomata by a transpiration stream in the leaf apoplast. Abscisic acid translocation to stomata induces stomatal closure and decreases the stomatal conductance capacity. A higher stomatal resistance leads to lower water losses from the leaf surface, which is one of the earliest plant responses for resistance to water stress. However, low CO_2 uptake by stomata leads to a reduction in the photosynthesis rate in leaves (Akhtar and Nazir 2013; Bernacchia and Furini 2004; Bray 2001; Osakabe et al. 2014; Rangan et al. 2014; Salehi-lisar et al. 2012). In recent studies, the discovered family of proteins which are known as pyrabactin (4-bromo-N-[pyridin-2-yl methyl] naphthalene-1-sulfonamide) resistance (PYR)/regulatory component of ABA receptor (RCAR) has opened new hypothesis about how the ABA-signaling network operates (Cutler et al. 2010). PYR/RCARs are ABA-binding proteins which interact with two other protein classes, protein phosphatases 2C (PP2Cs), and SNF1-related protein kinases 2 (SnRK2s), leading to ABA recognition and signal transduction (Hubbard et al. 2010). Abscisic acid impacts on the genes related to ROS-detoxifying enzymes, enzymes involved in compatible solute metabolism, protein transporters, transcription factors, and enzymes contributing to phospholipid signaling (Cutler et al. 2010). In addition, ABA plays a key role in the regulation of aquaporin's activity as well (Bhargava and Sawant 2013; Farooq et al. 2009). It is well known that ABA accumulation under drought conditions reduces ethylene production (Bhargava and Sawant 2013; Bray 2001).

5.4.6.2 Auxins

The auxin indole-3-acetic acid (IAA) is synthesized in the rapidly dividing tissues such shoot apical meristems and young leaves of all plant species in order to normal plant growth and development (Ding et al. 2013; Nezhadahmadi et al. 2013). In contrast, auxins act as negative regulators of drought tolerance in plants because indole-3-acetic acid downregulation facilitates the accumulation of late embryogenesis abundant (LEA) mRNA. Abscisic acid induces the accumulation of LEA proteins, which are involved in plant adaptation to drought stress, especially in seeds (Bernacchia and Furini 2004; Bhargava and Sawant 2013; Ding et al. 2013; Nezhadahmadi et al. 2013). In addition, auxin has also been implicated in altering hydrogen peroxide dynamics with downstream signaling effects on stomatal closure and root morphology, both of which are important contributors to drought tolerance. Thus, it was observed that maintaining auxin homeostasis in the plant is an essential component of lateral root growth during drought stress (Song et al. 2006).

5.4.6.3 Cytokinins

Cytokinins (CKs) are well-known positive regulators of senescence under stress conditions (Chernyad'ev 2005). Endogenous cytokinin (zeatin) and gibberellin (GA_3) levels of plants decline rapidly under water stress situations. Cytokinins have been shown to delay senescence; hence, those could lead to better adaptation of plants by delaying drought-induced senescence (Bhargava and Sawant 2013; Chernyad'ev 2005). Cytokinins (exogenous or endogenous) enhance antioxidant capacity of plants either directly or indirectly during drought stress (Merewitz et al. 2011).

5.4.6.4 Gibberellins

Gibberellins (GAs) are a large class of plant hormones that are involved in the plant growth and developmental processes including seed germination, stem and root elongation, leaf expansion, sex determination, transition from juvenile to adult phases, and flower initiation (Taiz and Zeiger 2010). Gibberellins typically known as antagonistic to ABA and natural GA (GA_1, GA_3, GA_4, and GA_9) levels of plants decline rapidly during drought stress (Acharya and Assmann 2009). Gibberellin applications relieve oxidative stress and the rate of leaf senescence by increasing endogenous GA_4 and GA_7 due to effect on lipid peroxidation, hydrogen peroxide content, and SOD, POD, and APX activities (Yu et al. 2009). Already, direct impacts of GAs on the cellular expansion under drought stress are not clear well. It seems that GAs may affect cellular expansion under water-deficit situation due to GA_3 upregulating expansion genes including $EXPA_4$ and $EXPB_4$ and xyloglucan endo-transglycosylase (XET) genes such as XET1 and XET1 to maintain cell elongation rates (especially in leaves) (Xu et al. 2016).

5.4.6.5 Ethylene

Ethylene induces a well-known triple response on plant growth and development as well as is implicated in various aspects of plant stress responses. The ethylene signaling is initiated with ethylene sensing by ethylene receptors which act as negative regulators. Briefly, ethylene binds to the receptors and inactivates the receptor-CTR_1 complex. This event allows EIN_3 transcription factors to accumulate in the nucleus and express transcription factor genes and ethylene response factors (ERF_1) which has an effect on downstream genes (Stepanova and Alonso 2009). Studies have shown that expression of ERFs affects plant responses to osmotic stresses, including drought or salinity, thus promoting stress tolerance in plants (Trujillo et al. 2008). The effects of ethylene on leaf senescence and growth inhibition under drought stress which may help in plant tolerance are well known. The ethylene-mediated reductions in shoot growth and stomatal responses under drought stress are highly dependent on ABA accumulation in shoots, since ABA and ethylene are antagonism (Chaves et al. 2003).

5.4.6.6 Salicylates

Salicylic acid (SA) is a phenolic plant hormone which plays regulatory roles in plant responses to oxidative stress, chloroplast biogenesis, and photosynthesis (Hayat et al. 2010). High concentrations of SA within the plant systems lead to

induce responses that promote tolerance to osmotic stresses such as salinity and drought. Exogenous application of SA enhanced the drought tolerance of crop plants by increasing photosynthetic parameters, membrane integrity, leaf water potential, chlorophyll content, and/or activity of nitrate reductase and carbonic anhydrase (Hayat et al. 2008). Salicylic acid can promote drought tolerance in crops by enhancing the transcription of GST_1, GST_2, GR, and MADAR which facilitate the ROS scavenging. Interactions between SA and hydrogen peroxide affect the ROS accumulation in plant cells as well as oxidative stress-induced gene expression (Kang et al. 2013; Zhang and Liu 2001).

5.4.6.7 Jasmonates

Jasmonic acid (JA) is a biologically active lipid derivative that is involved in the regulation of various stress responses in plants such as leaf senescence, ROS and NO signaling, antioxidant metabolism, and stomatal movement (Taiz and Zeiger 2010). The application of JA can increase activities of SOD, POD, CAT, APX, and GR collectively and detoxified hydrogen peroxide. Furthermore, JA application enhanced the drought resistance of agronomic plants by increasing proline and soluble sugar content (Wu et al. 2012). Microarray analysis of *Arabidopsis* genes showed that the prevalence of 221 mRNAs was highly upregulated following MeJA (from JA derivatives) application and the upregulated mRNAs play key roles in oxidative stress responses, cellular homeostasis maintenance, as well as defense signaling (Schenk et al. 2000). Increasing in jasmonate content of plants under drought stress induce expression of specific NAC transcription. It appears that JA plays important regulatory roles during the ABA-related drought responses in plants, because JAZ (jasmonate ZIM domain) and drought-inducible $AtMYC_2$ transcription factors regulate gene expression in jasmonate pathway. Furthermore, the pretreatment of plants by MeJA before drought conditions has reversible effects on nitrogen uptake inhibition and remobilization of RuBisCO subunits in agricultural fields; however, JA-induced changes in these parameters remain unknown (Rossato et al. 2001; Schenk et al. 2000).

5.4.6.8 Brassinosteroids

Generally, drought leads to an increase in brassinosteroid (BR) accumulation in plants. Brassinosteroids increase water uptake and cell membrane stability and can also reduce ion leakage from membrane under drought stress conditions (Bhargava and Sawant 2013; Rahdari and Hoseini 2012).

5.4.6.9 Melatonin

Melatonin (N-acetyl-5-methoxy tryptamine) is a hormone that is produced by the pineal gland in animals and regulates sleep and wakefulness. Melatonin is also produced in plants, and it is a potent natural antioxidant that effectively scavenges ROS in the animals and plants (Arnao and Hernandez-Ruiz 2015). Furthermore, melatonin downregulates MdNCED3, an ABA synthesis gene, and upregulates MdCYP707A1 and MdCYP707A2, ABA catabolic genes resulting in reducing of ABA contents in drought-stressed plants. On the other hands, melatonin scavenges

H_2O_2 and enhances the antioxidant enzyme activities to detoxify H_2O_2 indirectly (Li et al. 2015). According to the obtained information through cloned gene (MzASMT1 or KJ123721) from apple rootstock (*Malus zumi* Mats.), N-acetylserotonin-O-methyltransferase (ASMT) is a specific enzyme required for melatonin synthesis (Lee et al. 2015; Zuo et al. 2014). The transgenic plants with overexpression of MzASMT1 (KJ123721) or melatonin application in the soils leads to a decline in intrinsic ROS and subsequently oxidative stress and delays leaf senescence under drought conditions (Wang et al. 2013; Zuo et al. 2014).

5.5 Oxidative Stress: Secondary Drought Stress Signaling

Exposure of plants to many environmental stresses such as drought leads to the generation of ROS, including superoxide radical ($O_2^{\bullet-}$), hydroxyl radical (OH), hydrogen peroxide (H_2O_2), alkoxy radicals (RO), and singlet oxygen. Reactive oxygen species accumulations were considered harmful to biomolecules, and it creates oxidative stress which negatively affects plant. Oxidative stress is known as a secondary stress and causes oxidative damage in cells (Bhargava and Sawant 2013; Farooq et al. 2009; Labudda and SafiulAzam 2014; Nezhadahmadi et al. 2013; Osakabe et al. 2014; Rahdari and Hoseini 2012; Salehi-lisar et al. 2012; Zlatev and Lidon 2012). Reactive oxygen species may react with proteins, lipids, and other important macromolecules and can denaturize the structure and function of the macromolecules (Arbona et al. 2013; Bhargava and Sawant 2013; Kheradmand et al. 2014; Mafakheri et al. 2010). Many cell compartments produce ROS under drought stress, such as chloroplasts, mitochondria, peroxisomes, and others (Farooq et al. 2009; Labudda and SafiulAzam 2014; Osakabe et al. 2014). Drought stress is a multidimensional factor that limits CO_2 fixation and reduces the $NADP^+$ regeneration in the Calvin cycle, resulting in the over-decline of the photosynthetic electron transport chain activity and generally leading to production of $O_2^{\bullet-}$ and singlet oxygen ($^1O_2$) in the chloroplasts (Shao et al. 2008b). The generation of ROS in biological systems is represented by both nonenzymatic and enzymatic mechanisms, which are dependent on some factors such as oxygen concentration in the cells (Farooq et al. 2009). Generally, ROS accumulation leads to DNA nicking, oxidation of amino acids, protein and photosynthetic pigments, lipid peroxidation, and so on (Farooq et al. 2009; Nezhadahmadi et al. 2013; Salehi-lisar et al. 2012). Plants have developed some mechanisms to avoid ROS damage. All these mechanisms form an antioxidant defense system, which includes both enzymatic and nonenzymatic components. Superoxide dismutase, CAT, POD, APX, and GR are some enzymes involved in the antioxidant responses of plants (Arbona et al. 2013; Bray 2001; Ding et al. 2013; Farooq et al. 2009; Jaleel et al. 2009; Labudda and SafiulAzam 2014; Nezhadahmadi et al. 2013; Zlatev and Lidon 2012). Glutathione (GSH), ascorbic acid (AsA), carotenoids, and α-tocopherol are some compounds involved in the antioxidant defense system of plants (Bhargava and Sawant 2013; Farooq et al. 2009; Jaleel et al. 2009; Salehi-lisar et al. 2012).

Already, the signaling function of ROS has been recognized as a fundamental principle in cellular communication. There are six functional elements that operate the redox regulatory network: (1) redox input elements that feed the redox regulatory network by electrons, such as NADPH, ferredoxin, and GSH, (2) redox transmitters that transfer and distribute the electrons to downstream proteins such as thioredoxin, (3) redox target proteins that have redox-sensitive thiols controlled by transmitters, (4) redox buffer proteins that are accumulated in a great amount in organelles such as the RuBisCo, (5) redox sensors that deliver information from ROS to the redox regulatory network and make the crosstalk with other signaling pathways, and (6) electron acceptors that are including low molecular weight redox species such as ROS, reactive nitrogen species (RNS), reactive sulfur species (RSS), and reactive carbonyl species (RCS). Plant cells can sense, transduce, and translate the ROS signals into the effective cellular responses by redox-sensitive protein involvement (Baxter et al. 2014). Mechanisms underlying the sensing of ROS in the plant cells have not known well; however, three mechanisms of ROS sensing were introduced: 1) unidentified receptor proteins, 2) redox-sensitive transcription factors, and 3) phosphatases (Huang et al. 2012). Recent studies have shown well that ROS interact with other signal transduction components, such as phytohormones, MAPK cascades, and calcium ions, although the ROS perception in the plant cells is yet a mystery (Xia et al. 2015). After ROS sensing by cells, downstream signals amplify the ROS signal and transduce the response to counteract with the environmental stresses such drought which includes mechanisms that implicate the Ca^+ ions, calcium-binding proteins such as calmodulins, G proteins, and phospholipids that mediate phosphatidic acid accumulation (Sagi and Fluhr 2006; Steinhorst and Kudla 2013; Suarez Rodriguez et al. 2010). Accordingly, there are some molecules such as calcium, protein kinases, and hormones that transduce and amplify the ROS-produced signal.

5.5.1   Calcium

Calcium (Ca^{2+}) is an important second messenger in response to biotic and abiotic stresses as well as developmental processes in plant cells (Steinhorst and Kudla 2013). Calcium has different functions in plants, and its cellular accumulation patterns are called calcium signature that temporal and spatial feature, amplitude, frequency, and duration encoding can give more information about plant stress responses (Dodd et al. 2010; Kudla et al. 2010). An increase in ROS production started in plant cells in response to abiotic stresses such as drought, and neighboring cells produce a long-distance signal called the ROS wave (Gilroy et al. 2014). This event is associated with the Ca^{2+} wave through the action of vacuolar ion channel which leads to calcium-induced calcium release, Ca^{2+}-dependent protein kinase (CPK) activities, and subsequently the ROS production in the other cells that do not expose to the stress yet. Wonderfully, the Ca^{2+} wave propagated through the root cortex and endodermis layers demonstrates that the roots were implicated by stresses and root cells were specialized in Ca^{2+} wave production and propagation (Choi et al. 2014).

5.5.2 Protein Kinases

Protein kinase (MAPK) cascades connect environmental and developmental signals to intracellular responses. Sequential phosphorylations due to activated MAPKs eventually lead to phosphorylation of MAPKs downstream proteins, which include other kinases, enzymes, or transcription factors (Suarez Rodriguez et al. 2010). Protein kinase-mediated drought responses through ABA and ROS signaling pathway is the well-known function of these molecules. The expression patterns of MAPKs suggested that activities of MAPKs are molecular mechanisms of drought tolerance in several crop plants such as rice, malus, and maize (Peng et al. 2006; Wang et al. 2010).

5.5.3 Hormones

Hormones are known as plant development regulators and manage stress tolerance in plant often through the activation of NADPH oxidases and ROS production (Sagi and Fluhr 2006). According to the literature, there is a close relationship between oxidative stress and ABA in ROS-dependent drought responses. Abscisic acid is a stress hormone that plays a key role in plant development and being a key regulator of plant responses in abiotic stresses as well (Xiong et al. 2002) that is explained previously with details.

5.6   Plant Responses and Resistance to Drought Stress

Plants are sessile organisms and must tolerate environmental stresses; hence, they have developed various mechanisms for resistance to the stresses. Plant responses to environmental stresses such as drought are complex because plants are multicellular organisms (Bhargava and Sawant 2013; Khan et al. 2011; Nezhadahmadi et al. 2013; Rana et al. 2013; Salehi-lisar et al. 2012). Generally, plant resistance to environmental stress is divided into two main strategies: stress avoidance and stress tolerance. Plant adaptation to a water deficit is made possible by physiological, morphological, phenological, biochemical, and molecular responses. The responses can range from being at a molecular level to being at a whole plant level. In this chapter, plant strategies to cope with drought are summarized in the next two subsections including avoidance and tolerance. Although escape is generally a part of plants' avoidance strategy, plants that escape from drought are not exposed to a water deficit that is less important in agronomic plants. Therefore, we do not explain it in this chapter.

5.6.1   Avoidance

The main aim of this strategy is the preservation of a high water potential in plants. The reducing of water loss from plants by stomatal control of transpiration and maintaining of water uptake from the soil by an extensive and prolific root system

are the chief characteristics of this strategy (Bray 2001; Farooq et al. 2009). A deep and thick root system is helpful for exploring water from a considerable soil depth and at a large distance from the plant (Akhtar and Nazir 2013; Farooq et al. 2009; Franco 2011). The cuticle and hairy leaves help to maintain high tissue water potential within plant and are considered a xeromorphic trait for drought tolerance. The production of these structures leads to a decreased crop yield due to the energy consumed to produce them. Therefore, plants that use the avoidance strategy to maintain a relatively high water potential are generally small in size (Farooq et al. 2009; Khan et al. 2011; Salehi-lisar et al. 2012).

5.6.2 Tolerance

In this strategy, plants limit the number and area of leaves in response to water deficit; however, this strategy leads to crop yield loss (Akhtar and Nazir 2013; Bray 2001). In addition, these plants show some xeromorphic traits such as hairy leaves and the production of trichomes on both sides of leaves (Farooq et al. 2009; Khan et al. 2011; Salehi-lisar et al. 2012). Hairiness reduces the leaf temperature, while it increases light reflectance and minimizes water loss by increasing the boundary layer resistance to water vapor movement away from the leaf surface. Inter- and intracellular changes in leaves are visible (Bray 2001; Farooq et al. 2009; Salehi-lisar et al. 2012). The root is the main organ involved in the uptake of water from the soil. Hence, the root growth rate, density, proliferation, and size are key factors influencing plant responses to drought stress. Studies have shown that an alteration in the root system architecture is an important factor in plant tolerance, especially when tolerance is defined as the ability of a plant to maintain its leaf area and growth rate during a prolonged vegetative stage (Farooq et al. 2009; Salehi-lisar et al. 2012). The accumulation of compatible solute and osmotic adaptation, the induction of an antioxidant system, an alteration in metabolic pathways, an increase in the root/shoot ratio, and closure of the stomata are other mechanisms involved in plant tolerance to drought.

Moreover, some physiological mechanisms such as glyoxalase pathway, sulfur metabolism pathway, AsA-GSH cycle, heat-shock protein function, and plant regulator signaling are involved in plant response and resistance to drought stress and promoted plant tolerance in this situation (Bray 2001; Farooq et al. 2009; Khan et al. 2011; Salehi-lisar et al. 2012).

5.7   Drought Management in Agricultural Fields

5.7.1   Using Priming Methods

Plant priming is a general concept that can include several strategies to increase plant tolerance to various abiotic and biotic stresses. Priming may be also an effective method for alteration of plant's natural response to several environmental

stresses such drought that it does not naturally utilize as a survival mechanism (Paparella et al. 2015). The best priming strategy to be used is largely dependent on the type of compounds and plant species. Nowadays, there are different compound groups in order to plant priming for drought tolerance including (Mondal and Bose 2014; Paparella et al. 2015):

1. Inorganic compounds such as macronutrients (e.g., K, Ca, and P), micronutrients (e.g., Fe and Zn) or supplemental nutrients (e.g., Si and Se), and polyethylene glycol (PEG).
2. Amino acids such as proline.
3. Non-protein amino acids such as GB, γ- aminobutyric acid (GABA), β-aminobutyric acid (BABA), and 5-aminolevulinic acid (ALA) that their drought tolerance effects have been proven. Some other non-protein amino acids can be used for priming including p-aminophenylalanine, L-azetidine-2-carboxylic acid, δ-,4-aminobenzoic acid, ornithine, citruline, homoserine, L-3,4-dihydroxyphenylalanine (L-DOPA), and 5-hydroxy-L-tryptophan (5-HTP).
4. Polyamines such as free polyamines putrescine, spermidine, and spermine.
5. Reactive oxygen and nitrogen compounds like H_2O_2 and NO.
6. Antioxidant compounds including AsA or vitamin C and GSH.
7. Plant hormones such ABA, JA, SA, and GA.
8. Organic alcohols including polyols or sugar alcohols such as mannitol, glycol, sorbitol, myoinositol, and glycerol.
9. Volatile organic compounds (VOCs) such as terpenes, ethylene, methanol, isoprene acrolein, and other plant volatiles.
10. Microorganisms including mycorrhizal fungi and rhizobacteria.

Priming methods to cope with drought are summarized in the next three subsections including seed, foliar, and root priming.

5.7.1.1 Seed Priming

Seed priming is a very common action in the agricultural seed industry including chemopriming, hydropriming, osmopriming, solid matrix priming, biopriming, thermopriming, and halopriming (Paparella et al. 2015). Commercial seeds are currently primed for enhanced germination potential or prolong dormancy under stress conditions. Typically, priming seeds for promoting crop tolerance to biotic and abiotic stresses is less common than other seed priming practices (Mondal and Bose 2014; Paparella et al. 2015).

5.7.1.2 Foliar Priming

Exogenous application of various compounds such as hormones in the aerial parts of plants is a common practice in plant research and agriculture to increase crop yields specially under stress conditions. Foliar priming practices to improve both annual and perennial crop tolerance to drought are more important in agriculture

because of some priming compounds such as nature, low seed priming efficiency, and so on (Mondal and Bose 2014; Paparella et al. 2015).

5.7.1.3 Root Priming

Root priming can be effective for priming compounds that are not uptaken readily by aerial parts but are uptaken easily by water flow through plant roots (Mondal and Bose 2014). Besides, root priming is a common research practice for plant exposure under uniform conditions to accurate evaluation of compound effects, such as in hydroponics, tissue culture, or various potting media types (Mondal and Bose 2014; Paparella et al. 2015).

5.7.2 Using Breeding Methods and Transgenic Technology

Scientists have tested many techniques to improve drought tolerance in crop plants (Bhargava and Sawant 2013; Bray 2001; Nakashima et al. 2014; Salehi-lisar et al. 2012; Xoconostle-Cazares et al. 2010). The production of transgenic plants is one of the well-known methods for this purpose (Khan et al. 2011; Nakashima et al. 2014; Salehi-lisar et al. 2012; Xoconostle-Cazares et al. 2010). The wide range of drought-related genes in the plant genome has opened amazing opportunities for crop improvement (Khan et al. 2011; Khan et al. 2013; Nakashima et al. 2014; Xoconostle-Cazares et al. 2010). With all these interpretations, in practice the generation of transgenic plants cannot be completely effective for the production of drought-tolerant plants, because it requires a very complex and expensive laboratory method and generally its success rate is low (Khan et al. 2011; Nakashima et al. 2014; Nezhadahmadi et al. 2013; Xoconostle-Cazares et al. 2010). Traditionally, there have been several efforts to generate drought-tolerant crop plants through usual breeding methods (Nezhadahmadi et al. 2013; Rana et al. 2013; Salehi-lisar et al. 2012). In this method, two groups of plants with desirable traits are selected and crossed to exchange their genes; therefore, the offspring have new genetic arrangements (Khan et al. 2011; Xoconostle-Cazares et al. 2010). Important traits to use in plant breeding might include water-extraction efficiency, water-use efficiency, hydraulic conductance, transpiration efficiency, canopy temperature, light interception and radiation-use efficiency, stomatal characters, root traits, osmotic and elastic adjustments, and modulation of leaf area (Bhargava and Sawant 2013; Ding et al. 2013; Farooq et al. 2009; Nakashima et al. 2014; Nezhadahmadi et al. 2013; Rana et al. 2013; Salehi-lisar et al. 2012; Xoconostle-Cazares et al. 2010). Genetic data can improve the efficiency of the breeding method. Genetic improvement can assist by using recognizable tags to target genes; these are known as polymorphisms based on molecular markers that occur naturally in the DNA sequence (Xoconostle-Cazares et al. 2010). Different methods are employed to recognize linked markers, including restriction fragment length polymorphisms (RFLPs), sequence-characterized amplified regions (SCARs), random amplified polymorphic DNA (RAPDs), simple sequence repeats (SSRs), amplified fragment length polymorphism (AFLPs),

and others (Khan et al. 2011; Khan et al. 2013; Xoconostle-Cazares et al. 2010). The genetic factors involved in quantitative characteristics of phenotypes are called quantitative trait loci (QTLs) (Arbona et al. 2013; Bhargava and Sawant 2013; Nezhadahmadi et al. 2013; Rana et al. 2013; Xoconostle-Cazares et al. 2010). The use of plant breeding methods has an enormous potential to accelerate drought-tolerant plant production and help drought management assist these plants (Farooq et al. 2009; Xoconostle-Cazares et al. 2010). A QTL mapping approach has identified several QTLs with major effects on grain yield and flowering under particular hydrological conditions in crops (Bhargava and Sawant 2013; Khan et al. 2011; Rana et al. 2013; Xoconostle-Cazares et al. 2010). Nowadays, 17 QTLs for leaf water status traits under drought stress and 23 QTLs for seed yield under normal-watered and drought-stressed conditions in both agricultural field and greenhouse trials are identified by scientists (Du et al. 2009).

5.7.3   Using Planting Strategy in Agricultural Fields

In addition to commercial and laboratory techniques, there are several strategies for drought management in agricultural fields including irrigating during periods of low soil moisture, especially for young plants, using modern and effective methods, selecting the appropriate place and imitating good planting practices, selecting native plants or matching plant species to site conditions, using mulch to maintain soil moisture, eliminating any dead or weak tissues to resist secondary problems such as insects and herbivore invasions (Farooq et al. 2009; Khan et al. 2011; Nezhadahmadi et al. 2013; Rana et al. 2013), and inoculating plants with symbiotic microorganisms such as arbuscular mycorrhizal fungi (AM) (Abdelmoneim et al. 2014; Chepsergon et al. 2012).

5.8   Conclusion

Drought is a multidimensional stress factor; therefore, its effects on plants are complex and can affect different aspects of plant growth, development, and metabolism. There are several reasons for drought in agriculture system; hence, plants have developed diverse mechanisms for resistance to drought, generally classified as avoidance and tolerance strategies. The alteration resistance capacity of crops' seeds and young seedlings by priming methods, production of tolerant crops by traditional breeding methods, and the generation of transgenic plants by gene manipulation are useful procedures in order to minimize the negative effects of drought on agronomic plants. In addition, several strategies for drought management in agricultural fields on multiple levels can be effective. The causes of drought, its effects in plants, plant responses in order to resist drought, and some strategies that can be useful for drought management are summarized in Fig. 5.1.
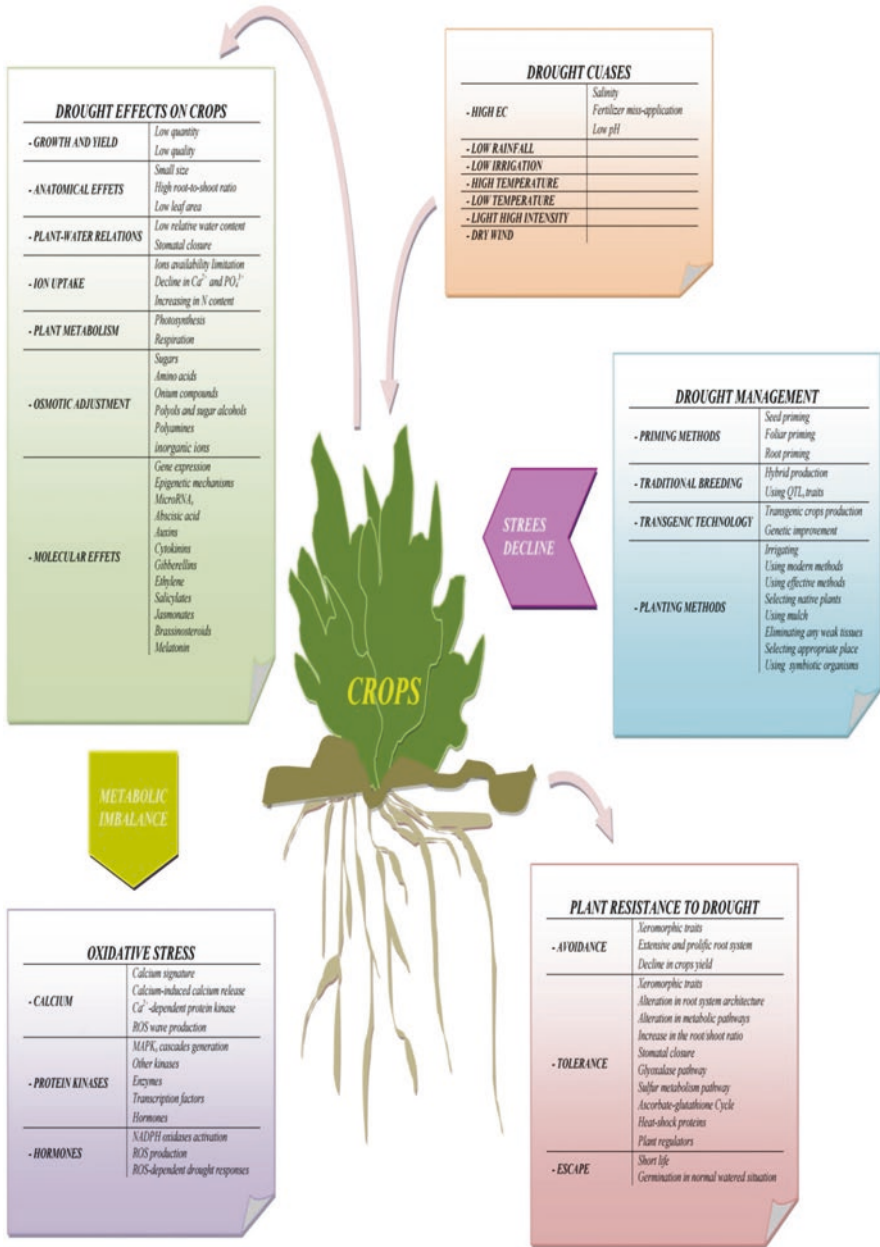
Fig. 5.1 Causes of drought and its effects on plants, plant responses to drought and mechanisms involved in resistance, and some useful strategies for drought management

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The Response of Major Food Crops to Drought Stress: Physiological and Biochemical Responses

6

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Abstract

Prevailing conditions of the climate have had a drastic effect on global food security. Various types of stresses have been producing havoc by reducing crop production. One of the primary causes has been observed in the form of drought. Drought generally has various kinds of impacts on human life, but its main victim is food crops. A plant has specific defense systems to combat and stay unchanged in an environment with water stress, but this ability decreases as the lack of water increases for a long time. The average globular yields of these primary agricultural products are admirably purposeful by enactment of crop performance in millions of fields distributed transversely in series of management practices for soil and climatic regimes; even with the global food supply complications, here we illustrate some simple measures of most widely germinated crops based upon the location, temperature, and precipitation. The types of responses, like reactive oxygen species (ROS), root signaling. Antioxidant enzymes, photosynthesis, etc., discussed in the context will help us to understand the situation with more clarity. The possible mitigation measures are also discussed in detail. A plant may be mitigated at different levels including breeding progress in drought condition, cellular and molecular adaptations, or using supplemental irrigation practices. In this paper, authors have reviewed all the aspects that encapsulate drought stress and its response to major food crops.

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6.1   Introduction

Abiotic stresses, mainly drought, salinity, temperature extremes, flooding, toxic metals, high light intensity, UV radiation, herbicides, and ozone, are the crucial factors worldwide in lowering the crop yield in arable land. This causes a vibrant treat to agriculture and food security (Tuteja and Gill 2013). Drought is an abiotic stress condition and a serious threat to agriculture resulting in deteriorating the environment and a primary cause of crop loss worldwide, reducing average yields for major crop plants such as maize, barley, wheat, rice, etc. by more than 50% (Bray et al. 2000). Abiotic stress leads to a series of morphological, physiological, biochemical, and molecular changes that unfavorably disturb crop productivity (Wang et al. 2003). The best option for crop production, yield improvement, and yield stability under soil moisture-deficient conditions is to develop drought-tolerant crop varieties (those crops which can even survive in low water level conditions) (Turner 1989). For developing new varieties, physiological approach is much practical, but breeding for specific, suboptimal environments involves a deeper understanding of the yield-determining practice (Valipour 2016). Drought, salinity, extreme temperatures, and oxidative stress are often interconnected and may induce similar cellular damage. For example, drought and salinization are established primarily as osmotic stress, resulting in the disruption of homeostasis and ion distribution in the plant/crop cell (Serrano et al. 1999). The alteration in global productivity of major food crops is a crucial driver of change in the cost of food, the land use decisions, and the nutritionally adequate supply of food. Like barley, wheat and maize show a definite negative (undesirable) yield response globally to the vibrant rise in temperature. It is estimated that due to these pragmatic climate trend sensitivities, the increase in temperature since 1981 brings about $5 billion per year or 40 Mt. roughly annual combined loss of these three crops as of 2002. The results demonstrate that the negative impacts directly impinge the crop yield on a global scale (Lobell and Field 2007).

6.1.1   What Is a Drought?

Drought is a prolonged period of abnormally less rainfall or precipitation (for days, months, years) in a given region, resulting in a persistent shortage of water supply, whether atmospheric, surface water, or groundwater, depending upon the conditions of a specific area. Drought causes noteworthy impacts upon the ecosystem and agriculture of the affected region and harm to the local community. The annual dry seasons in the tropics significantly increase the chances of drought development and subsequent bushfires. Periods of heat can considerably worsen drought conditions by accelerating evapotranspiration (Australian Drought and Climate Change 2007). Drought is the combined result of water deficiency, elevated temperature, and increase in population.

6.1.2   Types of Drought

The experts use some indicators to declare a drought condition; these gages help local authorities, states, and governments to mitigate these drought situations appropriately in an affected area. Some of them are as follows:

6.1.2.1 Meteorological Drought

Meteorological drought is usually determined by the overall moisture lack in weather/atmospheric precipitation. The factors which contribute to meteorological drought are dry wind, increase in temperature, etc. It is used as a global indicator of the potential water crisis if the condition prolonged. This category of drought begins and ends instantaneously.

6.1.2.2 Agricultural Drought

Agricultural drought is defined as the reduction in atmospheric precipitation or moisture to the extent that the soil moisture is also being affected. This kind of drought affects both crops/plants and animals because the evapotranspiration is very low (types of drought, 2018). This accounts for the water needs of crops during different growth stages. For instance, not enough moisture at planting may hinder germination, leading to low plant populations and a reduction in yield. Agricultural drought can be seen when the meteorological drought is at play.

6.1.2.3 Hydrological Drought

In this type of drought as from its name, it is clear that the shortage or absence of ground and surface water in a region causes hydrological drought; these result from excessive surface water reliance and less water precipitation. Water is also required for farming, energy, and human activities which accelerate hydrological drought. It has worsened impacts on living organism. Hydrological drought usually occurs or happens at the same time as meteorological drought. The decline in the quantity and quality of surface and subsurface water is the effect of meteorological drought.

6.1.2.4 Socioeconomic Drought

This condition occurs when the demand for water exceeds the supply, i.e., the quantity of drinking water and food is reduced and threatened by the alteration in meteorological and hydrological conditions. Other contributing factors may be growing population and unnecessary demands of such goods that create stress on little/less water availability. Socioeconomic drought condition takes a very long period to get into full paraphernalia and along to recover as well. Examples of this kind of drought include too much irrigation or when low river flow forces hydroelectric power plant operators to reduce energy production (Wolchover 2018). This chapter covers the functions of drought stress in food crops, responses, and tolerance to abiotic stresses on crop yield.

6.2   Food Crops and Their Hydrophilic Requirements

Pakistan is blessed with four different seasons; every region of the country has its variety of crops that flourish in the native environment to fulfill their needs. Specific climatic factors also define the water requirements of an individual crop. These are defined in Table 6.1.

Water need of a plant may also depend on the growth stage, type of plant, environmental factors, and the total growing period. Food crops in Pakistan are divided into two major categories, i.e., Kharif and Rabi crops. Figure 6.1 determines the water requirements of Kharif crops (growth period = July to Oct also known as summer crops) at its highest stage of growth. Type of plant is also a significant factor to understand the fluctuation in the water requirements of a plant. A fully grown maize crop with large leaves would require more water than onions and radishes at their peak stage. Figure 6.2 constitutes Rabi crops (grown period = Oct to March also known as winter crops) along with their irrigation and average water depth requirements.

6.3   Crop Responses

Due to various biotic and abiotic stresses, food productivity is being affected and is decreasing every passing day. Plant growth and development is severely impaired due to environmental abiotic stresses, such as high salinity, cold heavy metals, high temperature, and drought. Drought being the most significant environmental stress not only severely affects the plant growth and development but also affects the plant production and the performance of crop plant. Minimization of these loses is a major concerning part because of the ensurity of food security under climate change (Shao et al. 2009). Drought is experienced either when there is a shortage of water and water supply to roots becomes difficult or when the transpiration rate increases, and as a result, moisture is not carried by the roots of the plants to the small pores. We have also seen in recent years that the water resources for successful crop production are decreasing, and scientists have also suggested, in many regions of the world, that crop losses due to increasing water shortage will further worsen its impact with time (Van Loon et al. 2016). Drought stress affects cellular membrane integrity, osmotic adjustment, water relations, pigment content, and photosynthetic

Table 6.1 Water need and climatic factors

	Crop water need	
Climatic factor	High	Low
Sunshine	Sunny (no clouds)	Cloudy (no sun)
Temperature	Hot	Cool
Humidity	Low (dry)	High (humid)
Windspeed	Windy	Little wind

Fig. 6.1 Summer crops and their hydrophilic requirements

activity as well as the growth and yield of the plant (Benjamin and Nielsen 2006; Praba et al. 2009). Climatic, edaphic, and agronomic factors affect the drought stress, and factors that determine the dependence of stress degree of plants to drought include plant species, their developmental stages, and some other different accompanying stress factors. Deficiency of water leads to adaptive changes in the plant growth and physiobiochemical processes so plants can adjust and survive in the new environment. These changes include modification in plant structure, growth rate, tissue osmotic potential, and antioxidant defenses of the plant (Duan et al. 2007). It is now imperative to clear the reaction and adoption of crops to the water-deficient environment and to take measures to improve their ability to resist drought and water deficiency and ensure high crop yield in these new stresses (Asner et al. 2016).

For example, in comparison with other crops, potato is considered a sensitive plant to a water stress (Salter and Goode 1967) with its yields very much affected by drought in most environments in which crop is grown up. The effect of water stress on the plant very much depends upon the timing of the stress (Shi et al. 2017). There are some water stresses that last for a short time which is induced due to the high evaporative demand, particularly in hot sunny conditions when evaporative demand exceeds the capacity of roots to supply water to shoots, and it may have an

Average Water depth	Irrigation requirements
Wheat	
37.5 cm	3-4 times Watering
Gram	
30 cm	Irrigated when leaves get dry
Barley	
30 cm	2 times Watering
Potatoes	
60-90 cm	usually irrigated
Mustard	
45 cm	Irrigated at intervals of 15 days
Sugercane	
90 cm	5 or 6 watering of 10 cm or more

Fig. 6.2 Winter crops and their hydrophilic requirements

acute temporary effect on the growth of the plant even in well-watered crops. The prolonged drought may induce a chronic impact on plant growth and lead to premature agedness unlike the acute implications caused by hot sunny weather only. The type of water stress experienced by the crop may also determine the different physiological and morphological characters of the crop. MacKerron and Jefferies (1985) also proposed that the total yield of the potato crop is the product of four processes.

Drought affects the height of the plant by the crop canopy, and then height affects the proportion of dry matter. The portioning of that dry matter in the tuber and into the tuber is quantifiable like another process, which is indirectly linked to the stress of drought on the crop growth and yield (Jefferies 1995).

6.3.1   Morphological Responses

Plants are responding to a wide variety due to environmental stresses on them; these range from a change in gene expression and cellular metabolism to a change of growth in plant and its production (Shah and Steinberg 2017).

Morphological characteristics of the plant, i.e., a number of branches, their size, and spatial distribution, primarily depend on the environmental conditions in which they are planted. Species of plant and its soil resources also had a significant role in it. Properly branched and the fully developed root system is also providing good stability to the whole plant.

6.3.1.1 Seedling Origination and Formation

In this chapter, we will combine the different effects and the crop response and their adaption to the condition of drought and their final effect on a crop, with implication for plant breeding. Plant breeding is a risky course of action, so a relation must be established between the biological process and its final contribution to "value" at the crop level. Drought has multidimensional stress on the plant, whereas the investigation of unidimensional/singular effects of drought on the plant can also be explored by scientific methods; due to insufficient information, the integrated thesis may look practical and too simple and other times too speculative. A very brief discussion on the response of the plant/crop to stress caused by drought is later discussed, leading to the question of adaptation. The most common problem in a drying seedbed in a drought-prone area is mortality (Johnson and Asay 1993). During the emergence of young plant and its establishment, high soil temperature causes many growth-related problems (Peacock et al. 1990). The embryo within the dry seed is definitely dormant, and its tolerance to extreme dryness also attracts and holds water in it. Upon germination and emergence of the young plant, the seedling loses its tolerance. The tolerance to severe dryness was assessed of the germinated seedling, in wheat, by the recovery of germination upon rehydration (Blum et al. 1980). In wheat, when the coleoptile was fully grown, 6 cm in length, a relatively sharp reduction in germination recovery occurred that was from 67.2% to 32.5%, while upon the seedling development from the onset of germination, desiccation tolerance gradually declined (Marengo et al. 2017). There is some information seriously missing upon the loss of desiccation tolerance upon germination, while some information is only available on the acquisition of embryo desiccation tolerance in the developing seed. In the case of wheat, crop management and the genetic improvement of its seed are not easy because of the function of seminal roots in its life. Drought also affects the characters of the development of plant which affect seed establishment that is co-related to the development of grown roots, seminal roots, and leaves in grasses (Johnson et al. 1996). Under drought stress, traits such as seed size may influence the establishment of seed (Mian 1994). To understand the interactions such as the process of establishment, germination, and emergence with the status of seed and plant is still not well known. Biochemical and physiological factors are more important here as compared to developmental factors (Blum 1996).

6.3.1.2 Growth

A complete understanding of the process is required which involves plant growth and its development, for the confirmation of food supply with population size. Under different environmental conditions, crop growth and sustainability depend on

the regulations of plant reproductive and vegetative growth patterns. Two principal organs that make the plant growth functional are the root system and the shoot. Both act as the source and sink of the plant body. The primary factor that temporarily or permanently disturbs the plant development and its growth is the deficiency of water. Water is the main component of photosynthesis and other functions of plant, and its lack hampers more than any other environmental aspect. The primary effect of this deficiency contributes more to poor stand formation and impaired seed germination (Harris et al. 2002).

The most drought-sensitive physiological processes that are affected by a reduction in turgor pressure are cell growth. In the result of the subsequent immense expansion of the young cells and daughter-cell production by meristematic cell, plants usually grow. Due to the interruption of water flow from the xylem to the surrounding elongating cells, the phenomena of cell elongation of higher plants are significantly affected (Nonami 1998).

Water scarcity also causes genetic issues in plants such as impaired mitosis, cell expansions, and elongations that also result in the reduction of growth of plants (Hussain et al. 2008). Water deficits reduce the number of leaves per plant and individual leaf size and leaf longevity by decreasing the soil's water potential. Leaf area expansion depends on leaf turgor, temperature, and assimilating supply for growth. Drought supressed photosynthesis process which results in reduced leaf area (Rucker et al. 1995).

Drought also causes a reduction in the size of individual leaf and the number of leaves per plant. The decrease in the photosynthesis process leads to the suppression of leaf growth because leaf area growth depends on the temperature, turgor pressure, and integrating supply for growth. The decline in soil's water potential also had a significant effect on the leaf longevity and reduction in production of fresh and dry biomass (Zhao et al. 2006). Khan et al. (2001) led a study called "control (six irrigations)" that is comprised of six treatments, i.e. one, two, three, four, five, and six irrigation in maize. The results of this study show that leaf area, plant height, and stem diameter are noticeably decreased due to increase in water stress. One of the main factors that cause a reduction in plant height is a disturbance of decline which plays an essential role in cell enlargement (Manivannan et al. 2007).

In the case of maize, drought has adverse impacts on a number of leaves/plants, leaf area, cob length, plant height, and shoot fresh and dry weight. Kamara et al. (2003) also revealed that maize biomass is reduced at the grain-filling period by 34%, maturity by 21%, and silking by 37% due to water deficiency.

6.3.1.3 Yield

Water stress had a great impact on the yield-determining processes in plants. Yield integrated many complex processes. So, it is very difficult to interpret how plants accumulate, combine, and show the indefinite and ever-changing processes over the whole life cycle of crops. Grain yield is the result of association and expression of several plant growth components. The deficiency of water leads to a severe decline in yield traits of crop plants probably by disrupting leaf gas exchange properties which is not only limited to the size of the source and sink tissues but also to the

phloem loading, assimilate translocation, and dry matter portioning which are also impaired (Farooq et al. 2009a, b). Drought stress inhibits the dry matter production mainly through its inhibitory effects on leaf expansion, leaf development, and consequently reduced light interception (Nam et al. 1998). Drought at flowering commonly results in barrenness. A significant cause of this, though not the only one, was a reduction in assimilate flux to the developing ear below some threshold level necessary to sustain optimal grain growth (Yadav et al. 2004). When maize plants were exposed to drought stress at teaseling stage, it led to substantial reduction in yield and yield components such a kernel rows/cob, kernel number/row, 100 kernel weight, kernels/cob, grain yield/plant, biological yield/plant, and harvest index (Anjum et al. 2011a). Drought-related reduction in yield and yield components of plants could be ascribed to stomatal closure in response to low soil water content, which decreased the intake of CO_2, and as a result, photosynthesis decreased (Chaves 1991; Cornic 2000; Flexas et al. 2004a, b). In summary, prevailing drought reduces plant growth and development, leading to hampered flower production and grain filling and thus smaller and fewer grains. A reduction in grain filling occurs due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes (Anjum et al. 2011b).

6.3.2 Physiological Response

6.3.2.1 Root Signaling

In plants, the primary source of water and minerals from root to shoot is xylem. The drive of water through the plant is smoothed by xylem which is composed of cell wall substantial with specific possessions. Under drought conditions, plant growth and transpiration reduced from root to shoot as a result of alterations in sap composition, which is important in plant growth and development (Alvarez et al. 2008). A widespread root structure is beneficial to upkeep plant growing at the early crop development stage and uptake water from low soil layers that are then merely lost by vaporization. The effect of drought on crop root signaling has many divisive pieces of evidence. A better root development due to drought was observed in *Catharanthus roseus* (Anjum et al. 2011b). Under drought, the soil becomes arid; xylem causes transportation of root-sourced signals to leaves, which reduces water loss at various stages and ultimately leaf growth. There are various chemicals present in xylem sap. Cytokinin (CK), pH, abscisic acid (ABA), malate, a precursor of ethylene, and other anonymous issues have all been concerned in root to shoot motioning in water stress (Schachtman and Goodger 2008).

Abscisic acid has usually been observed as a hormone with diverse controlling properties in growth and development. Under drought condition in all crops, the level of ABA rises in both roots and leaves and causes physical response such as stomatal closure due to alterations in genes. Under normal circumstances, a low amount of ABA improves root development. Abscisic acid has been commonly considered a growth that is limiting stress hormone in all crops (Brunner et al. 2015). Abscisic acid encourages stomatal shutting by triggering Ca^{2+}, K^+, and anion

channels in guard cells (Becker et al. 2003). Due to high stress on roots, ultimate stress on leaves also occurs. A way of protecting plants against a root or shoot dehydration, water loss which sometimes causes cell death, and runaway xylem cavitation is leaf closure or initial response in crops. The general mechanism of drought on leaves is multifaceted since at a given time many other factors are involved such as CO_2 and light intensity (Chaves et al. 2003). As a result of low water obtainability of roots in field-grown maize crop, there is a decrease in leaf extension lead and stomatal closure under drought circumstances (Bahrun et al. 2002).

Cytokinins control crop development via a composite system of CK signaling. Mutual signaling behaviour exist in the CK, and ABA metabolism and signals are underlying altered procedures in changeable plant adaptation to stressors (Nishiyama et al. 2011). Cytokinins are usually deliberated as opponents of ABA action on stomata. It is concluded that due to low water availability, CKs must decrease. The change in the ratio of ABA:CKs was observed as, 50% decrease in zeatin and zeatin riboside in both stems and shoots of grape plant under low water. In sunflower, reduction in cytokines and many clashes about other plants are detected (Davies et al. 2005).

6.3.2.2 Photosynthesis

Photosynthesis along with cell growth are the primary affected mechcanisims of plant under drought stress. The effect can be direct, e.g., due to flow limits through the stomata and mesophyll or the changes of photosynthetic metabolism, and can immensely disturb leaf photosynthetic mechanism and decrease CO_2, and secondary effect can raise, i.e., oxidative stress (Chaves et al. 2009). Across worldwide, it is observed that limitation of photosynthesis, crop yield, and growth is due to low water availability. Drought affects the diffusion of CO_2 by stomatal closure predominantly in C_3 plants, i.e., wheat, rice, maize, beans, potatoes, etc. (Flexas et al. 2004a, b).

Drought cause stomatal closure and change metabolism processes, but usually, stomatal closing is a primary response which reduces the rate of photosynthesis even at mild drought. When there is inhabitation in metabolism, it causes a reduction in RuBP concentration which causes CO_2 incorporation in the process of photosynthesis. Now it is clear that stomatal closure causes a decrease in photosynthesis metabolism due to drought than relative water content or leaf water potential. At early stages of drought, reduced ATP production is observed (Flexas and Medrano 2002). It is observed that damaged ATP and photophosphorylation were the main influences of restrictive photosynthesis in sunflower even in slight water scarcity. It is now fit to recognize that there is a drought-brought root-to-leaf signing, endorsed by low water and attainment of the vegetation through the transpiration creek, which persuades closure of stomata and decreases photosynthesis (Medrano et al. 2002). The decrease in photosynthesis may be from stomatal or nonstomatal factors. Maize is the third most important crop and sensitive to water availability across the world. It needs 500–800 mm of water throughout life series of 80–110 days. Water stress led to failure in photosynthesis, evapotranspiration rate, stomatal activity, water use

effectiveness, prompt water use efficacy, and intercellular CO_2 in contradiction to well-watered (Anjum et al. 2011b). The effect is on net CO_2 endorsement and entire series electron carriage as assessed by leaf chlorophyll fluorescence capacities. Due to stomatal closing, less CO_2 is subjected to plant and low photosynthesis. In food crops, lower net CO_2 lead toribulose-1,5-bisphosphate oxygenation upsurges and develops the critical basin for photosynthetic electrons (Cornic and Fresneau 2002).

6.3.2.3 Contents of Chlorophyll

The visible light absorption, the photochemical capabilities, chemical stability, and abundant supply of redox level are requirements of photosynthesis which are accomplished by chlorophyll (Mauzerall 1976). Under the drought stress condition, symptoms of oxidative stress may be the result of pigment photooxidation, and chlorophyll degradation is due to a decrease in chlorophyll content. Photosynthetic colorings are significant to florae mostly for reaping light and manufacture of dipping powers. Both chlorophylls a and b are disposed to soil dryness (Farooq et al. 2009a, b). Drought has a direct effect on the plant such as dispersion limitation of gases through stomatal closure and changes in mesophyll and metabolism of photosynthesis and has indirect effects in multiple forms such as oxidative stress which occur from the superimposition of various stress (Chaves et al. 2009).

The primary cause of inactivation of photosynthesis under drought is loss of chlorophyll. Loss of chloroplast skins, extreme bulge, misrepresentation of the lamellae vesiculation (nodules on the surface), and the arrival of lipid descents are due to a shortfall of chlorophyll under water scarcity and arid soil conditions. Due to low water availability in drought, primary production can deficit due to a small number of chlorophyll pigments and the low photosynthetic ability of crop. From a physical viewpoint, leaves' chlorophyll concentration is a limitation of critical attention. Due to water scarcity, mostly effects occur on mesophyll cells but lesser amount from sheath cells as a response to chlorophyll lessening in crops (Anjum et al. 2011b).

Nikolaeva et al. (2010) have shown that three varieties of wheat crop under drought behave differently for chlorophyll content, and at initial period, crops resist drought and low water loss from leaves, but after 1 week due to little water obtainability, the content of leaf water reduced by 5.2–6.8%. Initially, chlorophyll content raised in the first 2 periods, but in the next period, chlorophyll content decreased by 13–15%. This reduction was not attended by variations in chlorophyll *a/b* relation.

6.3.3 Biochemical Responses

Biochemical responses of certain food crops combine biological catalyst to increase the chemical reactions proceeding in a specific organic species. These responses define the exact response of a molecule while it is going through conditions of drought.

6.3.3.1 Reactive Oxygen Species

In a eukaryotic cell, reactive oxygen species (ROS) is the essential biochemical reaction that proceeds in the presence of any stress. It is the early stage defense by a crop suffering from the water-stressed environment. As soon as drought occurs, the ROS levels dramatically fluctuate which may result in the oxidative destruction of proteins, lipids, and DNA (Apel and Hirt 2004). $O_2^{\bullet-}$, H_2O_2, and $OH^{\bullet}$ ions might attack the cell membrane and increase fat peroxidation (Mittler 2002).

Another very important drought-induced ROS is malondialdehyde (MDA) which is the main marker of oxidative damage. This might decrease the membrane stability as the major constituents of the cell membrane are lipids and proteins (Møller et al. 2007). Malondialdehyde defines the range of lipid peroxidation which further induces a radical reaction in the tissues (Anjum 2011b).

In pea plants, the range of lipid peroxidation increases 2 to 4 times under drought conditions which were found to be correlated with the amount of protein peroxidation in the cell (Moran et al. 1994).

6.3.3.2 Antioxidant Enzymes

All the plants have a natural defensive clean up system which helps them to withstand possible injury caused by the elevated active oxygen presence (Horváth et al. 2007). To minimize the action caused by oxidation, plants have come up with a mechanism requiring the use of antioxidants, for example (Caverzan et al. 2016):

1. ROS-scavenging enzymes, i.e., catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD), superoxide dismutase (SOD), etc.
2. Low-molecular-mass antioxidants such as glutathione (GSH), carotenoids, and ascorbate (AsA) (Apel and Hirt 2004).

Under drought condition, SOD and POX decrease in the plant. For wheat, the pretreatment of the seeds enhances drought tolerance levels (He et al. 2009). This is achieved by specific aluminum exposer which reduces ROS accumulation (Xu et al. 2011). Maize plant presented a different reaction to seed pretreatment, i.e., increased salt tolerance which directly relates to the amount of water uptake (Gondim et al. 2010). For rice plants, H_2O_2 is also associated with inducing cadmium, salinity, and abscisic acid stresses (Kao 2014).

6.3.4   Role of Plant Hormones in Drought

The yield and production of crops are reduced due to water scarcity and drought condition. The major phytohormones, which regulate the processes in plant adaptation under drought conditions, are ABA, gibberellic acid (GA), ethylene, auxin, and CK (Wilkinson 2012). In the situation of drought stress, ABA is produced in roots and transmitted to leaves to start the adaptation process in the plant to tackle the drought situation through stomata closure and discrete the growth (Wilkinson and Davies 2010). Cytokinin is known to delay premature leaf senescence and death of

plant under drought stress. This adaptive trait of the plant is very functional for enhancing crop production in drought (Peleg 2011). Gibberellic acid is referred to as a positive regulator (Wang 2008). Ethylene is referred to as a negative regulator because of boost senescence of leaf and stops the growth of roots and enhances the shoot development and growth (Munné et al. 2004).

Drought causes a series of negative impacts on growth, fiber quality, and yield of the cotton crop (Feng and Stewart 2003). Cotton is among the deadliest drought-sensitive crop; it can lead to a devastating reduction in yield and quality. Drought stress affects the growth and physiology of cotton plant (Iqbal 2013). In cotton crop, biomolecules and growth regulators like brassinosteroids and polyamine have become a recognized process for an increase in crop yield in a situation of drought (Ahmed 2017).

By modifying the plant genetic and molecular makeup for enhancing the plant's tolerance via manipulation and modification of polyamine levels can be acheived by the inclusion of brassinosteroids in signal pathway under abiotic stress such as drought. The procedure is useful in Bulgaria and Egypt to increase the tolerance level of plants (Todorova 2016). Putrescine at 2 ppm and 24-epibrassinolide at 10G[7] M applications generally increase the tolerance of Egyptian cotton and recorded the highest value of yield during experimentation (Ahmed 2017).

By using plant growth-promoting rhizobacteria (PGPR), drought tolerance is increased. Rhizobacteria are advancing by plant growth, and these microorganisms colonize the rhizosphere of plants increasing the tolerance of plant by producing certain hormones like phytohormones, exopolysaccharides, 1-aminocyclopropane, and 1-carboxylate (ACC). These hormones lead to induce accumulation of osmolytes and decrease the regulation of stress response-related genes and altered the morphology of root to tackle the drought stress. (Vurukonda 2016).

The senescence-associated gene OSAP which is identified in rice (*Oryza sativa*) is involved in encoding certain protein. This protein engaged in antiapoptotic activities which present in yeast to regulate the multiple stresses. In abiotic stress such as drought, plant is overexpressing OSAP about the balance of the hormones such as GA, jasmonic acid (JA), phytohormones, ABA, and zeatin (Ubaidillah et al. 2016).

6.4 Possible Mitigation

The decline in the income of farmers as a result of less production of crops and its yield basically attributed to drought and heat. According to an observation, the maize yield reduced up to 40% and wheat up to 21% as a result of a 40% reduction in water quantity (Daryanto et al. 2016). According to the report of the Intergovernmental Panel on Climate Change (IPCC), the atmospheric and oceanic temperature has become warm, and the number of greenhouse gases has sharply increased (IPCC 2014). The big challenge to food security and livelihood security is due to climate change. The supportive activities for agricultural adaptation also intensified food security. The adjustment in the field of agriculture must be considered at policy and management level in a country or worldwide (Lobell 2008). The

crop management practice application and implementation have significantly reduced the damaging effects of heat stresses and drought and basically include management of soil and culturing practices, the extent of irrigation, residues of crops and mulching, and useful crop selection. Irrigation is the primary source of drought tolerance and avoidance process. The significant advantages of irrigation are to intensify the crop production and the stabilization of the income. Besides it, the irrigation significantly depends upon the various social, economic, and environmental factors (website). The pressure on water supplies is basically from other users than agriculture, and to save water and to increase agricultural production have gained significant importance for countries as more crop per drop (Luquet et al. 2005). The essential adaptive measure taken into account to mitigate the less production of crop yield (due to drought) includes the creation and use of more drought-resistant genotypes (Salekdeh 2009). The primary mitigation and adaptation measures by plants for drought stress are as follows.

6.4.1　Breeding Progress for Limited Water Environments

For water-restricted environment, plant breeding is always a significant problem in dryland and rainfed agriculture. The research and methodology in the sphere of plant breeding have been dispersed due to collaborative effort. In the present condition, due to the vibrant issue of global warming and the crisis of water supply, the issue has gained more significance (Asif and Kamran 2011). The plant breeding for drought resistance and tolerance is increasing for resistance against diseases in conceptual design and framework. Drought resistance can be achieved by attaining its components which are avoidance of drought, understanding of drought, and drought reduction or elimination (Farooq et al. 2017). The widely used and applied mechanism for drought resistance in crops and plants is to avoid dehydration, which is plant's ability to maintain its water balance. The dehydration tolerance is rare but essential in which the plant can function in a dehydrated state.

The yield enhancement due to plant breeding can be determined by assessing the experiments of historical cultivators for a variety of crops (Castleberry et al. 1984). The application of stress-tolerant crops has shown a high population density of plants, etc. The comparison of 36 successfully grown hybrids in the USA from 1934 to 1991 has depicted the increased improvement in tolerating the abiotic stresses such as heat, drought, too cold and too hot weather, low soil fertility, etc. (Duvick 1997).

It was observed that during drought condition, the genetic increase in yield was 124 kg/h/year in flowering and 91 kg/h/year in mild grain filling.

The drought-resistant crops have developed certain physiological traits which increases their yield during stress condition. Modern soybean species have high water potential than old ones (Boyer 1980). Modern maize species also have high possibility to access the soil water than the previous ones (Hammer 2009). Earlier studies of wheat in the UK suggested that modern cultivars have large stem storage for flowering (Shearman et al. 2005) which sustains grain filling under pressure.

The breeding germplasm of wheat yield is high in dehydration avoidance due to genetic variation (Blum 2018). In conclusion, the dryland and rainfed crops have been improved successfully for drought resistance. As a whole, the efforts in plant breeding cause genetic variation which in turn causes resistance in drought and heat.

6.4.2   Protection of the Cells against Osmotic and Oxidative Damages

Drought resistance in crop plants has to follow two main aspects, i.e., dehydration avoidance and dehydration tolerance. Dehydration avoidance takes into account the capacity of plant cells and tissue to avoid being dehydrated during water stresses. The ability to sustain function when the plant is dehydrated defines dehydration tolerance. Plant survival can go through either of both situations. The superior protection of plants in drought condition is to avoid osmosis and oxidative damage (Ostad-Ali et al. 2017).

6.4.2.1 Osmotic Adjustment

The phenomena of osmotic adjustment (OA) relate that it is a process of accumulation of solute in dividing cells in a case when the water supply or potential is less; so far it helps in the regulation of turgor (Chaves and Oliveira 2004). The growth of cells of the plant is purely dependent on the availability of water and helps in turgor maintenance. The growing parts of plants like stem and leaves exhibit less reduction during turgor measurement, but the enlargement of the cell is stopped during drought condition and is mainly due to OA (Meyer and Boyer 1972; Serraj and Sinclair 2002). Various plant phenomena like stomatal conductance, photosynthesis, and leaf growth have been maintained due to osmotic adjustment under drought conditions (Oosterhuis 1987; Chaves and Oliveira 2004). In drought conditions, the water supply is reduced, and there are so many changes like an increase of salt concentration, etc. (Sauter et al. 2001). During drought stress, the solutes that accumulate are inorganic cations, organic acids, carbohydrates, amino acids, etc. Previous researchers have explained that drought-resistant wheat varieties yield more than less resistive varieties and have a considerable extent of osmoregulation (Serraj and Sinclair 2002). The suitable solutes for plants like proline and glycine betaine help plants against the adverse impacts of drought not only by ROS detoxification but also by osmotic adjustment, conservation of membrane, and regulation of enzymes (Ashraf and Foolad 2007). Enzymes like betaine aldehyde dehydrogenase (BADH), pyrroline-5-carboxylate reductase (P5CR), and ornithine δ-aminotransferase (OAT) have been revealed to play main roles in osmotic adjustment. Overexpression of *Arabidopsis EDT1/HDG11* was exposed to rise DT of poplar and cotton over greater accrual of solutes such as proline and soluble sugars and also increases the yield of cotton in the field (Yu et al. 2016). There are some plants within which sugars are the most osmolytes that play a prominent role in OA, together with saccharose, trehalose, glucose, and ketohexose. Earlier studies have revealed that

overexpression of the *sucrose:fructan-6-fructosyltransferase* (*6-SFT)* gene from *Psathyrostachys huashanica* in tobacco and the trehalose-6-phosphate phosphatase gene *OsTPP1* in rice confers abiotic stress tolerance (He 2015; Ge et al. 2008).

6.4.2.2 Antioxidation

To repel the toxicity of active oxygen species, the plant cells should have a competent antioxidative defense system. The GSH prevents various cellular components and protein status of thiol against oxidative stress, and it represents an efficient defense system for enzymic and nonenzymic components (Pamplona and Costantini 2011). The antioxidants become unstable and reactive when they lose or accept electrons in the presence of reactive species. In these cases, the antioxidants show prooxidant impacts and can be dangerous, but Damiani et al. (2008) described that the antioxidant that gives less oxidant reactivity with a less capability to produce peroxidation is a good antioxidant. Plant tissues basically contain a variety of enzyme scavengers of ROS to regulate the level of ROS under significant stressed conditions (Mor et al. 2014). Both nonenzymatic and enzymatic reactions represent the process of formation of ROS in biosystems (Zorov 2014). Nonenzymatic antioxidants contain low-molecular-weight compounds, such as vitamins C and E, beta-carotene, uric acid, and GSH, a tripeptide that comprises a thiol (sulfhydryl) group (Blokhina and Fagerstedt 2010).

6.4.3 Managing Drought Stress by Supplemental Irrigation

Supplemental irrigation (SI) is defined as the addition of a small amount of water in rainfed crops in a situation of water scarcity, shortage of rainfall, and drought. Supplement irrigation has furnished the moisture to prove moisture for proper growth and yield. The concept of supplement irrigation has three aspects. Supplement irrigation can provide water and rain throughout the year, but it makes sure that crops get the minimum amount of water for growing crops during a situation of drought to get maximum yield. There are particular schedule, timing, and amount of SI during the year. Supplemental irrigation is dependent on precipitation, the major water resources for SI in surface water, but shallow groundwater and treated sewage effluent are also used to provide water to crops (Oweis 1997).

6.4.4 Molecular Mechanisms Regulating Plant's Response Toward Drought Stress

Under environmental stress, plants have developed subtle procedures to manage them. Due to exposure to drought stimuli, extracellular indicators seem creation of ROS in crops, ABA response, and spread over signal transduction forces. After receiving and broadcasting of the signals, a figure of stress-related genes is persuaded, important to stress alteration in plant cells. The typical growth pattern is recovered by functional protein mechanism which protects from stress, by

restoration of cellular homeostasis. As the osmotic pressure in the cytoplasm decrease, the defensive cellular task of cellular arrangements constituents by a buildup of friendly solutes such as amino acids, quaternary and other amines (e.g., glycine), sugar, and sugar alcohols (e.g., mannitol) (Gao et al. 2008). Research shows that a cluster of soluble organic mixtures are added and play a role as osmo-protectants through osmotic stress (Bartels and Sunkar 2005). Genes which work in abiotic stress reaction and acceptance can be recognized by genetic and molecular methods. While numerous genes had been recognized with the abundant possibility for abiotic stress engineering, many of them can shake rice plant form, when they are essentially overoccurred (Su and Wu 2004; Roy and Wu 2002; Gao et al. 2008). The manifestation of genes can be changed in transgenic plants in command to get an accepting phenotype. In some circumstances, alteration of gene method has been positive in growing agronomic enactment of florae in the field. Consequences of nine field tests over six harvesting periods, in wheat crop, exhibited that the HVA1 protein put substantial security from water tension in comparison to (LEA) proteins (De Leonardis et al. 2012). In the field of technology, a very low amount of seed plasm has been partitioned for famine acceptance. Uniting genetic factor from both wild and cultured kind of maize crop displays potential to get genotypes with advanced stages of patience (Manavalan et al. 2009).

6.5 Recovery After Stress Dictates Survival

After the drought stress, recovery of plant carbon balance depends upon the severity and duration of drought. Studies have shown that maximum recovery of photosynthesis cannot be achieved and is slow and incomplete. Recovery in photosynthesis of some plants can be raised by adding photosynthetic proteins and by rewatering (Sofo et al. 2004; Galle et al. 2007). Recovery after a severe drought is very slow. The limiting recovery of leaf-specific hydraulic conductance is the cause of down-regulation in plant recovery. Due to stomatal closure, the photosynthesis process also slows down (Bogeat et al. 2007; Galmés et al. 2007). In maize, electrical signals can regulate stomatal recovery quickly than hydraulic regulation. The study has shown that CO_2 is also a factor, limiting the recovery of photosynthesis. In summary, recovery of plant photosynthesis process is dependent upon multiple factors and upon specific plant species, and then there is a need to study other factors (Grams et al. 2007; Ennahli and Earl 2005).

6.6 Conclusion

With varying environmental conditions and abiotic stresses by each passing day, crop productivity is decreasing severely. The global crop supply and quality are deprived due to the problem of drought, and the phenomenon of climate change is causing the circumstances more severe. Drought can affect seedling origination, formation, the growth of plant roots and branches, and yield of the crop. The

response of the plant to water deficiency is determined by severity, timing, and duration. Under water stress, root signaling and closure of stomata cause a decline in the rate of photosynthesis process. The reduction in the tolerance level of the plant is also reduced due to alterations in pigments and chlorophyll content. The protective leaf guards are then quickly activated to defend photosynthesis, so that it cannot affect irreversibly. Following drought stress, a natural defense mechanism in plants become active by generating ROS and antioxidative enzymes, plant hormones, and stability of cell membrane which are vital for drought tolerance.

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Rice Production, Augmentation, Escalation, and Yield Under Water Stress

7

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Abstract

Rice (*Oryza Sativa*) is a grass and highly stipulated cereal crop. Water stress is an existing and future trauma to rice production. It severely manipulates plant growth and production that ultimately results in yield loss. Cell size, molecular activities, tissue formation, organ establishment, flower formation, reproduction mechanism, grain fabrication, and seed maturation are partially or fully interrupted. Flowering stage is more susceptible to water stress. Reproductive organs are structurally and functionally influenced. Fertilization failure or grain filling loss and immature seed formation could result. Yield loss happens less severely when water stress occurs during vegetative phases but is more severe during panicle growth. Water stress and its tolerance to rice crop are therefore considered the critical issue under study and research. Various institutes and scientists worldwide are trying to explore new ways and schemes to overcome this strain. New ways are being investigated by providing suitable alternative rice harvesting strategies than traditional ways of cropping. Most of the Asian countries are still habitually grown rice in abundance water as they are doing so from over the years. In different agro-ecosystems, water is going to scarce, but it is provided by the farmer by fetching through different sources. Because farmers are in fear of

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crop loss and yield loss in case water is unavailable to their routine cropping, they must be encouraged by introducing water efficient use and water stress-tolerant practices in rice cropping. Scientific exertions in this contemplate still in progress to achieve free of yield loss adopted policies and approaches. This assessment is a part of scientific advancement to examine and inspect rice crop effects under water stress.

7.1   Introduction

Annual production of rice is vital in human foundation food. It is worldwide a chief trade commodity and major source of about 20% dietary energy supply from rice (FAO 2006). A biotic variation has an adverse effect on plant growth, development, production, and yield. Rice crop from its semiaquatic origin and growth with a diversity of ecosystems is traditionally dependent on adequate water supply, so water stress is more vulnerable for this cereal than others (O'Toole 2004).

Under water stress, all physiological processes of rice plant are distressing. Though all growth and reproductive phases are influenced, flowering stage is more susceptible because it depresses grain formation (Boonjung and Fukai 1996). However, various study approaches show major defects in different stress conditions that appear in reproductive growth during meiosis, production of mother cells, and maturation of anther, fertilization, seed establishment, and grain yield.

Research institutes are trying to sort out rice traits linked with tolerance toward different stress conditions by developing DNA-based techniques, to get precise and rapid reproduction varieties. In this stair to verdict tolerance, different concepts, theories, and practical efforts have been conceived. Two ways to illuminate are suggested as (a) activating stress receptive genes to alter biochemical levels and (b) alteration strategies to existing soil and traditional cropping. These progressive steps will surely promote (a) achieving tolerance against single stress and (b) developing tolerance to numerous stresses. To treat water stress, flowering stage screening is more practical in breeding plants. Breeding approaches toward water stress tolerance are dependent of parent selection. From the last 80 years, these breeding activities are in progress to achieve the desired yield against different environmental stresses (Teekam Singh et al. 2015). Rice production with elevated yielding varieties with massive fertilizers, biocides, and rich irrigation is in practice (Hossain and Fischer 1995). In the future, rice with the same dietary preference (Rosegrant et al. 2001; Sombilla et al. 2002) must achieve yield stability in the presence of inevitable abiotic challenges.

"More crop per drop" (Molden 1997) is a decisive objective of all these research-based study efforts. This appraisal is also an effort to consider the severity of water deficit and its effects on rice crop. Water stress influences rice plant physiology, grain formation, and seed development with resultant low production and yield loss. A slight stance is added to future management and alterations to water stress tolerance achievement in rice production.

Table 7.1 Nutritional composition of rice on average in different varieties[a]

Nutrients	Approximate gram %
Moisture	10.8
Protein	9.8
Fat	1.7
Ash	0.6
Carbohydrates	73.0
Dietary fibers	2.6
Amylose	26.6
Energy	349
Vitamins	0.39 mg/100
Mineral and trace elements	22.81 mg/100 g

[a]Different varieties: DRRH-3, Jaya, Lalat, NDR 97, PR 113, Salivahana, Sayasree, Savithri, TellaHamsa, Triguna, Varalu

7.1.1   Nutritional Composition of Rice

Rice is the second major source of human diet. Its energy content is high with protein, fat, carbohydrate, calcium, iron, vitamins, minerals, and fibers (Prasad et al. 2017; Table 7.1). Nutritional value of rice depends on various factors like grain type, soil fertility, fertilizer practices, and environmental conditions (Oko et al. 2012). Rice varieties are continuously derived with existing traits and tolerance of drought and salinity (GRiSP 2013). In all genotype of rice grain, high percentage (about 80%) of carbohydrates is present. It comprises of glucose, starch, sucrose, and dextrin. The percentage of content of various nutritional substances varies in different varieties. It is possible through genetic engineering to get the desired variety of rice with required nutrient values (Yousaf 1992). A variety could have the highest crude proteins, while the other could have the highest fat content, etc. The least and highest energy value is analyzed to be ranging from 262.94 to 398.82 J/kg. Moisture content also varies in different varieties. Its least value is analyzed as 5.0%, while its very high value is found as 9.6%. The choice of rice varieties to the farmers and consumers is principally dependent on their nutritious value (Oko et al. 2012).

7.1.1.1 Rice Protein

The protein substance assortment is 7.4% to 12.49%. Besides the genetic variations, agroclimatic factors and irrigation also control protein content of rice grains (Prasad et al. 2017). Rice protein is quality wise very good in comparison with other cereal crops (Juliano 1993). Protein quality is dependent on amino acid composition and digestibility (Frei and Becker 2003). Rice protein with excellent biological value, a balance of amino acids, with higher concentration of lysine, is highly digestible (WHO 1998). Branched amino acids like isoleucine, leucine, and valine are present (Shobana et al. 2011). Rice amino acid is elevated glutamic and aspartic acid (FAO 2006).

7.1.1.2 Rice Lipids

In all rice varieties, the total fat substance ranged from 1.45% to 2.03% (Prasad et al. 2017). The outer layer of the grain is its total oil content. The bran fraction and aleurone layer have chief lipid bodies. Rice lipids are highly unsaturated fatty acids, so considered blood cholesterol-lowering effects. Among this oleic acid is a mono-unsaturated acid, while linoleic acid is a polyunsaturated fatty acid (Probart et al. 1993).

7.1.1.3 Rice Mineral Fractions

Mainly K, Mg, Zn, Mn, Fe, Cu, Na, and Al represent the mineral content of rice grain, while Mo, Ni, Co, Cr, Li, and Pb are the trace elements. In different varieties of seed, these mineral contents greatly vary in their concentration. To pile-up, these mineral substances in a grain variety greatly depend upon its genetic variability, soil micronutrients, and soil conditions. Some varieties possess the highest content of a substance, while the other may just have its least amount (Prasad et al. 2017; Table 7.2).

7.1.1.4 Rice Dietary Fibers

Total dietary fibers in rice are classified as insoluble dietary fibers and soluble dietary fibers. These also vary in their gram percentage in different varieties of rice. Taking an average of different varieties, total dietary fiber is about 3.05 gram, insoluble dietary fiber is 2.95 gram, and soluble dietary fiber is 0.97 gram (Prasad et al. 2017).

Table 7.2 Mineral and trace element content in rice on average in different varieties

Mineral	mg/100 g
P	174
K	129
Mg	52.7
Ca	5.02
Zn	1.6
Na	0.78
Mn	0.80
Fe	0.58
Cu	0.20
Al	0.31
Mo	0.0829
Ni	0.0096
Co	0.0044
Cr	0.0016
Cd	0.0005
Pb	0.0012

7.1.2 Irrigation and Water Stress

Water is essential for rice production. Both soil and seed are active in rice growth in specific wetness. Rice harvesting is dependent on irrigation or rainfed wet soils. Rice is traditionally grown by seed raised in the seedbed, direct wet seeding, or direct dry seeding. Once the crop is established, the field is then kept in continuous pond water state. Rice crop by nature for its growth and yield depends on the balance of water availability and its outflows (Smith and Hornbuckle 2013). Water requirement for land preparation ranges from 100–150 mm (Bouman 2007) to 940 mm (Tabbal et al. 2002). This is due to the soaking and transplanting time differences ranging from a few days to 2 months and water management control in fields (Smith and Hornbuckle 2013). Soil type is a key factor in water management control. In heavy clay soils, 1–5 mm per day and 25–30 mm per day in sandy soils, percolation, and seepage are estimated (Bouman and Tuong 2001). Other water losses from the field (Bouman 2007) involve transpiration about 70% and evaporation about 30% of total evapotranspiration (Bouman et al. 2005), depending on the dryness or wetness of climatic conditions (Smith et al. 2001).

Rice production area is going to increase and water tables are going to decrease. Water input rates from rainfall and irrigation, soil texture for water retention, and shallow and deep groundwater for capillary rise must balance with water losses and outflows. Alteration of water flows to rice field results in stress. If climatic conditions, soil type variation and ground water kept aside, the adaptation can be acheived by choosing selective crop varities and water managment practices.

7.1.3 Augmentation Effect to Water Stress

The growth cycle of the rice crop is mainly divided into three phases: vegetation, reproductive, and ripening or grain filling phase (Singh et al. 2015). All these phases are affected by water stress, but it is more vulnerable at flowering that discourages grain formation (Boonjung and Fukai 1996). Reduced spikelet fertility due to the drought during meiosis in spore mother cells, resulting in premature abortion of seeds. It also inhibits the formation of reproductive organs, i.e., ovary (Saini et al. 1983) and pollen (Saini 1997), is followed by functional failure or seed premature abortion (Saini and Westage 2000). Pollen survival ability and fertility loss under water stress are reported because of diverging anther maturity in a flower cluster (Jin et al. 2013). Water stress causes inhibition in different progression steps as the spontaneous opening of anther, pollen peeling, pollen emergence, and fertilization (Satake and Yoshida 1978; Ekanayake et al. 1990).

7.1.4   Escalation Effect to Water Stress

Rice dry matter fabrication is low during and in subsequent periods of water stress. It is sternly experienced during grain filling phase when it results in early maturity. Eventually, individual grain mass reduced to 20% and filled grain declined to 40%. Low dry matter production is subjective by growth phase's combat due to water unavailability. The growth rate is influenced by soil water accessibility (Boonjung and Fukai 1996).

7.1.4.1 Nutritional Manipulation

Water stress affects starch synthesis genes; thus, abnormal starch accumulation and distribution are examined (Jin et al. 2013). Carbohydrate availability influences pollen maturity, and its deficiency can cause pollen grain abnormality (Saini et al. 1984; Saini and Lalonde 1998; Joppa et al. 1996; Devries and Le 1970; Lalonde et al. 1997). With soil moisture deficit, brown rice protein substance is raised, and immature grain percentage is lowered (Renmin and Yuanshu 1989). Elevated protein can increase the dietary value of milled rice, but it can negatively link with taste. Protein content also negatively relates to amylose content, because amylose content decreases under water stress (Ishima et al. 1974).

7.1.4.2 Rice Plant Physiology

Water is a solvent and is the main element for translocation of minerals and metabolites. It works as a reagent in plant tissue for chemical reactions. It is crucial for turgor pressure and cell size (Carlos et al. 2008). Water stress affects photosynthesis and transpiration influencing plant growth and activities; thus, grain filling poorly occurs (Samonte et al. 2001).

7.1.4.3 Metabolism Persuaded

Water stress causes reprogramming of abscisic acid catabolism and gibberellin acid signaling (Jin et al. 2013). Molecular level studies show chromosomal abnormalities in moderate intensity water stress. During meiosis, certain defects appear as prophase unpaired chromosomes; in metaphase and anaphase, chromosome segregation; and in telophase, micronuclei formation. With the persistence of these defects, 20–30% pollen grains appear nonviable (Namuco and Otoole 1986). The specialized nutritive cell layer within anther is tapetum; microspores separated from it cause disruption in nutrition and signaling (Jung et al. 2005; Li et al. 2006; Shi et al. 2011; Hu et al. 2011; Zhu et al. 2013). Starch synthesis and accumulation disruption and pollen growth abnormality are connected to the reduced activity of invertase. Alterations in anther carbohydrate metabolism are due to water deficiency at meiotic stage (Dorion et al. 1996; Sheoran and Saini 1996; Koojul et al. 2005, Zhang et al. 2010).

7.1.4.4 Grain Quality

Grain quality is directed genetically as well as environmentally (Krishnan and Rao 2005). Grain filling is critical for grain quality and is subjective to water status

(Dingkuhn and Gal 1996). In milled rice, with soil moisture deficit, protein content is raised to relate to some extent with grain quality attributes like grain size, look, and viscosity (Ishima et al. 1974). Extra centered whiteness of grain that affects cooking traits is also observed in Basmati rice under water stress (Pandey et al. 2014). Grain filling, grain weight, and ultimately grain yield are significantly reduced with normal nitrogen supply under water stress (Cai et al. 2006).

7.1.5   Yield Effect to Water Stress

Loss of yield of rice and other cereal crops is estimated in Asia due to less rain, El Nino events, and increase in temperature (Aggarwal et al. 2000; Fischer et al. 2002). In the rainfed systems, rice production is most severely affected as it has an estimated area of 13 million ha lowland and ten million ha upland in Asia (Pandey et al. 2007). Food insecurity and rural poverty will rise in tropical and subtropical areas (Bates et al. 2008). Yield loss is small when water stress is experienced at the vegetative phase. About 30% yield reduction is estimated at the flowering stage with a compact number of the spikelet in a panicle. Yield reduction is more severe when water stress is practiced at a panicle growth stage (Dorion et al. 1996; Sheoran and Saini 1996; Wang et al. 2011). The number of spikelets is reduced to 60% and flower functioning deferred and diminished are reasons to percentage loss of grain filling (Boonjung and Fukai 1996).

7.1.6   Breeding Approaches to Water Stress

The desired cultivar must be tolerant of known stress. Alternating stress is examined with controlled irrigation during selected phases of rice plant growth. The most severely water stress targeted phases flowering and grain filling, are selected for ranking cultivars. This natural selection is adaptive to stress resistance (Lafitte and Courtois 2002). Rain fed rice breeding, by direct selection, without depriving yield potential are also in the inspection. With defined breeding lines these varieties are working better over the years during mild and stern water deficits (Verulker et al. 2010). Stable genotypes with high yield in different stress levels at different places are recognized (Kumar et al. 2012).

7.1.7   Agronomic Prospects

Rice production systems with water productivity (Molden 1997), are in demand. Irrigation needs and water stress studies have evolved a number of policies, elucidations, and tactics to deal with these constraints. But these strategies and solutions are still not fully practiced because farmers are not precisely acknowledged to the severity of the water loss persistence. They are trying to provide required water if not one source they approach to others although with paying the cost. There is a dire

need to save water with less investment (Lampayan et al. 2004). Against habitual cropping approach with extensive water supply some future terminations and alterations are as follows.

7.1.7.1 Aerobic Rice System

Non-soaked and non-deluged rice grown under non-saturated soil state is a new water economy strategy. It saves 73% water at land preparation phase and 56% water in the growing phase (Castaneda et al. 2003). This system is based on biocides and nutrients provided to accommodate their unavailability in aerobic assert. It is water and labor securing scheme could be mechanized (Belder et al. 2004). Yield outcomes accounted by this system show a specific rise in upland rainfed varieties while a distinct fall in lowland varieties (Farooq et al. 2009).

7.1.7.2 Intermittent Irrigation Management

In general practice rice is grown under pond condition, that is, a nonflooding particularly dry soil with saturated or under low standing water irrigation (Won et al. 2005). It is by reducing the unwanted excessive runoff of flooding irrigation (Bouman and Tuong 2001). This is efficient water using strategy it's working capacity changes with soil type and seed type. It is also proficient for better yield, as it involves soil aeration, nutrient conscription, root magnification and intensification (Arif et al. 2013).

7.1.7.3 Soil Saturation Culture

This is also an efficient use of water by reducing unnecessary losses, by keeping the soil saturated and reducing surface elevation. It secures 34% water than conventional ways of rice cropping (Borrell et al. 1993). Experimentation revealed this scheme is decreasing water input without compromising yield (Bouman and Tuong 2001).

7.2   Conclusions

World's food and economy both transactions are equally sharing rice significance. Not only agricultural countries others as well depending on rice production and yield due to its vitality as a food component. Increasing needs and feeds raised dependency on existing abiotic sources. Water is essential for rice crop from its origin and nature. With increasing demands of huge population cultivated land area has been raised. But existing limited available water sources are insufficient and going to scarce in future in many regions.

Rice is an elementary component of food. Its nutritious value is high with carbohydrates, proteins, and minerals. Rice plant nourishing is reliant on its seed type, seed quality, soil type, soil quality, environmental aspects, and climatic circumstances. Water stress is a rigorous situation for rice plant growth, acceleration, and propagation. Water unavailability or limited supply dislocates its wholesome intake. It disturbs plant structure and function.

Water intake of rice is through rain water and irrigation. Soil moisture and field irrigation requirements are largely dependent on climatic conditions. Water discrepancy is influencing during different phases of plant growth especially flowering. During meiosis1 chromosomal disruptions, anther and pollen structural and functional abnormalities are observed. Afterward collapse of fertilization, grain establishment and seed maturation are also disturbed.

Water stress imbalanced rice plant's biochemical processes, physiology, and functioning. Grain filling defeat and seed immature abortion result yield loss. However, it is examined that more yield loss occurs when water deficit is experienced during the flowering phase in comparison with the vegetative phase. Rice is an essential component of food and will be in the future. Its production loss is not favored at any cost. Therefore, new ways, schemes, and technologies are continuously being introduced to overcome water stress. Breeding and agronomical approaches are in practice to gain water productivity. Customary ways of flood irrigation are not long lasting in the current scenario. Limited irrigation, Soil moisture consumption, and direct seeding are going to be common practices being water efficient policies. Selected breeding and more resistant, adaptive gene mechanisms are also introduced and experimentally examined in rice research institutes world over. To gain rice tolerance against water stress is decisive to achieve the desired quantity and quality production.

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Role of Mineral Nutrition in Improving Drought and Salinity Tolerance in Field Crops

8

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Abstract

Balanced nutrition is one of the key factors that contribute to optimum crop production under various environmental stresses including drought and salinity. Proper management of fertilizers leads to improved tolerance against these abiotic factors. In contrast, nutrient deficiency is a widespread problem, worsened by the non-availability of water or excessive salts in the soil. The impact of nutrient deficiencies includes reduced biomass accumulation, increased susceptibility to pathogens and diseases, and stunted plant growth directly linked to yield potential of most arable crops. Moreover, reduced tolerance to drought and salinity is also associated with low nutrient uptake and accumulation in crop plants. In this chapter, we highlighted the importance of mineral nutrients such as nitrogen, phosphorus, potassium, calcium, magnesium, sulphur, zinc, and boron to crop productivity under drought and salt stress conditions. In addition, interactive effects of mineral nutrients are also discussed and reported.

Keywords

Mineral elements · Nutrient deficiency · Drought · Salinity · Crop yield

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Abbreviations

5-ALA   aminolevulinic acid
AAO   ascorbic acid oxidase
ABA   abscisic acid
APX   ascorbate peroxidase
AQPs   aquaporins
B   boron
Ca   calcium
CAT   catalase
K   potassium
MDA   malondialdehyde
Mg   magnesium
N   nitrogen
Na   sodium
NaHS   sodium hydrosulfide
P   phosphorus
PAL   phenylalanine ammonia lyase
POX   peroxidase
ROS   reactive oxygen species
S   sulfur
SA   salicylic acid
SOD   superoxide dismutase
Tre   trehalose
Zn   zinc

8.1   Introduction

Plants being sessile face multiple adverse environmental conditions throughout their life known as abiotic stresses, more precisely defined as any environmental factor which exerts negative effect on optimum plant functions. The major abiotic stresses are drought, salinity, and low and high temperature which negatively influence the biomass production, economical yields, and ultimately survival of food crops up to 70% and hence are real threat to global food security. Drought stress affects various morphological and molecular cascades of plant at different growth stages. The general effects of drought stress take place at all growth stages irrespective of the plant species (Nawaz et al. 2012; Majeed et al. 2018). In addition, escalating soil salinity is the main cause of arable land degradation, 7% land area of the world is salt-affected, and worryingly, the extent of salinity of salt-affected soils and continuous spread is at alarming rate in densely populated countries (Vashev et al. 2010).

Plants adopt a wide range of resistance mechanisms to alleviate the adversities of abiotic stresses. The production of reactive oxygen species (ROS) under such environmental stress conditions results in activation of antioxidants such as catalase

(CAT), peroxidase (POX), ascorbate peroxidase (APX), glutathione reductase (GR), and superoxide dismutase (Wariach et al. 2011). Despite internal resistance of plants, balanced nutrient supply confers resistance against abiotic stress factors. Increasing evidence depict that reduced mineral nutritional status of plants has imposed deleterious impacts on plant resistance adaptations (Marschner 1995). It is evident that the reduced absorption of mineral nutrients to plants under abiotic stresses is because of disturbed activity of membrane transporters (Akram et al. 2009). Exogenous application of inorganic nutrients have proved an essential approach for improving stress tolerance in plants through cell expansion, osmotic adjustment, stomatal aperture, charge balance, protein synthesis, and homeostasis (Wasti et al. 2017) (Fig. 8.1).
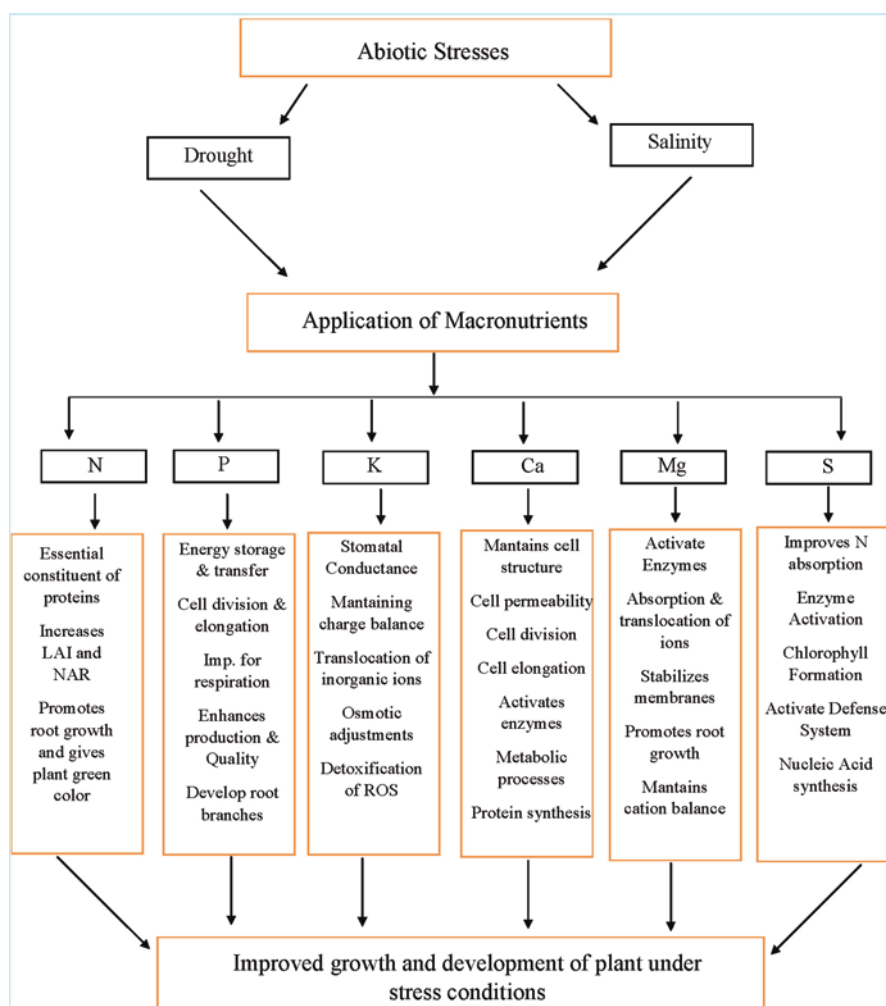
Fig. 8.1 Schematic overview of the role of mineral nutrition in improving drought and salinity tolerance in crop plants

8.2   Nitrogen (N)

Under water scarce conditions, absorption of N by the plants is essential for their growth because of its active role in structural and metabolic processes (Hassan et al. 2005). Its availability promotes the roots ability for more water and nutrients uptake. In N-deficient soils, the processes of cell division, cell expansion, and transpiration are severely affected through closing of stomata which contributes toward reduced growth (Vos and Biemond 1992; Waraich et al. 2011). Rufty et al. (1988) and Marschner (1995) suggested that enhanced N status of plants improves antioxidative defense system, carbon assimilation, accumulation of soluble sugars, and reduced photo-oxidation of chlorophyll pigments, resulting in higher cell growth and final leaf area. Improved photosynthetic ability of plants with higher light interception owing to expanded leaf surface area has also been supposed by N supply. The reduced activity of RuBisCO enzyme and chloroplast pigments during the process of photosynthesis is mainly due to limited N supply. Consequently, higher cell metabolic activities based on stromal and thylakoid proteins attributed to N addition. Under water-deficient conditions, morpho-physiological changes in plants like reduced leaf dry biomass, excised leaf weight loss, relative dry weight, relative water contents (RWC), and chlorophyll pigments could be alleviated with N fertilization. Drought-induced alterations in RNA contents accredited to increased activity of RNAse, leading toward reduced protein contents. In sunflower and wheat roots, nitrate reductase activity under drought stress conditions is severely affected by nitrate deficiency, but was contrasting in the roots of maize plants (Martin and Dasilva, 1972; Gimenez et al. 1992; Lawlor, 2002).

N maintains the metabolic function of plant at low tissue water potential, thereby playing an important role to alleviate drought stress in cereal crops. Application of N at vegetative stage mitigated the negative effects of drought stress in wheat (Abid et al. 2016). Low N supply (0.16 g/kg soil) reduced the grain filling duration and decreased final yield under water deficit conditions. However, high dose of N (0.24 g/kg soil) induced resistance against severe drought stress and increased grain yield, mainly due to enhanced antioxidative defense system and metabolic activities. Similarly, Shi et al. (2014) recorded a marked increase in nitrogen use efficiency (NUE), water use efficiency (WUE), as well as photosynthesis and biomass accumulation of wheat applied with N under drought stress conditions. Increased grain yield in barley, supplemented with N under drought stress conditions, provided further evidence that N supply directly influences quantum yield and activities of antioxidative enzymes to improve yield in crop plants (Movludi et al. 2014). Mannan et al. (2012) observed that increasing N levels improved growth and yield in rice under water deficit conditions. Recently, a comparative study involving application of ammonium (NH_4) and nitrate (NO_3) under limited water conditions showed that NH_4 was more effective than NO_3 to induce drought resistance in rice (Ding et al. 2015). Application of NH_4 significantly increased the root hydraulic conductivity, plasma intrinsic protein (PIP), expression of root aquaporins (AQPs), and protoplast water permeability suggesting positive association of NH_4 with AQPs.

Low winter rainfall and irrigation with brackish water are the primary causes of salinity in soils (Maggio and Cavallaro 2011). Salt stress reduces crop growth and production by adversely affecting metabolic activities and physiological process including assimilation, uptake, and translocation of NO_3 and increases sap osmolality from 305 to 530 mOs mol kg^{-1} in roots (Annunziata et al. 2017). Under salt-stress conditions, nitrate reductase enzyme of nitrate reduction pathway is severely affected by salinity. Increased activity of this enzyme in salt-tolerant plants than salt-sensitive means has vast capacity for inducing tolerance against salinity stress. The evidence from previous studies that glutamic acid, a primary product of N assimilation acts as a donor of amino group for many kinds of essential amino acids and actively involved in development of 5-aminolevulinic acid (5-ALA) and proline. Accumulation of proline in plants of salinity stress helps them to survive under such types of punitive conditions by adopting various biochemical adaptations. Its active role in osmotic adjustment as an osmolyte protects the DNA, membrane, and protein structures. Synthesis of ROS (O_2^{-}, H_2O_2, $^1O_2$) under salinity stress decreases with proline availability because of its scavenging ability for free radicals. Exogenous aminolevulinic acid (5-ALA) application alleviates the lethal effects of salt stress by dominating the anti-stress properties. Production of chlorophyll pigments, hemes, proteins stabilization, plant growth regulation, and cytokinins accumulation is attributed to 5-ALA synthesis (Kuznetsov and Shevyakova 1999; Watanabe et al. 2006). Application of N significantly improved the growth traits and root system because of increased activity of nitrate reductase. In barley plants, salinity stress has imposed serious impacts on reduced activity of nitrate reductase. Its reduced activity in salinity-induced plants caused accumulation of proline and 5-ALA. The decrease in protein contents owing to salinity stress caused significant decline in chlorophyll, 5-ALA, proline, and heme, based on N nutrition. Enhanced synthesis of these contents promotes the activity of peroxidases enzyme for inducing salt tolerance in ROS infected plants. It is well known that salinity has drastic effects on plants growth and development in terms of reduced respiration and the process of photosynthesis. Plants exposed to salinity stress provide protection to physiological processes during its adaptation through increased synthesis of proline, ALA, heme, and chlorophyll contents. Damage to thylakoid membrane results in inhibition of electron transport chain on account of reduced protein-pigment complexes in cytochromes, reaction centers, and antenna complexes of PS-I and PS-II, which consequently lowers the photosynthetic efficiency of plants. Hence, 5-ALA production in response to N nutrition is accountable to synthesis of heme and carotenoids, and mediating the plant growth through enhanced activities of antioxidants as catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), and ascorbate peroxidase (APX) (Parida et al. 2003; Averina and Yaronskaya 2012; Averina et al. 2014).

In pearl millet, application of N at the rate of 225 kg ha^{-1} increased grain production by 34% compared to 150 kg ha^{-1} N supply under salts stress conditions (Heidari and Jamshid 2010). Likewise, Abdelgadir et al. (2010) noted that increasing N level significantly increased the straw and grain yield in salt-stressed wheat plants. A marked effect of N fertigation (110 kg ha^{-1}) was also observed on NaCl-treated

wheat seedlings by Fallahi et al. (2012). Application of maize with high N dose of 300 kg ha^{-1} decreased the sensitivity of plants to salinity stress resulting in high yield (Azizian and Sepaskhah 2014). Esmaili et al. (2008) observed that N induced salinity tolerance in sorghum was associated with increased uptake of nutrients and suggested that application of N fertilizers after seedling emergence could minimize N leaching in plants. Similar results were reported by Rawal and Kuligod (2014) in maize exposed to salinity stress. They recorded maximum nutrient uptake and highest yield in plants supplemented with 200 kg ha^{-1}.

8.3   Phosphorus (P)

Phosphorus (P) is actively involved in plant growth and development. Its deficiency reduces the uptake and assimilation of nitrates by affecting the nitrate reductase enzyme activity (Pilbeam et al. 1993). A strong relationship between leaf turgor pressure and stomatal conductance has been reported by Radin (1984). Under drought conditions, the deficiency of P is prevalent through impaired root absorption rate and translocation toward shoot. The relative growth rate and photosynthetic ability of plants is negatively affected with P deficiency by reduced cell turgidity. Indeed, P actively involved in energy processes, enzyme regulation, transport of carbohydrates, and building of adenosine triphosphate (ATP), phospholipids, nucleic acids, and phosphorus-proteins. The decline in net photosynthesis is attributed to decreased regeneration capacity of ribulose 1,5 bisphosphate and stomatal conductance. In addition, plants in P-deficient soils are unable to consume photoassimilates for growth processes (Brooks 1986; Fredeen et al. 1989). The earlier effect of water scarcity in plants is the P deficiency. Its availability improves plant growth even under mild drought stress because of its active role in water status, photosynthesis, stomatal conductance, and cell membrane stability index. Phosphorus induces drought tolerance ability in plants through promoting symbiosis association of roots with mycorrhiza, leading toward enhanced water and nutrients uptake. The more absorption of water and nutrients, in turn, improves nitrate reductase activity for assimilation of nitrates. It is suggested that priming with P nutrient also improves the growth processes under drought stress (Ajouri et al. 2004; Waraich et al. 2011).

A drastic change in morpho-physiological mechanisms through distraction in intercellular osmotic gradient is the main cause of salinity stress. The disturbed functioning as decreased protein synthesis, photosynthesis, enzymatic activity, P, K$^+$, Ca^{2+} imbalances, water relations, membrane stability index is responsible for decreased stem width, length, diameter, pith, leaf thickness, xylem vessels, and length of leaf vascular bundles (Semida et al. 2014). Higher salinity tolerance with P supply has been suggested in previous reports. It is well documented that only moderate supply of P is essential for salinity tolerance in rice plants while its higher concentration leads toward toxicity in cells, which in turn decreases crop productivity (L'taief et al. 2012). Plants exposed to salt stress conditions causes a significant decline in chlorophyll pigments. The decrease in green pigments reduces

photosynthesis, which is a principal source of energy for physiological and bio-chemical processes. A considerable decline in chlorophyll contents might be caused by disoriented thylakoid membranes and degraded chlorophyll pigments. Indeed, the synthesis of chlorophyllase enzyme, a proteolytic enzyme, is the cause of rapid degradation of chlorophylls, attributed to reduced growth and assimilation rates (Rong-hua et al. 2006).

The production of osmo-protectants like total soluble sugars, proline, and free fatty acid contents are improved in plants of salinity stress, while its concentrations further increase in P-rich plants. These osmo-protectants are involved in salt-tolerant mechanism of osmotic adjustment for plants' survival under salt-induced conditions (An and Liang 2013).The biosynthesis of osmo-solutes also adopts strategy against salinity stress by acting as protectants for cellular and enzymes structures. Another reason for salinity tolerance by producing osmolytes is that behavior like N storage compounds. The salinity tolerance responses of osmolytes in terms of N fixation and plant development have been reported in *Proteus vulgaris*, *Phaseolus acutifo-lius*, and *Medicago sativa* (Taie et al. 2013). P's role in mitigating the salinity-induced adversities in *Pistacia vera* is because of its contribution to increased sugar contents. P's active role in osmotic adjustment is because of higher concentrations of produced osmolytes. Addition of P to salt-stressed plants provides support in the pathway of sugar synthesis and its structural formation. The decrease in mineral elements like K^+ under prevalent saline conditions could be related to selective absorption and gradient competition between Na^+ and K^+ resulted in increase in uptake of Na^+ in spite of K^+. This synergistic effect of P upon Ca^+, Mg^+, and K^+ may be responsible for osmotic adjustment in plants for improved tolerance to salinity stress (Shahriaripour et al. 2011; Bargaz et al. 2016).

8.4   Potassium (K)

Potassium (K) is considered the most effective element for inducing drought toler-ance in plants. It is involved in various physiological and biochemical mechanisms such as enzymes activation, photosynthesis, turgor pressure maintenance, and pho-tosynthates translocation (Mengel and Kirkby 2001). Increased photosynthesis and plant growth under drought stress conditions is attributable to improved K nutrient status of plants. The possible way for alleviating drought adversities in drought-stressed plants by K supply is the higher water use efficiency. Improved tolerance ability of K-rich plants is due to its crucial role in the maintenance of osmotic poten-tial and turgidity of the cells, which regulates the proper functioning of the stomates (Kant and Kafkafi, 2002). K protects the plants against harmful effects of drought by efficient utilization of soil moisture, maintaining high stroma pH, and reduced photo-oxidative damage to the chloroplast (Cakmak 1997). Plants suffering from abiotic stresses require more K to ameliorate their adverse effects. A high demand for K is relatively linked with its critical role in assimilation of CO_2. The decreased leaf water potential due to drought stress conditions causes stomatal closure, which eventually reduces CO_2 fixation. Among the harmful effects of environmental

stresses like drought stress is the formation of reactive oxygen species (ROS). Its increased production induces oxidative damage to the chloroplast particularly during the process of photosynthesis. The abnormalities in photosynthesis and carbohydrate metabolism are also associated with ROS synthesis. A more decrease in photosynthesis in K-deficient plans under drought stress conditions is due to decrease in K within the chloroplast and further synthesis of ROS. Therefore, to lessen the severity of drought stress, K could be the possible way to avoid the disorders of water relations, stomatal opening, cell oxidative damages, and finally photosynthesis (Mengel and Kirkby 2001; Jiang and Zhang 2002; Waraich et al. 2011).

Exogenous K supply enhances the biomass accumulation and influences grain weight and yield by increasing the translocation of dry matter into grain. Moreover, K plays a critical role in drought tolerance by increasing water use efficiency, maintaining water balance, regulating stomatal conductance, and improving carbohydrate content (Hussain et al. 2016). It decreases the risk of cavitation under low water availability, thus enabling the plants to tolerate drought stress (Trifilo et al. 2008). Application of KCl and K_2SO_4 was observed to increase drought tolerance in rice by increasing proline content and activities of antioxidative enzymes (Zain and Ismail 2016). In addition, K-induced high transpiration rate increased uptake of nutrients to alleviate the damaging effects of drought stress. Foliar spray of K (using K_2SO_4 as a source) before silking stage reduced kernel abortion and significantly increased grain yield and K concentration in maize under water deficit conditions (Shahzad et al. 2017). Similarly, soil applied with K (100 mg kg^{-1} of soil) increased growth and yield of two contrasting maize hybrids, viz., 32F-10 (drought tolerant) and YH-1898 (drought sensitive), under drought stress (Aslam et al. 2013). Hussain et al. (2017) reported that combined application of K with Zn (150 kg ha^{-1} K + 12 kg ha^{-1} Zn) was more effective than individual application of these nutrients to mitigate drought stress in maize.

In wheat, K application was observed to increase pigments (chlorophyll and carotenoids) and activity of aminotransferase resulting in improved RWC and yield under water deficit conditions (Jatav et al. 2014). Recent studies by Shah et al. (2017) also showed a marked increase in wheat yield by exogenous K supply. Exogenous K supply improves water relations and prevents the degrardation of pigments and plasma membrane proteins under water stress conditions (Alam et al. 2011; Zareian et al. 2013). Safar-Noori et al. (2018) provided evidence that K application along with salicylic acid (SA) could increase nutritional quality and grain yield of wheat under drought stress. They observed a significant increase in water-soluble pentosan and starch content by SA + K treatment. Likewise, Rohbakhsh (2013) reported a marked increase in forage yield and quality of sorghum by K application under limited water conditions.

Salt-induced effects on crop growth and productivity could be alleviated by K application because of its direct involvement in photosynthesis, synthesis of proteins, regulation of stomata, and turgor-pressure-driven solute transport in the xylem (Ashraf 2004). Furthermore, type of cuticle or wax deposition on leaf surface, type, source, type and applied concentration of K, growth conditions and its absorption are the basis for its effective utilization. K deficiency causes a significant decline in

growth of plants due to its active role in photosynthesis. The decline in leaf K contents in K-deficient plants is responsible for disturbed stomatal regulation, consequently affecting the rate of photosynthesis. Availability of K in guard cells, epidermal cells, and leaf apoplast is considered to be essential for mediating the proper functioning of stomates. It has been reported that K contributes to optimize the water balance and assimilate partitioning in salt-stressed plants. Its essential role as osmotic adjustment into the vacuole helps the plants to survive under stressful environment by maintaining their water relations (Shabala et al. 2002; Akram et al. 2009). ROS production in salinity-induced plants is the main reason of unbalancing of homeostasis, resulting in ion toxicity, osmotic stress, and lipid peroxidation, eventually reducing permeability of cell membrane for ion leakage (Sairam et al. 2002; Kukreja et al. 2005). Improvement in salinity stress in K-enriched plants has been reported in corn, rice, and wheat by its imperative role in activation of antioxidants. A major decline in ion leakage by K supply has also been reported in salt-induced spinach plants. Availability of K to salt-stressed plants showed positive response in mitigating its drastic effects because of its antagonistic behavior for uptake of Na ions. The enhancement in growth by K application under salinity stress was also reported in rice plants (Lynch and Lauchli 1984; Kaya et al. 2001). A significant decline in chlorophyll contents (*a* and *b*) was observed in maize plant when exposed to salt stress conditions. The biochemical alterations which are responsible for reducing chlorophyll pigments in salt-affected plants could be due to degradation of proteins, chlorophyll enzymes, and chloroplast structure. It is suggested that lethal effects are also in terms of reduced K^+/Na^+ ratio of salt-stressed plants. Addition of K improved the K nutrient concentration in plants, resulting in higher K^+/Na^+ ratio, which is responsible for salinity tolerance (Hernandez and Alamansa 2002; Abbasi et al. 2012).

8.5 Calcium (Ca)

Calcium (Ca) is considered most effective in enhancing drought tolerance ability in plants by maintaining the integrity of cell wall. It also facilitates the plants to acclimatize and recover from drought injury by its critical role in plant metabolism. To reduce the severe effects of drought, the possible way is the improved Ca nutrition in drought-stressed plants. Calcium protects the plant from drought injury by regulating the enzymatic activity of plasma membrane ATPase. This enzyme is actively involved in pumping back those lost nutrients during cell damage because of Ca deficiency (Palta 2000).

Imbalance nutritional status of salt-stressed plants is due to interaction and competition of Na^+ and Cl^- with other nutrients, leading to nutrient deficiencies, particularly uptake of Ca and N. Calcium is considered an essential element for ameliorating drastic effects of salinity because of its active role in varying mechanisms such as cell wall stabilization, functional and structural integrity of plant membrane, signaling processes, regulation and selectivity of ion transport, and enzyme activities of cell wall (Hadi and Karimi 2012). Salinity stress causes a decrease in Ca contents in the

cytoplasm, attributed to lower Ca signals required for stress tolerance. In various bio-logical systems, Ca acts as messenger for inducing salt tolerance ability in plants under harsh conditions by stimulating the system of signal transduction (Parre et al. 2007).

It has been reported that Ca has protective role in plant growth and development even under high salinity stress. Cell reproduction and volume in cotton roots was stimulated with supplemented Ca nutrition. Lowering of Na^+/Ca^{2+} ratio has signifi-cant impacts on cell shape and its production. The root cells become thinner and longer due to narrow Na^+/Ca^{2+} ratio (Leidi and Saiz 1997; Cramer 2002). Transport of water across root cell membranes from roots to leaves is affected when plants are exposed to salinity stress because of reduced hydraulic conductivity of roots with increased Na^+/Ca^{2+} ratio. Exogenous Ca has potential to avoid the inhibition of roots hydraulic conductivity under Na-stress (Azaizeh et al. 1992). Cell wall extension under salinity stress is reduced with increased Na^+/Ca^{2+} ratio as it affects biosynthe-sis of cell wall. Under high salinity levels, the biosynthesis of cellulose and non-cellulosic polysaccharide in the cell wall is affected in cotton roots with increased contents of uronic acid of cell wall, which eventually lose the integrity of cell wall. Modifications in concentration of cellulose and uronic acid is prevented if plants are supplied with Ca nutrition. With increased evidences, it is suggested that inhibition in enzymes activity and degradation of polysaccharides could be reduced by supple-menting Ca. Ca-deficient plants under sodium stress were observed with changed composition of cell wall, specifically that of pectic polysaccharides (Hadi and Karimi 2012).

8.6   Magnesium (Mg)

Magnesium (Mg) is an important element for plant development because of its direct involvement in physio-biochemical mechanisms. Transport of photosynthates from source to sink is prompted with Mg nutrition supply. Sufficient Mg nutrient increases water and nutrients uptake because of increased root growth, helps in export of carbohydrates, reducing ROS production and photo-oxidative damage to cells under drought stress conditions. An enhanced chlorophyll is directly linked with Mg that is bound in the chloroplast. Interveinal chlorosis in drought-stressed plants is mostly prominent by Mg deficiency. Another reason of its deficiency in plants is presence of competing cations such as Ca, Al, H, NH_4, and Na. Reduction in export and carbohydrates accumulation in Mg-deficient plants is the major cause of restricted CO_2 fixation. Utilization of electrons is being limited to CO_2 fixation due to impaired photosynthetic electron transport chain, thereby leading to ROS generation, which causes damage to membrane lipids and chlorophyll pigments. Tolerance to drought stress in plants is induced, however, by activating various kinds of enzymes such as RuBisCO, protein kinases, and ATPases by Mg supply (Mengel and Kirkby 2001; Mittler 2002; Shaul 2002; Epstein and Bloom 2004).

Harmful effects of salt stress on account of reduced photosynthesis may be due to alterations in stomatal conductance. More negative leaf water potential and osmotic potential under adverse conditions of salinity mediates turgidity of stomatal

cells, which ultimately reduces stomatal regulation in plants. Crop productivity may eventually decrease in relation to depressed photo-assimilation during the process of photosynthesis (Xu et al. 1994). It is depicted that under salinity stress, even plants are osmotically adjusted; water absorption could not regain their turgidity. To balance the water loss, Mg has strong impact on maintaining the water status of salt-stressed plants. Higher leaf stomatal conductance in Mg rich plants might be because of decreased leaf water potential and subsequent increase in leaf turgor pressure. Mg is involved in many enzymatic reactions, protein synthesis, osmoregulation, and growth of salt-stressed plants (Furriel et al. 2000).

8.7   Sulfur (S)

Sulfur (S), due to its importance in plant growth, development, and involvement in several defense mechanisms, is now being considered as fourth major macronutrient required by plant. Its importance is evident from the fact that it is a vital constituent of vitamins, pantothenic acid, and prosthetic groups. S-containing compounds like GSH, thiols, and sulfolipids are involved in defense mechanisms and also normal functioning of plants (Brychkova et al. 2007; Münchberg et al. 2007). In addition, it plays key roles in enzyme activation, chlorophyll formation, increasing photosynthesis, and synthesis of nucleic acids (Kaur et al. 2013). Glutathione, an S-containing compound, is involved in improving the assimilation of other nutrients. Furthermore, it stimulates the defense system against oxidative stress (Münchberg et al. 2007).

Sulfur plays an important role in plant growth, tolerance mechanisms, and formation of root nodules in legumes. Assimilation of S begins from the absorption of S from soil by SULTR (sulfate transporters) genes present in the roots. However, in S-deficient soils, plants can also absorb foliar S especially through hydrogen sulfide (H_2S) (Koralewska et al. 2008). Plants response to stress results in increased sulfate flux compared to other ions like NO_3 or PO_4 showing that there is a high demand for S under abiotic stress (Ernst et al. 2010). S nutrition can enhance the efficiency of essential primary macronutrients like N and P (Azza et al. 2011), and plant needs similar amounts of S and P (Ali et al. 2008). In cereals, S nutrition improves the efficiency of N absorption and assimilation because the enzymes involved in metabolism of N have S as their vital constituent (Salvagiotti et al. 2009; De Bona et al. 2011).

During drought stress, when leaves are only site for ABA synthesis, sulfate in the xylem of plant acts as chemical signal for closing stomata. In addition, it also acts as a chemical signal for ABA-dependent stomatal closure in leaves during early stages of water stress when ABA biosynthesis is restricted to leaves (Ernst et al. 2010). In recent years, important roles of S in alleviating various stresses have been studied in detail (Rausch and Wachter 2005). In wheat, exogenous sodium hydrosulfide (NaHS) supply increased RWC and biomass accumulation at seedling stage compared to control plants under water deficit conditions. Moreover, it also upregulated the ABA catabolism genes, ABA reactivation genes, and expression levels of

ABA synthesis in the roots of wheat plants. The results from this research indicated that exogenous NaHS can mitigate drought stress by the participation of ABA. Shan et al. (2011) evaluated the effects of H_2S application on ascorbate and glutathione assimilation in wheat leaves under drought stress. Sodium hydrosulfide (NaHS; H_2S donor) was used as a source of S. Pretreatment with NaHS reduced the contents of malondialdehyde (MDA) and electrolyte leakage caused by drought stress. Moreover, pretreatment with S enhanced the activities of GR, APX, gamma-glutamylcysteine synthetase (γGCS), and dehydroascorbate reductase (DHAR) compared to control plants. Application of trehalose (Tre) and SA resulted in increased activities of peroxidase (POD) and phenylalanine ammonia lyase (PAL), increased ascorbic acid oxidase (AAO) under stress, and decreased level of lipid peroxidation, preventing membrane leakage (Aldesuquy and Ghanem 2015). They concluded that SA and Tre are very effective in mitigating the negative effects of drought stress in wheat.

Salinity stress severely affects stomatal conductance leading to the restriction of gaseous exchange in plants. Hence, CO_2 absorption and availability in plants reduce, resulting in decreased rate of photosynthesis (Flexas et al. 2007). S-containing compounds have the ability to modify the physiological processes of plants to increase tolerance of plants under saline conditions (Khan et al. 2014). Hazardous effects of salinity on rice yield and quality can be alleviated by combined application of gypsum and S (Shaban et al. 2013). They reported that application of gypsum and S can be very helpful in improving vegetative growth, grain yield, and quality of rice grown under saline conditions. Supplementation of wheat with $CaSO_4$ at the rate of 150 kg ha-1 markedly increased tillers, spike length, 1000 grain weight, grains spike^{-1}, and straw yield under salt stress conditions (Arshadullah et al. 2013). Furthermore, increase in Ca, Mg, and S and a decline in Na were also observed in grains compared to control plants, indicating that $CaSO_4$ application can significantly increase essential macronutrients Ca, Mg, and S and avoid uptake of Na. Khan et al. (2006) investigated the importance of S in increasing the yield and yield-related traits of maize under saline conditions and concluded that fertilization with 60 kg ha^{-1} S markedly improved biomass (41%), 1000-grain weight (5%), and total grain weight (43%) in salt-stressed plants. In rice, application of 600 kg ha^{-1} S along with 6-day irrigation interval resulted in the highest water productivity rates and significantly improved grain and biological yield under saline conditions (Zayed et al. 2017). Maize seedlings treated with 60 and 80 mM $CaSO_4$ exhibited the highest germination percentage, mean emergence time, germination energy, mean daily emergence, and germination speed under salt stress conditions (Riffat and Ahmad 2016). Ye et al. (2015) reported that pretreatment of wheat grains with H_2S during imbibition can increase the germination of wheat seeds by reducing the inhibitory effects of salt stress. In addition, seeds treated with NaHS showed higher activities of esterase and amylase compared to control plants. It also reduced the levels of MDA and the alterations made in solidarity of plasma membrane by NaCl particularly in the tips of radicle.

8.8   Boron (B)

Boron (B) is considered as essential element because of its primary role in the integrity of cell wall. Mineral nutritional supply of B plays a vital role in stimulating plant resistance against drought stress factor. Reduced stunted growth of plants under drought stress is related to the fact that B nutrition helps to strengthen the plants through promoting flower retention, pollen tube formation, sugar transport, and carbohydrates metabolism. A wide range of physiological and biochemical changes at molecular and cellular levels are induced in drought-stressed plants. Alleviation of these drought adversities by B nutrition is because of increased uptake of water from the soil rhizosphere with more root hairs and mycorrhiza production, resulting in higher CO_2 assimilation and stomatal conductance (Bartels and Sunkar 2005; Christensen 2005; Gustav et al. 2008). Accumulation of polyamines and chlorogenic acid and reduced biosynthesis of indole acetic acid (IAA) and cytokinins (CK) in drought-stressed plants might be due to B deficiency. Crop productivity increased because B has a role in improving photosynthesis, water use efficiency, and pollen viability and assimilates partitioning under water deficit conditions. Imposition of drought stress caused considerable decline in leaf water potential, while B supplementation changed the water potential more positively. More negative leaf water potential was also perceived in B-deficient legume plants due to reduced transpiration efficiency in response to water scarcity conditions (Wei et al. 2005; Will et al. 2011; Upadhyaya et al. 2012).

Salt-induced reduction in growth of plants could be minimized in the presence of B. Its increased supply causes accumulation of B in different plant organs such as shoot, root, style, stigma, and ovary, which results in better pollination, seed setting, and vigorous grain formation. Improved salinity tolerance in rice plants seems possible due to ion exclusion mechanisms (Mehmood et al. 2009: Aftab et al. 2015). Reduced transpiration rate because of salinity stress has been suggested to affect the interaction of B with salinity, its uptake through the roots, and translocation to shoot. The root uptake of B is severely affected in salt stress conditions. Uptake of B is predominantly based on membrane permeability in plants subjected to salt stress. Salt-induced changes in membrane composition, changed aquaporin functionality, or membrane damage, resulted in reduced B translocation to shoots. Salinity-induced changes in transpiration rate of plants might be caused by closed stomata and transpiration-driven water flow (Hu and Brown 1997; Wimmer and Goldbach 2012).

8.9   Zinc (Zn)

The possible way to mitigate the damaging effects of drought stress in plants is the efficient use of Zn nutrition. The decrease in crop productivity under environmental stress conditions is only because of Zn deficiency. Zn supplementation under drought conditions balances the hormonal status of plants and ensures its survival under adverse conditions of drought. It has been suggested that drought stress alter the

normal functioning of auxin in plants. Its application under such harsh conditions acts as co-enzyme for the synthesis of tryptophan, a precursor for auxin production, and thereby increases root development for improved water status of plants. In previous studies, stunted growth and chlorotic leaves in maize, reduced photosynthesis because of decreased intercellular CO_2 concentration, carbonic anhydrase activity, and stomatal conductance in cauliflower, lowered osmotic potential in cabbage, and declined transpiration rate in pecan plants were observed in Zn-deficient plants. In addition, Zn nutrition protects the plants from oxidative damage of ROS by enhancing the activities of antioxidants and reduced activity of membrane-bound NADPH oxidase under drought stress conditions (Waraich et al. 2011). Improvement in drought tolerance in crop plants by Zn application is also because of protein and carbohydrate metabolism, starch formation, and membrane integrity (Fageria et al. 2002).

Zn-nutritional status of plants is essential for higher crop productivity. Its deficiency is considered a most limiting factor for plant development under salinity stress environmental conditions (Khoshgoftar et al. 2004). It seems in previous studies that improvement in salt tolerance in plants could be possible by Zn additive. Plants exposed to saline conditions have higher concentrations of Na^+ and Cl^- ions. Generally, reduced drastic effects in salt-stressed plants with supplemented Zn are because of increased membrane stability index. Enriched plants with exogenously applied Zn have critical role in mediating the permeability of membranes by sustaining the membrane lipids that are active structurally and functionally. Instability of cellular membrane due to Zn deficiency in salt-affected plants is attributable to excessive uptake of Na^+ and Cl^- ions at toxic level, indicating damage to membrane permeability (Kong et al. 2005; Aktas et al. 2006). Tavallali et al. (2009) also suggested a possible role of Zn in improving salt tolerance in plants with reduced uptake of Na^+ and Cl^- ions. Absorption of Na^+ and Cl^- ions under salt stress conditions is the major reason of declining leaf RWC that in turn affect the relative growth rate, which is most prominent in Zn-deficient plants. Supplemented Zn nutrition ameliorates the drastic effects of salinity in terms of maintained water status of plants attributable to improved vascular tissues. By maintaining the Zn requirement of plants accumulates the Ca and K ions in the cell that provides protection to salt-stressed plants against osmotic stress and helps the roots for more water absorption (Gadallah 2000; Mehrizi et al. 2011).

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Drought Stress Tolerance in Legume Crops

9

Savita, Ajay Tomer, and Saurabh Kumar Singh

Abstract

The environment is defined as the sum total of all biotic and abiotic factors other than individual concerned. The various factors are called biotic and abiotic depending upon their biological and non-biological nature. When some environmental factors interfere with complete expression of cultivars/varieties potential, they are known as stress. Stress is categorized into two types: (a) biotic stress that includes pathogen, pests, weeds, etc., and (b) abiotic stress due to moisture (excess/deficit), temperature (high/low), minerals (deficiency/toxicity), salinity, soil pH, air pollution, etc. Drought, which is a major and most important abiotic stress, acts as a constraint to productivity of legumes. It is a meteorological phenomenon which implicit the lack of rainfall for a long period of time which caused moisture reduction in soil and water shortage with a deficiency of water potential in plant tissues. It inhibits the crop from achieving the potential yield and severely lowers the legume production. Generally, grain legumes depend on rainfall and are susceptible to irregular drought stress throughout its vegetative and reproductive growth phase. During pod filling stage, drought stress is very common in legume crops and reduced yield in the crops grown with current rainfall. It can be minimized by developing cultivars tolerant to drought stress.

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9.1   Introduction

Stress may be described as any environmental condition which hinders the plant from reaching its full genetic yield potential (Atkinson and Urwin 2012). Harmful effect on the living organisms by the non-living factors in a specific set of the domain is called abiotic stress (Satyanarayana et al. 2012). These are severe intimidation to agriculture. Furthermore, it causes lesser yield due to changes in soil–plant–atmosphere continuum. In the world, India is the leading producer, consumer, and importer of pulses. Despite various efforts of the Government of India, the pulse production from an area of 23.0 million ha has stabilized at around 18–20 million tonnes against the consumption of 22–24 million tonnes, which necessitates imports of 4–six million tonnes pulses each year, resulting in a loss of $ 2.3 billion foreign exchange each year (Business Line 2015). Even with this level of production and import, availability of pulses (47 g/capita/day) is far lower than the recommended minimum requirement of 70 g/capita/day.

The pulses have great potential to bear the vagaries of the changing climate, provided other crop management practices are strictly followed to harness achievable yields. Pulses can adapt to a diverse range of edaphic and environmental conditions, therefore, can constitute an important component of climate-change mitigation and adaptation strategy. Major pulse crops in India grown during the rainy (kharif) season (June–October) include pigeonpea, urdbean, mungbean, and cowpea, while during the winter (rabi) season (October–April), chickpea (*Cicerarietinum* L*.)*, lentil (*Lens culinaris* Medikus), and peas (*Pisum sativum* L.) are grown. Choudhary (2013) and Pooniya et al. (2015) reported that yield gaps in pulses at research farms and farmer's field ranged from 368–492 kg ha^{-1} in urdbean, 220–417 kg/ha in kidney bean (*Phaseolus vulgaris* L.), 477–563 kg/ha in pigeon pea, 372–494 kg/ha in cowpea, 225–601 kg/ha in chickpea, and 253–510 kg/ha in lentil. So, a comprehensive study of crop reaction to the stress is the basis for regulating crops appropriately. There are significant differences in the tolerance of plants to drought stress depending upon duration and intensity of stress, species, and developmental stage of the plant (Singh et al. 2012).

9.2   Drought Stress

Drought stress is one of the most important challenging factors faced by legume crop producers worldwide. It can persistently limit production, and extreme events can lead to total crop failures. There may be a reduction in yield by 50% due to drought and heat stress, basically in arid and semiarid regions (Nam et al. 2001). Drought stress regulates normal physiological, biochemical, and morphological reactions of crops, which lastly reduces crop yield (Malik et al. 2006). All the legume crops (pea, French bean, cowpea, broad bean, Indian bean, black gram, green gram, lentil, pigeonpea, urdbean, mungbean, and chickpea) are vital sources of amino acids and quality protein for mankind. In several food producing

countries, severe droughts conditions take place from time to time, with comprehensive effects on world food production and supply (Edmeades et al. 1992).

9.3 Drought Stress Response in Legumes

Drought stress responses categorized as morphological, physiological, biochemical, and molecular are apparent at every phenological stage of plant growth. A comprehensive description of different types of drought responses is given below:

9.3.1 Morphological Responses

Growth is recognized through cell division, enlargement, and differentiation. It involves genetic, physiological, biochemical, morphological, ecological events and their intricate interactions. The growth and development of the plant depend on these cases, which are affected by drought. Cell growth is the most sensitive physiological processes of drought because of the low turgor pressure (Taiz and Zeiger 2006) and is a complex interaction between sources and sink. Drought debases mitosis; cell elongation and expansion, and resulted growth reduction (Hussain et al. 2008). Deficiency of water either permanent or temporary critically bonds the growth and development of plant more than the other climatic factors. The primary and leading effect of drought is low germination and development of weak plants (Harris et al. 2002; Kaya et al. 2006).

9.3.2 Physiological and Biochemical Responses

Growth results in the production of daughter-cells, resulting in cell divisions of meristematic cells, followed by young cells expansion. Inhibition in cell elongation of higher plants by disruption of water flow from the xylem to the fencing elongating cells is due to severe deficiency of water (Nonami 1998). Water deficit condition to plants affected root-to-shoot signaling and inhibits the root and shoot growth, impaired photosynthetic machinery, oxidation of chloroplast lipids, early leaf senescence, and modification in structure of pigments and proteins (Menconi et al. 1995; Novak and Lipiec 2012; Anjum et al. 2003; Farooq et al. 2009; Estill et al. 1991). Abscisic acid (ABA), a growth inhibitor, has long been identified as stress signal root-to-shoot (Schachtman and Goodger 2008). A signal cascade is stimulated by roots to the shoots via xylem during soil drying. Abscisic acid is composited in the roots and move in the xylem to the shoot through the transpiration stream, where it suppresses leaf expansion and the opening of stomata prior to altering leaf water and nutrient status (Wang et al. 2000; Guerrero and Mullet 1986).

Carotenes, isoprenoid molecules forms a major part of the plant defense system, but oxidative destruction is very common in these molecules. β-carotene is a part of the core complexes of PSI and PSII (Andrew et al. 2008; Havaux 1998), which is

destructed by the water stress (Kiani et al. 2008) due to development of reactive oxygen species (ROS) in the thylakoids (Reddy et al. 2004). Reactive oxygen species ($O_2^{\cdot-}$, H_2O_2 and $OH^{\cdot}$ radicals) levels increase noticeably and lead oxidative destruction to lipids, proteins, and genetic material of the cell (Apel and Hirt 2004; Farooq et al. 2009). The amount of highly reactive compound malondialdehyde (MDA) increases by ROS which has been responsible for oxidative damage (Moller et al. 2007). Antioxidant defense system presents in plants to regulate active oxygen damage and ensuring cellular function normally (Horvath et al. 2007).

For the maintenance of leaf turgidity assimilation of solutes takes place in the cell during drought stress. To raise tolerance level of plants to drought-stress, assembling and mobilization of proline has been reported (Nayyar and Walia 2003). The first response of plants under water stress condition is accumulation of proline (Anjum et al. 2011; Demiral and Turkan 2004), which act as a signalling molecule to modulate function of cell organelles, stabilize subcellular structures, scavenge free radicals, as well as cushioning cellular redox potential (Szabados and Savoure 2009; Ashraf and Foolad 2007).

9.3.3 Molecular Response

During the previous years, DNA-based markers have become available (Kumar et al. 2011). For transferring of resistance to stresses, DNA-based marker has been widely used into grain legumes (Choudhary et al. 2018). To identify quantitative trait loci (QTL) for specific drought-tolerance component traits can also be used to slice up the genetic basis of various characters linked to drought performance (Serraj et al. 2005). By using molecular techniques for many drought tolerance traits in chickpea varieties, one genomic region possessing quantitative trait loci have been identified and successfully accessed by using a marker-assisted breeding (Thudi et al. 2014). Inclusive work has been done to unravel drought tolerance mechanism in legume crops; however, the conception of the molecular basis of drought stress tolerance still needs more research.

9.4   Management Strategies to Minimize Drought Stress

9.4.1 Breeding Approaches

Conventional and non-conventional strategies of breeding have been used for improving drought tolerance in legume crops. The traditional breeding methods require large investments in land, labor, and capital with a little success rate of improvement. High root biomass, plant type, leaf trait, and cuticular wax present on leaves have been used as a marker in traditional breeding (Choudhary et al. 2018). However, DNA marker-based improvement method, which shows potential regarding the improvement of legume crops, specifically for those traits where the possibility of phenotyping is only late in the season of crop development, is not easy or

is uneconomical. Recently, progress in genomics gave a better understanding of physiological mechanisms of drought response. It added rapidness in progress of genetic improvement of drought tolerance of the crop.

9.4.2 Exogenous Application of Hormones and Osmoprotectants

Endogenous plant growth regulators take part in regulating the effects to abiotic stress by refining the growth and development system of plants. Overall, there are five major classes of PGRs: the auxins, gibberellins, cytokinins, ethylene, and ABA. Moreover, a broad range of chemicals have been accumulated with clear growth regulatory actions, and few of them have been illustrated to have extensive applications in getting better growth of the plant, as well as yield and quality (Upreti and Sharma 2016). Osmoprotectant protects cell membrane destruction by a high concentration of inorganic ions and oxidative damage. It has been hypothesized that installing osmoprotectant synthesis pathways is a potential way to breed stress-tolerant crops (Rathinasabapathi 2000).

9.5 Conclusions

Drought stress is a global problem, and this situation has been made dangerous by recent global climate change. It causes closer to stomata with a parallel decline in net photosynthesis and water-use efficiency. Progresses have been made to develop drought stress tolerance in legume crops through the application of conventional and non-conventional approaches of breeding. Besides that, hormones and osmoprotectants have been used for getting better performance of legumes. Furthermore, dissection of drought tolerance linked gene will open the way for improving the legumes.

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Drought Tolerance: Breeding Efforts in Sugarcane

10

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Abstract

Water is an essential necessity for proper crop growth and high yield. The requirement of water for the crop could not be fulfilled just by the uptake by crop roots from ground but by additional irrigation. The levels of groundwater is depleting with increase in time due to excessive usage /wastage and high temperatures this will cause defciency of water not only for irrigation but also for human consumption. Deficiency of water in crop leads to several changes in physiological and metabolic activities. In sugarcane crop, changes in leaf water potential, relative water content, osmoregulators, etc. have been observed. Sugarcane is an important crop in terms of economical purposes as it is the main producer of sugar and bio-energy all throughout the world. The prevailing drought condition due to the climate change scenario is hampering the productivity of the crop. To manage this problem, developing a tolerant variety for such a condition is the best option although there are several constrains in doing so. Furthermore, for breeding a tolerant variety, the breeder must keep in mind the selection criteria for choosing the right parent for achieving the correct result. This chapter is emphasizing on the breeding efforts in developing a drought-tolerant sugarcane variety.

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Abbreviations

DEF 1   disulfide isomerase protein 1
ERFs   ethylene-responsive factor proteins
HSP   heat shock proteins
IGS   indole-3-glycerol phosphate synthase
LEA   late embryogenesis abundance proteins
ROS   reactive oxygen species
Scdr 1   sugarcane drought-responsive gene 1
SOD   superoxide dismutase genes

10.1 Introduction

Sugarcane (*Saccharum officinarum* L.) is an important crop for sugar and bio-energy worldwide. It is one of the world's major C_4 crops that mainly grow in the tropic and sub-tropic regions. Weather- and climate-related events are the key factors for sugarcane production worldwide, especially in many developing countries (Zhao and Li 2015). Water is already a scarce commodity in many parts of the world, and as the climate is changing unpredictably, this will enhance such conditions in the near future. As the global temperatures are rapidly going up along with the frequency and precipitation level, the problem of water losses are predicted to enhance further through evapotranspiration (Lopes et al. 2011). Variation in climate is severely affecting the water sources, and as per the present scenario, the frequencies of occurrence of drought and floods will be increasing in times to come (Misra et al. 2016; Mall et al. 2017). Water is a requirement for any crop to grow properly which is not fulfilled through uptake of groundwater from the soil by its roots, but also additional irrigation is required for fulfilling the needs for the flourished crop. But if water needs are not fulfilled through external irrigation, then this would lead to groundwater depletion by the continuous usage of groundwater by plants for their survival (Oki and Shinjiro 2006). Water is essentiality not only for humans and animals but also for the plants for their proper growth and development (Larcher 2006). Several studies have revealed that deficiency of water causes changes in many physiological activities such as leaf water potential, relative water content, etc. (Nogueira et al. 2000; Graça et al. 2010; Silva et al. 2010). Also, as a result of water deficiency, metabolic processes were also altered like osmoregulators increased under such conditions (Nogueira et al. 2001; Guimarães et al. 2008; Silva and Barbosa 2009; Medeiros et al. 2012).

10.2 Breeding in Sugarcane

Drought is a complex stress that involves a large number of genes and regular elements, and breeding a drought-resistant variety is further a complex process for a polyploid crop. Several studies have been conducted on the way the elite genotypes

of sugarcane respond to drought conditions (Hemaprabha et al. 2004), but there is still a need for further study on this aspect to better understand the responses in sugarcane for developing better and improved drought cane variety (Sanchez et al. 2002). Involvement of candidate genes as molecular markers in breeding techniques had made a better understanding in this regard (Thorup et al. 2000; Huh et al. 2001). Breeding a new variety plays a direct relation to the sugar industries as an improved variety will cause a high production of sugar and alcohol. In India, the tropical zones favor the flowering production whereas the sub-tropical region lacks behind in this aspect due to which the flowering, seeds production and breeding techniques are performed in the tropical region for developing improved canes for cultivation, especially for sub-tropical regions (Scortecci et al. 2011). The basic target of a sugarcane breeding program is to improve the sugar content in plant with low inputs which will be profitable both for the cane growers and sugar millers (Jackson 2005).

10.2.1 Breeding Methods in Sugarcane

10.2.1.1 Traditional Method

10.2.1.1.1 Parental Selection

Parental selection is the most important trait for developing any good cane variety for any purpose. It is the most crucial step as yield has a direct relationship with the environmental conditions, and the environmental changes are unpredictable so for a breeder, the parental selection is of utmost importance (Pandey et al. 2018). In this method, parents are wisely chosen according to the desired traits they possess so that genotypes having a higher probability of that particular trait could be achieved. This is of interest in respect to commercial viewpoint (Matsuoka et al. 1999). In several stations of breeding, the selection rate for a parent depends on the progeny performance such as if the progeny performance is far better than the standard taken then in such a case the parent will be considered as proven parent and progeny obtained as proven cross (Breaux 1987; Hogarth and Skinner 1987; Berding and Skinner 1987; Heinz and Tew 1987).

10.2.1.1.2 Hybridization

Although the procedures and techniques used for crossing vary from breeders to breeders, the basic pollination procedure remains the same. Verret (1925) had shown that tassel stalks were harvested as soon as anthesis in flower starts, after which these stalks were kept in a shelter used particularly for breeding purpose in an acid solution of weak acidity. This is done to enhance the life of a flower and to make it either bi-parental or a poly-cross parent. In bi-parental crossing, the inflorescence possessing flowers are covered with bags (Sleper and Poehlman 2006). In poly-crossing, cane stalks possessing flowers are cut off and kept in crossing solution of a mixture of acids having diluted concentration. The use of a dilute mixture is to enhance the life of stalks and for providing nutrients (Cox et al. 2000). Similar to the bi-parental crossing, the flowers are also covered in lanterns where male flowers are kept above female flowers to allow the former to shed their pollen on to the latter

ones (Cox et al. 2000). After pollination has taken place, the stalks are kept in cross-
ing solution for 12–14 days (Buzacott 1965).

10.2.1.1.3 Progeny Selection

Mamet and Domainque (1999) had shown that progeny selection varies from place
to place and depends on the tenure of the life cycle and ratoon produced from plant
crop. Progeny selection for long duration crops depends on several factors such as
disease resistance, high sucrose content, more cane weight, etc., while for short life
cycle ones it depends on number of ratoons produced by the crop (Heinz 1987).

10.2.1.2 Molecular Method

Although selecting and breeding a cane variety are the best options for developing
a variety for stress conditions, the molecular and biotechnological approaches are
also emerging as the new approach to develop tolerant varieties for such conditions.
These approaches help in developing tolerant variety either for single stress or for
multiple ones. Epstein and Rains (1987) had shown a step-wise procedure for devel-
oping a variety of molecular means. In sugarcane, *Agrobacterium tumifaciens* medi-
ate transformation with two inclusion LBA4404 pB1 121 construct GLY1 bestowed
stress tolerance (Shaik et al. 2007). Any tolerance to drought and salinity in sugar-
cane was introduced in *Arabidopsis* tubes pyro-phosphatase (AVP1) factor which is
mediated by *A. tumifaciens* transformation (Kumar et al. 2014). Another way is the
involvement of candidate genes for developing a tolerant drought variety wherein
the candidate genes worked as a molecular marker (Huh et al. 2001; Thorup et al.
2000).

10.3 Constraints in Sugarcane Breeding for Stress

On a general basis, the following are the constrains in breeding a sugarcane stress-
tolerant varieties:

I. *Genetic improvement in sugarcane based on performance in yield:*

   Stress tolerance in sugarcane is necessary for rapid stalk development but the
accumulation of sucrose in the later stages, particularly in ripening period, is encour-
aged by the environmental stress that the cane faces (Viqueira et al. 1984). Desirable
parents are most important decision for any sugarcane breeding. Diverse parents
have different acclimatization, production and productivity, resistance to biotic and
abiotic stresses which are responsible for the development of varieties of different
target environment. So there is a need to develop drought-tolerant sugarcane variety
for different water regimes, poor rainfall pattern, and poor irrigation facilities.
Generally parentage for breeding for peninsular zones of India is very different
from North India parentage. In the view of high recovery percentage, breeding for
earliness and high sugar is the most important concern. But high sucrose and early
maturity have been found hard to associate with high yield. Cytogenetically,

sugarcane material is highly polyploid with high degree of genetical impurity. As per cytoplasmic studies, in sugarcane breeding more importance has to be paid to female parent than to male parent.

II. *Achieving high yield potential in sugarcane tolerant to stress:*

Another constrain for breeding variety for stress tolerance is to achieve high yield potential in canes having tolerant ability towards stress condition (Bell et al. 1995; Evans and Fischer 1999). Early stomata termination and leaf shedding leads to drought tolerance through breeding, but it is not necessary to increase yield under water-limiting condition because drought tolerance is a complex traits and involving the many dynamic interaction. During development of drought-tolerant varieties, the parameters like stalk number, height, diameter, and weight along with cane yield in sugarcane under water regimes should be selected. Generally yield associate having linear relationship with productivity but diameter are not a stable parameters under stress conditions. So to enhance the drought tolerance in sugarcane, associated trait must be selected for maximum yield under drought conditions. Accordingly, it is possible to select genotypes under water deficit with high yield and associated traits. Careful selection of suitable physiological traits and rapid/nondestructive methods of quantifying them would be very valuable in improving drought tolerance. To improve drought tolerance for target environment, a set of characters must be identified, which can be identified very soon and must be inexpensive during screening. In these circumstances, physiological parameters like chlorophyll, SPAD index, and thermal imaging are most valuable for rapid and non-damaging screening for drought tolerance.

10.4 Breeding Efforts in Developing Drought-Tolerant Cane Varieties

Since the past several years, cane varieties are being improved through breeding for high production of sugar and yield. Studies are being conducted to improve the cane yield and production in stress conditions as the frequency of occurrence due to climate change is enhanced and there is a need for developing cane varieties to flourish under such situation particularly drought. Sreenivasan and Bhagyalakshmi (2001) imparted drought tolerance to a variety Co 87, Co 263 wherein Co 312 worked as a parent. *S. spontaneum*, *Narenga* and *Erianthus* may also impart tolerance to a variety towards drought conditions when used as a parent for breeding the variety (Krishnamurthy 1989; Roach and Daniels 1987). Development of high yielding varieties for different zones is major objective of All India Coordinated Research Project on Sugarcane. Recently varieties for different zones, viz., Co 86032, Co 94008, Co 06207, CoH 119, CoPk 05191, Co 09004, Co 10026 (Peninsular Zone); CoLk 94184, Co 0233, (North Central & North Eastern Zones); CoOr 03151, CoA 05323 (East Coast Zone); CoLk 11206 (North West Zone) (Shukla et al., 2019). The development of drought-tolerant varieties will help in overcoming/minimizing the

problems associated with such conditions on drought especially in relation to production and yield.

10.4.1 Selection Criteria for Developing Drought-Tolerant Cane Varieties

Certain selection criteria required for the development of drought-tolerant cane varieties are as follows:

10.4.1.1 Physiological Parameters (Such as Relative Water Content, Stomata Conductance, Photochemical Efficiency (PS II))

Physiological parameters are important for characterizing drought tolerant genotypes (Buckley 2005; Vinocur and Altman 2005; Shao et al. 2008; Tezara et al. 2008). Hotta et al. (2010) had shown that these parameters along with the genes identified for this purpose can play an important role as a foundation for the development of new tolerant varieties. Azevedo et al. (2011) and Silva et al. (2007) had revealed that certain physiological and biochemical parameters gave positive results in identifying the sensitive and tolerant cultivars towards drought. Selection for physiological traits correlated with tolerance towards drought might augment the achievement of sugarcane breeding for this purpose. Decrease in stomatal conductance was seen with the size of the plant and also with age (Meinzer and Grant 1990). Meinzer and Grant (1991) had also shown that balance between loss in water by transpiration and hydraulic conductance has been known to maintain constant leaf water status when an alteration in environmental conditions occurred.

10.4.1.2 Assessment of Proline Content, Trehalose Content, and Photosynthetic Activity in Sugarcane Drought-Tolerant Varieties

One of the important characters often used to assess whether the variety is tolerant or not is the increase in proline content as well as photosynthetic activity in sugarcane (Ferreira et al. 2017). The former plays an effective role in stress phenomenon along with their functioning in cell osmotic adjustment acting as osmoprotectant, but Molinari et al. (2007) had shown its association with reactive oxygen species (ROS) scavengers. Several studies have reported that proline has been associated with drought tolerance in sugarcane (Rao and Asokan 1978; Paquet et al. 1994; Wahid 2004; Guimaraes et al. 2008). Molinari et al. (2007) had shown that transgenic cane plants indicated a positive association between increase proline content and biomass yield. Iskandar et al. (2011) had revealed that the mature canes possess an increased concentration of amino acids but it has the lowest amount of proline content under drought conditions. This amino acid could be used as a marker for assessing the tolerance in canes under drought conditions (Ferreira et al. 2017).

Trehalose in sugarcane has been known for having a role in stabilization of lipids and dehydrated enzymes (Pilon-Smits et al. 1998; Goddijn and van Dun 1999; Wingler et al. 2000; Garg et al. 2002). Trehalose phosphate synthase has also been

identified in drought-tolerant cane varieties (Vantini et al. 2015). It is an enzyme that plays a role in the formation of trehalose and its production is higher in plants under stress conditions especially under drought (Paul et al. 2008). Study on transgenic in sugarcane had revealed that transgenic sugarcane had a higher amount of trehalose content due to its transformation from *Grifola frondosa* trehalose synthase, but the higher accumulation of trehalose content had provided tolerance to cane towards drought condition (Zhang et al. 2006). Vantini et al. (2015) had also shown that in drought-tolerant canes high levels of trehalose genes have been expressed.

10.4.1.3   Maintenance of Yield Performance of Cane under Drought Condition as under Irrigated Condition

Drought tolerant canes should maintain its yield under drought conditions (Serraj et al. 2004). Drought is a frequent and sudden occuring stress in sugarcane and there is a need of variety with high yield potential under irrigated condition coupled with better water use efficient which can give substantial yield even under moisture stress condition (Mall and Misra 2017).

10.4.1.4   Performance of Cane Root System

To avoid drought, one of the important mechanisms that the crop adopt is the modification of its roots to capture the water for the process of transpiration (Fukai and Cooper 1995; Songsri et al. 2009). Root abundance, root distribution, and amount of total surface area used for absorption have been known as a trait used for selection of drought tolerance variety (Fitter and Hay 1987). *S. spontaenum* and its progenies are known to be higher tolerant for drought condition than *S. officanarium* (Evans 1935; Rao 1951). For breeding a good variety for drought condition, breeders emphasize on the variety having deep rooting system, good ratooning ability, as well as tolerance to disease, particularly smut mosaic and rust (Flores 2003).

10.4.1.5   Characteristics of Leaf

Another important trait considered for selection for drought tolerance is characteristics of leaf like the type of leaves, namely, short or erect or narrow, presence or absence of thick cuticles, pubescence, etc.

10.5   Drought-Tolerant Genes in Sugarcane

As an aid to the breeders for improving the cane varieties for drought conditions, molecular markers play an important and strong tool (Bundock et al. 2009; Parida et al. 2009). Detection of novel genotypes with the property of tolerance towards drought condition is necessary for agriculture as well as economics all around the globe. Genes associated with drought tolerance may enhance the knowledge of the evolutionary adaptation to such type of stress. These genes may be used in developing new tolerant varieties by the process of transformation (Nepomuceno et al. 2001; Lenka et al. 2011; Kido et al. 2012). A detailed knowledge of how the plants

will response under such condition at the molecular level is a pre-condition for managing such conditions. The genes in response to drought generally belong to two categories, i.e., genes encoding functional proteins and genes encoding regulatory proteins. The former consists of proteins like chaperones or proteases, detoxification enzymes, transporters, water channels, etc. The latter consists of those proteins whose functioning is either related to signaling the response or to the factors associated for the transcription process (Shinozaki and Yamaguchi-Shinozaki 2007). As signal transduction encourages response to plants under such conditions, one can easily predict whether these signals are for the adjustment of plant for such conditions or not (Zingaretti et al. 2012). Fujita et al. (2005) had shown that to succeed over the injuries occurred due to drought conditions, plants also develop complex pathways for transduction. In sugarcane, ScChi gene known as chitinase gene is known to be involved in host-pathogen interaction (Que et al. 2014), whereas for defense mechanism against eye spot diseases and smut, there has been an involvement of 62 differentially expressed genes (possessing 19 transcript derived fragments) (Borrás-Hidalgo et al. 2005) and for red rot infection differentially expressed EST clusters have been identified (Sathyabhama et al. 2015). Almeida et al. (2013) had revealed that as a response to foliar application of salicylic acid in drought conditions, genes were expressed that play a role in synthesis/ expression of trehalose 5-phosphate and sucrose-phosphate.

Due to the complexity in the sugarcane genome, the transgenic methodology has attracted the researchers for developing varieties having the quality of higher yield, high content, stress tolerance and disease resistance, etc. (Nerkar et al. 2018). A transgenic cane variety had been developed (by PT Perkebunan Nusantara (a state-owned sugar milling conglomerate), University of Jember (East Java), and Ajinomoto Co. Inc. Japan) for drought conditions that had shown to produce 20–30% more sugars than the commercial varieties under drought conditions in Indonesia wherein the use of bet A gene was involved. The bet A gene has been isolated from *Rhizobium meliloti* which has the capacity to produce an osmoprotectant known as glycine betaine for tolerance towards drought conditions (Marshall 2014; Waltz 2014).

10.5.1 Candidate Genes

Several studies on genomic and transcriptomic levels had paved the way for identification of candidate genes which provides tolerance towards various abiotic and biotic stresses. Superoxide dismutase and Indole-3-glycerol phosphate synthase genes have been identified and play an important role in improving the cane variety by molecular means and possess a promising future ahead in respect to drought conditions (Simon and Hemparabha 2010).

10.5.1.1 Superoxide Dismutase (SOD) Genes
In sugarcane, these genes play a role in modulating the drought conditions and studies have indicated that activity of such genes acts as primary line of control in

reactive oxygen species (ROS) scavenging process (Hemaprabha et al. 2004; Jain et al. 2015; Sales et al. 2015; dos Santos et al. 2015; dos Santos and de Almeida Silva 2015). Enhanced levels of these genes in canes impart tolerance towards drought conditions (Jangpromma et al. 2012; Simon and Hemaprabha 2010). It is known that different isoforms of SOD have been expressed in cane varieties and at times it may show a crucial effect in canes under drought conditions as an antioxidant response (Cia et al. 2012; Boaretto et al. 2014).

10.5.1.2 Indole-3-Glycerol Phosphate Synthase (IGS)
Another candidate genes identified in sugarcane for providing tolerance towards drought is IGS. In drought condition, auxin-related genes activates IGS and other related genes (Aloni et al. 2003).

10.5.1.3 Disulfide Isomerase Protein (DEF 1)
As a response to tolerance to stress, gene coding for disulfide isomerase protein (DEF 1) have been expressed in tolerant cane cultivars (Vantini et al. 2015).

10.5.2 Late Embryogenesis Abundance (LEA) Proteins

These proteins are hydrophilic proteins that majorly show their function in stress conditions, especially during drought (Magwanga et al. 2018). This gene is an important one in respect to stress response by plants. Besides, these genes are also accountable for the protection of macromolecules (Sakuma et al. 2006; Shinozaki and Yamaguchi-Shinozaki 1999). In sugarcane leaf, this gene was achieved under stress condition and being seen to play an essential part in canes that are tolerant to drought and salinity (JinXian et al. 2009; Iskandar et al. 2011).

10.5.2.1 Heat Shock Proteins (HSP)
HSPs are conserved polypeptides set which gets synthesized as a response to abiotic stress. The production of HSPs is a common incidence (Augustine 2016). The occurrence of these proteins is commonly seen in a normal condition in cytoplasm whereas, in stress condition, these proteins speedily reach to the nucleus of the cells (Lindquist and Craig 1988). These proteins are known to play an important part in plants grown under normal and stress conditions and help to understand the mechanism of signaling under such situation as well as another process like carbohydrate and amino acid metabolism, translation, etc. (Augustine 2016). About 44% of the genes belonging to Hsp 70 family along with its co-chaperone have been detected in sugarcane for biotic and abiotic conditions (Borges et al. 2001). Augustine et al. (2015) had shown that overexpression of *Erainthus arundinaceus* HSP70 (EaHSP70) in sugarcane enhances the tolerance ability of sugarcane towards drought.

10.5.2.2 Dehydrin Proteins (DHNs)
Dehydrin proteins are another type of LEA proteins of group II and have been known to be expressed in sugarcane and other plants under drought stress condition

(Close 1997). Wahid and Close (2007) had revealed the expression of DHNs and its association with water status in sugarcane. Three DHNs of different molecular masses have been revealed under drought condition and their expression was found to be irrespective of the alteration occurring in water content in leaves (Wahid and Close 2007). Iskandar et al. (2011) had also shown that under drought conditions, sugarcane expresses DHNs.

10.5.3 Ethylene-Responsive Factor (ERFs) Proteins

Allen et al. (1998) had revealed that these proteins consist of highly conserved DNA binding regions of 58–59 amino acids which were specific to plants. Singh et al. (2002) had identified two cis-elements in these proteins, namely, GCC box and C repeat (CRT) or dehydration-responsive element (DRE). In sugarcane, Trujillo et al. (2008) had identified a new sugarcane ethylene-responsive factor (SodERF3) which helps in increasing the tolerance under drought and salt stress conditions.

10.5.4 Sugarcane Drought-Responsive Gene 1 (Scdr 1)

In sugarcane, Scdr1 is upregulated and it was not associated with drought tolerance of some of the varieties of sugarcane. But, the transformation of tobacco, using this gene, conferred tolerance to multiple abiotic stresses like drought, salinity and oxidative stresses (Begcy et al. 2012). Utilization of these specific stress-induced genes and signaling cascades for inculcating stress resistance/tolerance in elite sugarcane varieties by their overexpressing or acting upstream in response to certain stress or multiple stresses may lead to the development of climate resilient sugarcane varieties which may sustain or even improve sugarcane/ sugar productivity in the climate change scenario. Not only this but some stress-upregulated genes in sugarcane like Scdr1 may confer tolerance to multiple abiotic stresses in some other plants like tobacco.

10.5.5 DEAD-Box Helicase Gene

Sugarcane transgenics overexpressing PDH45, a DEAD-box helicase gene isolated from pea, exhibited an upregulation of DREB2 (Dehydration responsive element binding proteins)-induced downstream stress-related genes and improved tolerance to drought and salinity (Augustine et al. 2015).

10.5.6 Other Associated Genes Related to Drought Tolerance

In sugarcane, there are several other genes which have been identified for drought tolerance like early response to dehydration protein 4 (ERD4) (McQualter and

Dookun-Saumtally 2007), upregulation of genes regulating intracellular redox status (Prabu et al. 2011), RAB (responsive to abscisic acid), osmotin, choline oxidase, and annexin (Nair 2011), etc.

10.6 Conclusion

Sugarcane is an important crop not only for sugar industries but also for bio-fuel industries. It is one of the crops that have been bestowed with a large number of natural qualities for facing abiotic stress. But the unpredictable changes in the environmental conditions like prolonged conditions of abiotic stress are also causing an effect on its productivity. Drought is one such stress which is now being frequently observed in many sugarcane-growing areas, and sugarcane being a water-loving crop faces difficulty in growing under such conditions. In this respect, improving the cane varieties either through breeding (conventional or molecular approach) or by using tissue culture methodology (such as somaclonal variation) is the need of the time. Furthermore, in developing an improved cane variety for drought conditions, there is a need for identifying newer genes and their response (expression patterns) to manage cane growth and productivity in such conditions in the near future.

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High-Temperature Response and Tolerance in Agronomic Crops

11

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Abstract

Extreme temperature (cold and heat) is one of the major threats to crop production globally. These conditions have affected the growth and development process of a plant. High-temperature stress can lead to the poor establishment, low floral fertility, pollen sterility, and improper grain filling which ultimately reduces the crop production. With the course of time, to escape or avoid the stress conditions, plants have developed morphological, physiological, biochemical, and molecular responses. Increased temperature along with drought stress has reduced the crop yield by 50%. It is a well-known fact that increasing population and decreasing agricultural productivity will lead to foodless days for many individuals especially in developing countries. Thus, to increase the crop productivity, there is a need to develop smart crops which are tolerant to both biotic and abiotic stress and have a high yield. Breeding programs have great importance in providing resistance to high yielding crops. On the other side, knowledge of heat tolerance molecular mechanism could help the scientists to develop smart crops in lesser time than the breeding program. This chapter will provide an overview of morphological, physiological, biochemical, and molecular response to

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high-temperature stress and will discuss the approaches that can be utilized to provide tolerance that will ultimately result in improved crop production.

11.1 Introduction

Plants are sessile organisms; they have no option to escape from abiotic and biotic stress prevailing around it. So, they have developed well-conserved but complex mechanism involving many cellular compartments, to cope up the ill effect of various stressors. Among abiotic stressors, the high temperature is most commonly found in many regions of the world particularly tropical and subtropical regions, along with drought. According to Intergovernmental Panel on Climate Change (IPCC), an increase of 4 °C in global atmospheric temperature has been recorded since the late twentieth century (Porter et al. 2014). Warming will continue, but variability will be there according to region. Projected surface temperature change has been shown in Fig. 11.1. Temperature plays an important role in plant growth, development, and yield (Wheeler et al. 2000; Tubiello et al. 2007; Lobell et al. 2011). Each crop has its threshold temperature (temperature at which reduction in the rate of growth and development of plant take place). However, the temperature at above or well below the optimum temperature hampers the normal growth and development of plant (Wahid 2007) (Fig. 11.1). Optimum temperatures for some agronomic crops are displayed in Table 11.1. These biotic and abiotic stresses have a great impact on plant, i.e., it alters the morphological, physiological, biochemical, and molecular parameters of a plant. Numerous researches have been conducted at breeding and biotechnological levels to understand the stress tolerance mechanism in the plant. However, scientists across the world are successful in understanding the mechanism until a certain level. With the advancement in science and technology, various approaches have been utilized to develop stress-tolerant plants. In the present chapter, we will discuss the impact of high-temperature stress on agronomically important crops and various approaches involved in the development of high-temperature stress-tolerant crops.

11.2 Types of Heat Stress Response Exits in Plants

There are two main types of plant response to high temperature, namely, basal and acquired thermotolerance. Basal thermotolerance refers to sudden direct exposure of the plant to a high temperature without any acclimation. Whereas, in acquired thermotolerance plant is subjected to a moderate temperature (priming) before exposing to high temperature. It is the nearest mimicry of prevailing natural
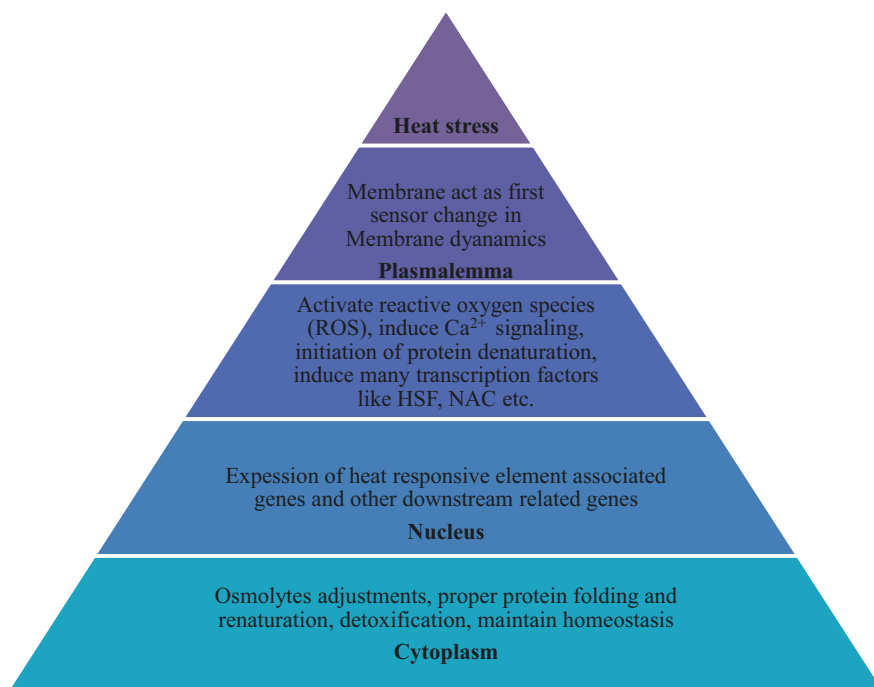
Fig. 11.1 Diagrammatic representation of molecular response during heat stress. Relatively adopted from Wahid et al. 2007

Table 11.1 List of crops with their optimum temperature

Crops	Optimum temperature	References
Rice	34 °C	Morita et al. (2004)
Wheat	26 °C	Stone and Nicolas (1994)
Pearl millet	35 °C	Ashraf and Hafeez (2004)
Cool season pulses	25 °C	Siddique et al. (1999)
Groundnut	34 °C	Vara Prasad et al. (2000)
Cotton	45 °C	Rahman et al. (2004)

high-temperature condition. The survival rate is more in acquired thermotolerance as compared to basal thermotolerance (Mittler et al. 2012).

11.3 Biochemical, Physiological, and Phenological Aspects with Respect to Cereal Crops

Of the environmental variants, the temperature is one of the major stress causing gradients in plants, largely the cereal crops viz., wheat, rice, maize, sorghum, and other coarse grains are among key sufferer. As per forecast made by IPCC, the

average temperature of earth's surface would increase in the range of 1.4–5.7 °C by the end of 2100 (Anonymous 2007). This prediction regarding the climatic variability would exert deleterious impact on the primary trophic level in terms of phenology, physiology, and biochemistry of plants.

11.3.1 Phenological Aspects

Phenology is the study of cyclic and seasonal natural phenomenon especially in relation to climate and plant life (Keller 2015). With regard to plant phenology, high temperature generates the alterations in biological events, such as bud break, flushing, flowering, and fruit development (Gray and Brady 2016). Although all developing stages are highly temperature sensitive, pollination is among the most susceptible phenological stages, as the viability of maize pollen reduces significantly with exposure to temperatures above 35 °C (Herrero and Johnson 1980; Schoper et al. 1987; Dupuis and Dumas 1990). According to literature, the optimum temperature requisite for wheat cultivation ranges between 18 and 24 °C and a slight increase (1–2 °C) in the required range is projected to alter the wheat phenology and production by 6% (Asseng et al. 2015). At this increased temperature range, plants exhibit accelerated rate of anthesis, shorter grain filling rate and duration, reduced pollen sterility, declined germination ratio, and suppressed yield (Yin et al. 2009; Chakrabarti et al. 2013; Barlow et al. 2015; Kumar et al. 2017). Besides mentioned alterations, the warming climate has also been recognized as a shifting factor in the flowering regime of the wheat crop. The strong correlation between traits like pollen viability, pollen production, anther dehiscence, and seed-set under heat stress has made these traits important parameters of reproductive success. These parameters can be used as candidate traits for selection in breeding programs. It is reported that in rice, anthers dehiscence is easier in heat-tolerant cultivars than susceptible cultivars (Prasad et al. 2006; Jagadish et al. 2010).

11.3.2 Physiological Aspects

Among physiological processes, photosynthesis has known as a significantly weaker section in response to elevated temperature. In general, the rising temperature remarkably affects the photosynthetic activity of plants, influencing moisture content of leaves, opening, and closing of stomata, level of CO_2 concentration within the cell (Allen and Ort 2001; Anjum et al. 2011). According to Hatfield and Prueger (2015), high temperature speeds up the phenological processes. However, no significant impact on leaf area or vegetative biomass could be seen in maize, besides the reduction in grain yield. The structural components of the chloroplast are greatly affected, including the variation in thylakoids, granum stacking, and swelling with markedly reduced photosystem II, causing damage to cellular cytoplasm, cell destruction, and hence cell death (Havaux 1993; Wang et al. 2009; Allakhverdiev et al. 2008; Chen et al. 2012). Moreover, the rising temperature disrupts the protein

machinery, RNA synthesis, enzymatic interaction, and activity of the cell. This cellular disturbance and imbalance and improper functioning consequently influence the growth and development in wheat, maize, millet, and other cereals (Das and Roychoudhury 2014; Ergin et al. 2016).

In general, certain plant species rely on temperature cues to regulate flowering under warmer conditions and greatly affected with rising temperature, resulting in altered flowering time, nectar, and pollen (Wigge 2013; Thines et al. 2014). Being temperature sensitive, physiology of flowering plants is regulated by various pathways, measuring day length, or photoperiod. Therefore, flower traits under warmer conditions differ in size, anthesis, scent, pollen, and nectar contents (Scaven et al. 2013). Sagae et al. (2008) illustrated the reduced floral scent and increased the content of nectar and sugar with increasing temperature. High temperature also governed the pollen performance as well as its composition within the plant species. A decline of 30–50% in pollen content and its viability was reported by Prasad et al. (2003). Furthermore, high temperature degrades pollen germination, pollen, and spikelet fertility beyond 33 °C in rice cultivation (Yang et al. 2017). Similarly, in wheat, shortened duration of grain filling, reduced weight of kernel and reduced yield are temperature determinants above 37 °C (Xie et al. 2015). Akin to variations above, sorghum exhibits compressed chlorophyll level, decreased photosystem II, weaken antioxidative capacity, decreased content of reactive oxygen species, and impaired thylakoid membrane at 40 °C (Prasad et al. 2008; Jain et al. 2010; Prasad et al. 2015). In maize, however, the temperature spectrum of 33–40 °C causes poor ear growth at pre-anthesis and silking stage, coinciding with 15 days of crop age (Lizaso et al. 2018).

The enzyme-mediated metabolic pathways are sensitive to the elevated level of temperature. It poses stress by generating the excessive amount of reactive oxygen species (ROS), leading to oxidative stress (Xia et al. 2015; Mignolet-Spruyt et al. 2016; Sewelam and Schenk 2016) within plant parts. The uncoupling might have caused the deposition of various components of stress causing agents, viz., superoxide radical, hydrogen peroxide, hydroxyl radical (Tripathy and Oelmuller 2012; Das and Roychoudhury 2014). Moreover, the oxidative stress is generated by means of ROS which is produced by the leakage of electrons into the thylakoid membrane of the chloroplast, wherein it disrupts the stability of the cell membrane. This thermal stress in plants enhances the enzymatic activity which consequently increases malondialdehyde (MDA) content in rice (Hurkman et al. 2009). However, in wheat, heat stress causes the enzyme deactivation and cell viability deterioration. Additionally, the high temperature is known to reduce the thermostability to the tune of 28% to 54% resulting into enhanced electrolyte leakage in wheat leaves (Xu et al. 2006). However, in sorghum, the peroxidation in lipid membrane causes injury to lipid membrane enabling the influx of H_2O_2 and O_2 (Cao et al. 2009; Tan et al. 2011). On the other hand, the root growth in wheat inhibited by the heat stress and significantly increased the concentration of reactive oxygen in root cell, and MDA content in seedlings was proposed by Rodríguez et al. (2005). The hindrance of the rate of evapotranspiration and soil moisture deficits may affect the agricultural activities due to climatic variability (Gunawardhana and Silva 2012).

Parameters like electron transport rate, enzyme viability, and membrane integrity have also been used for screening heat-tolerant crops (Cottee et al. 2010). In many crops, to characterize genetic variability in acquired thermotolerance, chlorophyll accumulation assays have been used (Selvaraj et al. 2011). In wheat, for instance, heat stress-induced damage of the thylakoid membrane is closely associated to chlorophyll loss, and detection of chlorophyll content has been proposed as high-throughput screening method for tolerance to heat (Shah and Paulsen 2003).

11.3.3 Biochemical Aspects

The biochemical reactions involved in plant growth are quite temperature sensitive; hence the vegetative and reproductive stages show increased activity of antioxidant enzymes, viz., peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT), under stress conditions. At extreme climate, particularly high-temperature stress, the plants show the accumulation of primary metabolites, including glycinebetaine, or soluble sugars. Among secondary metabolites, polyphenols like flavonoids, anthocyanins, and plant steroids are active to facilitate the protection, enabling the plant to withstand under adverse conditions (Wahid 2007; Bita and Gerats 2013). In addition to plant metabolites, the level of phytohormones like abscisic acid (ABA), salicylic acid, and ethylene rise, however, that of cytokinin, auxin, and gibberellic acids, declines in the response of high-temperature stress, resulting into premature plant senescence. This imbalance produced under stressed conditions in plants causes the nutritional alteration, undigestibility, and compromising yield quality (Larkindale et al. 2005; Bita and Gerats 2013). The raised polyphenol level plays a significant role in plant defense by ROS detoxification, reduction in microbial activity, and disintegration of enzymes. Besides polyphenol activity, high sugar content serves as a substratum in plant defense (Pandey and Rizvi 2009; Ferdinando et al. 2014).

11.4 Molecular Mechanisms of the Plant in Response to Heat Stress

Plasma membrane acts as the first sensor for heat stress, inducing changes in plasma membrane fluidity resulting in triggering downstream molecular responses (Mittler et al. 2012). At the molecular level, the change in response to heat stress is very complex but conserved across different plant species. There are many heat-responsive genes in plants identified via transcriptomic or proteomics approaches. It can be divided into two main groups, namely, transcriptional factors and structural genes. Transcriptional factors act as central regulators of the heat stress response such as heat shock factors (Hsf genes) (Scharf et al. 2012), (NAC genes) (Shahnejat-Bushehri et al. 2012), etc. Structural genes also play an important role in conferring thermotolerance such as heat shock proteins (Hsp) (Lindquist and Craig 1988), antioxidant enzymes, e.g., SOD, ascorbate peroxidase (APX), CAT, late embryogenesis abundant proteins (LEA), dehydrins, etc. (Mazorra et al. 2002; Wahid 2007).

11.4.1 Heat Shock Factor (Hsf)

Heat shock transcription factor belongs to winged helix turn helix types (Harrison et al. 1994). They possess various domains such as DNA binding domain, an oligomerization domain, nuclear export signal (NES), activation domain, and nuclear localization signal (NLS) domain. In the plant, there are three classes of Hsfs (classes A, B, and C); among these HsfA class especially HsfA1 and HsfA2 are mostly studied, and regulating mechanism in response to abiotic stress is well understood (Liu et al. 2011; Nishizawa-Yokoi et al. 2011). The HsfA1 group plays an important role in imparting thermotolerance in tomato (Mishra et al. 2002). Heat shock factors regulate the expression of heat shock proteins via heat shock elements in response to heat stress. Under normal condition, Hsf exists in monomer form in the nucleus. However, under stressed condition trimerization of Hsf monomer take place.

11.4.2 NAC Genes

The NAC genes constitute one of the largest plant transcription factors family, e.g., 151 in rice (Nuruzzaman et al. 2010). The NAC term derived from three genes, namely, no apical meristem (NAM), Arabidopsis transcription activation factors (ATAF), and cup-shaped cotyledon (CUC). The N terminal of NAC protein is highly conserved in nature but the C terminal shows divergent and it possessed functional domain (Ooka et al. 2003). Many of the NAC gene expression are induced by hormones like ABA and abiotic stresses such as *SNAC2*, *NAC6*, *NAC10*, etc. (Nakashima et al. 2009; Nuruzzaman et al. 2013). It is involved in the regulation and fine-tuning of many defense-responsive genes. The *ANAC042* enhances plant survival after heat stress via regulation of thermomemory-related expression (Shahnejat-Bushehri et al. 2012).

11.4.3 Hsp Genes

Many of Hsp genes are well characterized in regard to heat stress response. They help in proper folding of proteins, prevent denaturation, and aggregation (Borges and Ramos 2005). Based on their molecular weight, there are five main classes, namely, Hsp100, Hsp90, Hsp70, Hsp60, and small Hsp (Schlesinger 1990). The N terminal possessed ATPase activity and well conserved as compared to C terminal having peptide binding ability (Craig et al. 1993). The Hsp100 and small Hsps play an important role in thermotolerance, protein disaggregation, etc., whereas Hsp90 and small Hsps help in the stabilization of misfolded protein and interact with other signaling molecules. The Hsp70 and Hsp60 assist in proper folding of proteins (Park and Seo 2015).

11.4.4 Antioxidant Enzymes

Heat stress generates reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet-}$), hydroxide radical ($OH^{\bullet}$), etc., which has a toxic effect on the cell, cellular organelles, and other cellular functions. For example, the plasma membrane is the first to sense heat stress (Mittler et al. 2012). Lipid peroxidation and other redox reaction take place which results in a change in the level of membrane stability index. The level of ROS is checked by various antioxidant enzymes such as CAT, SOD, APX, etc. (Chaitanya et al. 2002). These antioxidant enzyme activities are used to observe and to estimate the degree of thermotolerance.

11.4.5 LEA Proteins

Late embryogenesis abundant proteins (LEA) name arise due to their high accumulation during seed maturation and have a significant role in overcoming water deficit condition. Based on motif types, there are five main groups, namely, LEA I, LEA II, LEA III, LEA IV, and atypical LEA proteins (Battaglia et al. 2008). LEA proteins secure integral membrane proteins and mitochondrial membrane during dehydration condition via behaving itself as water replacement molecules (Caramelo and Iusem 2009).

11.5   Approaches to Tackling Heat Stress in Agronomic Crops

11.5.1 Conventional Breeding

Since the onset of civilization, agriculture was considered as one of the major sources of livelihood. Earlier breeders select the naturally occurring wild type and cultivated field variants as better crops for breeding purpose. The selected better varieties were served as the donor parent for the development of high yielding varieties through conventional breeding. Conventional breeding or traditional breeding was used by the farmers since the origin of agriculture until the 1760s. The successful results of the first hybridization experiment carried out by Kölreuter limited the use of conventional breeding (Roberts 1929). Conventional breeding approach helped in reducing the negative effect of heat on the crop. In conventional breeding for heat stress tolerance, the development of high-temperature-tolerant plant is carried out in the climacteric region by selecting parent lines that perform well under hot conditions (Mickelbart et al. 2015). In regions with high temperature, the thermotolerant feature is mainly selected by local breeders as the crop from the warmer region is more tolerant to heat then the crops from the cooler region. This technique has proved great importance for developing thermotolerant crop via conventional breeding (Smillie and Nott 1979; Momonoki and Momonoki 1993; Tonsor et al. 2008; Yamamoto et al. 2011; Kugblenu et al. 2013). A cross between Indonesian "Peta" and Taiwan "Dee Geo Woo Gen" varieties leads to the development of semi-dwarf (sd1) IR8 was the

first variety of rice with higher harvest index. The sd1 IR8 rice variety performed better in nitrogen fertilizers conditions and became the symbol of a green revolution in spite of having poor grain quality (Khush et al. 2001). International Rice Research Institute had developed 200 rice varieties via the conventional breeding method. IR32, IR36, IR40, IR42, IR64, and IR72 are some of the superior rice lines developed by IRRI. One of the developed variety IR64 inherited the property of multiple and durable resistance to pests and diseases, tolerance to abiotic stresses, wide adaptability, and good response for agronomic practices and management (Khush 1997). Limitations of conventional breeding in developing heat-tolerant lines is that the physiological and genetic bases of the improvement is not clear in this method which further creates a hurdle for the development of markers (molecular and biochemical) that can be used for efficient breeding programs. Moreover, the use of cross-specific advanced starting material in conventional breeding program indicates that potential gain over heat stress is restricted by low genetic diversity (Ladizinsky 1985; Paran and Van Der Knaap 2007). The discovery of laws of heredity during the nineteenth and twentieth century provided the insight into hybridization in plant breeding and most of the breeding program presently involves the use of hybridization (Wilks 1990; Xu 2010). The limitation of the conventional breeding program was overcome by the introduction of modern or molecular breeding which involves the use of molecular markers.

11.5.2 Modern Breeding Approaches

The discovery of molecular marker in the nineteenth century and the limitations of conventional breeding create the platform for modern breeding approaches. Genetic correlation between different traits in a specific crop has made it difficult to improve all the desire traits at the same time. Improvement of the crop for a particular trait would influence the correlating traits both in the favorable and unfavorable way (Falconer and Mackay 1996). Pleiotropic genes, the physical linkage between genes in the chromosomes and population structure also affect the breeding techniques (Hartl and Clark 1997). Modern breeding includes marker-assisted selection, QTL mapping, and association mapping approaches to develop new and improved crop.

11.5.2.1　Marker-Assisted Selection

Marker-assisted selection (MAS) is one of the precise breeding techniques which is based on the utilization of marker (morphological, biochemical, and molecular) for selection of specific traits (e.g., biotic, abiotic stress tolerance, productivity, and quality) of a particular crop. This technique is an indirect selection method (Ribaut et al. 2001). The MAS technique has revealed the genetic basis of both biotic and abiotic stress tolerance in crops which helped the crop to cope up with these stresses (Lopes and Reynolds 2010; Thomson et al. 2010). Genotype × environment or gene–gene (i.e., epistasis) interactions resulting in low breeding efficiency has affected the MAS technique for heat stress which is a complex trait (Collins et al. 2008). Marker-assisted selection has been used in wheat for powdery mildew

disease (Zhou et al. 2005); in rice for bacterial blight (Chen et al. 2000, 2001), blast (Liu et al. 2003), deep roots (Chen et al. 2001) submergence tolerance (Mackill 2006; Toojinda et al. 2005), root traits and aroma (Steele et al. 2006); quality, disease resistance (Toojinda et al. 2005).

11.5.2.2 Qualitative Trait Loci Mapping

Qualitative Trait Loci (QTL) mapping is used to identify specific chromosome segments containing candidate genes for biotic and abiotic stress tolerance (Argyris et al. 2011; Zhang et al. 2012). The QTL mapping is a method of choice and is attaining attention across the globe because of its efficiency in identifying loci related to stress tolerance in crops. Qualitative trait loci-based mapping is used to have insight into the tolerance mechanism and to identify markers related to different stresses. Various reports on QTL-based stress tolerance studies have already been established earlier (Hirayama and Shinozaki 2010; Roy et al. 2011). Numerous QTLs related to heat stress tolerance have been reported in various bi-parental populations like in rice at flowering stages (Ye et al. 2012; Li et al. 2018), wheat (Paliwal et al. 2012) and maize (Bai 2011). The QTLs linked to different traits like thousand-grain weight (TGW), the GFD, CTD, yield are used to identify heat-tolerant varieties (Pinto et al. 2010). Traits related to plant senescence can also be used to identify tolerant varieties (Vijayalakshmi et al. 2010). Recently, a recombinant inbred line wheat population was used to identify QTLs related to well-irrigated, heat, drought stress conditions explaining variation up to 19.6% in grain yield in the drought, heat, and combined stress trials (Tahmasebi et al. 2016).

11.5.2.3 Association Mapping

Association mapping is a linkage disequilibrium (LD)-based high-resolution mapping method which is used to identify various biotic and abiotic stress-associated traits with the help of molecular markers (Varshney et al. 2009). Linkage disequilibrium is termed as the "non-random association of alleles at two or more different loci" in a population (Flint-Garcia et al. 2003; Slatkin 2008). The LD is the best method to study the strength of correlation between markers due to their shared genetic history. Pair of SNP marker helps in identifying the degree to which an allele of one SNP is inherited or correlated with an allele of another SNP within a population (Bush and Moore 2012). Association mapping studies are more advanced than QTL analysis because in the former, the mapping population is comprised of diverse germplasm. This approach required the phenotypic and genotypic data of the population along with the genetic knowledge of the germplasm (i.e., population structure) for identifying the association. Nowadays, association genetics could assist QTL mapping in identifying QTLs linked to a specific trait in different crop species (Ahuja et al. 2010; Yano et al. 2016). Based on the present knowledge of association mapping, there are two key factors which will help this approach in the near future: integration of functional analysis or gene annotation data, i.e., post-GWAS research (Zhang et al. 2014), and use of improved statistical and computational methods (e.g., STRUCTURE analysis, haplotypes, and SNP imputation). A

numerous heat stress tolerance genes in different crops have been identified via association mapping approach.

11.5.3 Biotechnological (Genetic Engineering) Approaches

The G × E interaction, epistatic effect, the effect of minor QTLs on major QTLs in breeding program, limits the importance of breeding in the development of tolerance crops. Moreover, the time is taken and intensive task in conventional breeding to produce an improved variety has also limited this technique used in developing tolerant crops. With the increase in population and a decrease in crop productivity due to global warming, there is a need to develop "smart crop" to feed the ever-growing population. Thus, to overcome this problem, genetic engineering an emerging field in biotechnology has gained worldwide attention. Genetic engineering helps in transfer of desire genes into a susceptible variety to develop transgenic crops. A desired gene can be transferred in a variety by direct and indirect transfer methods. Most commonly used transgenic method for development of transgenic crop is *Agrobacterium*-mediated gene transfer method and biolistic bombardment method. In this approach, firstly, desire gene is identified and then it can be transferred between the species and across the species either by a direct or indirect transfer technique. Like in gene pyramiding, multiple desire genes can be transferred via genetic modification in the same plant with the help of engineered promoters (Datta et al. 2002). The availability of standard transformation protocols for many food crop species has made the gene transfer process easy. In spite of great importance, transgenic crops are not used on a large scale due to certain restrictions and ethical issues. For cereal crops like wheat, rice and barley gene transfer methods have low efficiency due to the transfer of non-desire genes along with the desired ones or sometimes the desired gene does not express in the specific tissue (Takeda and Matsuoka 2008). Thus, to overcome this problem, stress-inducible and tissue-specific promoters have been used to provide stress tolerance along with high yield potential and prevent the negative effects of a stress gene on plant growth under favorable conditions (Nakashima et al. 2007). Recently, transcriptome engineering has been used to engineered stress-tolerant plants. In this method, specific transcription factors and signaling components are used to generate transgenic with an expression of various stress tolerance genes. Approaches like functional genomics, proteomics, metabolomics, and economics have also been used for the development of tolerant crop variety.

11.6 Conclusion

Identification of key heat-responsive genes and development of thermotolerance plant will be a crucial approach as per environmental changes prevailing now and anticipated near future is concerned. In addition, rapid population growth also posed

a threat to limited crop production. So, the development of thermotolerance plant will substantiate the crop production under global warming impact.

11.7   Prospect

Transgenic/trans-genomics and molecular breeding have a major role in the development of thermotolerance plant. Combination of functional genomics, proteomics, and phenomics will be the approaches in the near future that will help in clearing the pathways and their hierarchical order involved in thermotolerance.

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Agronomic Crop Responses and Tolerance to Metals/Metalloids Toxicity

12

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Abstract

The cultivation of crops for food production has been tremendously increased with the increasing world population. Various crops are being used for food, fiber and oil extraction, edible seeds and leaves, land reclamation, and fuel purposes. The applications of fertilizers has also been increased to fulfill high demand for agronomic crops. Several anthropogenic and natural activities have resulted in soil pollution in agriculture lands. Different types of contaminants including metals and metalloids accumulate in the soil ecosystem which are taken up by plant roots and cause various types of stresses in plant physiology which can lead to dysfunctions and disorders in many processes and mechanisms of plants. In response to the stress of metals and metalloids, plants show different types of mechanisms to resist or cope with this type of stress. Each and every plant shows different mechanisms against different heavy metals to reduce or tolerate their effects. Plants also secrete different enzymes through root exudates which also lessen the harmful impacts of metals and metalloids. Plants also exhibit defensive mechanisms by forming a mycorrhizal association. The tolerance of metals and metalloids stress is also governed at a cellular level, and different organelles are also involved in mitigating their toxic effects. Different cell organelles like plasma membrane and cell wall also show complete inhibition or permeable absorption of these contaminants. In response to the high stress of metals and metalloids, plants also secrete heat shock proteins to prevent the injuries caused by these pollutants. In addition to heat shock proteins, plants also excrete phytochelatins through their roots in the rhizosphere to fix these metals and their metalloids. Plants also exhibit

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response under these stresses at the molecular level and modify genes for expression of stress conditions. Therefore, it is clear that agronomic crops have adapted various kinds of mechanisms and processes which can reduce the toxic and harmful effects of metals and metalloids in order to show proper growth.

Keywords

Abiotic stress · Environmental pollution · Cadmium · Xenobiotics · Phytotoxicity

12.1   Agronomic Crops

With the increasing trend of the population, the demand for food has also increased day by day. To cope with this situation, different crops are being cultivated specifically for purposes such as (1) oil extraction, for example, canola, soya bean, sunflower, mustard, sesame, linseed, and flax; (2) fiber extraction, for example, cotton, jute, sun hemp, sisal, sun kukra, and flex – this fiber is used to make clothes, ropes, bags, and other accessories (Kranner and Colville 2011); (3) edible seeds, for example, maze, rice, wheat, oat, barley, sorghum, and millet; and (4) edible leaf, shoot, and fruit, for example, spinach, garden pea, pumpkin, tomato, cabbage, okra, eggplant, broccoli, asparagus, cucumber, and cauliflower (Shahid et al. 2015a, b).

Abovementioned crops are known as the agronomic crops. The science and technology that produces and uses plants for food, land reclamation, fuel, and fiber is known as agronomy. It involves the selective breeding of plant in order to achieve the best productions under different environmental conditions. This technology had increased the annual crop yields and also improved the nutritional values of various crops, including, soya bean, wheat, and corn. It has also helped in the development of new species of plants, for example, by cross-breeding rye and wheat, a hybrid grain called triticale was produced (Foucault et al. 2013). It contained more useable proteins than either wheat or rye. Agronomy has also played an important role in the research of production of fruits and vegetables. Agronomists are currently involved in dealing with many issues including food production, healthier foods, energy extraction from plants, and minimizing the environmental impacts of the agricultural techniques (Hasanuzzaman et al. 2014).

12.2   Metals and Metalloids Toxicity

In the present era, heavy metals are the most important and effective envoi mental pollutants. The toxicity caused by them is an issue of great importance on the impacts related to ecological and evolutionary processes and environmental and nutritional impacts (Nagajyoti et al. 2010). Heavy metal is a term used to refer to any metallic elements which possess a relatively high range of density. It is usually toxic and poisonous even if exposed at low concentrations (Akpor et al. 2014). These are a group of elements having an atomic number of more than 20 (excluding the alkali metals) and possess specific gravity higher than 5 (Rascio and Navari-Izzo

2010). Some researchers have also stated that these are the elements that have an atomic density greater than 6 gcm^{-3} (except B, Se, and As) (Park et al. 2011). Lead (Pb), nickel (Ni), iron (Fe), chromium (Cr), silver (Ag), cadmium (Cd), and platinum group elements are included in heavy metals. Some of the metalloids are significantly toxic due to the damage caused by them. These are the elements that possess properties in between metals and non-metals. Boron, germanium, silicon, antimony, arsenic, and tellurium are the most important metalloids. Although one member, selenium, is less commonly included in the group of metalloids, it is also toxic. This group mainly consists of transition metals, actinides, and lanthanides. These may be lethal and cause damage to the living organism if they are exposed to them at low concentration (Cuypers et al. 2009).

The 53 naturally occurring elements are reported as heavy metals. Most of these metals do not play any important role in plants functioning. These heavy metals play several different roles in crop production and are of different biological importance (Kavamura and Esposito 2010). The heavy metals that are involved in the important biological functions are Cu, Zn, Ni, Co, Cr, Se, and Mo. These metals have good impacts on plant productivity (Shahid et al. 2015a, b). On the other hand, the metals that are involved in the reduction of crop productivity when their concentration increases to supra-optimal values include Zr, As, Pb, Sb, Hg, and Cd. These elements do not have any important metabolic functions in the plants (Shahid et al. 2013). By the agency for toxic substances and disease registry, As, Pb, Cd, and Hg have been stated as most toxic. This classification was done on the basis of the level of their toxicity, exposure potential, and frequency of their occurrence (Pierart et al. 2015).

12.2.1 Sources and Impacts of Metalloids and Heavy Metals

There are several sources of heavy metals or metalloids contamination in the environment:

1. Industrial
2. Natural
3. Agricultural
4. Atmospheric
5. Domestic effluents

Heavy metal contamination can be caused by natural as well as anthropogenic sources. Large areas of the world have been contaminated by the activities that mainly include mining, agricultural, and smelting operations. China, Japan, and Indonesia are mainly effected by these heavy metals including Cd, Zn, and Cu (Herawati et al. 2000). North Greece is mainly affected by Pb, Cd, and Cu. Albania and Australia were affected by Pb, Cr, Cu, Ni, Zn, and Cd (Lee et al. 2006). Most of these heavy metals and metalloids also have a source known as lithogenic source. Heavy metals in the soil come from various anthropogenic sources and also from the soil parent material and these mostly involved several metalloids. Many of the human-imposed sources of heavy metal and metalloids pollution critically affect

both urban and agricultural soils (Alloway 2013). A localized source such as metals smelter can have a marked impact on the soils, on crops, and also on the health of the local community. This mostly occurs in the countries that have inadequate control techniques of emission and soil quality standards. Commonly at the industrial sights, soil is contaminated with specific groups of heavy metals. It depends on the nature of industries, the raw material used, and the products produced (Chen et al. 2008). Urban area soils are contaminated mainly with lead (Pb), zinc (Zn), cadmium (Cd), and copper (Cu). This occurs mainly because of paints, traffic, and many other non-specific urban sources. Heavy metal (loid) which is a composition of agricultural soils is driven and controlled by a number of other sources than its parent materials; sources include inputs from deposition of aerosol particles which are atmospherically transported from far areas. These occur because of fossil fuel combustion, organic material applications, and contaminants in fertilizers (Wei et al. 2011).

Considerable crop productivity and threats to the health of living beings result from the contamination of soil with heavy metals which causes accumulation of these toxic metals in plants parts. Stockpiling of heavy metals in food crops has been reported by many researchers. Research has highlighted the presence of heavy metals like Cd, Pb, and Zn in the land used for crop production in different parts of the world. Practically, a range of morphological, physiological, and biochemical disorders in the plants are induced because of heavy metals which result in a reduction of crop productivity (Babula et al. 2009). The intensity of toxicity induced by heavy metals may vary and mainly depends upon the exposure duration, concentration of heavy metal, stage of plant development, studied organ, and even plant species.

The most common physiological consequence of the heavy metals exposure to plants is a reduction in growth and development. Structure of leaf and physiology are changed. In addition, there is a reduction in photosynthesis and respiration. Due to the abovementioned changes, the process of metabolism in plants is affected, and there is a reduction in energy production. Moreover, it has also an adverse impact on the processes of transpiration and transportation of materials, between several organs. The ability of roots is also affected resulting in reduced nutrient and water uptake (Garg and Singla 2011). Hence, these mentioned changes in the operational process of the root and leaf affect various developmental processes, which include embryogenesis, flowering, and seed formation. Some direct and indirect impacts of heavy metals on plants are shown in Fig. 12.1 (Shahid et al. 2015a, b).

In plants, phytotoxicity is caused by toxic heavy metals. The phytotoxicity is followed by different disorders resulting in chlorosis, limited nutrient uptake, and decline in the plant growth, development, and yield. Because of heavy metal pollution entry into the food chain, agricultural yields are decreased, and also some hazardous health effects are observed (Carbonell et al. 1998).

Cadmium (Cd) is mainly considered a very toxic element for plants among various heavy metals. It results in restrain photosynthesis and reduces root and shoot growth. Cadmium, establishing a strong relation with the thiol group, results in limiting the activity of many. Furthermore, with lipid peroxide, it plays a role in the creation of different active oxygen species. These species include hydrogen
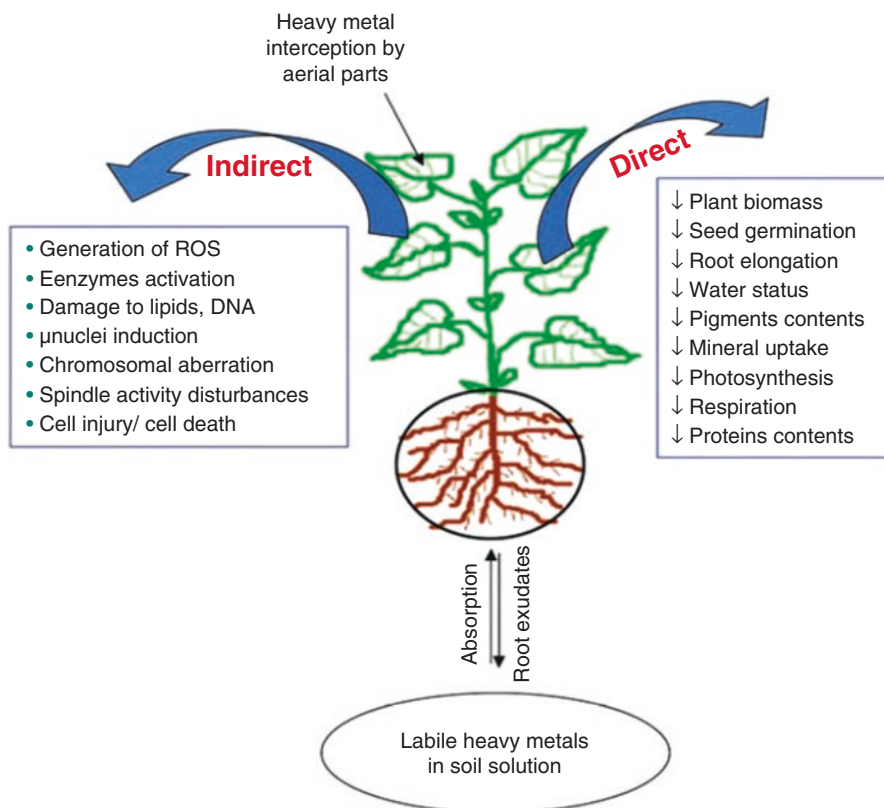
Fig. 12.1 Direct and indirect toxic effects of heavy metals uptake resulting in reduced crop production

peroxide, hydroxyl radicals, and superoxide, causing damage to cell membranes, as well as biopolymers (Ghosh and Singh 2005).

Lead (Pb) is one of the most plentiful toxic element found in the soil. It results in adverse consequences on photosynthetic processes, morphology, and growth of plants. It is also well-known for the inhibition of roots and stems elongation process, and expansion of leaves in *Allium* species, barley (Alloway and Jackson 1991) and *Raphanus sativas*. Moreover, it also causes inhibition of the seed germination in *Spartiana alterniflora* (Saeideh and Rashid 2014). Inhabitation of root elongation is dependent on the concentration of lead, pH of the medium, and ionic composition.

Chromium (Cr) compounds which are toxic are detrimental in plant growth and development, although low concentrations of Cr do not affect some species (3.8 9 10-4lM). For the higher plant species, Cr is toxic at the concentration of 100 l kg-1 dry weight (Kumar et al. 2016). The first physiological process which is adversely affected by Cr presence is seed germination. About 25% reduction was noticed in the process of seed germination of the wild plant Echinochloa colony with 200 lM Cr,

while reduction noticed by the presence of high concentrations (500 ppm) of hexavalent Cr in the bush bean *Phaseolus vulgaris* was about 48%.

Excessive deposition of manganese (Mn) mainly in leaves leads to decrease in photosynthetic frequency. Through the transpiration stream, Mn is transported from the roots of the plant to shoot, but after reaching the leaves, it does not readily remobilize through the phloem to other organs (Kastori et al. 1992). Symptoms of Mn toxicity are the presence of necrotic brown spots on leaves, stems, and petioles. The process of spotting mostly starts on the lower leaves, and then it spread towards upper leaves. The speckles, with time, can increase in both number and size resulting in necrotic lesions, browning of leaves, and eventually death.

The impacts of Cu on agronomic crops were also studied. The results showed that Cu in higher concentrations reduces the biomass because of chlorosis and also affects the photosynthesis by disturbing the electron transport system (Patsikka et al. 2002).

Due to various human activities, Ni concentration is increasing on different sites such as emission of smelters, mining activities, fossil fuels burning, sewage, pesticides, and phosphate fertilizers. The general range of Ni present in natural soils is 10–1000 mg/kg, whereas in contaminated sites, it is 20- to 30-folds higher (200–26,000 mg/kg) (Yusuf et al. 2011). High concentration of Ni in soil may cause various damages to plants including physiological alterations and different toxicity signs such as necrosis and chlorosis in various plant species (Rehman and Shah 2005). These damages were also observed in the rice. Also, the plants which grow in high Ni-contaminated soils displayed the impairment in nutrient balance and disorders of cell membrane function. A study on *Oryza sativa* shoots proved that high Ni concentrations affected the H-ATPase activity and lipid composition of the plasma membrane (Sharma and Dubey 2005).

Recent studies on Hg showed that it readily accumulates in aquatic as well as higher plants (Israr et al. 2006). Plants are badly affected by high levels of Hg, even cells are damaged. High concentrations of Hg cause visible damages and also physiological problems in plants (Savvas et al. 2010). The Hg results in the closure of stomata and physical barrier in the water flow by binding with the water channel proteins. Microbial activity is also affected by the high levels of Hg which ultimately results in oxidative stress. This results in the interruption of cellular metabolism and biomembrane lipids damage in plants (Pandey and Shama 2002).

12.3 Tolerance Mechanism to Metals Toxicity in Plants at the Cell Level

Tolerance mechanism is to infect the capabilities of the plant to survive under toxic conditions in the soil. It can also be defined as those changes in plants which occur due to exposure to high concentrations of metals and metalloids. Different types of mechanisms are involved at the cellular level to detoxify high concentrations of metals and metalloids (Kramer 2010). The tolerance mechanism of some of the metals has been discussed below.

12.3.1 Aluminum (Al) Tolerance Mechanism

Al is found in large quantity in earth's crust and immobilized in the form of alumino-silicates that secretes a phytotoxic ion (Al_{31}) under acidic conditions in the soil. From agriculture point of view, Al is the major restraint for the production of agronomic crops. It is presently ruining more than 40% of arable land worldwide (Chen et al. 2013). Therefore, it is crucial to convert these lands into productive ones for sustainable agriculture production. The Al toxicity causes inhibition of root length. In the root cells of plants, apoplastic injuries have been reported due to Al toxicity. Toxicity of Al also affects some crucial processes such as ion fluxes, characteristics of the plasma membrane, and cell wall assembly (Dawood et al. 2012).

The intercellular transport of different nutrients, water, and hormones (signaling molecules) is carried out by plasmodesmata. It is also known as symplastic intercellular transport to facilitate the movements of essential nutrients and other biomolecules. In context to aluminum (Al), it is not well identified whether Al could affect the transport of nutrients from one cell to another. It is very problematic for roots for being organs for the uptake of nutrients (Amsbury et al. 2017).

It is experimentally studied by injecting the Lucifer yellow carbohydrazide in the root cells of wheat which were sensitive to Al. It was reported that root growth inhibition induced by Al is linked with blockage of dye coupling from cell to cell transport induced by Al. Different techniques have confirmed 133-b-d-glucan (callose) that is the reason for the blockage of nutrients transport. An inhibitor for the synthesis of callose gave the idea that a decrease in callose particles is linked with developed dye coupling. It is analyzing the targeted tissues by dye coupling in mesophyll cells of tobacco (*Nicotiana tabacum*). Plasmodesmata linked proteins such as calreticulin and myosin VIII increased fluorescence with callose formation. Therefore, it is confirmed from this study that callose induced by Al can block the transport of nutrients and coordination in higher plants. The Al toxicity is linked with dysfunctions of mitochondria and reactive oxygen species (ROS) within plant cells (Sharma 2018).

12.3.2 Copper (Cu) Tolerance Mechanism

Copper is a very important nutrient for proper growth and development of plants. In addition to its essentiality, it is highly toxic at high concentrations. The Cu takes part in various physiological processes and acts as metalloproteins. The optimum concentration of Cu is required by the plants, and excess Cu concentration results in toxicity which creates a problem at the cellular level. Cu toxicity causes inhibition of plant growth and impairment of many cellular processes like photosynthetic electron transport. Therefore, Cu acts as an important nutrient as a cofactor and the toxic element at the same time depending upon the concentration and metal trafficking routes (Wang et al. 2018a, b, c). Several types of approaches have been introduced to maintain cells at homeostatic levels. These types of metals should avoid storage of metals in the active forms to detoxify the metal toxicity. This strategy is also involved in the transport of this nutrient to targeted metalloproteins. Several specified genes have been reported recently which act as copper transporters (Wang et al. 2018a, b, c).

12.4   Enzymatic Role in Response to Toxicity in Agronomic Crops

Different concentrations of metals and metalloids have been found in the soil deposited through industrial or agricultural activities. The uptake of these metals by the plants can result in several types of disorders and dysfunction in plants depending upon the concentration of metal and metalloids. These high concentrations can inhibit the activity of some enzymes and can also increase the induction or activities of others (Bolan et al. 2014).

Two mechanisms are involved in the inhibition of enzymes. First is the attachment of that specific metal to the sulphydryl groups which acts as catalytic action and structural integrity of various essential enzymes. Second is the deficiency of any crucial metal in metalloproteins which are later on associated with the alternative of harmful metal for the deficient nutrient or metal. In vivo, metal is accumulated in the cells of enzymes which is a requisite for inhibition of enzymatic activity (Caverzan et al. 2014).

The initiation of some enzymes is believed to play a vital role in the metabolism under stress conditions which is caused by metal toxicity. The induction of peroxidase is nearly linked to oxidative reactions in biomembrane. Various enzymes in the metabolism of different intermediates could be induced to balance for responsive metal crops. The isoperoxidase pattern is also affected by metal toxicity and can be treated as a tool to evaluate phytotoxicity in agronomic crops (Ent et al. 2012).

The toxic concentrations of various metals have been found in nature, but they are frequently originated by agricultural and industrial activities. Some of the sources include mining, pesticides, sludge, waste disposal, and fertilizers, and nonferrous industries are the major sources of pollution in aquatic and terrestrial environments (Hattab et al. 2015).

The interactions of enzymes with metal and metalloids interpret the toxicity of these compounds. These metals (Cu, Cd, and Zn) are toxic at different concentration to plants. These contaminants are found everywhere, and their concentrations can reach up to very toxic levels. These metals are absorbed by the roots of plants readily (Mitton et al. 2016). Some heavy metals are toxic under certain conditions of soil such as Ni, Co, and Pb. The bivalent cations of these metals are categorized in borderline class on the basis of their affinity for ligand formation (Toth et al. 2016).

The toxicity of various metals in appropriate concentrations causes chlorosis, red-brownish discoloration, and leaf epinasty. The enzymatic activity at cell level is inhibited substantially. Moreover, the activity of other enzymes can enhance significantly. The interaction of enzymes with metals is consisted of following aspects-.

1. The metals or metalloids should be absorbed by the plants and stored at their inhibitory concentrations in specific compartments of the enzymes. The interactions of metals deposited on the leaf surface or stored in apoplast, vesicles or vacuoles with most of the enzymes are not included.

2. In vivo, the chemical species of that particular metal must be interacted with enzymatic functional ligands. The formation of phytochelatins complexation and attachment of other compounds bound to metal.
3. The tendency of a metal to attach or bind with the functional ligand should be strong. The interaction involving SH-group is usually supposed as an important step for the mechanism.
4. The high concentration of metal uptake can cause a deficiency of many other essential nutrients which can ultimately affect the balance of cations at the subcellular level. Substitution or competition is involved, or binding site depends upon the presence of similar cations in concerned compartments of cells (Jaskulak et al. 2018).

12.5 The Defensive Mechanism by Plants Against Metals and Metalloids Toxicity

Heavy metals are very crucial for proper plant growth and development of all parts of plants. These metals are a very important part of several proteins and enzymes. The high concentration of macro and micronutrients can cause toxicity in the soil which will ultimately affect the plant growth when it becomes available to plants in excess amount. This toxicity results in different types of symptoms which can be observed at cell level as well. The activity of enzymes can be inhibited by combining these metals with sulphydryl groups of proteins (Aroca et al. 2015). Moreover, it can also cause displacement of crucial nutrients causing a deficiency of that element. Due to excess of these metals, free radicals and oxygen species can cause oxidative stress in the plants. It has been reported that plants have adopted some mechanisms in metalliferous soils to cope with high concentrations with homeostasis. Plants have several mechanisms at the cellular level to detoxify and tolerate high concentrations of metals (Boyd, 2007).

Various strategies have been shown in the plants to avoid metal toxicity. Extracellularly, plants exhibit roles for cell wall, extracellular exudates, and mycorrhizae. Cell membrane also plays its role in the reduction of uptake of heavy metals and stimulation of pumping the entered metals out from cytosol. Other mechanisms are also present within the protoplast such as the repair of damaged proteins due to metal stresses. Some proteins known as heat shock proteins or metallothioneins, which are responsible for metal chelation by producing amino acids or organic acids and their transport away from metabolic compartments in the vacuoles (Bothe, 2011).

The adaptive mechanisms to high toxic levels of metals are controlled only by some specific modified genes. Only a molecular change is needed to make the plant resistant or tolerant against any particular metal toxicity (Cappa and Pilon-Smits 2014). There are no co tolerance mechanism exits for more metals at the same time. For each metal, there is a specific mechanism which is involved for tolerance to its high toxic level. The most widely studied metals which lead to drastic changes in the plant functions and other metabolic processes are Cd, Cu, Zn, and Ni. Plants exhibiting tolerance to the high concentration of these metals are known as

hyperaccumulator due to their potential to accumulate more quantity or concentration of metals (Cui et al. 2014). So, there are different mechanisms which are involved in detoxification and tolerance to metals in agronomic crops.

12.5.1 Mycorhhizal Association

It has been reported that mycorrhizal association are also involved and ameliorate the toxic effects of metals. Metal tolerance with this association is very diverse and can vary from species to species of both plants and fungi. A research showed that an ectomycorrhizal fungus *Paxillus involutus* accumulated Zn contents and the toxicity to Zn in *Pinus sylvestris* was reduced. The amount of metals accumulated in different species of fungi also varies. The associated fungi with plants also exhibit the same mechanism to detoxify the metal stress by extracellular binding to materials and storage in the vacuoles (Chang et al. 2018). Different fungal species show different mechanisms to different metals toxicity. For example, *Paxillus involutus* shows the attachment of Cd to cell wall and accumulation in the vacuoles while *Pisolithus tinctorius* exhibited the tolerance to Zn and Cu by extrahyphal slime. Most of the processes are exclusion ones which prevent the entry to host plants (Huang et al. 2018).

Hyphal sheath is involved in the absorption of metals, metal chelation to exudates of fungi, and surface attachment on the external mycelium. Glomus isolate (Br1) obtained from Zn polluted soils has been reported to support the growth of maize and alfalfa on Zn contaminated soils. The microbeam analysis shows that the growth in maize plant was due to the immobilized form of Zn in the root tissues containing fungal hyphae (Zhan et al. 2018).

12.5.2 Cell Wall and Root Exudates

The properties of the cell wall to attach certain metals also remain of particular interest. The cell wall is in direct contact with the extracellular solutions and involved in less adsorption of metals and has little effect on the metal activity on the surface of the cell membrane. However, in some studies, it has been shown that a metal tolerant species *Silene vulgaris* stored a number of heavy metals inside into epidermal cells of cell wall by combining with proteins and silacates. In another study, it was found that Ni-chelating exudates have been stored in non-hyperaccumulators (Kumar et al. 2015).

Root exudates also play a vital role in tolerance to metal toxicity. These exudates consist of many compounds including metal chelators which can increase metal uptake sometimes. The compounds secreted by plants and fungi are large in number, these exudates might play a role in detoxification or tolerance to other elements toxicity. It can be explained with an example like buckwheat secrets oxalic acid under Al stress from the roots and store Al in the leaves (Wang et al. 2018a, b, c).

12.5.3 Plasma Membrane

The cell membrane is considered the first living structure which is exposed to metal toxicity. The functions of the plasma membrane are also affected by the metal toxicity. Under high concentrations of metals, the plasma membrane enhances the leakage of other essential nutrients from the cells as in the case of Cu (Hall 2002). It has been reported that under stress conditions of Cu, not Zn, the efflux of K^+ ions increased from the roots of *Agrostis capillaris*. Cu toxicity also causes damage to cell membrane due to ionic leakage from the cell. Cu and Cd also have a direct effect on the lipid composition of the cell membrane and also involved in the inhibition of certain cellular proteins. This metal toxicity leads to damaged permeability of cell membrane (Lange 2017).

In contrast to Cu, Zn plays its role to control leakage of ions from the cells and protects the membrane from oxidation. The integrity of the plasma membrane might be increased after damage in the presence of other heavy metals. The plasma membrane is also involved in the homeostatic conditions by preventing the entry of certain metals to cells due to its selectively permeable membrane characteristic. For example, in *Holcus lanatus*, the high concentration of arsenic (As) is controlled by arsenate-tolerant genotype which lowers the uptake of As from roots (Goolsby and Mason 2015).

12.5.4 Heat Shock Proteins

Due to the presence of these proteins, many organisms have shown their growth above their optimal growth temperatures. These proteins are present in all kind of living organisms and exhibit this phenomenon under stress conditions including high concentrations of metals as well. These heat shock proteins protect and repair proteins under metal toxicity (Becker and Dierschke 2008). It is reported that under high temperature and metal concentrations, these proteins in rice enhanced the number of mRNAs for low heat shock proteins. *Armeria maritima* also showed response to heavy metals by secreting HSP 17 which were expressed when this species was grown in Cu-rich soils. *Silene vulgaris* and *Lycopersicon perovianum* also showed an increased quantity of heat shock proteins under stress of various heavy metals (Antosiewicz et al. 2014).

12.5.5 Phytochelatins

Metal chelation in the cytosol of the cell due to ligands having a high affinity is the most important mechanism for the tolerance and detoxification of metal toxicity. These potential ligands consist of organic acids and amino acids. In addition to these ligands, there are other two classes, namely, metallothioneins and phytochelatins. A huge research has been made on the phytochelatins due to Cd tolerance in

plants. Phytochelatins belong to peptides which are produced under stress conditions of metal toxicity (Li et al. 2012).

In addition to phytochelatins, metallothioneins, organic acids, and amino acids are also involved in the tolerance and detoxification of metals. Vacuolar compartments are also involved in the storage of these toxic metals. This is also an important mechanism involved as others like a cell wall, root exudates, peptides, and plasma membrane (Dundar et al. 2015).

12.6 Coping with Various Toxic Levels of Metals

Pollution especially environmental pollution is a major threat to human life. Heavy metals which are toxic present as a component in soil can be transmitted to the environment through agricultural technologies and human activities (Dal Corso et al. 2008). Such contamination has two main aspects: firstly, reducing the yield of the crop by interfering the life cycle of the plant, and secondly, once these toxic metals are uptaken and stored in plant tissues, it will pass in the food chain and will cause damage to humans and animals (Bies-Etheve et al. 2008).

Like all other organisms, plants have developed a complex network of standardized mechanisms to minimize the damage caused from non-essential metal exposure. Plants have developed strategies active and passive to exclude heavy metal ions from the cellular environment to resist metal toxicity (Sharma and Dietz 2009). Plants have developed many strategies to deal with the adverse effects of heavy metals. In plants, the toxicity of heavy metals leads to excessive production of ROS, which leads to the peroxidation of many important components of the cell. To deal with this unfavorable situation, the plants have an effective defense system consisting of a group of enzymes and non-enzymatic antioxidants.

Many types of enzyme antioxidants consist of SOD (superoxide dismutase), POD (peroxidase), GST (glutathione-*S*-transferase), and CAT (catalase), which can convert superoxide radicals into hydrogen oxides, which is then converted to water and oxygen, while the non-enzymatic oxidation of low molecular weight antibodies consisting of proline, glutathione, and ascorbic acid neutralizes the toxicity ROS (Yadav et al. 2014). These two groups of antioxidants can address a wide range of toxic oxygen derivatives and retain the cellular structure of oxidative stress. Depending on the location of these antioxidants in the cell, the knockout system will vary. In this way, SODs are a group of accelerated metalloenzymes that convert superoxide roots (SOR, O_2^-) into hydrogen peroxide (H_2O_2) (Pourrut et al. 2013).

As they develop, how some plant species gain stress management mechanisms will allow the development of more stress-tolerant crops and make a significant contribution to increasing world food production to meet population growth needs.

Recently, the response of plants to harsh environmental conditions like saline soils, high temperature, and water stress conditions has become the subject of intensive studies up to molecular level (Cushman and Bohnert 2000; Mittler 2006). The extended EST panel and large-scale sequencing programs allow different crops to study these non-biological procedural genetic responses. Through genetic

engineering, transfers of the structural genes one or more than one are controlled by promoters to protect plants from environmental stress (Smirnoff 1998).

12.7 Tolerance Mechanism

The avoidance of stress and tolerance to stress is a general mechanism for plant responses to non-vital pressure, such as HM pressures in plants. Thus, plants stimulate the mechanisms of tolerance and tolerance for heavy metal stress through strategies such as regulation of permeability and rotation of the plasma membrane.

In addition, plant chelating agents (PC) and metallothionein (MTs) are the mechanisms by which plant toxins in plants can be removed (Cheng 2003). The plant chelating (PC) agent in cytosol is the best mechanism of detoxification under toxic conditions (Jan and Parray 2016). Plant stores heavy metals in cells that have special mechanisms.

When the concentration is high for quick removal, heavy metals are transported to the cytoplasm, so molecules containing thiols can separate cations into complexes. Tonoplast reduces the flow of heavy metals to cells through some osmotic mechanisms. Then remaining heavy metals will be stored in vacuoles and converted into crystals, and thus toxicity of heavy metals is reduced (Nies 1999).

The mechanism of transfer and accumulation of HMs to the cytoplasm is expressed as a facial indicator with extra heavy metals opens the door to cells (Nies 1999). The tolerance of plants depends on the tolerance of plant species. Some plant species can resist excess infiltration of heavy metals from the atmosphere. Some plant species can also accumulate excessively heavy metals in above-ground tissues, which may be toxic to most plants (Memon et al. 2001).

12.8 Molecular Effect of Heavy Metals on Wheat

Plant toxicity occurs when heavy metals accumulate in large amounts in different cells. Heavy metals are subdivided into two groups, i.e., redox active and inactive, like Fe, Cr, Co for redox inactive and Zn, Cd, Pb for redox active. Due to toxic levels of heavy metals, several series of physiological and metabolic changes activate when exposed to plants (Dubey 2010). There is a different effect of different heavy metals inside the plant, but the overall toxic effects differ. Effect of toxicity on plant causes reduced plant growth along leaf chlorosis, necrosis lost turgor, which is associated with the aging process or plant death (Bačkor et al. 2007). These effects are related to biochemical and molecular changes as well as total structure. Heavy metals also reduce carbon uptake by inhibiting the enzymes associated with the stabilization of carbon dioxide. Reduction in photosynthesis was seen at the time and dose-dependent response to various heavy metals (Gill et al. 2013).

Due to lead stress, *T. Aestivum* shows alterations in the biochemical pathways of significant enzymes, which in turn affects the expression of important genes. Reduced glutathione enzymes are important for the scavenging of reactive oxygen

species that are produced uninterrupted during abiotic stresses. (Hossain et al. 2012). In the presence of cadmium, the activity of glutathione reductase was increased in *T. aestivum*, *Arabidopsis thaliana*, and *B. juncea* (Khan et al. 2007; Mobin and Khan 2007). Stress and signaling of plant development are caused by PLDα gene and phosphatidic acid. Phospholipase D genes play a role in regulating stress and developmental responses. It is known that a gene from the ZIP family Zn, Fe, Mn, and Cd moves in a lot of abiotic pressure and shows a high level of expression in *Triticum aestivum* (Jamil et al. 2018).

12.9   Genes Expressed in the Presence of Aluminum

Aluminum is considered to exert and promotes oxidative stress in plants, and this is evident from the literature during recent years. Oxidative stress induced by the Al is not known yet whether it is primary or secondary and is still a question. However, an indication of early symptoms is lipid peroxidation. Several genes have been reported earlier that overcome the Al-induced oxidative stress that are glutathione-*S*-transferase, blue copper-binding protein, peroxidase, 1,3-b-glucanase, phenylalanine ammonia lyase, and cysteine proteinase (Cruz-Ortega et al. 1997). Expression study of these genes shows that in a transgenic plant like *Arabidopsis thaliana*, it enhances oxidative stress. In wheat, ALMT (aluminum-activated malate transporter) enhances the gene that encodes the member of ALMT family that are made of membrane-bound protein (Delhaize et al. 2007). TaALMT1 acts as an Al31 anion channel and releases malate from the root cells. It has been shown that many other members of the ALMT family contribute in the same way to the resistance of Al31 in the grain and non-cortical species (Poot-Poot and Teresa Hernandez-Sotomayor 2011).

12.10 Conclusion

It is concluded from the above detailed discussion about the response of agronomic crops under stress of heavy metals and metalloids. The natural and anthropogenic activities can contribute to the accumulation of these metals and metalloids in the agriculture soils. Each plant shows its specific mechanism to tolerate a particular kind of heavy metal or metalloids. The research showed that plants adapt different mechanisms and pathways to reduce the effects of metals and metalloids in order to keep nutrient balance for proper growth. Various mechanisms have been reported which plants can adapt to minimize the harmful and toxic effects of metals and metalloids. Several enzymes, hormones, phytochelatins, association with other organisms (mycorrhizae), cell organelles (plasma membrane, cell wall), and heat shock proteins are involved in coping up with high concentrations of these contaminants. Further, modified genes also expressed in plants to face stress conditions of pollutants at the molecular level.

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Arsenic Contamination in Major Food Crops: Issues and Mitigation in Indian Subcontinent Perspective

13

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Abstract

Widespread chronic arsenic (As) poisoning is a global concern due to consumption of arsenic-contaminated drinking water. Arsenic contamination in groundwater through geological sources and anthropogenic activities has been detected in many countries like the United States, Argentina, Taiwan, China, Hungary, Vietnam, India, and Bangladesh. Serious health hazards and deaths for millions due to As poisoning have been reported by many workers. While As contamination in drinking water has attracted much attention, its contamination in food chain has become a menace, particularly in intensively cropped areas of Bengal delta basin (India and Bangladesh). Growing crops in arsenic-contaminated soils with groundwater irrigation is primarily responsible for As contamination in food crops. The uptake of arsenic depends on various factors like type of crop, crop-growing condition (aerobic or anaerobic), water requirement, etc. During the post-monsoon season, crops like wheat, potato, winter vegetables as pea or French bean, and summer crops thrive more on groundwater-supported irrigation, making them vulnerable to arsenic contamination. Tolerance level of crops therefore becomes an important yardstick in mitigating arsenic stress along with interventions in water management, cultural practices, soil amendments, and fertilization with use of organics. Understanding the nature of arsenic contamination and its uptake helps in formulating appropriate strategies to ameliorate the negative impacts of As-stress limiting crop productivity and subsequent health hazards. This chapter would be handy to the students, agricultural researchers, and policymakers to acquaint themselves with the issue toward research and development programs to alleviate As-stress in major food crops.

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Abbreviations

AMF	arbuscular mycorrizal fungi
AOB	As(III)-oxidizing bacteria
APX	ascorbate peroxidase
As	Arsenic
As_2S_2	orpiment
As_2S_2	realgar
ASC	ascorbic acid
As^{III}	arsenite
As^V	arsenate
CAT	catalase
CPE	cumulative pan evaporation
DAT	days after transplanting
DMA	dimethylarsinic acid
EDI	estimated daily intake
EDTA	ethylenediaminetetraacetic acid
EFY	elephant foot yam
ETc	crop evapotranspiration
FCT	flue cured tobacco
FeAsS	Arsenopyrite
FeOB	Fe(III)-oxidizing bacteria
FeRB	Fe(III)-reducing bacteria
FYM	farm yard manure
GPX	glutathione peroxidase
GR	glutathione reductase
GSH	glutathione-*S*-transferase
IW	irrigation water
MAC	maximum acceptable concentration
MDA	malondialdehyde
MIPs	major intrinsic proteins
MMA	monomethylarsonic acid
MT	metallothioneins
NIPs	nodulin 26-like intrinsic proteins
PC	phytochelatin
Pht1	Phosphate transporter 1
SOD	superoxide dismutase
STW	shallow tube well
TF	translocation factor

13.1 Introduction

Arsenic, a notorious poison, is one of the world's greatest environmental concerns, and millions of people are suffering from arsenic (As) poisoning globally. Presence of high concentrations of arsenic in drinking water due to groundwater arsenic contamination is a major public health issue globally (Mukherjee et al. 2006). It is reported that approximately 140 million people over 50 countries have been drinking the contaminated water with As levels higher than the old WHO permissible limits of 50 ppb (Ravenscroft et al. 2009). The presence of arsenic at concentrations exceeding the maximum acceptable concentration, MAC (0.05 mg l^{-1}) in groundwater, was first detected in 1978, while in 1983, the first case of arsenic poisoning of a human being was diagnosed at the School of Tropical Medicine in Kolkata (Acharya 1997).

Long-term exposure to arsenic leads human health to an array of medical issues mainly known as arsenicosis. The symptoms include muscle weakness, mild psychological effects followed by characteristic skin problems like changes in skin pigmentations, painful skin lesions, i.e., keratosis. Besides these, arsenic poisoning can cause a wide range of health problems like diseases of the liver and kidney, neurological disorder, cardio-vascular and peripheral vascular diseases, diabetes, and cancers (skin, lung, kidney, liver, bladder, and prostrate) (Abernathy et al. 2003).

Groundwater As contamination has been reported in Argentina, Canada (Ontario), the United States (Arizona, California, Washington etc.), Chile (Antofagasta), Mexico, Poland, Greece, and several other countries. Widespread environmental problems due to the leaching of the metal from mine trilling in Australia, Canada, Mexico, Thailand, the United Kingdom, and the United States was reported by Jones (2007). As-contaminated aquifers in Argentina, Bangladesh, Cambodia, Chile, China, Ghana, Hungary, Inner Mongolia, Mexico, Nepal, Taiwan, the United States, and Vietnam have been reported (Wilson 2002).

Among the Asian countries, groundwater arsenic contamination was reported in Bangladesh, India, and China before 2000. After that, arsenic-related issues were emerged in different Asian countries, including new sites in China, Mongolia, Nepal, Cambodia, Myanmar, Afghanistan, DPR Korea, and Pakistan (Mukherjee et al. 2006). Bangladesh has a high mortality rate of 20,000 annually due to arsenic toxicity, and 50 million people are at risk for severe health issues (Pearce 2001; Choudhuri 2004). The World Health Organization (WHO) described the situation as "the largest mass poisoning of a population in history" (Smith et al. 2000). During the last few decades, groundwater in the Gangetic alluvial zones of West Bengal, India (covering 38,865 sq. km area) was affected by arsenic contamination resulting in arsenic-related health hazards for millions (9–10 millions) of people (Das et al. 1995; Mitra et al. 2002; Sanyal and Dhillon 2005) with 42.7 million people vulnerable to As-associated danger (Rahaman et al. 2001).

Contamination of arsenic in soils occurs through geogenic sources and anthropogenic activities. Soil arsenic is mainly controlled by parent rock materials, volcanic activity, weathering history, transport, sorption, biological activity, and precipitation
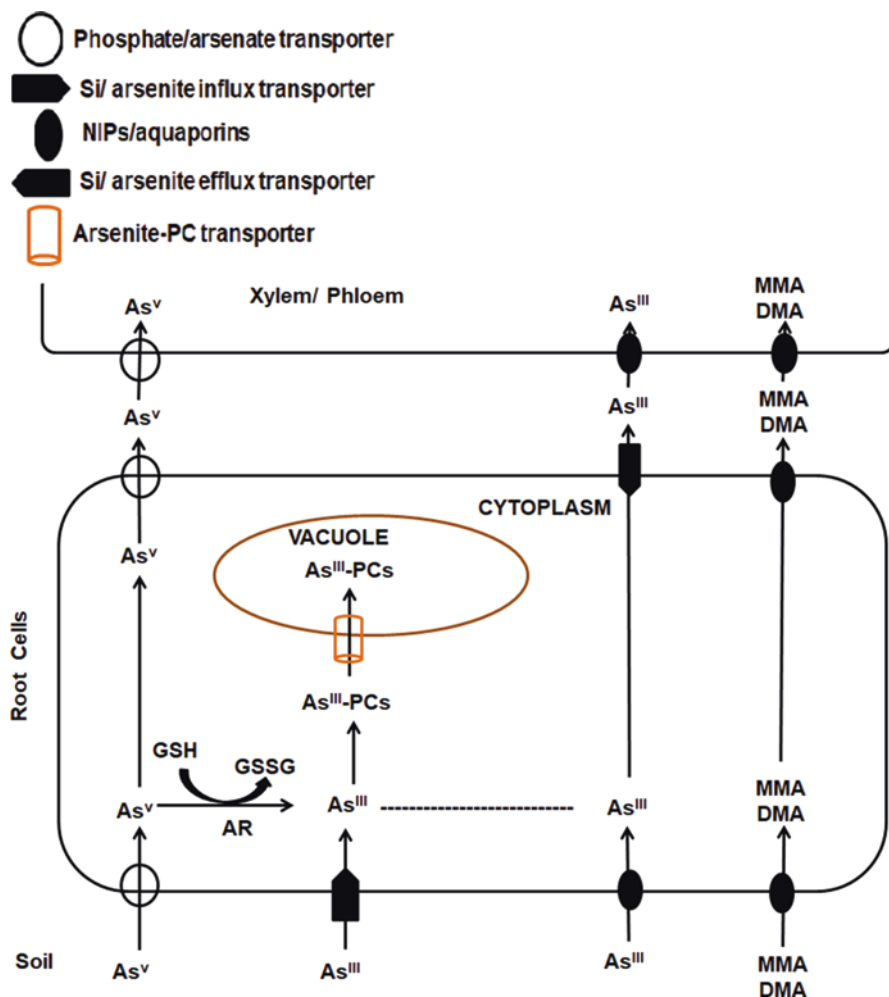
Fig. 13.1 Generalized diagram of arsenic uptake by plant roots, where GSH- glutathione; AR, arsenate reductase; GSSG-oxidized glutathione; PCs- phytochelatins. (Adopted and modified from Ma et al. 2007; Ali et al. 2009; Zhao et al. 2009)

(Kabata-Pendias and Adriano 1995). Arsenic accumulates in soil and water due to weathering of rocks and minerals containing arsenic ores and their subsequent translocation. As is a major constituent of more than 200 minerals, including elemental As, arsenides, sulfides, oxides, arsenates, and arsenites. Arsenopyrite (FeAsS), realgar (As_2S_2), and orpiment (As_2S_2) are the most important minerals. Anthropogenic activities such as combustion of municipal solid waste, application of arsenical pesticides (herbicides, fungicides, and insecticides) (Matera and LeHecho 2001), land application of solid waste/sewage sludge, river and irrigation waters (Kabata-Pendias and Adriano 1995), mining and smelting, combustion of

fossil fuels (especially coal), landfilling of industrial wastes, manufacturing of metals and alloys, petroleum refining, and pharmaceutical industry (Ning 2002) are responsible for spiking As contamination in soil.

Initially, the focus of attention was mainly on contamination through drinking water. But, a higher concentration of arsenic was observed in the urine samples of some people having no history of consumption of contaminated water (Sanyal 2005). Consumption of food crops irrigated with As-contaminated groundwater may lead to higher As levels in humans. It is noteworthy that more than 90% of the contaminated groundwater is used for crop-irrigational purposes and quantifying the influence of arsenic in soil-plant-animal systems is essential (Sanyal and Nasar 2002). The food chain is ultimately getting contaminated when the crops are grown in arsenic-contaminated soil and/or irrigated with contaminated water (Abedin and Meharg 2002; Ghosh and Bhattacharyya 2004; Jones 2007). Arsenic accumulation is higher in crops requiring more water (such as summer rice) compared to crops with low water requirement (such as food legumes, some vegetables, etc.) (Mondal et al. 2012a). Therefore, the population with rice-based diets is more susceptible to As toxicity (Sinha and Bhattacharyya 2015). So, an understanding on the source of arsenic to crop plants and the factors that influence them is of utmost importance to minimize human exposure to this poison.

The build-up of arsenic in the soil is a continuous process (William et al. 2007). Prolonged irrigation with contaminated groundwater eventually leads to As accumulation in soil, particularly in areas with groundwater-irrigated rice (Hossain 2005; Khan et al. 2009). The gradual build-up of As in rhizosphere over time can result in contamination of the succeeding crops, therefore leaves the entire cropping system vulnerable to severe phytotoxicity. Thus, high levels of As in irrigation water can cause soil pollution that alone can endanger the productivity and food safety of the agricultural produce (Heikens 2006).

Rice, the staple food of many Asian countries, mainly, Bangladesh and West Bengal has high export value (particularly Basmati rice). Its high water requirement is mainly met through groundwater withdrawal that further leads to As accumulation in rice grains and hampers the food safety. The outflow of contaminated products to local, national, and international markets may be further reduced by sanitary and phytosanitary measures. The Codex Alimentarius Commission Committee on Contaminants, therefore, met to discuss on the setting of limits for arsenic in rice at its eighth session held on 1 March to 4 April 2014 in The Hague, The Netherlands (SPS 2013–2014). The maximum permissible limit of arsenic in polished rice is 0.2 mg kg^{-1} for international market (European Commission 2015). Establishment of international limits is bound to affect the export market of the products grown on arsenic-contaminated soil with contaminated water. Thus, the complexities of arsenic problem in the management system, as emphasized above, needs sustained research work to characterize the entire range of the intricacies of arsenic toxicity in groundwater – soil – crop continuum, and come up with the effective remedial measures to contain the toxic effect of arsenic thereon.

13.2 Tolerance of Food Crops Toward Contamination: Uptake and Translocation

Arsenic is a metalloid of group VA of the periodic table, and it is similar in oxidation state and electron orbital status with phosphorus. Arsenic exists mainly in four oxidation states, + V, + III, 0, and – III. It occurs in the environment both in organic and inorganic forms. The most important inorganic species are arsenate (As^v) and arsenite (As^{III}), while the most important organic species are monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA). The toxicity of arsenic is mainly dependent on the forms of arsenic. Inorganic As species are more toxic to living organisms than organic forms (Meharg and Whitaker 2002).

At first, As enters into the root apoplast through the space between the cells. Then, As cross the plasma membrane of endodermal root cells to enter into the root symplast or cytosol probably through the action of a membrane pump. Localization of arsenic in the apoplast may make a significant contribution to the total amount of it in a plant. Plants take up arsenic primarily through the roots, but submerged plants may also absorb As through the leaves (Wolterbeek and Van der Meer 2002). The factors that affect bioavailability, uptake, and toxicity of arsenic in field crops are (i) arsenic speciation, (ii) redox condition and soil texture, (iii) phosphate levels, (iv) soil pH, (v) soil organic matter, (vi) microbial activity toward volatilization, (vii) genotype variation in crop, and (viii) distance of the crop field from the source of irrigation (Lawgali and Meharg 2011; Delgado and Go'mez 2016; Azam et al. 2016).

Plants can take up arsenic from soil and subsequently translocate from roots to other aerial plant parts with different pathways (Fig. 13.1) and rates. The uptake of inorganic species of arsenic, i.e., arsenite (As^{III}) and arsenate (As^v), occurs by two mechanisms. The transport of arsenate takes place from soil solution to aerial parts of the plants through high-affinity phosphate transporter (Wu et al. 2011). Being analogous to each other, uptake of arsenate and phosphate occurs through the same transport pathway in higher plants and the uptake mechanism involves co-transport of phosphate or arsenate and protons (Ullrich-Eberius et al. 1989). Phosphate transporter 1 (Pht1) family is involved in the expression of over 100 phosphate transporters which are strongly expressed in roots (Bucher 2007). Arsenite (As^{III}), the predominant form of arsenic in reducing environment, is taken up by root cell through aquaporin or water channels (Li et al. 2009; Ma et al. 2008). Aquaporins are nodulin 26-like intrinsic proteins (NIPs) which represent one of the four subfamilies of the plant major intrinsic proteins (MIPs). In rice, two silicon transporters, viz., Lsi-1 (a silicon influx transporter) and Lsi-2 (a silicon efflux transporter), are mainly involved in entry of arsenite (Ma et al. 2007). The uptake mechanisms of methylated species such as monomethyl arsonic acid (MMA) and dimethylarsinic acid (DMA) are less extensively studied than inorganic arsenic species. Monomethyl arsonic acid and DMA are also taken up by plant roots, but generally in a less efficient manner than inorganic arsenate or arsenite (Carbonell-Barrachina et al. 1998; Marin et al. 1992). MMA and DMA are taken up through the nodulin 26-like intrinsic proteins (NIPs) (Rahman et al. 2011). Although inorganic arsenic species (As^{III} and As^v) are more efficiently absorbed by roots than methylated arsenic species (DMA

and MMA), their translocation rate in plant shoot is much lower than methylated arsenic species (Raab et al. 2007).

Arsenic is primarily stored in the plant roots. Rahman et al. (2007a) reported that As concentration in rice roots was 28 to 75 times higher than that of shoots. However, a higher As concentration in the shoots compared to radish roots has been observed (Smith et al. 2008). After the entry into roots, a small fraction of arsenic is transported to the shoot via the xylem as oxy-anions (arsenate and arsenite). Inside the plant tissues, arsenate is reduced to arsenite by the activity of arsenate reductase utilizing glutathione as reductant followed by complexation of arsenite to phytochelatins. The complex is then sequestered into root vacuoles or is translocated to the shoots from where it is distributed to various organs (Zhao et al. 2010). The flow of the xylem sap transports the element to the leaves once it is loaded into the xylem.

Once taken up by plants, As toxicity adversely affects crop growth and physiology in numerous ways. Both arsenate and arsenite disturb central cellular functions. However, the mechanisms of arsenic toxicity significantly differ among these inorganic species. Arsenate can replace phosphate in aerobic phosphorylation and disturbs the phosphate-based energy-generating processes, thereby inhibiting oxidative phosphorylation (Hughes 2002; Markley and Herbert 2009) while arsenite disturbs protein functioning by binding to sulfhydryl groups in the proteins such as pyruvate dehydrogenase and 2-oxoglutarate dehydrogenase (Ullrich-Eberius et al. 1989; Ozturk et al. 2010). Therefore, As disrupts the biochemical function of cells and different plant metabolic processes viz. photosynthesis, transpiration, respiration, and other physiological functions by reacting with proteins and enzymes and eventually ceases plant growth (Meharg and Hartley-Whitaker 2002). It is noteworthy that As phytotoxicity in different plant species largely depends on the chemical state of arsenic compounds (Yoon et al. 2015). Some phytotoxic responses of plants to arsenic and respective tissue concentrations in various crops are given in Table 13.1.

Plants vary greatly in their tolerance to arsenic. When all major crops show their sensitiveness to arsenic, some species like *Holcus lanatus* and more specifically *Pteris vittata* (Chinese break fern) can tolerate to extremophiles such as that which can accumulate 2% of its dry weight as arsenic (Wang et al. 2002). In plant roots, a common mechanism of detoxifying arsenic is its complexation via sulfur bonds (Lin et al. 2006; Tripathi et al. 2007). It is assumed that a substantial proportion of As^{III} may be chelated in this way to minimize cytoplasmic exposure. Phytochelatins (PCs), having a general structure (k-Glu-Cys)n-Gly, play very important roles in eliminating toxicity through sequestration of this toxic metalloid into the vacuole as As^{III} -PCs complex since PCs have a high affinity for As^{III}. Essential roles of PCs in both constitutive and adaptive plant tolerance to arsenic have been pointed out by Raab et al. (2004).

13.3 Strategies to Mitigate Arsenic Contamination

There are several strategies to mitigate arsenic contamination in food crops as well as to reduce the buildup of As in rhizosphere. Rationing of groundwater use for irrigation purposes, appropriate measures to improve the water use efficiency of

Table 13.1 Phytotoxic responses of plants to arsenic and respective tissue concentrations in various crops

Crop	Arsenic conc.	Phytotoxicity	References
Rice	2 mg l^{-1} soil solution	Inhibition of germination by 10%	Abedin and Meharg (2002)
	0.5 mg l^{-1} soil solution	Inhibition of root growth by 20%	
	0.5 mg l^{-1} soil solution	Reduction of shoot height by 30%	
	10 mg kg^{-1} soil	More than 45% grain yield reduced	Jahiruddin et al. (2004)
	25 mg kg^{-1} soil	Dry matter reduction by 50%	Onken and Hossner (1995)
	30 mg kg^{-1} soil	Both chlorophyll-a and chlorophyll-b contents in rice leaf decreased significantly	Rahman et al. (2007b)
	60 and 90 mg As kg^{-1} soil	No rice plant survived up to maturity stage	
Maize	12.5 and 25 mg kg^{-1} soil	Promoted maize growth and the nutritional quality of the grain	Ci et al. (2012)
	50 and 100 mg kg^{-1} soil	Toxic effects for the crop	
Barley	20 mg kg^{-1} tissue	Growth inhibition	Davis et al. (1978)
Mustard	150 μM in hydroponic solution	Inhibition in shoot length, chlorophyll, carotenoid and protein	Praveen et al. (2017)
Potato	290 mg kg^{-1} soil	No growth inhibition	Codling et al., 2016)
Soybean	>1 mg kg^{-1} tissue	Yield reduction	Deuel and Swoboda (1972)
Cotton	>4 mg kg^{-1} tissue	Yield reduction	

crops and minimal withdrawal of contaminated groundwater is of prime importance in alleviating As toxicity. Other practices like choice of crops or varieties, nutrient management, organic intervention, and related measures also play key roles in reducing As accumulation in food crops (Heikens 2006; Mitra et al., 2017; Mondal et al. 2012b). Mitigation options appropriate for different crops should be identified, tested, and propagated in all countries suffering from As pollution of soils and crops as soon as possible. Mitigation strategies might be practical. But due to local climatic, soil, agricultural, and hydrological complexity and differential rates of As accumulation in soils, different methods might be required within individual tube well command areas (Brammer 2009).

13.3.1 Choice of Crops/Cropping Systems

In arsenic-contaminated locations, it is essential to choose crops on the basis of water requirement. The emerging problem of groundwater As contamination due

to the lifting of excessive groundwater for the cultivation of crops in the lean period when groundwater recharge is at its minimum needs immediate attention (Mandal et al. 1996; Sanyal 2005). Cropping systems with less irrigation requirement should be selected in high As prone areas. Depending on the location and soil conditions, *summer* rice, a high water-demanding crop, must be replaced with dryland crops like wheat and maize (Heikens 2006) or tubers (like potato, elephant foot yam, etc.) with less water requirement (Mondal et al. 2012b; Mondal and Bandopadhyay 2014). In Table 13.2, the relationship between the water requirement and As accumulation crop is presented. The abundant ferric ion under aerated soil condition rapidly immobilizes As in irrigation water (Brammer 2009). Low water requiring dryland crops are therefore a good choice in As prone areas. Therefore, drastic alteration of soil and land use is needed to accommodate dry land crops replacing summer rice (Brammer 2009). Since rice is the staple food crop of South and South East Asia, rice cultivation may be continued in the prevalent lowland rice ecosystems characterized by heavy soil texture and poor drainage condition, supported with monsoon rains.

As food legumes require much less water, green gram can be a better substitute for summer rice (Mondal et al. 2012a) when the objective is to reduce the contamination. So, incorporation of legumes or oilseeds (green gram or sesame) in the cropping sequences can reduce the total arsenic uptake of the system (Mondal et al. 2018). Profitability, however, is an important factor that determines a farmer's receptivity to a new crop/system. The inclusion of remunerative food legumes such as pea, cowpea or French bean in cropping systems not only reduces arsenic loading but also fetch a better price to the farmers (Mondal et al. 2015; Mondal et al. 2018). Due to its ability to thrive on a much lesser amount of water than summer rice, high-value crop strawberry crop cultivation is a profitable farming option in As-ridden areas (Das Roy 2017). Governments need to consider appropriate policies to phase out summer rice cultivation with suitable crops and provide subsidies for the matter.

Table 13.2 Water requirement and arsenic accumulation of major food crops

Crop	Season	Water requirement (mm)	As accumulation (mg Kg^{-1})
Summer rice	Summer	900–2500	1.07–1.84
Wheat	Winter	450–650	1.23–1.35
Maize	Winter	500–800	0.02–0.40
Green gram	Summer	200–250	0.03–0.18
Sesame	Summer	350–400	1.03–1.34
Pea	Winter	350–500	0.71–1.14
French bean	Winter	300–500	0.05–0.17
Potato	Winter	500–700	0.56–0.94
Elephant foot yam	Monsoon	Rainfed	0.30–0.40
Strawberry	Winter	175	0.07–0.22

Source: Mondal (2010); Agropedia (2010); Muñoz et al. (2002); DasRoy (2017)

13.3.2 Choice of Varieties/Plant Breeding Approaches

Selection or breeding of cultivars that have a low arsenic uptake or tolerant to soil arsenic levels is important. Varieties should be screened in arsenic prone locations to identify the suitable arsenic tolerant variety. Varieties may show variation in their response to As exposure. Researches revealed that As accumulation, uptake, and phytotoxicity significantly differ among the cultivars (Rauf et al. 2011; Hua et al. 2011).

Development of crop varieties which accumulate less arsenic in their edible part can be a potential strategy to reduce human exposure to the dietary arsenic intake. Advanced genetics and traditional plant breeding techniques using knowledge of arsenic uptake and tolerance characteristics of plants are the useful approaches to develop varieties and ideotypes with desired characteristics (Punshon et al. 2017). Many rice cultivars with less arsenic in their grain have been screened (Norton et al. 2009), and use of such As-resistant lines in hybridization programs with stable yielding genotypes is a promising breeding intervention. In Table 13.3, a list of a

Table 13.3 Low arsenic accumulating variety of major food crops

Crop	Varieties	Varieties with less As uptake	References
Rice	IR-36		Kundu et al. (2012a)
	Kakdwip Sel-1		
	Satabdi	√	
	Ratna		
	Jaldi Minikit (local)		
	Rasi		
	Khitish		
Wheat	Kalyansona		Kundu et al. (2012b)
	Sonalika		
	UP-262	√	
	Local variety		
Maize	Azad Kamal		Mallik et al. (2011)
	Azad Uttam		
Potato	Kufri Jyoti	√	Kundu et al. (2012c)
	Kufri Naveen		
	Kufri Jawahar		
	Kufri Chandramukhi		
	Kufri Badshah		
	Kufri Pukhraj		
	Kufri Bahar		
	Super six		
	Lal alu (local)		
Sesame	SWB-32-10-1		Kundu and Pal (2012)
	BT-893		
	Pragati		
	UTS-8		
	Rama	√	
	Tilottama		

low arsenic variety of major crops from India and Bangladesh is given. Plants can grow in a medium containing toxic concentrations of arsenic through overexpression of *Arabidopsis* ABC-type transporters, and it helps in sequestering arsenite-PC complexes into the cell vacuole (Song et al. 2010). Since rice ABC transporter $OsABCC_1$ limits arsenic transport to grains by sequestering arsenic in the vacuoles of the phloem companion cells directly connected to the grain and as such excluding the function of $OsABCC_1$ transporter results in higher levels of grain arsenic. Thereby, the overexpression of OsABCC1 can be an efficient strategy to develop arsenic tolerance and low-arsenic accumulating rice cultivars. Besides expression of arsenate efflux transporter from yeast (*Saccharomyces cerevisiae*) in rice leading to 20% reduction of arsenic accumulation in brown rice can be another way of arsenic loading in rice (Duan et al. 2011).

13.3.3 Water Management

13.3.3.1 Alternate Source of Irrigation

The best possible way to alleviate As contamination in soils and crops is to limit As addition to soils. This can be done by using safer sources of irrigation water instead of As-contaminated groundwater. It will vary with location, surface water sources like rivers, major reservoirs, or small reservoirs ("tanks" or "ponds" in the Indian subcontinent), or deeper uncontaminated aquifers. Irrigation from these surface water sources is reported to reduce arsenic uptake in individual crops (Mondal et al. 2012b; Mondal et al. 2015) and cropping systems (Mondal et al. 2018). Table 13.4 reflects the variation in As accumulation in crops with different sources of irrigation. Irrigation from these alternative sources is more costly to provide, operate, and maintain than the existing shallow tube wells (STWs). Appropriate policies to provide surface water support to compulsive summer rice areas should be considered for the matter. It will not be possible to provide safe irrigation supplies in all areas. In areas with the limited possibility of safer irrigation support, the best alternative is water treatment to reduce the amount of As in irrigation water (Brammer 2009).

Table 13.4 Effect of sources of irrigation on arsenic accumulation ($mg\ kg^{-1}$) in major food crops

Crop	As content in economic produce	
	Irrigated with water from shallow tube well (STW)	Irrigated with PW (Pond water)
Summer rice	1.61	1.33
Winter rice	0.90	0.74
Potato	0.93	0.61
Cowpea	0.52	0.29
Jute	0.60	0.46

Source: Mondal (2010)

13.3.3.2   Water Treatment

The water treatment methods recommended for purification of As-contaminated drinking water are not feasible options for purifying huge quantities of irrigation water because of the cost implications. Though simple means to reduce the amount of As, reaching fields is the co-precipitation of As with application of ferric hydroxides in irrigation distribution channels (Brammer 2009). It may provide the most realistic and economical method to reduce As contamination of crops and soils. But, these methods need to be tested, validated, and then introduced for their safer implementation.

13.3.3.3   Irrigation Management

Proper irrigation methods should be adopted to use irrigation water judiciously, implying reduced application of water without affecting the growth and productivity of the crop. In the case of rice, the conventional cultivation method of rice (flood irrigation) requires a large amount of water. Flood irrigated soil is not a biological requirement of rice plants. Flooding is mainly used to control weed and vermin, for mobilization of key nutrients such as iron, phosphate, and zinc, and most importantly, flooding discourages the buildup of root nematodes due to multiple years of rice cropping. But, under flooded condition, As is quickly released due to reductive dissolution of Fe (oxyhydr)oxides and the arsenate reduction to the more mobile arsenite (Xu et al. 2017; Takahashi et al. 2004). Non-flooded or aerobic conditions can reduce arsenic uptake in rice by restrictive dissolution of arsenic. However, rice grown in non-flooded or aerobic conditions has a significantly lower yield than intermittent ponding or continuously flooded rice (Sarkar et al. 2012; Li et al. 2009; Grassi et al. 2009; Arao et al. 2009). Reduction in the amount of irrigation water at stress tolerable stage of the crop can enhance crop water productivity without a significant decrease in rice grain yield (Sarkar 2001). Intermittent ponding is more promising management technique to reduce arsenic levels without significantly affecting grain yields than aerobic or continuous flooded rice cultivation (Hu et al. 2013). Sarkar (2001) reported that intermittent ponding during 15–45 days after transplanting (DAT) has no significant effect on grain yield. However, the authors observed that grain yield reduced significantly in case of intermittent ponding during 46–60 DAT and 61–75 DAT (Sarkar 2001). It can be recommended from pot experiments that water management strategies applied during the heading period of rice (when the rice panicle has emerged from the stem and is fully visible, just before flowering) can moderate arsenic concentration in the grain (Arao et al. 2009). Maintaining the oxidative condition after heading significantly reduces the grain arsenic concentration (Matsumoto et al. 2015a). Use of sprinkler irrigation in rice can substantially reduce a substantial amount of arsenic uptake by the crop (Moreno-Jimenej et al. 2014). Spanu et al. (2012) reported that As uptake in rice decreased up to 50-fold under sprinkler irrigation compared to rice grown in traditional flooded irrigation. However, purchase, maintenance, and operation of a sprinkler system are expensive rendering them unaffordable for the small and marginal farmers. A more viable option for reducing arsenic uptake in many areas of South and Southeast Asia is to grow rice in raised beds and delivering irrigation water through furrows.

Growing rice on the permanent raised bed is another suitable water management technique to mitigate As accumulation in both straw and grain of rice. The furrow irrigation method of the permanent raised bed reduces irrigation input by 29–31% in *summer rice* and 27–30% for *winter* rice resulting in 30% less As deposition in the soil through irrigation (Talukder et al. 2011).

To mitigate arsenic contamination, reduced water use in crops can be an effective strategy which also improves upon water productivity. In the case of dryland crops, different water-saving technologies and deficit irrigation methods (sprinkler and drip) coupled with mulching can be helpful in reducing the irrigation water requirement. Das Roy (2017) reported that drip irrigation at 0.8 ETc and 1.0 ETc reduced the irrigation requirement by 44% and 30%, respectively over surface irrigation at IW/CPE = 1 in strawberry. In addition to that, mulch application improved water productivity by 34–121% depending on different types of mulch in comparison to bare soil. Therefore, in case of dry land crops, these water-saving technologies can be adopted in arsenic prone areas.

13.3.3.4 Soil Amendment and Fertilization Practices

Application of soil amendments like Fe, P, Si, S, Se, and organic manures has potential role in alleviating As toxicity by reducing its uptake and translocation to the edible part of the food crops (Bakhat et al. 2017; Mitra et al. 2017; Matsumoto et al. 2015b; Moulick et al. 2016).

13.3.3.4.1 Iron

Use of iron-based amendments increases the concentration of free iron oxide in the soil, impeding the release of arsenite from the solid phase into soil solution (Bakhat et al. 2017). This free iron oxide reduces arsenic uptake in food crops in the following ways: (1) deposition of iron oxide in the rhizosphere decreases arsenic uptake in roots and (2) increases iron and arsenic co-precipitation and (3) desorption of soluble arsenic decreases due to adsorption of As(V) on iron surface. Steel slag amendment (rich in Fe and silicate) is a common practice in rice production systems of Southeast Asia.

Anaerobic rice cultivation also promotes the Fe plaque formation around the rice roots. Due to high affinity toward As (V), Fe-plaques play a significant role in reducing the As uptake in rice. Studies have indicated that the Fe plaque may be able to sequester the As, which ultimately decrease As translocation from roots to shoots (Liu et al. 2004). Further, Fe-redox cycling influences the As fractionation and As bioavailability in rice soil. Uptake of As mainly depends on the bioavailability of As in soil. Amorphous iron oxide acts as a sink of arsenic (Liu et al. 2015). When iron is supplemented with arsenic, there is a concomitant decline of hydrogen peroxide (H_2O_2), malondialdehyde (MDA) contents, along with ascorbate (AsA) and glutathione (GSH) levels in both root and shoot. Again, catalase (CAT) and superoxide dismutase (SOD) activities were reduced in Fe supplemented seedlings. From these reviews, it may be concluded that oxidative stress in rice plants may be moderated by iron supplementation (Nath et al. 2014). Application of iron oxides (at a rate of 2%) was more effective than phosphate amendment in lowering grain arsenic

content (Farrow et al. 2015). Grain arsenic content was reduced with iron oxide addition and constant flooding (Honma et al. 2016).

A combination of ethylene diamine tetraacetic acid ferric sodium salt (iron EDTA) and calcium peroxide was effective in remediating arsenic uptake by vegetable crops (lettuce, Chinese cabbage, and radish) due to immobilization of As (Chou et al. 2016) and chemisorptions by oxides and hydroxides of Fe and Al in the soil surface. In addition, at lower pH range, arsenic immobilization is the maximum and is highly influenced by soil phosphorus concentration that strongly competes with arsenic. However, a pertinent question arises whether iron oxide amendment application only temporarily reduces arsenic bioavailability (Tiberg et al. 2016), which should be further studied and validated.

13.3.3.4.2 Phosphorus

Phosphorus (P), being the second most important nutrient, plays an important role in plant physiology and biochemistry. Phosphate (PO_4) and As (V) share the same pathway of translocation for uptake in plants (Wu et al. 2011). Several studies have reported that the application of phosphatic fertilizers helps in reducing the uptake of arsenate from soil solution (Pigna et al. 2010; Rahman and Hasegawa 2011). A plant with higher P content was reported to have lower arsenate toxicity. Thus, an increment in external P application can alleviate the problem of arsenate toxicity in plants (Mondal et al. 2015; Mondal et al. 2012b). The important factors for controlling As uptake in rice grown in As-contaminated soils are soil properties, concentration of As in soil solution, and application of phosphatic fertilizers (Geng et al. 2005; Farooq et al. 2016; Lee et al. 2016). The most important factor in the reduction of arsenate uptake by plant roots depends on the affinity of the plants or competitive uptake in rice roots. The competition between As (V) and PO_4 for adsorption sites on soil particles, competition between phosphate and As in rice roots for uptake, and the role of PO_4 in translocation of As from root to shoot are the factors that influence the effect of PO_4 on As mobility in soil and its uptake in rice (Lee et al. 2016). Phosphate plays a potential role in the paddy field because it regulates As solubility in soil and its uptake by plants (Peryea 1991; Fitz and Wenzel 2002). Moreover, As mobility in As enriched soils can be reduced by a co-application of calcium and P that forms Ca-P-As complex (Neupane and Donahoe 2013). Geng et al. (2005) observed that when PO_4 concentration increases, the amount of As decreases in Fe-plaque. Liu et al. (2004) reported that sufficient P resulted in less Fe-plaques on the rice roots, but the P-deficient solution increased the Fe-plaque formation on the roots. Oxygen transport in rice roots can be increased by less P concentration in plant tissues (Kirk and Van Du 1997) which may stimulate Fe plaque formation on the roots.

In anaerobic conditions, there is less influence of PO_4 in As reduction because, in flooded (anaerobic) soil, As (III) is the predominant form of As and As (III) is not an analog of PO_4. No significant effect of phosphate application was observed on As uptake in rice under flooded conditions (Abedin and Meharg 2002). However, there are also some contradictory reports of P application on As uptake in rice. Several workers reported that the application of P increases As accumulation in rice grains

(Jahiruddin et al. 2004; Talukder 2005; Hossain et al. 2009). However, there are the certain possibility of oxidation of As(III) into As(V) in the rice root zone as aerobic conditions prevail around the roots (Armstrong 1967). Therefore, a comprehensive study on the effect of PO_4 on As accumulation in major food crops is required. Much elevated phosphate application might be useful to compete for uptake with As in plants (Mondal et al. 2012b). In contrast, the enhanced application of As in highly As-contaminated area can aggravate the As toxicity problem due to the desorption of As in soil solution. However, an elevated dose of P higher than the requirement of the plant may influence the soil and environment. Therefore, further experimentation with foliar applications of P under As stress may be worked out to address the interaction of P and As with minimum negative impact on soil and environment (Lee et al. 2016).

13.3.3.4.3 Sulfur

Sulfur (S) is a vital element for plant growth and development. S-metabolism produces S-rich low molecular weight non-protein thiols like glutathione (GSH) and phytochelatin (PC). It plays a crucial role to regulate As through formation of a complex with As by S-containing ligands glutathione and phytochelatins (Srivastava and D'Souza 2009; Mishra et al. 2013). It is an important element to tackle As translocation as well as accumulation in plants. In the As detoxification process, As(V) is converted to As(III) and the sulfhydryl groups of GSH and PCs acts as the binding sites for the As(III) (Muñoz-Bertomeu et al. 2009). Then, As-thiol complexes are subsequently transported to vacuoles (Song et al. 2010). Moreover, with increased application of S, the transcript level of Lsi2 that helps in As translocation in shoots was reduced (Dixit et al. 2016) and the accumulation of As was increased in roots. Duan et al. 2011 reported that As accumulation in rice grain and concentration of PCs was negatively correlated.

Additionally, S helps to moderate oxidative stress due to As by reduction of H_2O_2 and influencing the activities of antioxidant enzymes such as SOD, ascorbate peroxidase (APX), glutathione peroxidase (GPX), and CAT.

The effect of sulfate (SO_4) on As accumulation in paddy soils is of great significance. Sulfate has a strong affinity toward As under anaerobic conditions as it leads to precipitation of insoluble As sulfide (Signes-Pastor et al. 2007). Sulfate uptake in plants is regulated by different SO_4 transporters like high-affinity SO_4 transporters (HASulTs), low-affinity vascular transporters (LASulTs), and vacuolar efflux transporters (Buchner et al. 2004). Up-regulation of the SO_4 transporters maintains a continuous supply of sulfur which helps in the formation of phytochelatins and thereby sequestration of the metalloid in vacuoles. It has been reported that sulfate uptake and transportation systems are activated upon As exposure in various plants like rice (Srivastava et al. 2015). Further, up-regulation of different genes which are involved in S transport and metabolism has been reported in rice under As^V exposure (Norton et al. 2008). It was also reported that S reduces uptake of As, possibly due to the formation of Fe plaque (Hu et al. 2007), which reduced the As concentration in soil solution (Liu et al. 2005). However, some studies suggest that Fe-plaque acts as a buffer that enhances the As concentration in soil solution and to plants

(Tripathi et al. 2014). Moreover, SO_4 also compete with As(V) as both of them use the same pathway in the same way that PO_4 compete with As(V) for transport and metabolism (Ballatori 2002).

13.3.3.4.4   Silicon

Silicon is an essential nutrient for the plant. It is beneficial to plants even if when it is present in an excess amount in soil (Ma et al. 2001). Si plays an important role in alleviating both abiotic and biotic stresses in plants (Liang and Ding 2002). Due to physicochemical similarities between silicic acid and (As[III]) arsenous acid (Ma et al. 2008), As is taken up by the silicon membrane transporter (Lsi1) into rice root cells and presence of silicon inhibits arsenite uptake. Application of Si fertilizer may be a potential mitigation strategy to decrease As accumulation in plants grown in As-contaminated soil (Zhao et al. 2010; Gupta and Khan 2015). Furthermore, significant inhibitory effects of Si on As uptake and content in straw and grain of rice were reported either by the presence of indigenous silicic acid in the soil solution (Bogdan and Schenk, 2008) or by supplementation of Si externally (Seyfferth and Fendorf 2012). It has been reported that Si supplementation has reduced the As accumulation in the shoot. Changes were observed in related stress parameters (cysteine and proline), antioxidant enzymes (SOD, CAT, and APX), and oxidative stress markers (MDA and H2O2) in As stress condition, which were moderated on co-application of Si as compared to As[II] treatment (Praveen et al. 2017). The presence of Si helps to mitigate As contamination by moderating those related stress parameters and antioxidant system in mustard (*Brassica juncea*).

Rice plants take up high concentrations of silica. It constitutes up to10% of dry matter in the straw and husk of the plant (Penido et al. 2016). The use of synthetic silicon fertilizers, such as calcium silicate or silica gel, is prohibitively expensive for smallholder farmers in developing countries; however reusing the silicon-rich parts of the rice plant that remain after harvesting and grain processing may provide a sustainable solution that also addresses the ongoing issue of silicon depletion of the soil (Penido et al. 2016). Soil incorporation of fresh rice husks, or the ash that remains after burning the husk and straw for energy, can provide silicon without increasing methane production and decreases either total or inorganic arsenic in rice grain (Seyfferth et al. 2016).

13.3.3.4.5   Selenium

Selenium (Se) plays an important role in crops in providing protection against environmental stresses. The synergistic and/or antagonistic effect of Se with As is a well-established phenomenon (Han et al. 2015). Selenium (Se) at lower concentration (1.0 mg L^{-1}) is reported to stimulate crop growth and it has also an antagonistic behavior with As. However, Se concentration more than 1.0 mg L^{-1} has been proved to be toxic in case of higher plants like mungbean, but the lower dose less than 1.0 mg L^{-1} has a beneficial effect on crop growth (Malik et al. 2012). Se also has antagonistic effect against a wide range of heavy metals like cadmium, chromium trivalent, chromium hexavalent, antimony, mercury, and lead by inhibiting their uptake and/or translocation in plant system under in vitro condition (Feng et al.

2013). Seed priming with Se improved seed germination and seedling growth by reducing As uptake, suppressing the oxidative damage by increasing antioxidant accumulation in rice seedlings. Seeds primed with 0.8 mg Se L^{-1} were more effective in enhancing germination and seedling growth of rice, compared to 1.0 mg Se L^{-1} (Moulick et al. 2016). Malik et al. 2012 reported that the oxidative damage due to As was reduced with the application of Se. It might be due to elevated levels of enzymatic [SOD, CAT, APX, glutathione reductase (GR)] and non-enzymatic [AsA and GSH] antioxidants. Moreover, metallothioneins (MTs), thiols, and GST activity were found to be high in Se-treated mungbean plants. This might be the reason behind the detoxification mechanisms. The promotion of the growth of flue-cured tobacco (FCT), i.e., *Nicotiana tabaccum* L., were realized because low Se dose (0.1 mg L^{-1}) alleviated the toxicity of the high As dose, and the addition of As counteracted the toxicity of high Se dose (5 mgL^{-1}) (Han et al. 2015). The antagonistic effect of Se with As was mostly reported from Petri plates and hydroponic studies. But, recently, Moulick et al. (2018) concluded from a pot experiment that Se-primed plant enhances growth and yield by reducing As translocation from root to aerial parts, expressed as translocation factor (TF). A reduction of TF root to shoot (46.96%), TF root to husk (36.78–38.01%), and TF root to grain (39.63%) was recorded among the Se-primed plants than unprimed plants both cultivated in similar As stress. Besides these, consumption of cooked rice obtained after cooking of brown rice of Se-primed plants can help in reduction in estimated daily intake (EDI) and cancer risk than their unprimed counterparts.

13.3.3.4.6 Organic Manure

The role of organic matter to mitigate arsenic accumulation in edible parts of plants was reported by several workers. Organic matter application can reduce up to 75% of As accumulation in a vegetative part of the plant (Huq and Joardar 2008). The lowest arsenic uptake was recorded in pea and EFY with a combination of inorganic fertilizers and organic manure (FYM) with or without elevated levels of phosphate compared to inorganic fertilizers only (Mondal et al. 2012b, 2015). FYM facilitates absorption of As in the soil matrix (Mukhopadhyay et al. 2002). Application of FYM was reported to minimize As accumulation in both the soil and rice crop (Mukhopadhyay and Sanyal 2000). Humic/fulvic colloids of the native soil form organo-arsenic complex with the incorporated organic manures (Mukhopadhyay 2002). In this way, it can be expected to minimize the risk of As toxicity. Combined applications of different types of organic manure can reduce the As accumulation by 33.47% and 36.87% in whole grains and milled grains, respectively, compared to treatment without such manure (Rahman et al. 2011).

Unaffordable costs limit the use of soil amendment to reduce arsenic bioavailability or prevent plant uptake of arsenic either in smallholdings in Asia or affluent in the United States or Europe (Punshon et al. 2017). In non-rice agricultural systems, arsenic is tightly bound to the solid phase; significant crop uptake from oxidized soil is likely to be a result of extreme contamination, in which case effective mitigation is restricted to redirecting land use away from edible crops.

13.3.3.5 Role of Soil Microorganism

Soil microorganisms have a potential impact on arsenic biogeochemistry through a number of mechanisms including mobilization, sequestration, redox, precipitation, and methylation transformation that directly control the fate and transport of arsenic in the environment (Huang 2014). The mostly accepted As detoxification mechanism is binding of As on extracellular surface of soil microorganisms which has uronic acids and proteins and amino sugars with a hydrogen-bonding potentials (Bakhat et al. 2017). Several studies reported about the adsorptions of various inorganic and organic species of arsenic by various soil bacteria: *Bacillus* sp., *Rhodococcus* sp., and *Halobacterium* sp. The activity of Fe(III)- reducing bacteria (FeRB) and As(V)-reducing bacteria can increase the bioavailability of As from soil Fe (hydr)oxides into the porewater (Zhu et al. 2014). Conversely, in the proximity of oxidation zone of rice roots, As(III)- and Fe(II)-oxidizing bacteria (AOB and FeOB) can decrease its bioavailability by the formation and co-precipitation of As with Fe minerals (Das et al. 2016). Microorganisms can manipulate the speciation in rice grains. A large number of genes are available in bacteria and archae that encode enzymes and transporters which are useful for As processing. These enzymes help to reduce As^V to As^{III}, oxidize As^{III} to As^V, methylate As^{III}, and extrude As^{III} from the cell (Cavalca et al. 2013). Several studies revealed that methylated As found in rice grains are derived from the activity of rhizospheric microorganisms, not produced by the plant (Arao et al. 2011; Zhao et al. 2013). Therefore, an understanding of the potential role of microorganisms, which type of microbes are involved in As methylation within the rhizosphere and the conditions for their growth, is of great importance.

Arbuscular mycorrhizal fungi (AMF) also play an important role. It helps to moderate arsenic translocation by suppressing mRNA expression of OsLsi1 and OsLsi2, the mediators of AsIII transport (Mitra et al. 2017). Thus, AMF facilitates to enhance biomass and yield without increasing the grain arsenic content under As stress. This option can be sustainable to develop a remunerative mitigation strategy.

13.4 Conclusion

Arsenic contamination in food chain either through drinking water or food has severe human health consequences. In the Indian subcontinent (mainly Bangladesh and India), widespread groundwater As contamination is of great concern. The prevalent *summer* rice, grown during the lean period of December to April, mainly depends on groundwater irrigation support. Rice is the staple diet and consumption of As-contaminated rice is primarily responsible for As-related health hazards in the said region. Plants vary greatly in their tolerance to arsenic, and all the major food crops are susceptible to As toxicity. Arsenic contamination varies with crop-growing condition (aerobic and anaerobic), water requirement, growing season, etc. Crops and cropping system requiring less irrigation water holds promise in the endemic areas. *Summer* rice must be replaced with low As accumulating dryland crops like

wheat, maize, tubers (potato, elephant foot yam, etc.), or food legumes having low water requirement. Additionally, soil amending properties of food legumes make them a better alternative when the objective is to reduce the contamination. Inclusion of pea, cowpea, or French bean in cropping systems not only reduces arsenic loading but also fetches better remuneration to the farming community. Cultivation of fruit crop like strawberry is also a lucrative farming option in this regard. Crop varieties accumulating less arsenic in their edible part can be a potential strategy to reduce human exposure to the dietary arsenic intake. Increasing crop water productivity and implementation of different water-saving technologies like mulching and deficit irrigation methods (sprinkler and drip) minimizes groundwater use and can be helpful in alleviating As-stress. Fertilization with Fe, P, Si, S, Se, and organic manures play crucial role in mitigation of As by reducing uptake and translocation to the edible part of the food crops. The mineral nutrients are involved in co-precipitation of As and minimizes As accumulation in crops. They play an active role in preventing As-induced oxidative damage to the crop. Additionally, Fe-plaque formation with As due to application of Fe amendments also helps in minimizing As uptake. Since $PO4$, SO_4, and As^V involve same uptake pathway, application of PO_4 and SO_4 amendments can effectively curtail down arsenate uptake in crops. Selenium at lower concentration exhibits antagonistic behavior with As. Application of FYM reduces As accumulation in both the soil and rice. Humic/fulvic colloids present in organic matter form organo-arsenic complex in soil, thereby decreasing arsenic uptake and accumulation in crops. The mostly accepted As detoxification mechanism by microorganisms is binding of As on extracellular surface of soil microorganisms which has uronic acids and proteins and amino sugars with a hydrogen-bonding potentials. AMF also helps to moderate arsenic translocation. Holistic management practices comprising of moderated irrigation water use, the addition of adequate soil amendments, use of tolerant varieties, and microbiological intervention can go a long way in ensuring food, nutritional, and livelihood securities in the As-ridden areas.

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Responses and Tolerance of Cereal Crops to Metal and Metalloid Toxicity

14

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Abstract

Soil acts as a sink for a number of organic and inorganic pollutants, through which these enter into the food chain and become a potential source of human diseases. Heavy metal (Cd, Cu, Cr, Fe, Ni, Pb, Zn) and metalloid (As, Sb) contamination of soil resources is increasing due to natural and anthropogenic activities. Currently, metal(loid) accumulation is one of the most serious environmental concerns owing to their toxicity to crops. Agronomic crops, mainly cereals (wheat, *Triticum aestivum*; maize, *Zea mays*; rice, *Oryza sativ*a), are cultivated on large area and, thereby, are more vulnerable to metal(loid) toxicity, affecting crop growth (seed germination, root/shoot length, and biomass), physiology (water relation, pigmentation, photosynthetic machinery), and metabolic processes (reactive oxygen species (ROS), lipid peroxidation, protein degradation). However, to counter these anomalies, crops are equipped with antioxidants

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(CAT, POD, SOD, APX, GR, proline, phenolics) to detoxify metal-induced ROS and proteins (phytochelatins, PCs; metallothioneins, MTs) to sequester metal(loid)s. Thus, further insight into these processes is important to exploit better metal-contaminated areas for raising crops, generate revenue, and feed ever-increasing population. Therefore, we present an overview of heavy metal(loid) pollution in soil; their toxicity to cereals (wheat, maize, rice) at morphological, physiological, and cellular levels; and their tolerance mechanisms. At the end, we explore the symbiotic association of cereal crops to a microbe in scavenging metal toxicity.

Abbreviations

AI	acid invertase
APX	ascorbate peroxidase
AsA	ascorbic acid
ATP	adenosine triphosphate
CAT	catalase
CCA	copper-chromium-arsenic
DHAR	dehydroascorbate reductase
ETS	electron transport system
GDH	glutamate dehydrogenase
GOGAT	glutamine oxoglutarate aminotransferase
GPOD	guaiacol peroxidase
GR	glutathione reductase
GST	glutathione-S-transferase
HMW	high molecular weight
IAA	indole-3-acetic acid
IBA	indole butyric acid
MDA	malondialdehyde
MDHAR	monodehydroascorbate reductase
MT	metallothioneins
NAA	naphthaleneacetic acid
POD	peroxidase
SOD	superoxide dismutase

14.1   Introduction

Soil contamination and metal pollution are the most imperative concerns in the industrialized world due to harmful effects on the biological system (Kisku et al. 2000). Heavy metals and metal(loid)s include cadmium (Cd), copper (Cu), chromium (Cr), iron (Fe), nickel (Ni), lead (Pb), zinc (Zn), arsenic (As), selenium (Se), and antimony (Sb) (Yadav 2010). Plants obtain the necessary and beneficial nutrients from organic matter or soil; however, the plants can also uptake and accumulate nonessential toxic metal(loid)s when these are bioavailable in soil (Kisku et al. 2000; Houshm and Moraghebi 2011). Heavy metal(loid)s are present in the soil naturally due to weathering of minerals, erosion, and volcanic activities; in addition to them, anthropogenic activities such as mining, electroplating, wood preservation, pesticides, industrial effluent, and fossil-fuel burning are also polluting our environment and thus have adverse impact on the biological entities (Alloway 2013). Heavy metals and their oxides are long persistent after their introduction and change their chemical forms with the varying bioavailability in most of cases; they do not undergo microbial or chemical degradation. Soil contamination by the heavy metals has a risk and adverse impact on human health by the direct ingestion or contact with contaminated soil, through the food chain or drinking the contaminated water (Alloway 2013; Singh et al. 2011). The main reasons for the toxicity of the metalloids are the mining process, manufacturing of the synthetic product, and their uses. Landfill sites and old orchards have a potential risk of arsenic due to excessive use of insecticide in the past for different purposes and the dumping of industrial hazardous waste or chemical waste (Alloway 2013).

Heavy metal(loid)s do not perform any known physiological function in the plants. Some metals are necessary for normal growth and required for the metabolism of the plants such as Co, Cu, Fe, Mn, Mo, Ni, and Zn, but they can harm when the concentration of any element is higher than the optimal level (Penna and Nikalje 2018; Alloway 2013; Krantev et al. 2008). The heavy metal contamination not only has an adverse impact on different constraints relating to plant quality and its yields but also alters the population size, composition, and activity of microbial community residing in the rhizosphere (Alloway 2013). Metals influenced the enzyme activities by the different approaches due to the disparate chemical affinities of the enzymes in the soil system; for example, the Cd toxicity is higher toward enzymes than Pb because it has greater mobility and lesser affinity to the soil colloids (Verma and Dubey 2003). Cr (IV) is a highly toxic and strong oxidizing agent, and its high concentration can cause harmful effects on the microbial cell metabolism (Shanker et al. 2005). Heavy metals can also affect the microbial reproduction in the composting process and cause morphological and physiological changes (Alloway 2013; Shanker et al. 2005).

Abiotic stresses such as heavy metal(loid)s, drought, salinity, water logging or flooding, and extreme temperature have adverse impacts on germination, growth, development, and seed quality of field crops; in some cases, these stresses reduced production rate up to 60% (Chapagain et al. 2017). On the other hand, global food production requirements increase day by day that would double in 2050 to meet the

needs of the growing population. Hence, one of the best way to ensure food security for the future generation is to develop the various stress-tolerant crop varieties. Extensive increase in the intensity and frequency of tremendous weather event and unpredictable monsoon rainfall has caused intense and frequent cycles of drought and flood. Rising temperature causes water stress condition and heat; predominantly, regions like arid and semiarid consequentially reduce agriculture productivity. Heavy metal(loid) stress also caused a decrease in plant nutrient contents, leaf area, shoot growth, root length, dry matter production, and seed germination effects of many cereal crops such as wheat, maize, and rice (Ahmad et al. 2015; Chapagain et al. 2017). Seed germination and seedling growth of wheat and maize cultivars were reduced on exposure to Cd (Ahmad et al. 2012, 2013).

Cadmium has adverse effects on photosynthetic rate, chlorophyll content, and intracellular CO_2 concentration (Krantev et al. 2008; Alloway 2013). The other metals such as Ni, Cu, Mn, and Zn also reduce photosynthetic efficiency by decreasing chlorophyll pigments (Krantev et al. 2008; Penna and Nikalje 2018). Chromium inhibits cell division, severely disturbs the cell cycle, and also reduces the root growth in the plants at the cellular level (Hu et al. 2014). Different crop plants (wheat, rice, maize) are very sensitive to metal stress; thus, some plants are referred as non-accumulator plants, whereas some plants are hyperaccumulators (*Brassica* sp., *Salix* sp., *Alyssum* sp.) and are able to tolerate toxic metals at higher level. Plant species can manage metal(loid) pollution through one or combination of these mechanisms: (i) remove the toxic metal(loid)s from the soil, (ii) avoid uptake of metal(loid)s to the plant roots, (iii) minimize the competition between metal(loid)s and fundamental nutrients that are required for the growth and development of the plants, and finally (iv) prevent movement of toxic metals into shoots. The most important thing is to be identifying the heavy metal fraction, controlling reaction mechanism, and monitoring the activities of metals and their bioavailability to the plants (Penna and Nikalje 2018).

Toxicity of metals also obstructs nitrogen metabolism, which is the important physiological processes that play a vital role in the growth and development of plants (Ma et al. 2017). Nitrate metabolism, inhibition of nitrate uptake, and its transportation are severely affected by Cd, which changes the primary nitrogen assimilation processes (Benavides et al. 2005). Plants are synthesizing and secreting many hormones which can improve plant tolerance against abiotic stresses (Chapagain et al. 2017; Penna and Nikalje 2018). Toxicity of metal(loid)s affects plant growth and development directly by causing oxidative stress and cytoplasmic enzyme inhibition, and indirectly, disturb ion homeostasis in plants, and excessive reactive oxygen species (ROS) to oxidize biomolecules in the plant (Wang and Zhou 2005; Chapagain et al. 2017). Production of the ROS is due to the effect of any type of stress. Mostly, the ROS is produced in the chloroplast, peroxisomes, and mitochondria. The heavy metal accumulation is the consequence of the disruption of CO_2 in the chloroplast so that it reduced the electron transport chain in the photosynthetic process and production of ROS. In the plant metabolism, ROS plays a dual function under optimum concentration; they are involved in various physiological processes and act as stress sensor. The fate of ROS totally depends on the

scavenging system if the ROS scavenges efficiently so that it works as a signaling molecule. If the production of ROS is much higher and cannot be regulated to the scavenging system, it becomes toxic (Wrzaczek et al. 2013; Penna and Nikalje 2018). The antioxidant mechanism protects cells from detrimental effects of ROS. The antioxidant system includes enzymatic component that consists of glutathione reductase (GR), catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), etc. The antioxidant enzymes are used for the mitigation of induced damages of metals. It is well known that ROS generation increased by metals and in response the activity of antioxidant enzymes (POD, SOD, APX) also increased (Yang et al. 2011; Penna and Nikalje 2018).

The cereal crops (wheat, maize, and rice) are staple foods in different parts of the world; therefore, in this chapter, we discuss the toxic effects of metal(loid)s to cereal crops and find out the tolerance mechanisms they have to rectify metal(loid) stress. We also identify the role of plant growth-promoting bacteria (PGPB) and cereal interaction for the alleviation of metal(loid) stress.

14.2 Pollution of Metal(loid)s in Soil

The terrestrial environment is the principal sink of heavy metal(loid)s coming from geogenic and anthropogenic sources (Fig. 14.1). Metalloids such as As and Se are mainly accumulated in soil through natural resources; for instance, 45,000 tons of As is released in the environment through burning of coal on annual basis; igneous rocks contributed 100 mg As kg^{-1} while manganese ores 15,000 mg As kg^{-1} (Bolan et al. 2014); similarly, Se-rich shales, limestones, and mudstones are the source of Se in soils found in the USA and India (Bolan et al. 2014).

Many countries in the world are poorly designed and implement the environment act; thereby, they are facing the problem of heavy metal(loid) accumulation in the terrestrial and aquatic environment. Those having frequent use of lead gasoline have the problem of Pb accumulation in air and soil (Wuana and Okieimen 2011). Lead is a toxic element, it is present in rocks (1–150 mg kg^{-1}), and thereby, it has been included in new European REACH Regulation (EC1907/2006) (Kushwaha et al. 2018). Some countries are using intensive pesticides (Bordeaux mixture), and phosphate fertilizer (rock phosphate) has been reported for Cu, Cd, and Pb pollution (Wuana and Okieimen 2011; Bolan et al. 2014). The mixture of copper-chromium-arsenic (CCA) is being used for preservation of wood in the USA; Cr is also frequently used for the treatment of tanneries (Bolan et al. 2014; Robinson et al. 2006). Soil irrigated with wastewater was contaminated with heavy metals (Cd 5, Co 13, Pb 21, Cr 33, Cu 43, Mn 64, and Zn 83 mg kg^{-1} soil) in Lahore, Pakistan (Mahmood and Malik 2014). They further reported the health hazard impact of these metals especially Cd and Mn via consumption of leafy vegetables cultivated in metal-contaminated soils. Heavy metal(loid)s can be divided into three distinguished hazardous classes on the basis of their toxicological profile; for instance, Dutch has divided metal(loid)s on the basis of their toxicity in soil (Vodyanitskii 2016): (i) highly hazardous (Cd, Be, Se, Sb (< 1 mg kg^{-1} soil)), (ii) moderately hazardous (As,
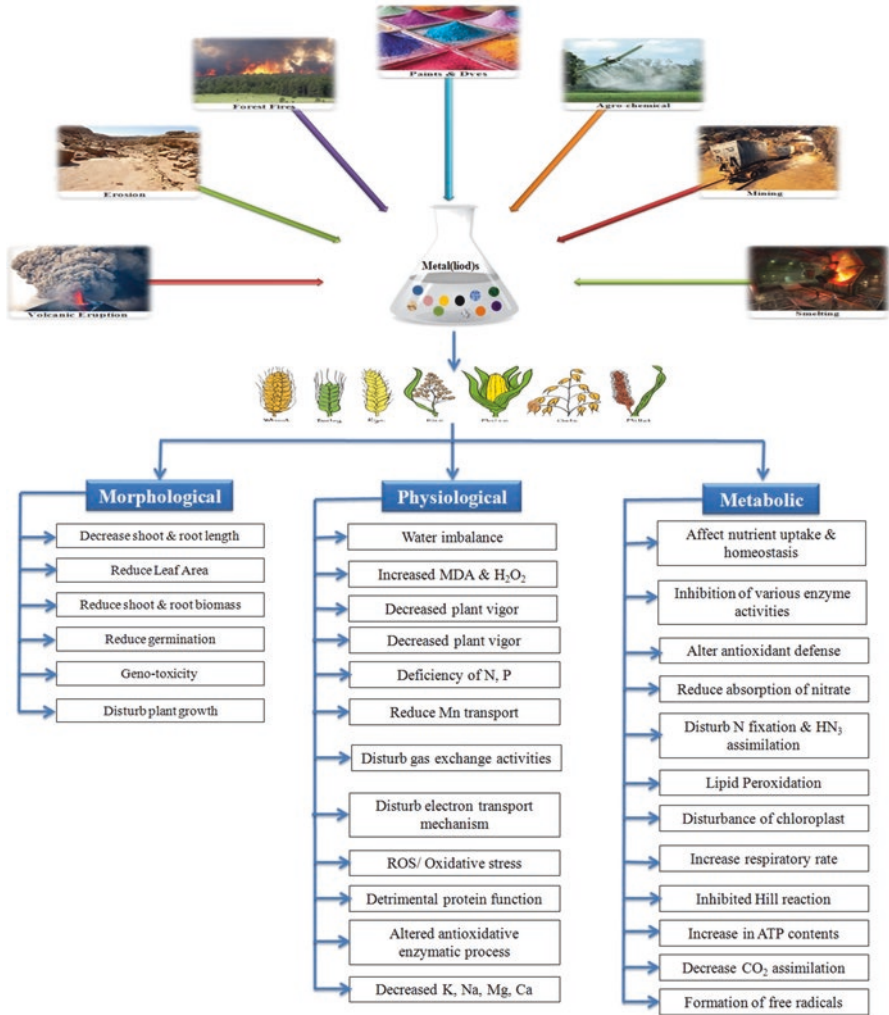
Fig. 14.1 Sources of heavy metal(loid)s and their toxic effects on cereal crops

Ba, Cu, Cr, Hg, Ni, V (1–10 mg kg^{-1}soil)), and iii) low hazardous (Co, Ce, Pb, Zn (> 10 mg kg^{-1} soil)). Heavy metal(loid) contamination in soils of various countries has been summarized in Table 14.1. The soils of Ghana, the European Union, and Greece were contaminated with As, whereas Bangladesh soil was contaminated with Cd higher than the values of these metals in world soil (Table 14.1). Similarly, river basin of Columbia showed higher levels of Cu, Ni, and Zn, whereas agricultural soils of Khyber Pakhtunkhwa, Pakistan, showed higher values of Zn than their respective world level (Table 14.1).

Table 14.1 Heavy metal(loid) contamination in soils of various countries

Sample	Country	As	Cd	Cr	Cu	Hg	Ni	Pb	Zn	References
		mg kg^{-1}								
Soil	Average Ghana	4	0.052	21	6.2	0.32	3.7	7.2	39	Bortey-Sam et al. (2015)
Soil	Tamso, Ghana	27	0.43	77	16	0.42	28	14	118	Bortey-Sam et al. (2015)
Agricultural soil	Average European Union	4	0.09	22	13	0.04	18.36	15.3	–	Tóth et al. (2016)
Soil	Dhaka, Bangladesh	–	11	54	39	–	58	50	115	Ahmad and Goni (2010)
River basin	Columbia	–	0.040	–	1149		661	0.071	1365	Marrugo-Negrete et al. (2017)
Argolida basin	Peloponnese, Greece	6.95	0.54	83	75	–	147	20	75	Kelepertzis (2014)
Agricultural soil	Almería Spain	–	0.4	30	26	–	27	26	66	Rodríguez-Martín et al. (2013)
Agricultural soil	Piemonte, Italy	–	–	46	58	–	83	16	63	Facchinelli et al. (2001)
Agricultural soil	Huizhou, China	–	0.10	28	17	–	15	45	57	Cai et al. (2012)
Agricultural soil	Yongji, China	–	0.22	54	32	–	–	12	107	Yangchun et al. (2017)
Agricultural soil	Thiva, Greece	–	–	277	32	–	1591	24	67	Antibachi et al. (2012)
Agricultural soil	Zagreb, Croatia	–	0.66	–	21	–	50	26	78	Romic and Romic (2003)
Agricultural soil	KPK, Pakistan	–	–	0.9–67	7–28	–	5–52	–	41–217	Rehman et al. (2017)
World soil value		1–1.5	0.07–1.1	5–120	6–60	0.07	1–200	10–70	17–125	Kabata-Pendias (2011)

14.3   Metal(loid) Toxicity to Cereal Crops

Heavy metals and metalloids are ubiquitous in the environment; however, they affect crops mainly due to their contamination in soil and water. The farmers are using untreated industrial effluent to irrigate fields, chemical fertilizers, and pesticides to increase economic yield at the cost of soil pollution and quality. The exposures of heavy metal(loid)s to cereal crops are causing morphological, physiological, and metabolic changes which are elaborated here (Fig. 14.1).

14.3.1 Morphological Effects of Metal(loid)s

Heavy metal(loid) toxicity severely affected the plant growth and development more than any other environmental stress. Heavy metal toxicity has decreased morphological attributes of cereal crops and also caused genotoxicity. It is essential for metals to be available in sufficient amount in soil for plant uptake; once it is accumulated in plants through either H+/ATPase pump or Ca channels, it disrupts the synthesis of enzymes and proteins that inhibit seed germination and growth of plants (Kushwaha et al. 2018). They further reported that Pb toxicity also limits leaf water contents, stomatal closure, and mineral nutrients. It is reported that heavy metal (Pb) has decreased the seed germination, root/shoot length, and biomass of many cereal crops such as maize (Ghani 2010; Hussain et al. 2013; Singh et al. 2015), wheat (Yang et al. 2010; Lamhamdi et al. 2013; Ramesar et al. 2014), and rice (Gautam et al. 2010; Khan et al. 2018). Verma and Dubey (2003) examined the effect of high dose of Pb (1000 mM) to rice seedlings that caused a reduction in shoot/root length (31–40%) and shoot/root fresh weight (29–43%). Very recently, Khan et al. (2018) determined the toxicity of Pb to rice crop cultivated in nutrient-sufficient or nutrient-deficient conditions. They observed Pb toxicity to aerial part of rice; however, it did not cause any toxicity to belowground part of rice under a limited supply of essential nutrients. The short-term effects of Pb on wheat seedling were observed by Lamhamdi et al. (2011), while long-term effects were reported by Ramesar et al. (2014). They concluded that this metal has reduced seedling growth of wheat at either short- or long-term Pb exposure.

Leaf concentration determines the toxicity of Cd; Lux et al. (2011) reported that Cd causes toxicity to plants if its concentration in the leaf is >10 µg g^{-1}. They also noted the toxic effects of Cd on root anatomy of the plant that is due to high accumulation of this metal in plant roots. Seed germination and initial growth stages of wheat are very crucial and sensitive to Cd toxicity (Ahmad et al. 2012, 2013). Many investigations reported that Cd has decreased root/shoot length, biomass, and chlorophyll content of cereals (Ahmad et al. 2016; Rizwan et al. 2016; Ansarypour and Shahpiri 2017). However, in some cases due to a higher concentration of Cd, crops showed phytotoxic symptoms such as browning of roots, leaf epinasty, and leaf chlorosis and necrosis (Dong et al. 2005; Lux et al. 2011). Cadmium-induced genotoxicity damages DNA, growth, and mineral uptake in plants (Benavides et al. 2005); in another study, Cd caused an acute reduction in growth, biomass, and water contents in sorghum (Roy et al. 2016).

Higher Cr accumulation may cause inhibition in seed germination and thus cause a reduction in crop growth (Adrees et al. 2015; Tripathi et al. 2015). Chromium has caused the oxidative stress in cereal crops that disturbs not only the biochemical but also the morphological functions of plants, resulting into loss of economic yield of crops (Ma et al. 2017; Handa et al. 2017). Mathur et al. (2016) examined the effects of Cr on wheat and noted that growth of wheat is inhibited due to impairment of photosynthetic and internal metabolic machinery. Wyszkowski and Radziemska (2013) reported negative effects of Cr on growth and biomass of oat.

Previous studies revealed that germinating seeds and seedling growth of rice were decreased due to toxicities of metalloids in hydroponic (Khan and Gupta 2018). Among these metal(loid)s, arsenic (As) toxicity becomes a worldwide environmental problem (Zhao et al. 2009). Zhang et al. (2016) exposed the resistant and sensitive cultivars of rice to As in a pot experiment with and without mycorrhiza. They found less accumulation of As in grains of resistant rice cultivars as compared to sensitive; however, flooding conditions promote the As accumulation in resistant cultivar when compared with aerobic conditions (Zhang et al. 2016). The authors urged the farmers to adopt these agronomic (water management) and genetic engineering-cum-breeding techniques to avoid As toxicity to rice (Zhang et al. 2016). An excellent review has been published by Islam et al. (2016a) elucidating the toxicity of As in rice. They argued that rice is more efficient at accumulating As in grains as compared to other cereals, and thereby, this is prone to relatively greater As toxicity in terms of growth and quality of rice grain. However, at the same time, the authors address some management practices to reduce As toxicity in rice. Arsenic was loaded into crop cells following the same route as followed by the essential elements and has caused morphological and metabolic effects on cereal crops (Abedin and Meharg 2002; Zhao et al. 2009). It has reported that As caused severe damage to root/shoot biomass, seed germination, and economic yield of crops (Abedin and Meharg 2002; Armendariz et al. 2016). Maize seedlings were exposed to 0–5 mg As L^{-1} in hydroponics for 5 days (Stoeva et al. 2003); they observed a significant reduction in maize growth, biomass, and leaf area. Similar to other metalloids, selenium (Se) stress decreased growth and biomass of lowland rice (Mostofa et al. 2017).

14.3.2 Physiological Effects of Metal(loid)s

Lead (Pb) toxicity has caused a significant reduction in chlorophyll contents of wheat (Lamhamdi et al. 2013; Ramesar et al. 2014) and maize (Singh et al. 2015), and the effect was aggravated with elevated concentrations of Pb. Similarly, Zn stress significantly decreased chlorophyll a and b of wheat leaves (Li et al. 2013). It has been reported that Pb stress generated ROS in many crops (Fahr et al. 2013); consequently, it increased malondialdehyde (MDA) and H_2O_2 contents in wheat (Kaur et al. 2012). Similar kind of effects was reported in other studies; for example, MDA concentration has increased in maize (Gupta et al. 2009), rice (Thakur et al. 2017), and wheat (Yang et al. 2011; Kaur et al. 2012) in hydroponics under different Pb concentrations and time of exposure. The increased MDA and H_2O_2 contents in

wheat and maize are rectified in plants by activating internal antioxidative system (Kaur et al. 2013, 2015; Singh et al. 2015). However, the ability of cereal crops to respond to Pb toxicity and detoxification mechanisms varies with growth conditions and plant species.

Cadmium ions cause inhibition in physiological machinery of cereal crops that decrease plant strength and hamper cereal crop growth (Nahakpam and Shah 2011; Ahmad et al. 2015, 2016). Leaf chlorosis, reduction in seed germination, growth and cell division, and limited uptake of water, phosphorus, and nitrogen in cereal crops are some common causes of Cd toxicity (Benavides et al. 2005; Lux et al. 2011; Shah et al. 2013). The presence of Cd^{2+} is associated with the occurrence of oxidative stress (Nahakpam and Shah 2011; Ahmad et al. 2016). Also recently, it was demonstrated that Cd^{2+} causes a series of ROS generation, viz., hydrogen peroxide, superoxide anion, and hydroperoxides in crop cells (Garnier et al. 2006). Effects of Cd toxicity are employed to the plasma membrane within the cell of the crop (Lux et al. 2011). Cd^{2+} when taken up by the roots is moved to xylem cells through an apoplastic or a symplastic pathway for its transportation into leaves (Lux et al. 2011); however, most of this metal is restricted at roots (Ahmad et al. 2014). Such accumulation and translocation of Cd^{2+} in roots to leaves differ considerably among species and even among varieties of the same species. Mostly, Cd^{2+} gets deposited and binds largely in the cell walls adjacent to the plasma membrane and to the endomembrane compartments; however, in leaves, Cd^{2+} is found to accumulate in vacuoles as well (Jin et al. 2015; Liu and Kottke 2004). The first visible effect of Cd toxicity was an enhancement of vacuolation in the meristematic cells and the appearance of electron-dense granules between the cell wall and plasma lemma in plant roots (Liu and Kottke 2004). At high concentration of Cd^{2+}, the cell death occurs owing to severe plasmolysis, shrinkage of cytoplasm, and reduction in a number of ribosomes and mitochondrial cristae (Liu and Kottke 2004).

Cr largely targeted the green pigments and photosystem and inhibited carbon assimilation in wheat (Ali et al. 2015; Mathur et al. 2016). The process of photosynthesis, enzymatic reactions, and chlorophyll (a, b, and carotenoids) content of maize were inhibited in the presence of Cr in the growth media (Islam et al. 2016b). Similar to other metals, Cr generates ROS in plants that cause specific damage, and sometimes, it spreads to whole-plant level (Anjum et al. 2014; Gill et al. 2016); this condition causes severe destruction in physiological processes of plants due to oxidative stress, which oxidizes proteins, lipids, and nucleic acid and inhibits enzymes leading to cell death in cereal crops (Adrees et al. 2015).

Selenium has generated ROS such as H_2O_2 and damaged cell membrane of rice plant by the production of high-lipid peroxidation that ultimately hampered the morphology of rice (Mostofa et al. 2017). ROS are considered as an indicator of stress in plants, and thus, it acts as signaling molecules (Wrzaczek et al. 2013; Luo et al. 2016). Higher concentration and accumulation of Se in crops decreased the amount of green chloroplasts and degradation of the organelles in plant root cells (Ślusarczyk et al. 2015). The increased lipid peroxidation in wheat seedlings and enhanced antioxidant activity in barley are indicators of ROS generation and accumulation in these cereals cultivated in Se-contaminated media (Akbulut and Cakır 2010; Łabanowska et al. 2012). The inhibition of green pigments, reduction in water

contents, enhanced production of hydrogen peroxide, and lipid peroxidation are the major consequences of Se stress in lowland rice plant (Mostofa et al. 2017). They also noted that rice plant in Se stress showed upregulation of some antioxidant enzymes (SOD, GPX) while downregulation of others (AsA, CAT, GR). Selenium caused toxicity to cereal crops due to attachment of Se to Cys/Met complex in protein chain and resulted in formation of selenoproteins (SeCys/SeMet); this complex impairs protein functioning. The formation of SeCys complex is more detrimental to protein synthesis than SeMet, the former having more toxic nature; however, both complexes are very reactive and easily deprotonated and inhibit enzyme functions (Hondal et al. 2012). The other studies reported specific inhibition of glutathione synthesis in model plants in response to Se stress (Hugouvieux et al. 2009; Grant et al. 2011).

The As exposure to maize seedlings causes a significant reduction in green pigments that lead to lower efficiency of photosynthetic machinery (Stoeva et al. 2003); the As stress also increased lipid peroxidation and antioxidant enzyme peroxidase activity in the same plant. The As toxicity to maize seedlings is rendered due to metabolic impairment in maize cell for uptake of phosphate ions which are known analogue of arsenate ion and share the same path to enter in root cell and are transported to shoot (Stoeva et al. 2003; Smith et al. 2010). Another reason to this toxicity is the conversion of As (V) to As (III) in the cytoplasm of plant cell (Meharg and Hartley-Whitaker 2002; Stoeva et al. 2003), which causes cellular damage through generation of ROS, inhibiting enzymes and proteins (Meharg and Hartley-Whitaker 2002; Smith et al. 2010).

14.3.3   Metabolic Effects of Metal(loid)s

In cereal crop, toxic effects of Cd on metabolism have been observed, for instance, reduced uptake of nutrient (Sandalio et al. 2001), hampering of various enzyme activities (Obata and Umebayashi 1993), and production of oxidative stress (Romero-Puertas et al. 1999; Sandalio et al. 2001), including changes in enzymes of the antioxidant defense system (Benavides et al. 2005). Cd also decreased the accumulation of nitrate and its transport from roots to shoots, by damaging the nitrate reductase activity in the shoots of the plant. Cadmium also decreased the process of absorption of nitrogen fixation and primary ammonia in plants during Cd treatments (Balestrasse et al. 2001). Cadmium produces changes in the functionality of membranes by destroying lipid peroxidation and disturbances in chloroplast metabolism by damaging chlorophyll biosynthesis and decreasing the activity of enzymes involved in CO_2 fixation.

Wheat seedlings are exposed to Pb stress in hydroponics to determine its effect on nutrient uptake and metabolic products (Lamhamdi et al. 2013). They found decreased uptake of nutrients (Ca, Mg, Cu, Zn) and synthesis of proteins while increased Mn in wheat under Pb stress. Kaur et al. (2012) reported membrane instability and alteration in enzyme activities in wheat in response to Pb stress. Heavy metal stress (Ni, Cd, Pb, Zn) inhibits phosphorylation reaction and impairs electron transport system in the plant (Romanowska et al. 2002, 2006); another study

reported alterations in dictyosomes, endoplasmic reticulum, and mitochondrial cristae under Pb stress (Jiang and Liu 2010). The chromosome damage and decreased in mitotic and cell division in maize cells are the consequences of Pb stress (Jiang and Liu 2000). The exposure of C_3 and C_4 plants to Pb oxidized many important substrates of Calvin cycle in mitochondria which affects respiration rate of maize and barley (Romanowska et al. 2002); moreover, Pb stress triggers ATP production in these cereals (Romanowska et al. 2002, 2006).

The scientist identified many biomarkers in plants to quantify metal stress. Among them, phytochelatins are the most common proteins produced in plants in response to heavy metals. Keltjens and van Beusichem (1998) reported the toxicity of Cd and Cu on maize and wheat metabolic activities. They observed a close association of Cd and PC contents in plant tissues; thereby, they considered PC as a biomarker of Cd stress in these cereals. Cadmium exposure to sorghum increases or decreases the expression of many proteins responsible for the metabolism of carbohydrates and protein synthesis. These factors have a major role in lowering of growth and biomass of sorghum (Roy et al. 2016). The high concentration of Zn in the growth media caused inhibition in kinase and dehydrogenase enzymes in wheat roots (Li et al. 2013); however, Zn stress does not affect hydrogen peroxide, MDA, and SOD activities in leaves of wheat. The Cu exposure to cereal crops induced metabolic and anatomical changes; for instance, it induced lipid peroxidation in wheat, maize, and rice (Adrees et al. 2015).

The high concentration of Cr decreased NO_3-N and increased accumulation of total N in oat (Wyszkowski and Radziemska 2013). The toxic effect of Cr on the yield of barley was also reported that was due to decreased accumulation of N compounds in this cereal crop (Wyszkowski and Radziemska 2010); interestingly, the same study compared the toxic effect of Cr on maize which showed tolerance compared to barley. This tolerance was due to greater accumulation of NH_4-N in maize. Exposure of plants to Cr-induced changes in their metabolic activities; in some cases, it disturbs hydrolytic enzymes (amylase) during seed germination, nitrate and nitrite reductases essential for nitrogen metabolism, and carbohydrate metabolism in plant leaves (Singh et al. 2013). The other studies also reported similar effects of Cr on nitrogen metabolism (Kumar and Joshi 2008); they observed reduced activities of urease, nitrate/nitrite reductases, glutamate synthase, and dehydrogenase in root and shoot of sorghum. Twenty-two different kinds of proteins were identified in maize exposed to Cr stress, of which six proteins were associated with sugar metabolism, three proteins were related to stress tolerance, and four were responsible for antioxidant production (Labra et al. 2006). Similarly, Ding et al. (2009) reported Cr-induced activities of protein kinase in maize, which is inactivated upon production of hydrogen peroxide scavenger. The activity of NO- and Ca-dependent kinase increased in maize exposed to Cr, and it followed the ZmMPK5 pathway for expression of these enzymes (Ding et al. 2009). Based on microarray analysis, Dubey et al. (2010) found up- and downregulation of genes in rice grown under Cr stress; these genes were involved in metabolism, transport of sugar and nutrients, and homeostasis of Cr stress by either production of antioxidant enzymes or osmolytes.

Łabanowska et al. (2012) investigated Polish and Finnish wheat seedlings exposed to Se for a two-day period. They observed increased metabolism of carbohydrates and enzymatic antioxidants in Polish than Finnish wheat that might be the reason for better Se tolerance in Polish-originated wheat cultivars. Selenium in the form of selenate is metabolized in chloroplasts via sulfur reduction process, and its toxicity is mainly due to alteration of cysteine to selenocysteine in proteins. The formation of the process of nonspecific selenoproteins in iron-sulfur clusters has reduced the rate of photosynthetic electron transport in selenate-treated wheat plants (Hondal et al. 2012). So, evidence from previous studies suggests that Se toxicity can also be increased due to the ability to catalyze the process of the oxidation of thiols and to generate ROS (Hondal et al. 2012). Selenium stress in rice plant inhibits the activity of glyoxalases and causes toxicity of methylglyoxal to rice (Mostofa et al. 2017). They also found Se toxicity on the synthesis of proteins, reducing sugars and enzymatic antioxidants in rice. Lipid peroxidation, denaturation, and disruption of many enzymes and processes in the model plant *Arabidopsis* were due to Se-induced oxidative stress (Hugouvieux et al. 2009), and moreover, it inhibits the accumulation of APX, POD, and ETS in plant cells.

Another important metalloid is As; many studies have reported metabolic-level toxicity of As in crops including cereals (Stoeva et al. 2003; Smith et al. 2010). Normally, As is transported to plant shoot, usually arsenite following the silicon while arsenate following the phosphate pathway (Meharg and Hartley-Whitaker 2002; Zhao et al. 2009; Zhu and Rosen 2009). The SH groups of proteins are mainly influenced by As, and thus, it causes conformational changes in the structure of proteins in plant cells (Van Assche and Clijsters 1990; Delnomdedieu et al. 1994). The metabolic response of six rice lines exposed to As revealed accumulation of phytochelatins in roots and grain while no production observed in leaves; instead, glutathione activity increased in leaves (Heuschele et al. 2017); similarly, As-induced lipid peroxidation and peroxidase activity were observed in maize seedlings (Stoeva et al. 2003). Studies revealed that inorganic As is converted into organic form in rice grains; for instance, Marin et al. (1992) noted that rice seedlings exposed to organic and inorganic forms of As showed that the former is a dominant species in rice grain. The summary of the physiological and metabolic effects of metal(loid)s on cereal crops is given in Fig. 14.1.

14.4 Responses of Plants to Heavy Metal Stress

Plants are usually immobile, and therefore, they have to face unwanted environmental variations. Cereal plants have to evolve a large number of strategies ranging from physiological and biochemical to maintain adverse effects of metal(loid) toxicity. These plants recognize stress signal and then transduce and transmit the signal into the cell and activate the response to offset the unwanted effects of stress by redesigning the biochemical processes of plant cell (Fig. 14.2). Understanding the variations in the signal transduction in plants in response to metal(loid) stress is difficult at the whole-plant level. This might be possible to monitor initial responses like
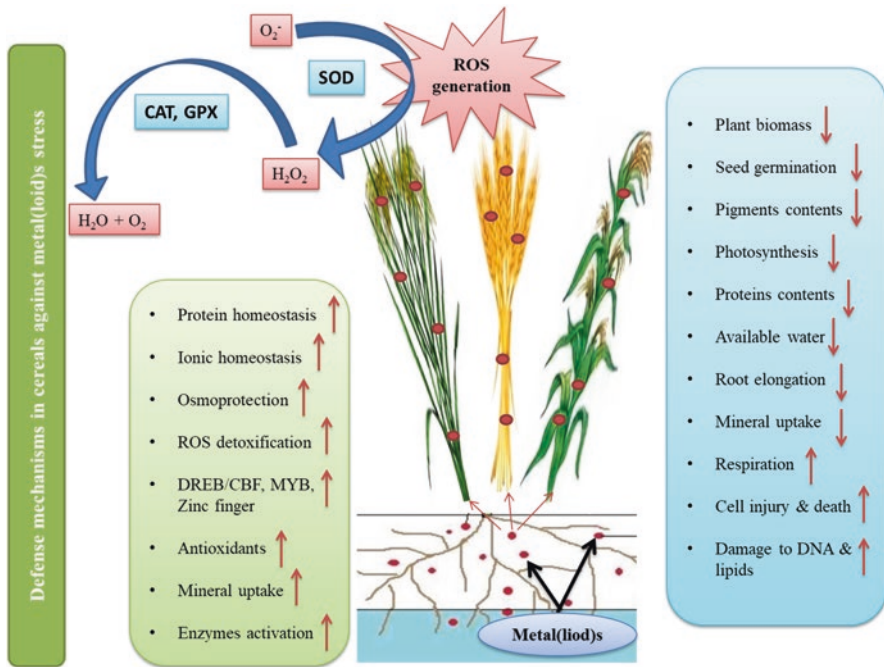
Fig. 14.2 Possible defense mechanism activities in cereals to mitigate heavy metal(loid) stress

metabolite accumulation, oxidative stress, and transcriptomic and proteomic changes, and this will help in the recognition of changes that occur in cereal plants after heavy metal stress exposure. The similarity between heavy metals and essential plant growth elements causes competition in absorption from the soil. The presence of heavy metal(loid)s in soil competes with phosphorous and zinc and restricts their absorption from soil to plants which cause a nutrient deficiency. Heavy metal(loid)s bind with functional protein sulfhydryl group and disturb its function essential for normal plant growth and function (Lux et al. 2011; DalCorso et al. 2013; Sharma et al. 2016).

In some plants like cereal (barley), metal toxicity symptoms are similar to drought stress symptoms, and therefore, overexpression of genes related to water stress tolerance is the basic mechanism adopted by these plants that enable them to withstand metal stress (Tamas et al. 2010). Restricted seed germination and growth of seedling in wheat, decreased photosynthetic activity, chloroplast membrane damage, limited enzymatic activity, reduced plumule and radical growth, imbalanced protein metabolism, and nutrient status are the responses of cereal plants when exposed to heavy metal stress (Ahsan et al. 2010; Li et al. 2013; Ahmad et al. 2012; Ahmad et al. 2015; Singh et al. 2015, 2018). Suppression in root growth due to prolonged cell cycle and decreased cell division (decreased mitotic activity) has been reported in many cereal crops under metal stress (Jiang and Liu 2000; Kikui et al. 2005; Lux et al. 2011; Hayat et al. 2012; Anjum et al. 2014). The copper toxicity alters auxin distribution

restricted root growth that causes limitation in water and nutrient uptake, and ultimately, it reduced shoot growth of cereals (Wang and Zhou 2005).

Cereal plants adopt following basic three types of mechanisms to mitigate the effects of heavy metal stress. These include physiological, biochemical, and morphological adaptations: i) Physiological adaptations are osmolyte accumulation, higher leaf gas exchange, regulation of leaf water and chlorophyll contents, and vascular development; ii) biochemical strategies utilized by plants are the regulation of antioxidant production system and biosynthesis of enzymes. These physiological and biochemical changes help the cereal plants to tolerate toxic effects of heavy metal stress and lead to iii) morphological developments like leaf development, root and shoot length improvement, leaf cell proliferation, and better seed germination and increased the fresh and dry weight of plants (Shahzad et al. 2018). The following section elaborated the salient mechanisms reported in cereals and related plant species to dilute the effect of heavy metal(loid) toxicity.

14.4.1 Enzymatic Antioxidants

Plants experiencing stress usually generated ROS which are hunted by the production of enzymatic and nonenzymatic antioxidants (Dat et al. 2000). The phytohormone (brassinosteroids, BRs), e.g., 24-epibrassinolide (EBL), regulates the antioxidant production system of plants and helps to tolerate metal stress (Sharma and Bhardwaj 2007; Allagulova et al. 2015; Shahzad et al. 2018). Allagulova et al. (2015) investigated the effect of EBL hormone to mitigate Cd stress in wheat. They observed dehydrin protein accumulation in wheat seedlings is responsible for Cd tolerance. Regulation of chlorophyll contents, photosynthetic activity, and osmolyte production was accompanied due to phytohormone, i.e., EBL produced by plants under metal stress to tolerate heavy metal toxicity (Hayat et al. 2007). The cereal plants adopted many defense mechanisms to mitigate metal stress: the scientists noted enhanced production of enzymatic antioxidants (SOD, APX, CAT, GPOD) in root, shoot, and leaves of wheat, maize, and rice (Kaur et al. 2012; Islam et al. 2014; Ali et al. 2015; Kaur et al. 2015; Khan and Gupta 2018) and synthesis of EBL-hormone-induced dehydrin and steroidal compounds (Allagulova et al. 2015; Shahzad et al. 2018). Superoxide radicals are mutated to H_2O_2 due to the action of SOD, and H_2O_2 is further scavenged by CAT and APX (Gill and Tutija 2010). Increase in CAT, SOD, GPX, and GSH-PX in rice and brassica was observed in response to Cr and Ni stress (Arora et al. 2010; Sharma et al. 2016). Increased nitrogen metabolism due to increased activity of nitrate reductase and nitrite reductase; increased carboxylase and oxygenase activity; and increase in activity of glutamine synthetase, glutamate dehydrogenase, glutamine oxoglutarate aminotransferase (GOGAT), and glutamate dehydrogenase (GDH) has a vital role in detoxification of toxicants produced in metal-stressed plants. Enhanced protease activity is another phenomenon that takes place to cope with heavy metal stress. Toxicity of As in rice is ameliorated by the enhanced production of antioxidants (SOD, CAT, GPX, GST) in shoot and root (Khan and Gupta 2018).

14.4.2 Nonenzymatic Antioxidants

Along with enzymatic antioxidants, cereal plants possess a nonenzymatic antioxidant system to combat with deleterious effects of heavy metal exposure. Ascorbic acid is an important nonenzymatic compound produced in plants under metal stress (Gill and Tuteja 2010; Hasanuzzaman et al. 2012). It is used as a reducing agent by the enzyme ascorbate peroxidase to detoxify H_2O_2 in the ascorbate-glutathione cycle. Furthermore, ascorbic acid improves tolerance of plants to metal stress by protecting proteins and lipids and offsets the toxic effects on growth and physiology of plants (Akram et al. 2017). These mechanisms are also observed in other plant species: for instance, enhanced activity of carbonic anhydrase and monodehydroascorbate reductase (MDHAR) of ascorbate-glutathione cycle (Hayat et al. 2007; Yadav et al. 2018). The AsA is an important nonenzymatic antioxidant to alleviate metal stress, but it is oxidized to MDHA. Thanks to nature, plants have ascorbate-glutathione cycle which converted MDHA to AsA by the hormone MDHAR in the presence of NADPH. Maintenance of AsA pool is brought about by the increased activity of this enzyme. Toxic electrophiles are produced in plants under metal stress, and increased activity of glutathione-*S*-transferase (GST) has been found to be important in detoxification of these electrophiles (Edwards et al. 2000). Upregulation of genes encoding antioxidants like DHAR, GR, GST-1, and GSH-S was observed in previous study, and overexpression of stress-related genes in plants under metal stress suggested the role of upregulation and expression level in detoxification of stress-related toxicants and in enhancing the tolerance level of plants (Ashraf et al. 2010; Zhang et al. 2015). Glutathione is also capable of reducing ROS via the ascorbate-glutathione cycle by the action of GR as it converts GSSG to GSH at the expense of NADPH (Gill and Tuteja 2010; Foyer and Noctor 2011).

Phenolics are another important group of nonenzymatic antioxidants having at least one aromatic ring (C6) bearing one or more hydroxyl groups. Biosynthesis of phenolic compounds in wheat, maize, and barley under heavy metals like Ni, Al, and Cd, respectively, has been reported (Michalak 2006). Phenolic compounds have –OH and –COOH groups which may bind metals and lipid alkoxyl radicals and limit metal-induced oxidative stress. However, this activity directly relies on the number and position of –OH group in the molecules (Michalak 2006). Various types of peroxidases (POX) are operating in the plant system of which some use ascorbate or phenol to donate an electron. These perform a vital role in lignin formation in the plant cell wall that has restricted Cd entry into the plant by developing physical barrier (Loix et al. 2017).

Organic acids like acetic and citric acid produced biologically in plants have a carboxylic group in their structure and possess the ability to chelate heavy metal ions. Citric acid mobilizes the heavy metals in the rhizosphere and facilitates the phytoremediation process (Gao et al. 2010). It has been reported that citric acid induced protection by activating host antioxidant system against metal(loid) stress (Freitas et al. 2013). Synthesis and exudation of citric acid in wheat (Tahir et al. 2015) while cysteine and proline in rice (Khan and Gupta 2018) have been reported previously to overcome the oxidative stress induced by the metal(loid)s. Amino

acids like alanine, proline, cysteine, methionine, glutamine, and aspartic acid were produced in response to metal stress (Bhatia et al. 2005). Roots synthesize and deposit callose that helps them in restricting the entry of heavy metals into roots and thus avoid negative effects. Sequestration and stabilization of metals at the root level is an important strategy to avoid or protect shoot from metal-induced oxidative stress (Singh and Pandey 2011; Feigl et al. 2013). Auxin has a vital role in the improvement of root system properties like enhanced root length and root area to absorb more water and essential ions (Tahir et al. 2015). In metal-contaminated soils, cereal plants produce auxin compounds like indole-3-acetic acid (IAA), indole butyric acid (IBA), and naphthaleneacetic acid (NAA) to combat with osmotic stress caused by metal toxicity.

14.4.3 Protein

The activity of ATPase soluble proteins and nucleic acids mitigates the toxic effects of metal(loid) in plants (Ashraf and Foolad 2007; Choudhary et al. 2011; Madhan et al. 2014). Lipid peroxidation occurs in plants under metal stress, and plants produced membrane proteins that degrade ROS and minimize the effects of lipid peroxidation (Cao et al. 2005). Increase in free proline contents is another mechanism adopted by plants to tolerate metal stress. In the presence of elevated levels of heavy metals, plants synthesize two types of proteins, i.e., phytochelatins (PC) to chelate metal ions and metallothioneins (MT) in the cytosol for sequestration of metals in the vacuole (Hassan et al. 2017). The synthesis of S-rich proteins is known to induce stress tolerance in plants (Zagorchev et al. 2013); such kinds of proteins have been reported previously for sequestration and detoxification of metal(loid)s in plants (Clemens 2006; Viehweger 2014). In addition to heavy metal chelation and accumulation, PC also has a critical role in antioxidant production, homeostasis of metal ions, and complexation of metals with PCs (Jabeen et al. 2009; Furini 2012; Hasan et al. 2017). The heavy metal(loid)s sequestered by PC are transported from cytosol to the vacuole by ATP-dependent vacuolar pumps (V-ATPase and VPPase) and a set of tonoplast transporters (Sharma et al. 2016; Hassan et al. 2017). The advanced RNA-Seq and de novo transcriptome analysis revealed metal detoxification in plant cells is due to metal gene–encoded natural resistance-associated macrophage proteins (NRAMPs), permeases, and ATPases (Xu et al. 2015; Sharma et al. 2016; Hasan et al. 2017). Recently, Khan and Gupta (2018) identified various genes and proteins (NR, PH1, Apase, KAT1) that involved in upregulation of nutrients in rice plant under As stress. These genes along with the antioxidant defense system might involve in As detoxification in rice. In another study, various rice elite lines were screened against As stress (Heuschele et al. 2017). They found that synthesis of cysteine and phytochelatin proteins is involved in sequestration of As in rice tissue.

Metallothioneins (MT) are cysteine-rich proteins which can detoxify metal(loid)s through cellular sequestration and protection from oxidative damage (Kang 2006; Capdevila and Atrian 2011; Hassinen et al. 2011; Hossain et al. 2012; Hasan et al. 2017). The mechanism for ROS hunting is not yet clear; however, it is advocated that

metals are detached from MT-metal complex and replaced with MT-ROS complex that might alleviate metal-induced oxidative stress in plants (Hassinen et al. 2011; Hasan et al. 2017). Ansarypour and Shahpiri (2017) investigated the role of rice MT isoform-OsMTl-1b against Cd stress tolerance in *Saccharomyces cerevisiae*. They conferred that isoform of MT-induced tolerance in this yeast against Cd stress. In addition to these mechanisms, proteins also have a role in repairing of damaged proteins, tolerance of endoplasmic reticulum, heavy metal stress-induced denatured proteins, and autophagy in heavy metal-stressed plants (Hasan et al. 2017).

14.5 Crop-Microbe Interactions Under Metal and Metalloid Stress

Around the globe, abiotic stresses like salinity drought and metal/metalloid pose a challenge to the sustainable production of crop plants (Ahmad et al. 2012; Ditta 2013; Naveed et al. 2014). In the course of time, demand for food has forced the farming community toward intensive farming which is the production of more and more crops without taking care of the health of soil-plant continuum. This farming practice has deteriorated the vital component of ecosystem, i.e., soil-plant continuum with metal and metalloids with the application of different amendments (Gajdos et al. 2012). In order to cope with this situation, several phytoremediation strategies have been employed like phytoextraction and phytostabilization (Sessitsch et al. 2013). Another strategy that could be employed is the use of rhizospheric bacteria associated with plants that are well renowned for their plant growth promotion effect under normal (Ditta et al. 2015; Ditta and Khalid 2016; Ditta et al. 2018) and abiotic stress conditions (Ahmad et al. 2012, 2013, 2014, 2016).

Plant growth-promoting microorganisms especially plant-associated bacteria, i.e., rhizobacteria, improve growth and yield of various crop plants. In literature, various researchers around the world have reviewed their role under abiotic stresses like heavy metals (Glick 2010; Ma et al. 2011; Rajkumar et al. 2012; Sessitsch et al. 2013). It has been found that these bacteria not only enhance the plant growth but also employ certain mechanisms which help increase/decrease the availability of metals and metalloids under heavy metal stress. The plant growth-promoting mechanisms include the provision of micro- and macronutrients through the production of phytohormones, siderophores, etc. (Glick 2010; Ma et al. 2011; Rajkumar et al. 2012). The mechanisms related with increasing the availability of heavy metals in the soil include the secretion of certain organic acids which lower the rhizospheric pH. The low pH is suitable for improving the availability of heavy metals in the soil and ultimately helps in phytoextraction. Similarly, solubilization of metal minerals via lowering the pH of rhizosphere by increasing the release of root exudates results in more root growth and surface area for more phytoextraction of heavy metals (Sessitsch et al. 2013; Ullah et al. 2015; Sharma and Archana 2016). With the passage of time and advancement in technology, certain bacteria have been isolated that have the ability to reduce the availability of certain heavy metals via certain mechanisms, i.e., phytostabilization and bioaccumulation. In phytostabilization, the

Table 14.2 Plant growth promoting bacteria–induced metal stress tolerance in cereals

Cereal crop	Metal(loid)s	Effect of bacterial inoculation on cereal crops	References
Maize	Cd	Cd accumulated primarily in the roots and transported to the shoots was rather low	Gajdos et al. (2012)
Maize	Cd	Plants inoculated with bacterial strains exhibited greater root-to-shoot ratio and dry biomass in Cd-contaminated soil, caused a marked increase in Cd uptake. Bacterial strains were efficient colonizer	Ahmad et al. (2016)
Maize	Cd	Immobilization and low translocation to the shoots reduced metal accumulation	Moreira et al. (2014)
Maize	Cd	Promoted root and shoot length and dry biomass	Sangthong et al. (2016)
Maize and wheat	Cd	Significantly reduced the suppressive effect of Cd on growth and physiology	Ahmad et al. (2014)
Maize and wheat	Cd	Improved growth and yield parameters through phosphate solubilization, IAA, siderophores, ACC deaminase activity	Jiang et al. (2008)
Maize	Cr	Enhanced Cr tolerance in maize seedlings by decreasing Cr uptake from root to shoot, reduced oxidative stress by elevating the activities of enzymatic and nonenzymatic antioxidant, improved carbohydrate metabolism under Cr stress	Islam et al. (2016b)
Wheat	Hg	Growth parameters and relative water content were significantly higher and vice versa for proline content, electrolyte leakage, and malondialdehyde content (shoots and roots) in inoculated plants compared to uninoculated plants under stress condition	Gontia-Mishra et al. (2016)
Maize	Pb	Decreased soil pH which resulted in more accumulation of Pb in shoot	Hadi and Bano (2010)
Maize	Pb	Improved growth and yield parameters through phosphate solubilization, IAA, siderophores, ACC deaminase activity	Jiang et al. (2008)
Maize	Pb	Inoculated plants had maximal growth and yield parameters, photosynthetic pigments, proline, protein, peroxidase, glutathione-S-transferase, and catalase, while these plants had minimal Pb uptake in root and shoot	Hassan et al. (2014)
Wheat	Zn	Inoculation improved the uptake of P and N in wheat plants with an increase in leaf chlorophyll, total soluble protein, and plant biomass production	Islam et al. (2014)
Wheat	Zn	Increased various growth parameters, photosynthetic pigments, Zn content in plant, various compatible solutes such as proline content (30–65%), total soluble sugar (9–49%), total protein (16–52%), and decreased the malondialdehyde (MDA) content (38–47%) as compared to control, illustrating its protective effect under metal-induced oxidative stress	Singh et al. (2018)

(continued)

Table 14.2 (continued)

Cereal crop	Metal(loid)s	Effect of bacterial inoculation on cereal crops	References
Wheat	Cd, As	Significantly reduced water-soluble Cd and As concentrations, and increased pH and NH_4^+ concentration in the soil filtrate	Wang et al. (2018)
Maize	Cr, Pb	Siderophore promoted plant growth under Cr and Pb stress	Braud et al. (2010)
Wheat	Cd, Cr	Polymeric substances immobilized metals and decreased their uptake	Joshi and Juwarkar (2009)
Maize	Cu, Pb	The dry biomass of roots of inoculated plants grown with 2007 mg Cu kg^{-1} and 585 mg Pb kg^{-1} was increased by 28% and 20%, respectively	Rizvi and Khan (2018)
Barley	Cr, Co, Hg, Cd, Pb	Increased germination rate and growth parameters of barley under Cr, Co, Hg, Cd, and Pb stress	Bensidhoum et al. (2016)
Wheat	Cd, Cr, Cu, Mn, Ni	Inoculation decreased biological accumulation coefficient (BAC) as well as translocation factor (TF) for Cd, Cr, Cu, Mn, and Ni	Hassan et al. (2017)
Rice	Cd, Pb, As	Inoculation significantly improved the activities of protease and amylase, increased relative root elongation, germination percentage, root-to-shoot ratio, and overall biomass. Bacterial strains also decreased superoxide dismutase activity and malondialdehyde levels	Pandey et al. (2013)

bacteria help in immobilization of heavy metal, thereby decreasing their availability to the crop plants (Vangronsveld and Cunningham 1998; Zhang et al. 2012). In case of bioaccumulation, there are bacteria which have the ability to tolerate certain levels of heavy metals via accumulation of metals in their cell wall (Hussein et al. 2011; Govarthanan et al. 2016). Also, there are reports about microbial biotransformation of heavy metals from one form to another nontoxic form (Qian et al. 2012; Babu et al. 2013) (Table 14.2).

Keeping in view the scope and limitations of this chapter, reports about the impact of different rhizospheric metal/metalloid-resistant and plant growth–promoting bacteria on growth and yield of rice, maize, and wheat under different metal/metalloid stresses are given in Table 14.1. Under different heavy metal stresses, inoculation with heavy metal–resistant bacteria significantly improved growth, physiological, and yield parameters of maize, wheat, and rice through phosphate solubilization, scavenging reactive oxygen species, ACC deaminase activity, and decreasing rhizospheric pH through the production of organic acids (Jiang et al. 2008; Hadi and Bano 2010; Hassan et al. 2014). More specifically, under cadmium stress, the accumulation of Cd was reduced, and plant growth and yield were enhanced with the inoculation of Cd-resistant plant growth-promoting bacteria (Jiang et al. 2008; Gajdos et al. 2012; Ahmad et al. 2014; Moreira et al. 2014; Ahmad et al. 2016; Sangthong et al. 2016).

14.6 Conclusion and Perspectives

Heavy metal(loid) contamination of soil is ubiquitous, and reports have confirmed their augmentation across the globe. It is a major threat for sustainable production of crops especially cereals (rice, wheat, and maize) provide food for almost 3/4 of the world population. Metal(loid)s have toxic effects on cereals starting from seed germination to maturity; these show toxic effects to cereals at morphological, physiological, and metabolic levels. The most common factor is ROS generation in cereals under metal(loid) stress; however, these crops are equipped with ROS scavenging system (i.e., production of antioxidants and proteins, mineral, and ionic regulations) to mitigate metal(loid) stress. Another tool is the application of metal(loid)-resistant microbes to cereals. They have P-solubilization, IAA, ACC deaminase, and siderophore productions which are known to mitigate metal(loid) stress through a variety of mechanisms. However, their impact authenticity remains to be explored under natural/field conditions. Moreover, there have been many reports stating concerns about the shelf life of these metal/metalloid-resistant bacteria in biofertilizers. Therefore, it would be more imperative to explore how to increase their shelf life or more special microbes having the ability to survive under natural conditions. We suggest that genetic engineering approach may prove beneficial in this regard.

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Agronomic Crop Responses and Tolerance to Polycyclic Aromatic Hydrocarbon Toxicity

15

Mahdieh Houshani and Seyed Yahya Salehi-Lisar

Abstract

Polycyclic aromatic hydrocarbons (PAHs) are made up of only carbon and hydrogen and composed of two or more fused benzene cycles. It includes a large and heterogeneous group of organic contaminants that are mainly formed and emitted because of the incomplete combustion of organic materials. Polycyclic aromatic hydrocarbons are toxic for all living organisms, and their mutagenic and carcinogenic effects are well known. Hence, their fate and transport in the environment are of worldwide attention. Over 90% of PAHs in the environment reside in surface soils; therefore, plants grown in PAH-contaminated soils can uptake them, and that can make problems in terms of agronomic crop yield and contamination of food chains. Polycyclic aromatic hydrocarbons can enter the plant via stomata as well as the root system and can lead to a range of disorders in plants. Decrease in photosynthesis and respiration, changes in enzyme activities and photosynthetic pigment content, and injury to membranes by lipid oxidation are some known effects of PAHs in plants. The increasing load of PAHs to the environment can be a crucial factor for the future diversity of plant species in the habitat, and it may determine the level of possible economic yields. Thus, it is important to exactly understand how PAHs influence the overall plant growth and development. This chapter revises some concepts about PAH importance in the environment, those effects on plants, and plant responses to PAHs.

Keywords

Agronomic crop · PAHs · Physiological effects · Organic contaminants · Toxic effects

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Abbreviations

ABC transporter	ATP-dependent transporters
CAT	catalase
GPX	glutathione peroxidase
HMW	high molecular weights
IARC	International Agency for Research on Cancer
LMW	low molecular weights
LPO	lipid peroxidation
MDA	molondialdehyde
PAHs	polycyclic aromatic hydrocarbons
PSII	photosystem II
QA	quinone A
QB	quinone B
ROS	reactive oxygen species
SOD	superoxide dismutase
US-EPA	United States Environmental Protection Agency

15.1 Introduction

Polycyclic aromatic hydrocarbons (PAHs) are a large group of organic compounds, which are composed of only carbon and hydrogen (Gong et al. 2007). These compounds form a major group of pollutants and mainly are produced by anthropogenic activities especially incomplete combustion of fossil fuel (Lin et al. 2001). Some compounds of PAHs are carcinogenic and mutagenic, and therefore, they can be important for human health (Jian et al. 2004). Due to their high persistence, long-term toxicity, and accumulation in the environment, PAHs have attracted more attention in the recent decades (Parrish et al. 2005; Haritash and Kaushik 2009; Jajoo et al. 2014). Human and wildlife exposure to persistent and toxic environmental contaminants can occur as a result of bioaccumulation in plants and subsequent transfer through natural and agricultural food chains (Hung and Mackey 1997).

The uptake of PAHs by plants occurs by more than a few ways. The major ways of PAH entrance into plants are primarily through the roots and secondarily by the aerial parts (Gao and Zhu 2004; Meudec et al. 2006; Sun et al. 2014; Wild et al. 2005; Kang et al. 2010). Although there is more than one way for PAH entrance into plants, the main routes of PAH entrance and distribution in plants still remain ambiguous. The uptake rate of PAHs by plant root and the amount of its accumulation in different organs is related to a number of factors such as plant species (Lee et al. 2008; Watts et al. 2006), microbial population in soils (Kapustka 2004; Khan et al. 2008), the initial concentration of PAHs in the environment (Lee et al. 2008), and the structure of plant roots (Sun et al. 2014). Indeed, all stages of plant growth can be affected by PAHs from germination to production (Kummerova et al. 2012). Accordingly, some known effects of PAHs on plants resulted in biochemical and

physiological changes such as alterations in enzyme activities, reduction in photosynthesis as well as respiration, formation of reactive oxygen species, and injury to membranes by lipid oxidation (Alkio et al. 2005). Thus, it is important to understand the mechanisms upon which PAHs influence the overall plant growth and development. In this chapter, we discuss recent progress in understanding of PAH effect on plants as well as agronomic crop responses and tolerance to PAH toxicity. The revision of physiological and biochemical effects of PAHs, and those uptake, accumulation, transformation, and degradation in agronomic crops are the main aims of this chapter.

15.2   General Description of PAHS

Polycyclic aromatic hydrocarbons (PAHs) as potent environmental pollutants are composed of fused aromatic rings and existing in almost everywhere in the environment. They are typically formed during incomplete burning of organic materials such as wood, coal, oil, and gasoline and are also found in crude oil, coal tar, and asphalt (Fetzer 2000; Li et al. 2014). In the environment, they are primarily found in soil, sediment, and oily substrates, and their concentration in water or air is relatively small. Their presence in the environment is directly related to human activities within the environment especially in urban areas and in areas where bush burning for agricultural farming is commonly practiced as well as in petroleum exploration and refining operations (Fetzer 2000; Gong et al. 2007; Paiga et al. 2012). Also, the actual amount of PAHs emitted from agricultural bush burning varies with the type and nature of the fire and the intensity of the fire (Platt and Mackie 1980; Gao et al. 2006; Smith et al. 2006; Li et al. 2014). PAHs have adverse impacts on living organism, and some of the PAHs have been identified as carcinogenic, mutagenic, and teratogenic. Therefore, their large concentrations in environment are of great concern to humans (Larsson et al. 1983; Jian et al. 2004). The United States Environmental Protection Agency (US-EPA) has recommended 16 PAHs as priority pollutants for monitoring in the environment (Gao and Zhu 2004; Jan et al. 2014; Li et al. 2014) (Fig. 15.1), and International Agency for Research on Cancer (IARC) has reported that 15 PAHs are potential carcinogens (Chauhan et al. 2008).

   Polycyclic aromatic hydrocarbons are solid matters, generally colorless, white, or yellow under normal conditions. Their physicochemical properties change with molecular weight (Mackay et al. 1992). These compounds are hydrophobic compounds (they mix more easily with oil than water), and their aqueous solubility decreases almost linearly with increases in molecular mass (Parrish et al. 2004; Chang et al. 2004). Polycyclic aromatic hydrocarbons contain two- to seven-membered (fused) benzene rings and are generally divided in two groups including low molecular weights (LMW) and high molecular weights (HMW) PAHs. Low-molecular-weight PAHs have two or three benzene rings and are relatively water soluble, but HMW PAHs contain four or more benzene rings and are quite hydrophobic and insoluble in water (Cerniglia and Heitkamp 1989; Mandalakis et al. 2002; Gregoris et al. 2014). The higher molecular weight of PAHs generally leads
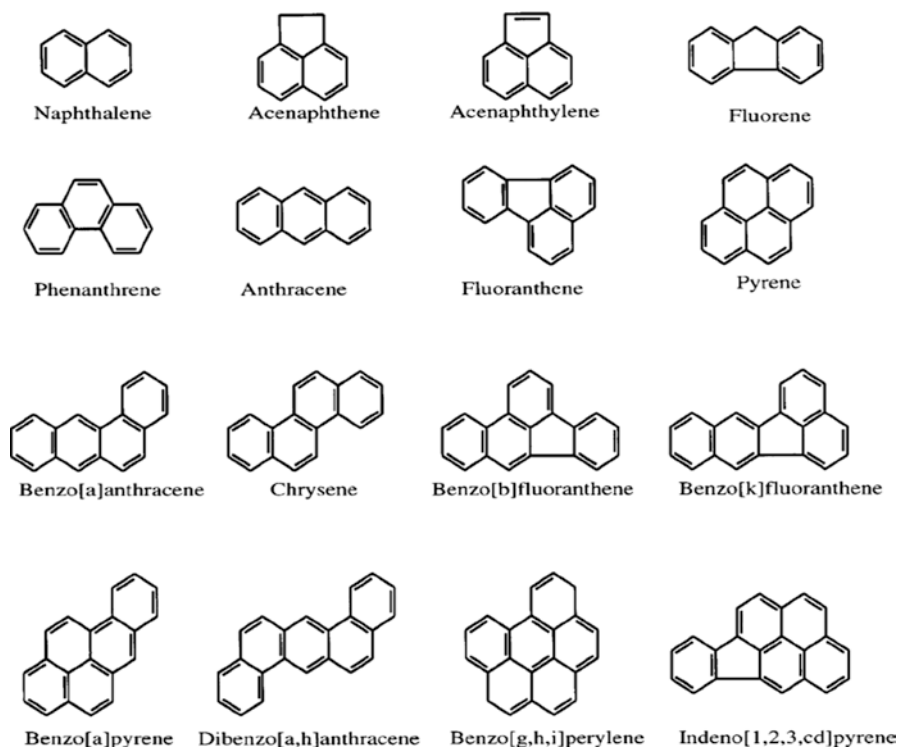
Fig. 15.1 Structure of 16 US-EPA priority pollutant PAH compounds (Lima et al. 2005)

to their higher absorption to soil organic matter, and this tendency to strong adsorption on particulate matter renders the HMW PAHs less available and thus less susceptible to remediation (Cerniglia and Heitkamp 1989). Due to the dense clouds of pi-electrons surrounding the aromatic rings, HMW PAHs have high resonance energies and are persistent in the environment and recalcitrant to degradation (Johnson et al. 2005).

Generally, by increasing the molecular weight of PAHs, their hydrophobicity, toxicity, biodegradation, and usually environmental resistance will be increased. Therefore, the difference in molecular weight among PAHs is one of the important factors effective in their distribution, accumulation, and persistence in the environment. Thus, low-molecular-weight PAHs such as naphthalene, because of their high solubility in water, are more toxic to aquatic organisms than high-molecular-weight PAHs. The half-life of phenanthrene as low molecular weight in the soil is 16–126 days, while high-molecular-weight PAHs such as benzo[a]pyrene have a half-life of 229–1500 days. Accordingly, high-molecular-weight PAHs are more tended to be bind to the particles of soil or sediments because of their low solubility in water (Parrish et al. 2006; CCME 2008).

15.3   Physiological Effect of PAHs on Plants

Polycyclic aromatic hydrocarbons are phytotoxic compounds affecting several biochemical and physiological processes in plants. These compounds, together with environmental factors, can cause acute and chronic injuries, depending on the duration of exposure and their concentration (Kmentova 2003). The long-term impact of toxic substances can affect the structure and function of ecosystems and the diversity of plant species, reduce the production of biomass and the production of oxygen, and ultimately lead to the destruction of the environment. The plant response to the presence of PAHs is induced after reaching a threshold concentration of PAHs. Most of the responses are linked with biochemical and physiological processes which are mediated by membranes (Vanova 2009).

The severity of PAH effects on plants depending on their concentration, time of exposure, and some other factors may stimulate or reduce the PAH effects in plants. The ontogenetic stage of development, the physiological state of organism, size and morphological characteristic of leaf area, cuticular permeability, transpiration rate, length of roots, and the activity of enzymes participating in the transformation of PAHs may be the factors affecting the sensitivity of plants to PAHs (Chroma et al. 2002). Harmful effects of PAHs on plants are very diverse including morphological, cytological, genetical, and metabolic disorders (Kvesitadze et al. 2006; Wilcke 2000) such as inhibition and reduction in seed germination (Huang et al. 2004; Reynoso-Cuevas et al. 2008; Tomar and Jajoo 2014), induction of oxidative stress (Liu et al. 2008; Paskova et al. 2006), and disruption in photosynthetic apparatus function (Huang et al. 2004; Liu et al. 2008; Tomar and Jajoo 2013).

15.3.1   Seed Germinations

The germination of plant seeds is associated with external factors such as water, temperature, pH, microbial activity, type and amount of toxin and also the morphological and anatomical structure of the seeds such as shell, amount, and type of storage material. As one of the external factors, PAHs can affect all stages of plant growth from germination to reproduction (Kummerova et al. 1997; Maila and Cloete 2002; Reynoso-Cuevas et al. 2008). The critical stages of development are primarily the early stages of ontogenesis, the germination of seeds, and the formation of root system (Baud-Grasset et al. 1993). Researchers have shown that the sensitivity of lettuce, barley, and millet germination to PAHs is much related to the length of root. Seed germination is an important sign against toxicity because of their effects on the spread of plant species in the ecosystem (Kmentova 2003; Kummerova et al. 2012).

Through a research that investigated the effect of phenanthrene on wheat plants, the results demonstrated that phenanthrene treatment inhibited the germination of wheat seeds especially at higher concentration and caused the reduction of growth

and chlorophyll content and increase of molondialdehyde (MDA) content and a decline of many antioxidant enzyme activities (Wei et al. 2014). In another research by Salehi-Lisar and Deljoo (2015), it was shown that fluorene as PAH had a negative effect on the rate of seed germination and seedling growth of wheat, alfalfa, and sunflower.

15.3.2 Photosynthesis and Respiration

Lipophilic organic compounds as well as the products of their transformation may create the changes in the structure and the function of subcellular substances. The membrane damage and changes in enzyme activity depending on the type and concentration of compound surely change photosynthetic, respiration, and transpiration processes (Huang et al. 1996). PAH compounds at low concentrations can penetrate to the chain of fatty acids and enhance the permeability of membranes. As additional effect, PAHs have inappropriate effects on cell metabolism as these compounds and the products of their transformation can penetrate into chloroplast and then enter into thylakoids and finally disrupt the performance of the electron transport chain (Duxbury et al. 1997).

As mentioned before, PAHs are able to penetrate into chloroplasts and influence the primary processes of photosynthesis. Accordingly, they can affect the stability and function of the photosynthetic apparatus and disturb the electron transport chain as the products of their transformation can interact with plastoquinones. Additionally, PAHs can block the photosystem II (PSII) on both acceptor and donor sides. On the donor side, between water oxidation complex on the lumena and reaction center of PSII, they resulted in lower fluorescence signal. On the acceptor side, between PSII, quinone A (QA), quinone B (QB), and plastoquinones, they resulted in some increase in fluorescence (Govindjee 1995; Kummerova et al. 2006).

Also, in investigation, it was set up on sunflower, wheat, and alfalfa indicating that photosynthetic pigment content of these species was changed differently depending on plant species (Salehi-Lisar and Deljoo 2015). By fluorene treatment in sunflower, chlorophyll a and chlorophyll b content was increased significantly as it was the most sensitive species to fluorene toxicity. But in both wheat and alfalfa plants, chlorophyll pigment content was decreased or unchanged, and these plants showed the highest resistance to fluorene toxicity. Accordingly, changes in photosynthetic pigment content cannot be a suitable marker for the evaluation of plant sensitivity or resistance to PAH contamination.

By another research conducted by using *Sorghum vulgar*, the treatment of plants by different concentrations of phenanthrene led to no considerable effect on the value of chlorophyll and biomass of the plant shoots, probably due to higher resistance of this plant to phenanthrene. It was concluded that because of having special biological and physiological conditions and also under greenhouse treatment, the selected plant was resistant to phenanthrene, and the relatively stable value of

chlorophyll and biomass was in fact the result of plant positive response to the presence of toxic level of pollutant (Alaei et al. 2010).

Further, the investigation of maize plants exposed to phenanthrene exceeding 50 mg kg^{-1} showed reduced transpiration and CO_2 absorption. This reduced photosynthetic carbon fixation could be the reason for lower biomass production (Dupuy et al. 2015).

15.3.3 PAHs and Oxidative Stress

Exposing of plant to PAHs can lead to some kind of oxidative stress. Generally, plants are equipped with enzymatic and nonenzymatic mechanisms for scavenging of reactive oxygen species (ROS) under oxidative stress (Alscher et al. 1997). According to the results of the study that was undertaken by Wei et al. (2014) to understand the responses of wheat to phenanthrene, it was revealed that PAHs can induce oxidative stress in plants. In this study, the activities of antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT) glutathione peroxidase (GPX), lipid peroxidation (LPO), and H_2O_2 were measured. The results demonstrated that phenanthrene enhanced the levels of LPO and induced H_2O_2 accumulation in leaf tissues in a dose-dependent manner besides the changes in the antioxidant status. With the increase of phenanthrene, the activities of antioxidant enzymes such as SOD, CAT, and GPX showed a decreasing trend. Therefore, phenanthrene could bring oxidative damages of wheat and also exert harmfulness mainly at higher concentrations.

Another research was conducted to study the enzymatic activity in the shoots, roots, and rhizosphere of alfalfa (*Medicago sativa* L.) grown in quartz sand treating with phenanthrene at concentrations of 10 and 100 mg kg^{-1}. The results showed that higher concentration of phenanthrene had a distinct phytotoxic effect on alfalfa through inhibiting seed germination, plant survival, and biomass accumulation, as well as an increase in peroxidase activity. Peroxidases were the predominant enzymes in the alfalfa shoots and roots, and alfalfa root peroxidases were the common enzyme systems in the rhizosphere sand revealing the possibility of involvement of the plant enzyme in degradation of the PAHs in the rhizosphere (Muratova et al. 2009). Based on Kraus et al.'s (1999) study, roots of soybean contacted with toxic chemicals like PAHs have induced peroxidase activity which may have an intracellular function as part of a defense mechanism and/or a direct involvement in the degradation of PAHs in the external medium.

15.4 Uptake, Translocation, and Accumulation of PAHs

Polycyclic aromatic hydrocarbons are hazardous for all living organisms with regard to their distribution in the biosphere, risk properties, and abilities of accumulation in animal and plant tissues. Plants as primary producers are essential components of terrestrial ecosystem (Sverdrup et al. 2003). The plants standing at the
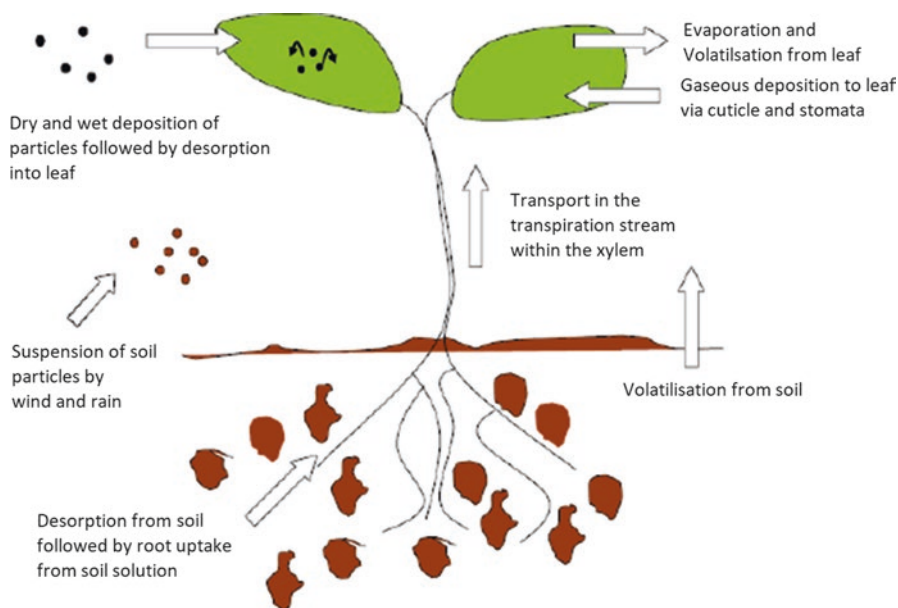
Fig. 15.2 Principal pathways for plant uptake of organic chemicals (Collins et al. 2006)

beginning of the food chains can uptake and provide contaminants to higher trophic levels (Aina et al. 2006; Zuo et al. 2006).

The plants have capacity to take up PAHs from the environment through four partial mechanisms (Fig. 15.2). These mechanisms or pathways include (1) passive or (2) active uptake through the root system, (3) gaseous and particulate deposition to aboveground shoots, and (4) direct contact between soil and plants aerial parts (Fismes et al. 2002; Collins et al. 2006; Wang et al. 2011; Marchal et al. 2014). The mechanisms are influenced by the chemical and physical properties of pollutants such as their lipophilicity, water solubility, and vapor pressure; environmental conditions such as ambient temperature and content of organic compounds; and the plant species and structure (Simonich and Hites 1995; Holoubek et al. 2000; Lee et al. 2008; Salehi-Lisar et al. 2015; Zhang et al. 2015). Additionally, some plants have more potential for uptake of some special pollutants because of root particular exudates which actively mobilize these pollutants from the soil and make these compounds available for uptake and translocation (Hulster et al. 1994; Mattina et al. 2002; White 2002; Gao and Zhu 2004; Kacalkova and Tlustos 2011).

Polycyclic aromatic hydrocarbon compounds are absorbed by plants through various ways. Such organic pollutants may enter the plants from polluted soil to the roots and then may be translocated by the xylem (Meudec et al. 2006; Zhan et al. 2013). They may also enter the plants from the atmosphere as gas or by particle deposition onto the waxy cuticle of the leaves or by uptake through the stomata and may be translocated by phloem (Holoubek et al. 2000; Piccardo et al. 2005; Tao et al. 2006; Yang and Zhu 2007). Due to leaves covered by wax and cuticle being

lipophilic structures, organic pollutants such as PAHs can simply penetrate into leaves through stomata or transcuticle absorption. The rate of such absorption depended on K_{OW} of compound, indicating compound lipophilicity. Generally, low-molecular pollutants enter the leaves through stomata, while high-molecular pollutions enter the leaves mainly through cuticle. Thus, the mechanism of uptake of high-molecular compounds is based on adsorption on cuticle leaf surface. Accordingly, leaves adsorb substances more selectively than roots due to the more simple mechanism of penetration (Korte et al. 2000).

More than 50% of total atmospheric PAHs are absorbed into soils and then transferred to lower layers and then may be absorbed by the plant roots. However, the availability of these compounds is very limited for root absorption mainly due to compound adsorption on soil particles and becomes inaccessible. The root uptake is especially determined not only by plant water relation but also by root surface and the ratio of lipid components in roots in that these lipid components enable easier absorption of lipophilic pollutants (Edwards 1983).

Gao and Zhu (2004) reported that pyrene uptake was 4–7 times higher than the uptake of phenanthrene by plants. Similar results were also indicated by Kang and Colleagues (2010). Accordingly, the uptake of pyrene by ryegrass roots was two times greater than that of phenanthrene. Generally, these results emphasized that pyrene exhibited higher uptake rate in comparison with phenanthrene. Lipophilic characteristics of pyrene (log k_{ow} = 5.32) were higher than that of phenanthrene (log k_{ow} = 4.46) (Kang et al. 2010). Therefore, lipophilic property of compounds is a determinant factor for their uptake magnitude by plants (Gao and Zhu 2004). Probably, this is the main reason for higher uptake of pyrene in comparison with phenanthrene.

Generally, phytotoxicity of PAHs is assigned by the ability of plants to uptake, accumulate, and transform rates of these compounds. Because plants are dominant component of terrestrial ecosystems with the ability of PAH uptake from the environment, the study of influence of selected PAHs on higher plants is very important. For these reasons, plants are used as early indicators of environment pollution, and some plant species can be used for detoxification of the environment.

The plants' ability to accumulate PAHs is very specific in terms of their species as well as organs and is depending especially on K_{OW} of compound and content of lipid components in plants. This fact is used for investigating and controlling of polluted environment. Plants like mosses, lichens, broadleaved and coniferous trees, grasses, some arable crop, and different plant materials like pollen or tree bark are especially used as to this aim. These species not only reflect short-term situation of atmosphere pollution but also are suitable for long-term condition (Vanova 2009).

The plants and tissues with high content of lipid components have high accumulation capacity for organic compounds. These compounds absorb on the lipophilic surface of the leaf wax and then largely accumulate in the cuticle and gradually enter into the internal components of leaf (Simonich and Hites 1995). Higher accumulation of PAHs by plants was proved by species with a large surface area of leaves compared to plants with a lower surface area. For example, vegetables like spinach and lettuce, because of having broad surface area of leaves, have a higher

potential to PAH absorption and accumulation (McGlynn and Livingston 1997). It seems that PAHs can accumulate on the trichomes and then gradually diffuse to the base of the cell and spread into the adjacent cells of the trichome basement, and finally, the trichome collapses. This fact that trichomes act as entering points for the PAHs or they import the PAHs coming from other cell types and tissues is still unclear. The special role of trichomes in detoxification of various compounds has been identified in previous studies. Based on these studies, trichomes of *Brassica juncea* and *Arabidopsis thaliana* have ability to accumulate cadmium and glutathione suggesting that trichomes may function as an efficient site of xenobiotic conjugation (Salt et al. 1995; Gutierrez-Alcala et al. 2000). Accordingly, trichome may play a good role in phytoremediation strategies by using engineering of PAH-degrading enzymes (Alkio et al. 2005).

15.5 Agronomic Crop Responses to PAH Toxicity

15.5.1 Transformation of PAHs

Plants have the enzymes involving in PAH transformation through which they can transform a more number of xenobiotics (including some kinds of PAHs) ranging from highly polar to nonpolar compounds (Kummerova et al. 1997). This feature is a species-specific process which may be unique to the given plant only at a specific tissue or organ or even in a specific developmental stage (Kmentova 2003). Some studies demonstrated that plants are able to transform benzene rings of PAHs. Low-molecular-weight compounds with two or three rings such as naphthalene, anthracene, and phenanthrene may be degraded more quickly than high-molecular-weight compounds such as pyrene, benzo[*a*]pyrene, and dibenzo[*a,h*] anthracene (Vanova 2009).

Plant transformation of xenobiotics can be divided into three phases: transformation, conjugation, and elimination reactions (Fig. 15.3). The reactions of first phase are oxidation, reduction, and hydrolysis. It is assumed that these processes are localized inside mitochondria or endoplasmatic reticulum. These reactions may modify compounds so that they enable the conjugation with amines, acids, and alcohols in the second phase of detoxification. The reduction reactions play relatively few roles in transformation, but oxidation is the most frequent observed reaction involving in detoxification of the organic xenobiotic toxicants. The main reaction in the process of oxidation is monooxidation (hydroxylation) where the active addition of oxygen to toxicant molecule takes place (Korte et al. 2000).

Hydroxylation detoxification is made with the presence of cytochrome P450 binding in the membrane of mitochondria or endoplasmic reticulum. Cytochrome P450 as a multifunctional enzyme catalyzes oxidation and reduction reactions (Korte et al. 2000; Bernhardt 2006) and is involved in the detoxification of various xenobiotics in the cells of higher organisms (Chroma et al. 2002). Cytochrome P450 is found in all kingdoms of microorganisms (Bernhardt 2006). More than 250 various forms of it have been found in the *Arabidopsis thaliana*, and even more than
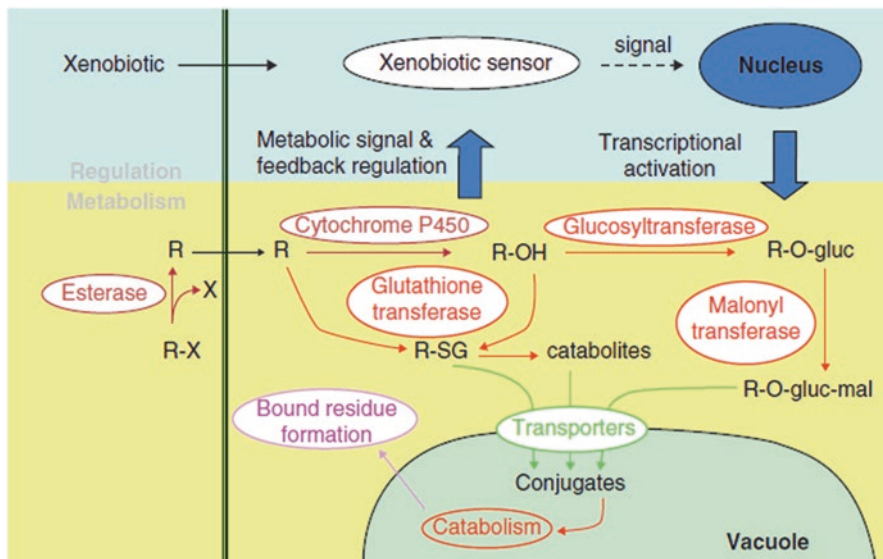
Fig. 15.3 Different phases of metabolism of xenobiotics in plant cells (Collins 2011)

1000 isoforms are expected in wheat. Also, cytochrome P450 plays a role in the metabolism of a variety of secondary metabolites in plant-insect interaction, herbicide metabolism, and other vital functions (Werck-Reichhart et al. 2000). Moreover, plant P450 has potential for engineering herbicide tolerance and bioremediation (Werck-Reichhart et al. 2000; Bernhardt 2006).

It was illustrated that the penetration of xenobiotics into the cell is a regulatory indication for initiating NADPH-dependent oxidation and converting cytochrome P450 activity from "endogenous" (metabolism) into "exogenous" (detoxification). This cytochrome transforms PAHs not only into different alcohols such as diols, triols, and tetrols, but also into carcinogenic and mutagenic epoxides and free radicals (Khatisashvili et al. 1997).

In the second phase (conjugation), compounds such as sugars, amino acids, organic acids, and peptides are added to the pollutant and produce their conjugated form. The reactions are catalyzed by relatively few specific enzymes such as transferase. For example, sugars are added to the contaminated through glucosyltransferase enzyme, and glutathione are added to the contaminated through glutathione transferase enzyme. At this phase, after the addition of glucose, another reaction is made including the addition of malonic acid by the malonyl transferase enzyme (Knejzlik et al. 2000; Collins 2011).

The third phase of biotransformation is detoxification. Created conjugations within the second phase transfer from the cytoplasm to the vacuole by transmembrane ATP-dependent transporters (ABC transporters) for accumulation. Alternatively, metabolites can be further processed by hydrolytic reactions within the vacuole and/or then re-exported into the cytoplasm for further metabolism (Brazier-Hicks et al. 2008).

Plants also can accumulate soluble conjugates in the vacuole for further metabolism and non-soluble conjugates in the cell wall (Trapp and McFarlane 1995). Also, many aromatic compounds that have hydroxyl, carboxyl, amine, or sulfhydryl groups are placed inside lignin or to other cell wall components such as protein, hemicellulose, or cellulose (Vanova 2009; Kang et al. 2010).

Based on a study by Wild et al. (2006), phenanthrene in maize can be metabolized into polar compounds, and in another study by Harms (1996), it was found that anthracene and its derived compounds are bound to cell wall components such as pectin, lignin, hemicellulose, and cellulose. Hence, the distributions of anthracene and its metabolites in maize illustrated that the metabolism of this compound takes place mainly in the cell wall (Briggs et al. 1983).

15.5.2 Phytodegradation

Phytodegradation is a technology employed by plants to detoxify pollutants from contaminated systems (Epuri and Sorensen 1997). Also, it is an important phytoremediation process indicating the role of internal plant mechanisms and processes in removing or detoxifying certain environmental pollutants to make them harmless (Newman and Reynolds 2004). Various grasses and leguminous plants have potential for phytodegradation of organic pollutants (Adam and Duncan 1999). Some tropical plants have also revealed effective degradation tendency because of their inherent properties such as deep fibrous root system and tolerance to high hydrocarbon and low nutrient availability (Dzantor et al. 2000). Based on recent reports, tall fescue grass (*Festuca arundinacea*) and switch grass (*Pannicum virgatum*) are able to degrade about 38% of pyrene during 190 days (Chen et al. 2003). Other studies on PAHs degradation have stated that plants in acidic soils have intensified phenanthrene and pyrene degradation rates. The combined plant cultivation has potential to enhance the degradation rate of PAHs (Chouychai et al. 2009; Cheema et al. 2009), and higher degradation rates of phenanthrene and pyrene were observed in the combined plant cultivation compared to the single plant cultivation in spiked soils. Accordingly, the presence of plants such as corn (*Zea mays*), alfalfa (*Medicago sativa*), rape seed (*Brassica napus*), *Festuca arundinacea*, and rice (*Oryza sativa*) can enhance the adsorption of PAHs and efficiently promote phytodegradation of PAHs in contaminated soils (Cheema et al. 2008; Du et al. 2011). Some researchers believe that the phytodegradation process is effective when it is used as a secondary treatment process for decontamination of PAHs from composted soils (Parrish et al. 2004). But, some other researchers believe that phytodegradation can be used as a primary remediation technology or even a final and comprehensive remediation technology for treating of PAHs-contaminated soils (Pradham et al. 1998). Study on *P. virgatum* and little bluestem grass (*Schizachyrium scoparium*) revealed their ability to decease PAHs concentration after six months. As another example, ryegrass

(*Lolium multiflorum*) and bermudagrass (*Cynodon dactylon*) can also degrade naph-
thalenes as two-ring PAHs (White et al. 2006). Moreover, the morphology of the
plant system affects the efficiency of plant uptake and metabolism of PAHs
(Simonich and Hites 1994; Bakker et al. 1999; Gao and Zhu 2004). For example, *L.
multiflorum* showed higher tendency for uptake of pyrene by the roots than other
PAHs (Kang et al. 2010; Ward et al. 2003).

   The ability of water hyacinth (*Eichhornia crassipes*) in degrading of organic pol-
lution was investigated, and based on the reports, it has higher efficiency for accu-
mulation of high levels of five-ring PAHs compared to two- and three-ring
compounds (Xia 2008; Moustafa and Shara 2009). According to Wolverton and
McDonald (1976), *E. crassipes* can very quickly absorb and metabolize organic
pollutants. Further study has shown that this plant can decrease naphthalene con-
centration in wastewater in 7 days (Nesterenko et al. 2012) and also reduce oil pol-
lutions in contaminated soils up to 18% (Nor 1994; Tang and Lu 1993). Overally,
these studies indicate that the plant has the potential to absorb phenolic compounds,
heavy metals, and inorganic material. Such findings emphasize the potential of *E.
crassipes* for absorption of hydrocarbons as well as its ability to absorb other com-
pounds such as inorganic compounds and pesticides (Reddy et al. 1989; Xia and Ma
2006; Rosas et al. 1984; Ebel et al. 2007; Ghabbour et al. 2004).

15.6 Conclusion

Polycyclic aromatic hydrocarbons are a diverse group of organic pollutants, mainly
produced by anthropogenic activities and existing in all parts of environment. They
are toxic for all organisms, and plants can uptake these compounds by various ways
and introduce them into food chains. They can affect different aspects of plants at
all stages of growth, and their harmful effects on plants are very diverse, including
morphological, cytological, genetical, and metabolic disorders. Inhibition and
reduction in seed germination, induction of oxidative stress, and disruption in pho-
tosynthetic apparatus function are some well-known effects of PAHs on plants. The
severity of PAHs effects on plants depends on plant species, structure of plant organs
specially roots, type and concentration of PAHs, and some other environmental fac-
tors. Plants can accumulate PAHs or transform them by their enzymes. This feature
is a species-specific process which may be unique to the given plant only at a spe-
cific tissue or organ or even in a specific developmental stage. Apparently, plants
have higher potential for biodegradation of low-molecular-weight PAHs such as
naphthalene, anthracene, and phenanthrene.

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Gene Pyramiding: An Emerging Control Strategy Against Insect Pests of Agronomic Crops

16

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Abstract

The present chapter is focused on the evolution of the insect's resistance against Bt crops and describes the most appropriate approach in order to cope with this serious issue. Different techniques have been used in the past to manage insect evolution against Bt crops. Among them, gene pyramiding, or stacked combinations of different genes in a single crop with their ability to target the same insect pest species, is proven to be a very powerful and effective tool in managing insect resistance problem. The principle goal of gene pyramiding approach is to develop transgenic plants with extra resistance against pests and to enhance crop yield. To obtain transgenic crops with durable and broad-spectrum resistance against insect pests and diseases, the pyramiding of predominant genes (multigene strategy) implying a unique mode of action is a powerful strategy. Gene pyramiding is a useful technique in controlling different insect species as compared to transgenic variety comprising of single toxin trait. Many studies have shown that gene pyramiding is advantageous in controlling different insect species in a single Bt crop, but due to continuous pressure on insect pests, there are chances that the herbivore may evolve resistance. Therefore, reliance only on gene pyramiding strategies is not a complete solution to Bt resistance. It is, therefore, necessary that different combinations of strategies like RNAi with gene pyramiding techniques will be required in the near future that will not only shield our crop against insect pest damages but also reduce reliance on heavy insecticide usage in crops.

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16.1   Introduction

Bacillus thuringiensis spores had been used as an insecticide many years before the identification of the bacterium. Some researchers suggested that the Bt spores had been used against insect pests by ancient Egyptian. This bacterium was first accidentally isolated in Japan in 1901 by the Japanese biologist Shigetane Ishiwatari from an infected silk worm's larva. He named this bacterium as *Bacillus sotto*. Approximately ten years later in 1912, German scientist Ernst Berliner isolated the same bacterium from an infected Mediterranean flour moth (*Ephestia kuehniella*), and he changed its name to *Bacillus thuringiensis*, since the infected moth was found in the German province of Thuringia (Siegel 2000). For over 70 years, Bt-based insecticides have been used in spray form in crops, containing a mixture of spores, and the related protein crystals stay valuable in organic and conventional agriculture to control various insect pests of field crops, vegetables, forests, and vector control. The first Bt-based commercial biopesticide formulations such as Dipel and Thuricide were marketed over 50 years ago. Currently, numerous sprayable formulations of Bt products with various endotoxins are available for commercial use against different insect pest species. However, the continuous use of these Bt-based products resulted in the evolution of resistance in some major pests. The very first report indicating the evolution of insect resistance against sprayed Bt spores was published online in early 1985; since then, many more such cases of field-evolved resistance have been documented in various crop pests. This problem was overcome by the development and introduction of transgenic crops. The first genetically modified crops containing endotoxin had been grown on a large scale in 1996 within the USA. Since then, different companies have launched different Bt transgenic varieties of different crops including potato, tomato, cotton, and corn. In this way, the integrated pest management program gained new momentum as these Bt crops were grown on a large scale with the aim of protecting the crops from insect pest damages. Since 1996, transgenic crops have been grown around the entire globe; they have shown to efficiently control various insect pests including tobacco budworm (*Heliothis armigera*), Colorado potato beetle (CPB) (*Leptinotarsa decemlineata*), cotton bollworm (*Helicoverpa armigera*), pink bollworm (*Pectinophora gossypiella*), southwestern corn borer (*Diatraea grandiosella*), and European corn borer (*Ostrinia nubilalis*) and helped the growers to reduce reliance on the usage of chemical insecticides. These Bt crops revolutionized the history of agriculture. With the advancement of genetic engineering and biotechnologies, the insect pest control program took a new dimension that has resulted in the development of different transgenic *B. thuringiensis* (Bt) varieties in corn, cotton, and potatoes. Currently, Bt transgenic crops are being extensively grown in many advanced and developing countries (Cohen 2005; Bravo et al. 2007). These Bt transgenic

crops have suppressed pest populations, reduced dependency on insecticide sprays, encouraged control via bioagent, and doubled farmer income (Shelton et al. 2000; Ferry et al. 2004; Tabashnik et al. 2010). These biotech crops were initially grown on 1.7 million hectare land in 1996. Since the start of commercialization, there has been a significant 100-fold increase in cultivated areas of certain Bt crops especially in Bt cotton and Bt corn. This year-wise increase is shown in Fig. 16.1. It is obvious in Fig. 16.1 that a total of 179.7 million hectares of genetically modified organism (GMO) were cultivated in a single year during 2015. Since 1996, a collective total of 2339.5 million hectares of GMO were planted around the entire globe (ISAAA 2017). From Fig. 16.1, it is assumed that these Bt-based crop technologies are readily accepted worldwide.

Agricultural production worldwide is constrained primarily by insect pests. Initially, chemical insecticides were found effective in controlling the major agricultural pests, but their continuous use resulted in so many problems like environment pollution, the effect on nontarget insect, and vertebrate insect resistance (Salim et al. 2016). The transgenic crops produce insecticidal crystal proteins or Bt toxins that are toxic to the insect. The mode of action (MOA) of these Bt endotoxins has been studied in detail by different scientists in various insect orders. From these studies, it is evident that the mode of action of this Bt protein relies on three different models. Two of them are based on pore formation activity, while the third one relies on signaling pathway model as shown in Fig. 16.2 (Zhang et al. 2005, 2006;
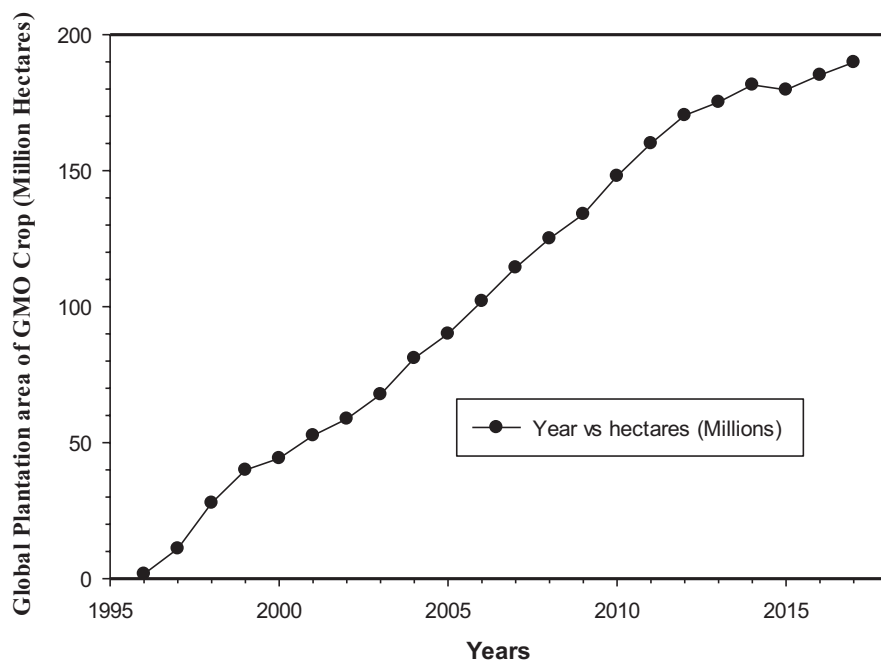
Fig. 16.1 Global GM crop plantation area (million hectares) from 1996 to 2017
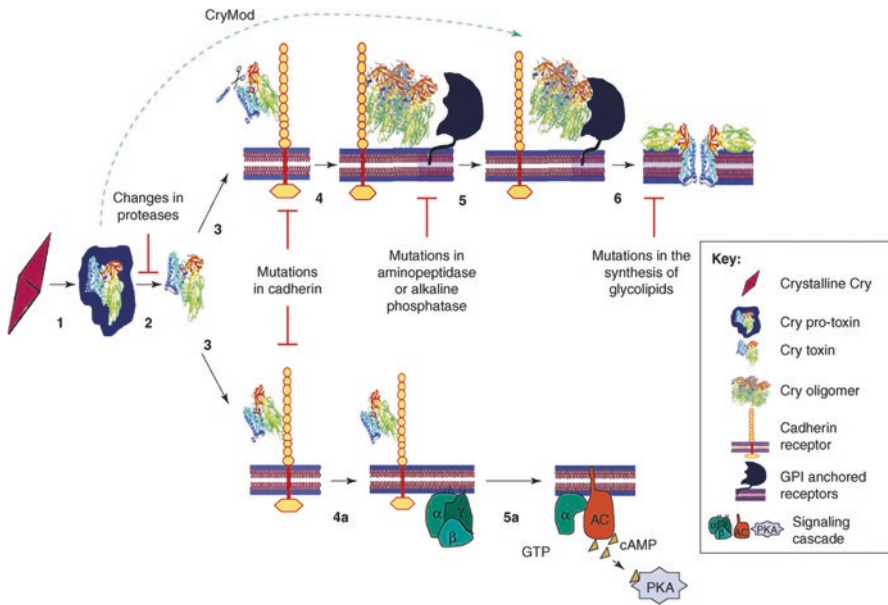
Fig. 16.2 Proposed models for Cry toxin mode of actions and ultimately resistance mechanism adapted from Bravo and Soberón (2008) with permission

Bravo and Soberón 2008). Unlike most other chemical insecticides, these Bt toxins don't act as a contact poison. To kill an insect, this Bt toxin must be ingested. The toxic pathway of these Cry toxins undergoes several steps that include crystal ingestion and solubilization by insect, release of protoxin and conversion into active toxin by midgut proteases (proteolytic activation), and cadherin receptor binding (active protein binds to cadherin receptor situated on the brush border membrane of midgut cells) leading to pore formation that causes swelling and leakage of the cells. The swelling continues, resulting in insect midgut cells bursting, allowing the insect midgut juices to pass into the hemolymph. As a result, insect blood pH rises; this results in insect paralyses and eventually death (Soberon et al. 2009; Bravo et al. 2011; Vachon et al. 2012). The third model regarding Cyt toxin which constitutes one-fifth of the size of the Cry protein suggest that they are dissolved and processed like Cry toxins; upon release, they secrete a toxic core which results in cell lyses. They act as a detergent or synergist, attack the lipid portion of the cell membrane resulting in cell lysis, or increase the activity of other Cry toxins.

As these first-generation transgenic crops (single toxin) have become more widely cultivated, some of their valuable environmental and economic benefits have disappeared, especially due to the sudden and rapid evolution of filed resistance by the insect pest to the first-generation Bt crops that produced only a single Bt toxin. These insect resistance reports have made the growers uncomfortable and have raised doubts about the future sustainability of these Bt crops. The first insect that has developed resistance to Bt cotton is known as bollworm (*Helicoverpa zea*)

Table 16.1 The featured Cry genes introduced to agronomic crops to encode insect resistance

Insect spp.	Bt crop	Bt gene	Detection year	Country	References
Helicoverpa zea	Cotton	*Cry1Ac*	2002	USA	Dennehy et al. (2010)
H. zea	Maize	*Cry1Ab*	2004	USA	Dively et al. (2016)
H. zea	Maize	*Cry1A.105*	2016	USA	Dively et al. (2016)
H. zea	Cotton	*Cry2Ab*	2005	USA	Ali and Luttrell (2007) and Tabashnik et al. (2013)
Busseola fusca	Maize	*Cry1Ab*	2006	South Africa	Kruger et al. (2011)
Spodoptera frugiperda	Maize	*Cry1F*	2006	USA	Farias et al. (2014)
Pectinophora gossypiella	Cotton	*Cry2Ab*	2014	India	Tabashnik (2015)
P. gossypiella	Cotton	*Cry1Ac*	2008	India	Dhurua and Gujar (2011)
Diabrotica v. virgifera	Maize	*Cry3Bb*	2009	USA	Gassmann et al. (2011)
D. v. virgifera	Maize	*mCry3A*	2011	USA	Gassmann et al. (2014)
D. v. virgifera	Maize	*Cry34/35Ab*	2013	USA	Andow et al. (2016) and Gassmann et al. (2016)
D. v. virgifera	Maize	*eCry3.1Ab*	2014	USA	Zukoff et al. (2016)
D. v. saccharalis	Maize	*Cry1A.105*	2014	Argentina	Tabashnik and Carrière (2017)
S. albicosta	Maize	*Cry1Fa*	2013	USA	Smith et al. (2017)
S. frugiperda	Maize	*Cry1F*	2011	Brazil	Monnerat et al. (2015)
S. frugiperda	Maize	*Cry1ab*	2010	Brazil	Farias et al. (2014) and Tabashnik et al. (2010)
S. frugiperda	Maize	*Cry1F*	2007	USA	Storer et al. (2010)

reported between 2003 and 2006 in Mississippi and Arkansas. Since then, many scientists in different parts of the world published different cases of insect resistance to transgenic crops. The different insect species that have evolved resistance against different transgenic crops around the entire globe are shown in Table 16.1. Most of the insect-resistant species have been reported on large-scale cultivated varieties of Bt corn and cotton. These reports suggested that the insect pests have evolved resistance to transgenic crops by two different mechanisms. In most cases, the primary mechanism of insect resistant to Cry protein is linked to defects in binding specific receptor that leads to reduce protease activation, higher immune response of the target insect pests, or enhanced esterase production. Mutations in the cadherin receptor in different lepidopterans are known to cause resistance against Cry1A toxins (Ferre and Van Rie 2002; Tabashnik et al. 2013, 2014). For example, resistance to Cry1Ac in *H. armigera* is conferred by a mutation in the promoter region of HaTryR. Lower expression of cadherin in *Diatraea saccharalis* was linked with resistance to Cry1Ab toxin; cadherin silencing with RNA interference (RNAi) was also related with tolerance to this toxin in *D. saccharalis* and *M. sexta* (Soberon

et al. 2007; Yang et al. 2011). Similarly, a mutation in three alleles of cadherin receptors confers resistance in *P. gossypiella* and *H. virescens* to Cry1Ac in Bt cotton (Morin et al. 2003; Xu et al. 2005; Fabrick et al. 2011; Ocelotl et al. 2015). Furthermore, resistance in *Plodia interpunctella* to Cry1A was due to inactivity of the midgut protease that resulted in decrease activation of Cry1A protoxins. Mutations in the aminopeptidase P of *O. nubilalis* were also related with resistance to 3d-Cry toxins (Khajuria et al. 2011). Resistance in *P. gossypiella* to Cry1Ac and Cry2Ab is due to a cadherin transmembrane mutation disturbing cellular trafficking in pink bollworm (Wang et al. 2018). Mutation in a single amino acid in ABC transporter gene has been linked to conferred resistance to Cry1Ab in silkworm (*Bombyx mori*). Resistance in *H. armigera* to Cry1Ac toxin has been related with their capability to break down long insecticidal bonds and to exclude these materials, resulting in increased production of gut esterase that bound and sequestered Cry1Ac protein (Atsumi et al. 2012).

Therefore, it is necessary to understand these molecular and genetic bases of resistance against various Bt toxins in different insect pest species. This will help to devise an integrated resistant management strategy to counter insect and pest problems in transgenic crops (Ferré and Van Rie 2002).

16.2 Pyramiding or Cry Gene Stacking Strategy

The problem of insect resistance to Cry toxin has evolved in single Bt crop due to the fact that insects may be able to adapt more rapidly to a single Bt toxin than to multiple ones (Roush 1998; Zhao et al. 2003). Thus, in order to delay the evolution of insect resistance to Bt crops, several insect resistance management (IRM) strategies have been considered for managing resistance to Bt transgenic crops (Shelton et al. 2000; Bates et al. 2005; Yang et al. 2011; Saljoqi et al. 2015). The primary strategy to overcome insect resistance is the use of high-dose refuge (HDR) (Gould 1998; Bates et al. 2005; Tabashnik et al. 2008). The HDR strategy requires planting a proportion of non-Bt host plants in close proximity as refuges to maintain an appropriate size of susceptible population. A drawback of this strategy is the economic loss to the non-Bt crops in the refuges (Hutchison et al. 2010).

To reduce the percentage of refuges required by the HDR, new generations of transgenic crops with two or more than two Bt toxins with different mode of action called pyramid Bt crops, plantations have been started in the USA, Australia, and elsewhere (Gould 1998; Ferre´ and Van Rie 2002; Zhao et al. 2003, 2005). The stacking of more than one useful transgene into plant genomes is called gene stacking or gene pyramiding (Berger 2000; Halpin 2005).

The logic behind the gene pyramid originates from the ancient philosophy when people were using insecticide mixtures to broaden the spectrum of insects controlled in one spray event. The gene pyramid is considered a permanent insect/disease resistance management strategy (Shelton et al. 2002). However, a closer look at the strategy shows that pyramid is developed as a practical strategy to expand the

range of insect species that were not adequately controlled by a single Cry toxin as in the case of transgene Bt cotton variety.

The main aim of gene pyramiding strategy is to develop transgenic plants with more resistance against pests and to improve crop yield. To obtain transgenic crops with durable and broad-spectrum resistance against insect pests and diseases, the pyramiding of major genes (multigene strategy) implying different mode of action will be a powerful strategy. This strategy has resulted in the so-called second generation of genetically engineered (GE) plants. Gene pyramiding has been principally obtained through crosses between GE plants with different biotech traits (hybrid stacking), such as in Agrisure™ and Viptera™ maize. Other methods involve plant transformation with two or more genes harbored in a single (linked genes or multigene cassette transformation, e.g., Herculex™ maize) or in separate (co-transformation, e.g., Knockout™ maize) gene constructs or the insertion of one or more genes into an already transgenic plant (retransformation, e.g., Bollgard™ II cotton). The first pyramided transgenic cotton plants expressing two 3d-Cry toxins, Cry1Ac and Cry2Ab with a different mode of action, were introduced in the USA in 2003. These two Cry proteins are known to have a different mode of action and bind to different receptors that result in significant delay in the evolution of any insect resistance. The rapid adoption rate of Bt pyramided plants has attracted the attention of its superiority over individual transgenic events. Biotech crops with multiple traits were planted on 77.7 million hectares in 2017, representing 41% of all biotech hectares planted worldwide and a 29% year-over-year increase (ISAAA 2017). To delay insect resistance to Bt crops and to improve efficacy against some pests and broaden the spectrum of pests controlled, most newer Bt crops produce two or more Bt toxins that have been commercialized in different parts of the world (see Table 16.2). Most of these products contain multiple Bt genes for managing major insect pests. The current predominant stacked trait crops are insect-resistant and herbicide-tolerant maize and cotton. These products often contain only two introduced genes, as the "effect" gene conferring herbicide tolerance can also be used as the selectable marker for transformed plant material. Many commercial companies such as Syngenta, Bayer Crop Science, Pioneer, Dow AgroSciences, and Monsanto are pursuing to achieve GM crops with stacked traits (see Table 16.2).

These results showcase gene pyramiding as a possibly useful tool that could be successfully applied to the combination of pests and diseases for delaying resistance development and in some cases can be successfully applied against the combination of biotic and abiotic stresses.

16.3   Strategies for Gene Stacking/Pyramiding in Plants

Several methods have been used to pyramid (or stack) transgenes into plants that range from using conventional sexual crosses of plants comprising of one single transgene or more of transgenes to be combined into single germplasm to biotechnologies. The three main strategies are discussed below.

Table 16.2 Some selected example of commercially released gene pyramiding crop events against major insects by different companies

Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Maize	Bt 176	(a) *Cry1ab* (b) *bar*	Microparticle bombardment of plant cells or tissue	(a) Damage midgut lining of *O. nubilalis* (b) Confers glufosinate herbicide tolerance in corn	*Bacillus thuringiensis* subsp. *kurstaki* *Streptomyces hygroscopicus*	Cry1Ab delta-endotoxin Phosphinothricin N-acetyltransferase (PAT) enzyme	Syngenta
Maize	CBH-351	(a) *Cry9c* (b) *bar*	Microparticle bombardment of plant cells or tissue	(a) Damage midgut lining of *O. nubilalis* (b) Remove herbicidal effect by acetylation	*Bacillus thuringiensis* subsp. *tolworthi* strain BTS02618A *Streptomyces hygroscopicus*	Cry9C delta-endotoxin Phosphinothricin N-acetyltransferase (PAT) enzyme	Bayer Crop Science
Maize	DBT418 (2006)	(a) *Cry1ac* (b) *bar* (c) *pinII*	Microparticle bombardment of plant cells or tissue	(a) Damage midgut lining of *O. nubilalis* (b) Remove herbicidal effect by acetylation (c) Increase defense against insect predators by reducing the digestibility and nutritional value of the leaves	*Bacillus thuringiensis* subsp. *kurstaki* strain HD73 *Streptomyces hygroscopicus* *Solanum tuberosum*	Cry1Ac delta-endotoxin Phosphinothricin N-acetyltransferase (PAT) enzyme Protease inhibitor protein	Monsanto

| Maize | Mon801 | (a) *Cry1ab*
 (b) *cp4 epsps (aroA:CP4)*
 (c) *goxv247* | Microparticle bombardment of plant cells or tissue | (a) Damage midgut lining of lepidopteran insect pests
 (b) Declines binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance
 (c) Confers tolerance in maize crops by splitting glyphosate into aminomethylphosphonic acid (AMPA) and glyoxylate | *Bacillus thuringiensis* subsp. *kurstaki*
 Agrobacterium tumefaciens strain CP4
 Ochrobactrum anthropi strain LBAA | Cry1Ab delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Glyphosate oxidase | Monsanto |
| Maize | Mon802 | (a) *Cry1ab*
 (b) *cp4 epsps (aroA:CP4)*
 (c) *goxv247* | Microparticle bombardment of plant cells or tissue | (a) Damage midgut lining of lepidopteran insect pests
 (b) Declines binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance
 (c) Split glyphosate into aminomethylphosphonic acid (AMPA) and glyoxylate resulting in increased tolerance to glyphosate herbicides | *Bacillus thuringiensis* subsp. *kurstaki*
 Agrobacterium tumefaciens strain CP4
 Ochrobactrum anthropi strain LBAA | Cry1Ab delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Glyphosate oxidase | Monsanto |

(continued)

Table 16.2 (continued)

Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Maize	Mon809	(a) *Cry1ab* (b) cp4 epsps (aroA:CP4) (c) *goxv247*	Microparticle bombardment of plant cells or tissue	(a) Damage midgut lining of lepidopteran insect pests (b) Declines binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance (c) Split glyphosate into aminomethylphosphonic acid (AMPA) and glyoxylate resulting in increased tolerance to glyphosate herbicides	*Bacillus thuringiensis* subsp. *kurstaki* *Agrobacterium tumefaciens* strain CP4 *Ochrobactrum anthropi* strain LBAA	Cry1Ab delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Glyphosate oxidase	Monsanto Company and DuPont (Pioneer Hi-Bred International, Inc.)
Maize	MON810	(a) *Cry1ab* (b) cp4 epsps (aroA:CP4) (c) goxv247	Microparticle bombardment of plant cells or tissue	(a) Damage midgut lining of lepidopteran insect pests (b) Declines binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance (c) Split glyphosate into aminomethylphosphonic acid (AMPA) and glyoxylate resulting in increased tolerance to glyphosate herbicides	*Bacillus thuringiensis* subsp. *kurstaki* *Ochrobactrum anthropi* strain LBAA *Agrobacterium tumefaciens* strain CP4	Cry1Ab delta-endotoxin Glyphosate oxidase Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme	Monsanto

Crop	Event	Genes	Method	Function	Source organism	Protein	Company
Maize	MON87427 x 59122	(a) cry34Ab1, cry35Ab1 (b) cp4 epsps (aroA:CP4)	Conventional breeding—cross hybridization and selection involving transgenic donor(s)	(a) Damage midgut lining of coleopteran insects, particularly corn rootworm (b) Decreases binding affinity for glyphosate, resulting in increased tolerance to glyphosate herbicide	*Bacillus thuringiensis* strain PS149B1 *Agrobacterium tumefaciens* strain CP4	Cry34Ab1 delta-endotoxin Cry35Ab1 delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme	Monsanto
Maize	33121	(a) cry2Ae cry1A vip3Aa20 (b) pat	*Agrobacterium tumefaciens*-mediated plant transformation	(a) Provides protection against feeding by lepidopteran insects by selectively damaging their midgut (b) Eliminates herbicidal activity of glufosinate (phosphinothricin) herbicides by acetylation	*Bacillus thuringiensis* subsp. *dakota* *Bacillus thuringiensis* *Bacillus thuringiensis* strain AB88 *Streptomyces viridochromogenes*	Cry2Ae delta-endotoxin Delta-endotoxin of the Cry1A group Vegetative insecticidal protein (vip3Aa variant) Phosphinothricin N-acetyltransferase (PAT) enzyme	DuPont (Pioneer Hi-Bred International, Inc.)
Maize	MON89034 (2010)	(a) cry2Ab2 (b) cry1A.105	*Agrobacterium tumefaciens*-mediated plant transformation	Damage midgut lining of lepidopteran insect pests	*Bacillus thuringiensis* subsp. *kumamotoensis*	Cry2Ab delta-endotoxin Cry1A.105 protein which comprises the Cry1Ab, Cry1F, and Cry1Ac proteins	Syngenta

(continued)

Table 16.2 (continued)

Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Maize	MON89034 x MON88017	(a) *cry1A.105* *cry2Ab2* (b) *cry3Bb1* (c) *cp4 epsps* (*aroA:CP4*)	Conventional breeding—cross hybridization and selection involving transgenic donor(s)	(a) Damage midgut lining of lepidopteran insect pests (b) Damage midgut lining of coleopteran insects, particularly corn rootworm (c) Decreases binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance	*Bacillus thuringiensis* subsp. *kumamotoensis* *Agrobacterium tumefaciens* strain CP4	Cry1A.105 protein which comprises the Cry1Ab, Cry1F, and Cry1Ac proteins Cry2Ab delta-endotoxin Cry3Bb1 delta endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme	Monsanto
Maize	3272 x MIR604	(a) *mcry3A* (b) *amy797E* (c) *pmi*	Conventional breeding—cross hybridization and selection involving transgenic donor(s)	(a) Damage midgut lining of coleopteran insects, particularly corn rootworm (b) Improve bioethanol production by increasing the thermostability of amylase used in degrading starch (c) Metabolizes mannose and allows positive selection for recovery of transformed plants	Synthetic form of cry3A gene from *Bacillus thuringiensis* subsp. *tenebrionis* Synthetic gene derived from *Thermococcales* spp. *Escherichia coli*	Modified Cry3A delta-endotoxin Thermostable alpha-amylase enzyme Phosphomannose isomerase (PMI) enzyme	Syngenta

Crop	Event	Genes	Method	Effects	Protein	Source organism	Company
Maize	4114	(a) *cry1F* (b) *cry34Ab1* (c) *cry35Ab1* (d) *pat*	*Agrobacterium tumefaciens*-mediated plant transformation	(a) Damage midgut lining of lepidopteran insect pests (b and c) Damage midgut lining of coleopteran insects, particularly corn rootworm (d) Removes herbicidal activity of glufosinate (phosphinothricin) herbicides by acetylation	Cry1F delta-endotoxin Cry34Ab1 delta-endotoxin Cry35Ab1 delta-endotoxin Phosphinothricin N-acetyltransferase (PAT) enzyme	*Bacillus thuringiensis* var. *aizawai Bacillus thuringiensis* strain PS149B1 *Streptomyces viridochromogenes*	DuPont (Pioneer Hi-Bred International, Inc.)
Cotton	SGK321	(a) *cry1A* (b) *CpTI*	Pollen-tube pathway (PTP)	(a) Damage midgut lining of lepidopteran insect pests (b) Provides resistance against wide range of insect pests	Delta-endotoxin of the Cry1A group Trypsin inhibitor	*Bacillus thuringiensis Vigna unguiculata*	Chinese Academy of Agricultural Sciences
Cotton	3006-210-23 x 281-24-236 x MON1445	(a) *cry1F* (b) *cry1Ac* (c) *pat* (syn)	Conventional breeding (cross hybridization and selection involving transgenic donor)	(a and b) Damage midgut lining of lepidopteran insect pests (c) Removes herbicidal activity of glufosinate (phosphinothricin) herbicides by acetylation	Cry1F delta-endotoxin Cry1Ac delta-endotoxin	*Bacillus thuringiensis* var. *aizawai Bacillus thuringiensis* subsp. *kurstaki* strain HD73	Monsanto Company and Dow AgroSciences LLC

(continued)

Table 16.2 (continued)

Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Cotton	3006-210-23 x 281-24-236 x MON1445	(a) cp4epsps (aroA:CP4) (b) *cry1F* (c) *cry1Ac* (d) bar, nptII, aad	Conventional breeding—cross hybridization and selection involving transgenic donor(s)	(a) Decreases binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance (b and c) Damage midgut lining of lepidopteran insect pests (d) Removes herbicidal activity of glufosinate (phosphinothricin) herbicides by acetylation, further allows transformed plants to metabolize neomycin, kanamycin, spectinomycin, and streptomycin antibiotics during selection	*Agrobacterium tumefaciens* strain CP4 *Bacillus thuringiensis* var. aizawai *Bacillus thuringiensis* subsp. *kurstaki* strain HD73 *Streptomyces hygroscopicus* *Escherichia coli* Tn5 transposon *Escherichia coli*		Monsanto Company and Dow AgroSciences LLC
Cotton	31707	(a) *bxn* (b) *cry1Ac* (c) *nptII*	*Agrobacterium tumefaciens*-mediated plant transformation	(a) Removes herbicidal activity of oxynil herbicides (b) Damage midgut lining of lepidopteran insect pests (c) Allows transformed plants to metabolize neomycin and kanamycin antibiotics during selection	*Klebsiella pneumoniae* subsp. *ozaenae* *Bacillus thuringiensis* subsp. *kurstaki* strain HD73 *Escherichia coli* Tn5 transposon	Nitrilase enzyme Cry1Ac delta-endotoxin Neomycin phosphotransferase II enzyme	Monsanto

Cotton	COT102 x MON15985 x MON88913	(a) cp4 epsps (aroA:CP4) (b) vip3A(a) (c) *cry1Ac* (d) aph4 (hpt)	Conventional breeding—cross hybridization and selection involving transgenic donor(s)	(a) Decreases binding affinity for glyphosate, resulting in increased glyphosate herbicide tolerance (b and c) Damage midgut lining, provides resistance against lepidopteran insect pests (d) Allows plant selection for resistance to the antibiotic hygromycin B	*Agrobacterium tumefaciens strain CP4* *Bacillus thuringiensis strain AB88* *Escherichia coli* *Bacillus thuringiensis subsp. kurstaki strain HD73*	Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme VIP3A vegetative insecticidal protein Hygromycin B phosphotransferase (hph) enzyme Cry1Ac delta-endotoxin	Monsanto
Potato	SEMT15-02	(a) cry3A (b) pvy_cp (c) nptII (d) aad	*Agrobacterium tumefaciens-mediated plant transformation*	(a) Damage midgut lining, provides resistance against coleopteran insects (b) Provides resistance to potato virus Y (PVY) (c) Metabolize neomycin and kanamycin antibiotics during selection (d) Allows plant selection for resistance to antibiotics	*Bacillus thuringiensis subsp. tenebrionis* Potato virus Y (PVY) *Escherichia coli* Tn5 transposon *Escherichia coli*	Cry3A delta-endotoxin Coat protein of the potato virus Y (PVY) Neomycin phosphotransferase II enzyme 3′′(9)-O-aminoglycoside adenylyltransferase enzyme	Monsanto

Table 16.2 (continued)

Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Potato	RBMT22-262	(a) *cry3A* (b) cp4 epsps (aroA:CP4) (c) plrv_orf1 2	*Agrobacterium tumefaciens-mediated plant transformation*	(a) Damage midgut lining of coleopteran insect pests (b) Decreases binding affinity for glyphosate, resulting in increased tolerance to glyphosate herbicide (c) Provides resistance to potato leaf roll virus (PLRV)	*Bacillus thuringiensis* subsp. Tenebrionis *Agrobacterium tumefaciens* strain CP4 Potato leaf roll virus (PLRV) Potato leaf roll virus (PLRV)	Cry3A delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Putative replicase domain of the potato leaf roll virus (PLRV)	Monsanto
Potato	SEMT15-07	(a) *cry3A* (b) *pvy_cp* (c) *nptII* (d) *aad*	*Agrobacterium tumefaciens-mediated plant transformation*	(a) Damage midgut lining of coleopteran insect pests (b) Confers protection against potato virus Y (PVY) through "pathogen-derived resistance" mechanism (c) Metabolize neomycin and kanamycin antibiotics during selection (d) Allows plant selection for resistance to antibiotics	*Bacillus thuringiensis* subsp. *tenebrionis* Potato virus Y (PVY) *Escherichia coli* Tn5 transposon *Escherichia coli*	Cry3A delta-endotoxin Coat protein of the potato virus Y (PVY) Neomycin phosphotransferase II enzyme 3″(9)-O-aminoglycoside adenylyltransferase enzyme	Monsanto

Potato	SEMT15-15	(a) cry3A (b) pvy_cp (c) nptII (d) aad	*Agrobacterium tumefaciens-mediated plant transformation*	(a) Damage midgut lining of coleopteran insect pests (b) Confers protection against potato virus Y (PVY) (c) Metabolize neomycin and kanamycin antibiotics during selection (d) Allows plant selection for resistance to antibiotics	*Bacillus thuringiensis* subsp. *tenebrionis* Potato virus Y (PVY) *Escherichia coli* Tn5 transposon *Escherichia coli*	Cry3A delta-endotoxin Coat protein of the potato virus Y (PVY) Neomycin phosphotransferase II enzyme 3″(9)-O-aminoglycoside adenylyltransferase enzyme	Monsanto
Potato	RBMT22-238	(a) cry3A (b) cp4 epsps (aroA:CP4) (c) plrv_orf1 2	*Agrobacterium tumefaciens-mediated plant transformation*	(a) Damage midgut lining of coleopteran insect pests (b) Confers herbicide tolerance in potato (c) Provides resistance to potato leaf roll virus (PLRV) through gene-silencing mechanism	*Bacillus thuringiensis* subsp. *tenebrionis* *Agrobacterium tumefaciens* strain CP4 Potato leaf roll virus (PLRV) Potato leaf roll virus (PLRV)	Cry3A delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Putative replicase domain of the potato leaf roll virus (PLRV)	Monsanto

Table 16.2 (continued)

| Crop name	Event name	Genes introduced	Method of trait introduction	GM traits/function	Gene source	Product	Developer
Potato	RBMT22–186	(a) cry3A (b) cp4 epsps (aroA:CP4) (c) plrv_orf1 2	Agrobacterium tumefaciens-mediated plant transformation	(a) Damage midgut lining of coleopteran insect pests (b) Confers herbicide tolerance in potato (c) Provides resistance to potato leaf roll virus (PLRV)	Bacillus thuringiensis subsp. tenebrionis Agrobacterium tumefaciens strain CP4 Potato leaf roll virus (PLRV) Potato leaf roll virus (PLRV)	Cry3A delta-endotoxin Herbicide-tolerant form of 5-enolpyruvulshikimate-3-phosphate synthase (EPSPS) enzyme Putative replicase domain of the potato leaf roll virus (PLRV)	Monsanto
Potato	HLMT15-46	(a) cry3A (b) pvy_cp (c) nptII (d) aad	Agrobacterium tumefaciens-mediated plant transformation	(a) Damage midgut lining of coleopteran insect pests (b) Confers protection against potato virus Y (PVY) (c) Metabolize neomycin and kanamycin antibiotics during selection (d) Allows plant selection for resistance to antibiotic	Bacillus thuringiensis subsp. tenebrionis Potato virus Y (PVY) Escherichia coli Tn5 transposon Escherichia coli	Cry3A delta-endotoxin coat protein of the potato virus Y (PVY) Neomycin phosphotransferase II enzyme 3″(9)-O-aminoglycoside adenylyltransferase enzyme	Monsanto

Fig. 16.3 Gene pyramiding via crossbreeding. Plants harboring transgene A or transgene B are crossed to produce plants with both transgenes
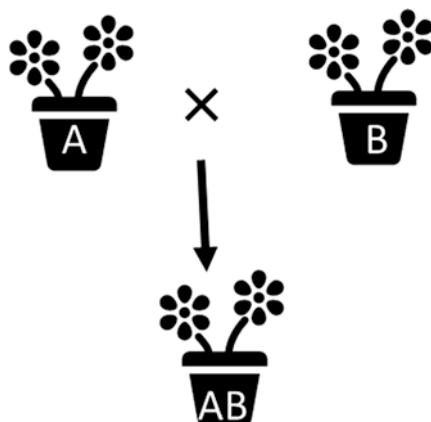
16.3.1 Iterative Procedure/Conventional Breeding

Plant harboring one or more transgenes can be successively introduced into another plant by conventional iterative procedures (Fig. 16.3). This method is also called sexual hybridization which results in the development of multi-stack hybrid. These techniques have been used to at least combine or enhance existing transgenic traits at the research level.

For example, combining herbicide-resistant event with an insect-resistant transgenic event, both being deregulated, can be performed through sexual crossing until all the required genes are present in the progeny. This has been the method to produce plants expressing different Bt toxins to delay the emergence of insect resistance to Bt crops as recently demonstrated in broccoli where pyramided *cry1Ac* and *cry1C* Bt genes controlled *P. xylostella* resistant to either single protein (Cao et al. 2002) and significantly delayed insect resistance development to Bt crops (Zhao et al. 2003). Iterative rounds of crossbreeding have also been used to introduce novel proteins or biochemical pathways into plants. For example, *Arabidopsis* plants tolerant of the environmental toxin (methylmercury) were produced by crossing plants containing two different genes for a bacterial organic mercury detoxification pathway (Bizily et al. 2000).

16.3.2 Retransformation

Retransformation is another valid gene pyramiding method, with which a plant harboring a transgene can be transformed with other multiple transgenes with several rounds of transformation (Fig. 16.4). For retransformation, every single transformation requires a new and different selectable marker from the original event, which is critical in this process. This method can be principally useful in crops that are uneasy to propagate by sexual crossings, such as trees or woody plants. This method has been proven in various research like a modification of flower colors in forsythia

Fig. 16.4 Pyramiding
genes A and B by
retransformation method
with which a plant
harboring transgene A is
retransformed with
transgene B
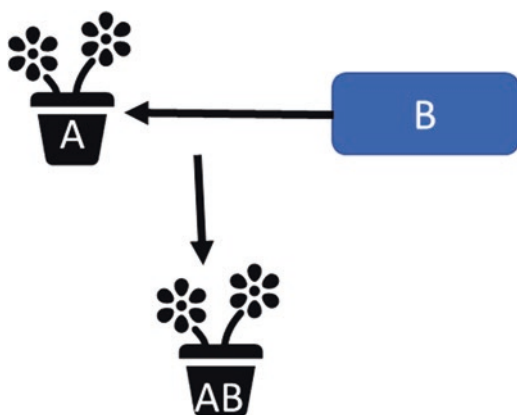
by inducing anthocyanin synthesis through sequential transformation with the genes
for dihydroflavonol 4-reductase from *Antirrhinum majus* (*AmDFR*) and anthocyani-
din synthase from *Matthiola incana.* This induced anthocyanin synthesis in the
double transformants which showed a novel bronze-orange petal color. This method
has also been used in trees to combine two genes involved in lignin biosynthesis by
introducing antisense transgenes in a way to reduce the environmental impact of
papermaking.

16.3.3 Co-transformation

Co-transformation is another method which has been proven to be one of the most
capable strategies taken to date for the introduction of multigenes into plants. In this
method, a plant is transformed with two or more independent transgenes. The trans-
genes of interest are in separate gene constructs and are delivered to the plant instan-
taneously. This strategy is divided into two categories: (a) single-plasmid
co-transformation of linked transgenes in which transgenes A and B are linked on
one piece of DNA, with each gene having its promoter, and transferred together into
a plant (François et al. 2002; Halpin and Ryan 2004) or (b) multiple-plasmid co-
transformation of unlinked transgenes in which transgenes A and B are on different
pieces of DNA and are transformed together into a plant (François et al. 2002).

The stacking of multiple genes via co-transformation is quick and easy and can
be used in a variety of species including biolistic (direct) and *Agrobacterium*-
mediated (indirect) transformation methods. Multiple-plasmid co-transformation
via biolistics has been successful in introducing up to 13 genes simultaneously into
plants at one or a few loci, and six-gene clusters by single-plasmid co-transformation
methods were introduced successfully into plants (Chen et al. 1998; Goderis et al.
2002; Thomson et al. 2002). A major advantage of this method is that the co-
introduced transgenes tend to co-integrate at the same chromosomal position in a

high proportion of transgenics. This confirms that "effect" genes are unlikely to segregate apart in subsequent generations.

Several studies have reported how transformation conditions might be manipulated to encourage co-transformation and/or co-integration. For example, one tobacco study using two T-DNAs recorded 100% co-transformation frequencies, with 40–50% of lines showing the capacity for segregational separation (McCormac et al. 2001). Presently, co-transformation methods via particle bombardment have resulted in the successful introduction of three insecticidal genes in *indica* rice. The resultant transgenes showed significant resistance against major rice pests (Maqbool et al. 2001). Similarly, co-transformation of modified cry1Ab and cry1Ac genes of Bt in chickpea has resulted in improved resistance to *H. armigera* (Mehrotra et al. 2011).

The proteinase inhibitors oryzacystatins I and II (OCI and OCII) genes were stacked into the potato genome by simultaneous co-transformation with both OCI and OCII genes. Expression of both OCI and OCII in potato resulted in increased resistance against CPB that caused a significant reduction in adult body weight and foliage consumption (Cingel et al. 2014). The strategy, therefore, has obvious advantages as a one-step procedure for the introduction of multiple "effect" genes into plants. Beyond the research level, co-transformation methods have been successfully used to produce some of the commercialized GM stacked crop events that are available in the market today.

16.4   Practical Merits of Gene Pyramiding

Problems related with engineering resistance through the genetic transformation of a single gene are that there is a possibility that pests may develop resistance to the transgenes used against them, resulting in the susceptibility of the transgenic plants to pest attack. Therefore, gene pyramiding or trestle transfer of multiple genes may be useful in conferring broad-spectrum resistance against different biotic and abiotic stresses. Essentially, gene pyramiding allows us to have a simultaneous expression of more than one gene(s) associated with resistance in a transgenic plant (Shelton et al. 2002). There is a broad agreement that pyramiding genes for resistance is a useful tool for increasing endurance with many known achievements. Stacked GMOs are an important component of insect-resistant management (IRM) strategies to delay development of resistance in pests against the transgenes. Gene staking allows the development of crops with combined protection against multiple pests and diseases as well as adverse environmental conditions such as heat, cold, and drought stresses. Second-generation dual Bt gene cottons Bollgard II® (*Cry1Ac + Cry2Ab*) and WideStrike™ (*Cry1Ac + Cry1F*) express two *Bt* toxins that were introduced in order to control *H. zea*, which was not satisfactorily controlled by the Cry1Ac toxin alone (Jackson et al. 2003; Ferry et al. 2004; Bates et al. 2005; Gahan et al. 2005). The *Cry1Ac* and *Cry2Ab* toxins have different binding sites in larva midgut and are considered to be a good combination to deploy in managing or controlling resistance evolution. This is due to the fact that a species cannot easily

evolve resistance to both toxins due to a different site of actions. Since different Cry toxins vary in their effectiveness against the individual species, this pyramiding of Bt genes in a single crop has effectiveness in controlling different species. Pyramiding may reduce the likelihood of developing resistance in the pest insects especially if the pyramided Bt toxins use different insect gut receptors (Bates et al. 2005). More recently released transgenic maize varieties have genes pyramided with lepidopteran-active *cry* genes to give concurrent protection against caterpillars and rootworm. For example, Dow AgroSciences' Herculex XTRA®, Syngenta's Agrisure CB/RW®, and Monsanto's YieldGard Plus®.

16.5   Gene Pyramiding with RNAi

Rapidly declining host plant resistance in Bt crops induced researchers to adapt gene pyramiding strategy in transgenic plants which produce two or more Bt toxins to kill one or more insect pest. Conversely, multiple resistance and/or antagonistic action among Bt proteins minimized the potential benefits of this strategy. The breakthrough technology RNA interference (RNAi) has provided promising results in managing insect pests (Lim et al. 2016; Mao et al. 2007; Tian et al. 2015; Yu et al. 2016). Being an eco-friendly technique, RNAi—small interfering RNA (siRNA)—silence only a particular sequence in the target gene to suppress the expression. The main goal of this strategy is to silence the expression of the gene(s) which is encoding protein(s) crucial for the growth and development of that specific insect pest. For example, promising targets for RNAi may include genes involved in synthesis of juvenile hormones (JHs), EcR genes, etc. (Asokan et al. 2014; Tian et al. 2015; Fu et al. 2016), which are essential for growth and development of insects, which are not present in other organisms (Belles et al. 2005). Concluding, pyramided cotton combining a Bt toxin and RNAi substantially delayed resistance relative to using Bt cotton alone (Ni et al. 2017). Larval gut genes have been reported as promising target sites for RNAi (Wynant et al. 2014). So, they can be easily combined with Bt crops to synergize their effect.

Proteolytic enzymes, also called proteases, make the most diverse class of enzymes. Hydrolytic cleavage can occur in some peptide bonds in the target enzymes due to the catalytic activity of these enzymes. These kinds of enzymes are distributed in approximately all living organisms, viz., plants, animals, and microbes. In fact, these types of enzymes are essential for the host organisms; however, their overexpression can be significantly detrimental especially in higher concentrations. That is why the bioactivities of these types of enzymes should be highly specified and controlled. However, due to several reasons, they can't provide full control of insect pest like Bt toxins. So, according to our point of view, combining these PIs with suitable RNAi can make them useful for making insect-proof crops.

Additionally, protease inhibitors (PIs) are considered as successful alternatives to Bt. Gut enzymes including cysteine proteases, intestains D and E, cellulases, serine proteases, and endopolygalacturonase can be underexpressed by RNAi.

Several other genes which are parallel to Bt like PIP-47Aa (Wei et al. 2018), GNIP1Aa (Sampson et al. 2017), and AfIP-1A/1B (Yalpani et al. 2017) can be used potentially in the near future. If we start considering their pyramiding with favorable RNAi, we can preserve these new insect toxins for more than a century without any resistance.

16.6 Conclusion

Pyramiding insecticidal genes in crops can theoretically counter the requirements for insecticide mixtures and can be efficiently used to delay the development of resistance in insect pests. Insecticidal genes that are expressed in the plant tissues can provide protection upon which the target pest feeds. Insecticidal Cry proteins from *B. thuringiensis* with high specificity have been identified and are achieved through specific midgut receptors and combinations with no cross-resistance in target pests. However, insecticidal gene combinations that are stacked against a particular set of pests may not be beneficial against all insect pests. For example, while WideStrike® is a stacked transgene event of cotton containing Cry1F and Cry1Ac, effective against the key cotton pests *H. virescens* and *H. zea*, the same product is not recommended for *P. gossypiella*, against which the pyramided toxins have little or no toxin activity, nor for *T. ni* or *S. exigua*, against which Cry1Ac has little or no activity. Similarly, VipCot® in cotton and Viptera® in corn with Cry1Ab and Vip3A toxins can provide protection against most key pests such as *H. virescens*, *H. zea*, and *D. grandiosella*; however, only Vip3A toxin in both crops has no activity against *O. nubilalis*. On the other side, SmartStax with only Cry1F is highly effective against *Striacosta albicosta* (western bean cutworm) and *Agrotis ipsilon* (black cutworm). Further evaluations may be required for such secondary pests, especially if they become more damaging or widespread. Crop having single transgene products is incapable of complete resistance against insect pests. In such circumstances, the pyramided toxins can be useful to withstand the insect damages and offer the most effective resistance management option. Different experiments show that genes pyramiding is more effective at delaying resistance than single traits and probably the most effective resistance management tool. Since pyramids can enable mixed refuges to provide effective resistance management. To overcome the stacked traits, the insect will need two or more than two different alleles. This means that the addition of a smaller and simplified refuge with pyramids can provide longer protection than larger refuges for single traits. Similarly, gene silencing with RNAI along with gene pyramiding strategies can further enhance pest control in various crops

including cotton, maize, and potato. From these integrated resistant management programs, growers can easily control major insect pests and related secondary pests resulting from the combinations of insecticidal traits. To achieve all these benefits from gene pyramiding of major crops, it is necessary that all stakeholders, including breeders, extension workers, crop advisors, farmers, and regulatory authorities, should continue to encourage the development, deployment, and adoption of stacked insecticidal crop product for enhanced yield and better insect resistance management.

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Agronomic Crops Response and Tolerance to Allelopathic Stress

17

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Abstract

Under agricultural situations, plants are often exposed to various environmental stresses, including biotic and abiotic stresses. Allelopathy is one of the most important interactions among plants. Nowadays, allelopathy is known as one of the biotic stresses affecting growth and development of plants, especially crops. Responsible compounds in allelopathy named allelochemicals are derived from the secondary metabolism of plants and are species and tissue specific. These compounds are released from the plants into the environment as leachates, volatiles, and root exudates and from biomass decomposition. Their action mechanism affecting the receiver plants also differs. Some of these compounds, such as volatile compounds, directly impact the receiver plant, while other compounds need microorganism's intermediation. Allelopathic stress is a multidimensional stress, and in receiver plants, it occurs at molecular, biochemical, physiological, morphological, and eventually ecological levels. In addition, it can negatively affect the quantity and quality of growth in agronomic crops. Plants have several resistance mechanisms to counteract the adverse effects of this phenomenon at physiological, biochemical, and molecular levels that all these mechanisms lead to the detoxification of allelochemicals. Generally, allelochemical's detoxification processes were aimed to facilitate allelochemicals' outlet from the cells that eventually leads to normal cell functions. Environmental stresses, viz., drought, deficiency and toxicity of nutrients, temperature stress, light stress, and biotic stresses can affect allelopathy and also influence it. Herbicide application in agricultural fields causes changes in plant's allelopathic interactions as well. Already, allelopathy has become a suitable tool for the transgenic plant production with desirable traits via biotechnology techniques, which promise the production of resistant cultivars to a variety of stresses.

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Abbreviations

ABA	abscisic acid
C_4H	cinnamate-4-hydroxylase
COMT	caffeic acid O-methyltransferases
CTK	cytokinin
F_5H	ferulic acid 5-hydroxylase
IAA	indoleacetic acid
MDA	malondialdehyde
PAL	phenylalanine ammonia lyase
PDMS	polydimethylsiloxane
QTL	quantitative trait locus
RAPD	random amplification of polymorphic DNA
ROS	reactive oxygen species
STME	silicone tube micro-extraction

17.1 Introduction

Under both natural and agricultural situations, plants are often exposed to various environmental stresses including biotic and abiotic stresses (Inderjit and Einhellig 1993; Maqbool et al. 2013).There is evidence that many plants prevent foreign species from entering their kingdom and continue to live as a dominant species. Growth decline in neighbor plants of certain species has also been reported frequently. This growth pattern cannot be justified only by the competition phenomenon, and it seems that other factors are involved in this event that today one of these factors is considered as allelopathic phenomenon (Kohli et al. 2001; Maighany 2003). "Allelopathy" is a word derived from two Grecian words "allelon" and "pathose," is mainly used as a negative word (Molisch 1937), and is a common biological phenomenon or ecological behavior in which one organism produces biochemicals, which are known as allelochemicals, that influence the growth, survival, development, and reproduction of other organisms (Einhellige 1996; Kohli et al. 2001; Singh et al. 2001). Exactly allelochemicals are the responsible compounds in allelopathic phenomenon (Kohli et al. 2001; Singh et al. 2001). Nowadays by science progress, allelopathy is known as biotic stress that affects plants' growth especially on the quantity and quality of crop growth and yield (Haddadchi and Massoodi Khorasani 2006; Maighany 2003; Menges 1988). Allelopathic stress is a multidimensional stress, and its effects on

plants occur at molecular, biochemical, physiological, morphological, and eventually ecological levels (Gniazdowska and Bogatek 2005; Inderjit and Einhellig 1993; Kohli et al. 2001). Plant allelopathy is one of the modes of interaction between receptor and donor organisms and may exert either positive or negative effects and is becoming important in the arable systems, particularly associated with intercropping and crop rotation (Iqbal et al. 2007; Liebman and Dyck 1993; Mahmood et al. 2013). According to the terms "allelopathy," "allelopathic stress," "allelopathic phenomenon," and "allelopathic interaction" can address different issues, and in this text we will use these terms in their certain mean.

17.2   Concept of Allelopathy

Allelopathy is one of the most important interactions among plants and is sub-discipline of chemical ecology (Einhellig 1995; Achigan-Dako et al. 2014). The word allelopathy was first used by Molisch in 1937. Allelopathy is a word derived from two Grecian words "allelon" and "pathose" and is mainly used as a negative word (Molisch 1937). The study on allelopathy increased in the 1970s to recent years and become a popular topic in botany, ecology, agronomy, soil science, and horticulture (Einhellig 1995, 1996). The effects of chemicals that are produced by plants or microorganisms on the growth, development, and distribution of other plants and microorganisms in natural and agricultural systems are very important. The allelopathic interaction can be one of the effective factors in second culture and crop rotation, especially in contact with crop–crop and weed–crop interactions (Chou 1999; Mallik 2003; Zheng et al. 2015). Allelopathy is now defined as any positive or negative response of a plant to the chemical produced by another plant (Bhadoria 2011; Einhellige 1996), however; an allelopathic interaction mostly ends with negative effects. Plants producing allelopathic compounds and plants affected by these compounds are named donor and receiver plants, respectively (Sodaeizadeh and Hosseini 2012; Soltys et al. 2013). In addition, recent information is suggested that the allelopathic chemical donor and receiver may include animals (Kong and Hu 2001). Some plant-secreted compounds also affect directly the growth and development of the donor plant, which is called as auto-toxicity. Auto-toxicity is a branch of the allelopathic phenomenon and is very common in plants, although plants with high allelopathic potential have auto-toxicity avoidance mechanisms as well (Singh et al. 1999; Kohli et al. 2001; Lv et al. 2002; Maighany 2003; Singh et al. 2001).

A remarkable point in the allelopathy is the chemical compounds that cause this phenomenon. The type of compound, concentration, toxicity, water solubility, and its sustainability in the environment are the main factors that are primarily determinative in allelopathic interactions. However, other factors are effective in the allelopathic phenomenon (Einhellige 1996; Kohli et al. 2001; Singh et al. 2001).

17.3 Allelopathy or Competition

Competition is another kind of plant interactions. In natural ecosystems and rarely synthetic ecosystems, the competition and allelopathy overlapped together in terms of the effects and involved factors and are hardly distinguishable from each other. So in the past, these two phenomena were introduced as a subset of a phenomenon called interference. The interference word was originally developed by Harper (1964), whose concept covers both competition and allelopathy (Chou 1999; Kohli et al. 2001; Maighany 2003). In fact, the main cause of interference is the use of limited resources (competition) along with the production and release of toxic substances into the environment (allelopathy). According to Zimdahl (1999), competition is the receiving of limited resources by a microorganism following by the reduction of resources in the environment and eventually leads to the growth decline of other microorganisms. Exactly, competition occurs when one (or more than one) growth factor was restrictive. Despite all similarities, there are numerous differences between the allelopathic phenomena and the competition (Chou 1999; Inderjit del Moral 1997; Inderjit and Einhellig 1993; Kohli et al. 2001; Leslie 2005; Maighany 2003; Willis 2007; Gioria and Osborne 2014), among which are:

1. Entry of allelopathic compounds into the plant environment against consumption of nutrients from the environment in competition.
2. Density, which has negative and positive effects on the allelopathy and competition, respectively.
3. Competition occurs merely between living organs, whereas in allelopathy, dead organs and tissues can be involved.
4. Growth and dimensions of the plant, which reduces the competition and increases the plant's allelopathic potential and vice versa.
5. In the allelopathic phenomenon, a donor plant can produce allelopathic compounds throughout its all phases of life cycle (especially the reproductive phase), while the competition between the species is limited to the early phase of the young plant establishment.
6. Only certain plant species (often weeds) can use allelopathy for dominance over other species, while competition is a common phenomenon in among all plants that are living in the extreme environments.
7. Allelopathic phenomenon is observed in the absence of a donor plant due to the existing of compounds in the environment, but the absence of competitor plant in the environment leads to lack of competition.
8. Allelopathy is the result of competition and is an advanced state of it, while itdoesn't lead to competition.
9. Allelopathy isn't artificially inducible, while competition is inducible under lab conditions by limiting the sources.
10. Poisoning, growth inhibition, cell death, and ultimately receiver plant death are the allelopathic effects, while the competition symptoms are limited to the nutrient deficiency and toxicity symptoms, and most plants can complete their life cycle under these conditions.

17.4   Allelochemicals: Responsible Compounds in Allelopathy

The responsible compounds in allelopathic phenomenon are called allelochemicals (Kohli et al. 2001; Singh et al. 2001). In the past, since these compounds were considered possibly a protein nature, they were called allelopatin, but with the analysis of soil extracts, the true and varied nature of these compounds was determined (Kohli et al. 2001; Soltys et al. 2013). Allelochemicals are species- and tissue-specific compounds, which are nonnutritive substances mainly produced as plant secondary metabolites, microorganisms, fungi, and virus or released due to decomposition of organic materials by microbes (Inderjit Nilsen 2003). All plants use primary metabolites for growth but differ in terms of the secondary metabolite production. Therefore, plants differ in terms of the ability to produce allelochemicals (Kohli et al. 2001; Maighany 2003). Allelochemicals are often toxic compounds, although, in some cases, stimulant compounds are also produced rarely (Bhadoria 2011; Einhellige 1996). The toxicity of the allelochemical compounds is dependent on their concentration, donor plant age, plant metabolism, type of tissue or organ in which it is produced, season, climate, and environmental conditions (Belz 2007; Iannucci et al. 2013; Khalaj et al. 2013; Khan et al. 2010; Kohli et al. 2001; Leao et al. 2012).

17.4.1   Sources

Allelochemical production sources are very diverse in the crop environment including microorganisms, certain weeds, and past or present crops (Einhellige 1996; Maighany 2003). In some cases, production of allelochemicals has been reported in primary plants, algae, and lichen as well (Pruvis 2000). In the whole plant, allelopathic compounds can be produced and accumulated in leaves, stems, fruits, rhizomes, roots, seeds, flowers, buds, or even pollen grains (such as corn), in which their concentrations are directly related to the type of organ (Anaya 1999; Kohli et al. 2001; Maighany 2003; Singh et al. 2001). At the cell level, these compounds are either accumulated in vacuole, away from the cell's metabolic center, or in storage structures. Generally, the storage location of allelochemicals is determined by their tendency to fat. For example, lipophilic compounds are found in secretion structures or in cuticular waxes, while hydrophilic compounds are stored in cell walls or vacuoles (Kohli et al. 2001; Maighany 2003; Shao-Lin et al. 2004; Singh et al. 2001).

17.4.2   Action Mechanisms in the Environment

In order to triggering allelopathic stress in crops, allelochemicals must be released from the plants into the environment as leachates, volatiles, and root exudates or from biomass decomposition (Maighany 2003; Sodaeizadeh and Hosseini 2012; Soltys et al. 2013). Some of these compounds are volatile and released into the

receiver plant atmosphere. Some compounds are root exudates and enter into the soil. Other compounds are produced as latex from green parts of plant and enter into the soil. Rainfall facilitates releasing of allelochemicals (Cheng et al. 2011; Inderjit Nilsen 2003; Khan et al. 2010; Shao-Lin et al. 2004). Their action mechanisms on the receiver plants also differ. Some of these compounds, such as volatile compounds, directly impact the receiver plant (Einhellige 1996; Maighany 2003; Sodaeizadeh and Hosseini 2012), while other compounds need microorganism's intermediation (Kohli et al. 2001; Sanchez-Moreiras et al. 2008; Singh et al. 2001; Soltys et al. 2013; Li et al. 2015). The action mechanisms of allelochemicals in the environment are summarized in Fig. 17.1.

17.4.3 Active Concentration and Half-Life of Allelochemicals

The effect severity of an allelochemical is dependent on the received concentration by the receiver plant (Kohli et al. 2001; Maighany 2003). In general, regardless of the stimulatory or inhibitory effect and the type of compound, the response of the plants to the allelopathic compounds in a curve against concentration is indicative of the concave pattern. For example, phenolic compounds at high concentrations are always inhibitory, although they may be stimulatory in very lower concentrations. Therefore, the concentration of allelochemicals is very important and a decisive factor in the evaluation of the effect of these compounds (Razavi 2011; Maighany 2003).The rapid decomposition of allelochemicals in the soil makes it difficult to determine the true concentration of these compounds. On the other hand, the effective concentration of these compounds in the soil and the controlled bioassay can be very different (Chou 1999; Leslie 2005; Peng et al. 2004; Shao-Lin et al. 2004). In this regard, determining the threshold for the activity of an allelopathic compound in the soil or any type of bioassays will be helpful in tracing the allelopathic activity. Today, many studies have been conducted to measure the concentrations of allelochemicals in soil and culture media. One of the most common and effective techniques available for this object is the use of polydimethylsiloxane (PDMS) microtubes (Dayan et al. 2009; Mohney et al. 2009; Weidenhamer 2005; Weidenhamer et al. 2009, 2014). In this technique, by using coated microtubes with PDMS fibers, the allelopathic compounds of plants are directly collected at a short distance from the hairy root over time. The PDMS is a powerful absorbent and used with the brand name of Dimethicone as a carminative drug (Dayan et al. 2009; Mohney et al. 2009). This technique is also known as the silicone tube micro-extraction (STME) and is very useful to determine the concentration of the compounds released from the roots rapidly without changing the compounds' characteristics. The biggest problem in using of STME technique is its inability to be used in the natural environment (soil) because of artifact results (Dayan et al. 2009; Mohney et al. 2009; Weidenhamer 2005; Weidenhamer et al. 2009, 2014).

Studies have been shown that the allelopathic behavior of the donor plants in vitro differs from the natural conditions (Inderjit Callaway and Vivanco 2006; Inderjit et al. 2011). Allelochemicals are decomposed after being released into the

Donor Plant   **Receiver Plant**

■ Volatile compounds
release directly into the
receiver pant atmosphere

■ Allelopathic compounds
of pollen grain can affect
receiver plant during
pollination phenomenon

■ Roots can also produce
volatile compounds, but these
compounds are mostly trapped
in the soil and altering by
microorganisms

■ Allelochemicals produced as
the latex from plant green parts
enter into the soil by rainfall

■ A few allelochemicals can induce other
microorganisms to produce new allelochemicals
that named secondary allelochemicals

■ Some allelochemicals
release into the soil as
root exudates

■ Some allelochemicals
are released from the
dead plantmaterials by
decomposition processes

■ Some allelopathic compounds needs
microorganism's intermediation to be
active compound

Fig. 17.1 Action mechanisms of allelochemicals in the environment

environment by various factors or by themselves. The half-life of allelochemicals varies from one to several months depending on their composition (Barto and Cipollini 2009; Demuner et al. 2005; Macias et al. 2005a, b; Wang et al. 2007). Moreover, the active concentration of allelopathic compounds, soil texture, microbial population, and vegetation structure of the region are very important (Gu et al. 2009; Kong et al. 2008; Macias et al. 2004; Understrup et al. 2005). Often, the conjugation increases the half-life of allelochemicals in the environment, and conjugative compounds, such as benzoxazinones, have a greater chance to affecting the target plant (Tabaglio et al. 2008; Understrup et al. 2005).

17.4.4 Classification

Already, various classifications were suggested for allelopathic compounds, but due to the functional (Leslie 2005; Shao-Lin et al. 2004; Weir et al. 2004) and structural (Inderjit and Einhellig 1993; Leslie 2005; Maighany 2003) variations of these compounds, as well as the unknown nature of some of them (Chou 1999; Weir et al. 2004), none of the presented models are comprehensive. Nowadays, these compounds are classified based on the structural similarities and biochemical behaviors into 14 categories including: (1) water-soluble organic acids; (2) straight-chain alcohols; (3) aliphatic aldehydes and ketones; (4) simple unsaturated lactones; (5) long-chain fatty acids and polyacetylenes; (6) benzoquinone, anthraquinone, and complex quinones; (7) simple phenols, benzoic acid and its derivatives, cinnamic acid and its derivatives, and coumarins; (8) flavonoids and tannins; (9) terpenoids and steroids; (10) amino acids and peptides; (11) alkaloids and cyanohydrins; (12) sulfides and glucosinolates; (13) purines and nucleosides; and (14) some plant's growth regulators, including salicylic acid, gibberellic acid, and ethylene, which are also considered to be allelochemicals (Rice 1974, 1984).

Although, according to the literature, the recent classification also has many shortcomings, it provides a general framework for the diversity of existing known compounds and groups. An old but common classification also is divided all allelopathic compounds into the three general groups including: (1) compounds with nitrogen base, such as alkaloids, nonprotein amino acids, and cyanogenic glycosides; (2) carbon-based compounds containing a hydrocarbon ring such as phenolic compounds; and (3) carbon-based compounds, lacking a phenolic structure, such as terpenoids (Kohli et al. 2001).

Among the various types of allelopathic compounds, some of them have high prevalence. The most important types are phenolic compounds, terpenoids, alkaloids, nonprotein amino acids, saponins, and benzoxazinones (Khan et al. 2010; Kohli et al. 2001; Razavi 2011; Soltys et al. 2013).

17.4.4.1 Phenolic Compounds

These compounds play an important role in the allelopathic interactions and ecological studies. Phenols play a role in the allelopathy of algae, fungi, lichens, mosses, pteridophytes, gymnosperms, as well as angiosperms (Odeyemi et al. 2013; Maighany 2003).

Among the most important phenolic compounds with a potential for allelopathy in the soil are 3-hydroxy-hydrocinnamic acid, benzoic acid, phenylacetic acid, syringic acid, ferulic acid, resorcinol, p-Coumaric acid, salicylaldehyde, and hydrocinnamic acid (Batish et al. 2008; Einhellig 1995; Maighany 2003). Studies showed that among all the phenolic compounds involved in the allelopathic phenomenon, the chlorogenic acid in the seeds and skin of the eggplant is the most toxic compound (Maighany 2003).

Phenolic compounds affect accumulation and availability of the soil nutrients, which can eventually lead to changes in crop growth and development (Bergmark et al. 1992; Li et al. 2010; Weston and Mathesius 2013).

17.4.4.2 Terpenoid Compounds

This group is important allelochemicals because they are active in the relatively low concentrations (1–3 μmoles). In addition, terpenoid compounds have the ability to transfer through the atmosphere to longer distances (Abrahim et al. 2003a, b; Maighany 2003). Alpha- and beta-pinene, camphene, picrol, cineol, podolactone, anomacilactone, nagilactone, and diterpenoid alkaloids are from the important terpenoid compounds involved in the allelopathy phenomenon (Abrahim et al. 2003a, b; Kato-Noguchi et al. 2013; Khan et al. 2010; Maighany 2003).

17.4.4.3 Alkaloids

Alkaloids are the most common nitrogen-based allelochemicals. These compounds are interesting for scientists due to their complex structures and properties, and they can also be fatal to human (Wink and Latzbruning 1995; Maighany 2003). They reduce the membrane stability, alter the enzyme kinetics, and affect photosynthesis, respiration, biosynthesis of proteins, signal transduction pathways, and DNA replication (Inderjit and Einhellig 1993; Li et al. 2010; Maighany 2003; Wink and Latzbruning 1995). The important alkaloids involved in the allelopathy are sapotine, aconitine, caffeine, cytisine, and gramine. Although alkaloids have a high structural diversity, they play a limited role in the allelopathy phenomenon (Inderjit and Einhellig 1993; Maighany 2003).

17.4.4.4 Nonprotein Amino Acids

These compounds are the nitrogen-based compounds and considered as analogous of standard amino acids (Maighany 2003; Rice 1974). An example of the nonprotein amino acids with known allelopathic activity is canavanine that is analogous of arginine and inhibits seed germination and growth of seedlings in plants such as lettuce (Inderjit Callaway and Vivanco 2006; Inderjit and Einhellig 1993; Maighany 2003). It is worth noting that nonprotein amino acids do not have auto-toxicity effects, because tRNA synthetase of plants has considerable ability for nonprotein amino acid recognition (Maighany 2003).

17.4.4.5 Saponins

Saponins are compounds with steroid or terpene skeletal system that are replaced by carboxyl, carbonyl, and hydroxyl functional groups (Maighany 2003). The action mechanism of saponins is not known as much as phenolic acids, but their herbicide

activity has been reported frequently. The most active and well-known saponin is the medicagenic acid, which is found abundantly in alfalfa roots (Anaya 1999; Kohli et al. 2001; Maighany 2003).

17.4.4.6 Benzoxazinones

These compounds were identified in the late 1950s as important natural products in the Poaceae family. Biological activities of benzoxazinones, such as the effect on aphids, fungi, and pathogenic bacteria as well as their allelopathic effects on plants, have been proven (Inderjit del Moral 1997; Inderjit and Einhellig 1993; Kohli et al. 2001; Schulz et al. 2013). Studies have shown that biosynthesis of benzoxazinoid compounds in the plants is dependent on tryptophan pathway and is structurally similar to auxins (Macias et al. 2005a; Maighany 2003). These compounds are found in the plant in the form of glycosylated (inactive), which in general terms are named as cyclic hydroxamic acid. During plant damage or due to the action of microorganisms in the soil, especially the gram-negative bacteria, beta-glycosidase enzyme hydrolyzes these compounds and creates a cyclic benzoxazolinone (more toxic aglycones) (Macias et al. 2004, 2005b; Maighany 2003). Unlike other allelopathic compounds that have the highest concentration at flowering time, concentrations of these compounds increase during seed germination, reach to the maximum in young seedlings, and thereafter decrease (Inderjit and Einhellig 1993; Kohli et al. 2001). By studying the effect of these compounds on the activity of enzyme systems, their inhibitory effect on the metabolism of chloroplasts has been confirmed (Kohli et al. 2001; Maighany 2003). It is notable that dicotyledon plants are more susceptible to benzoxazinoids than monocotyledon plants (Kohli et al. 2001). Like nonprotein amino acids, cyclic hydroxamic acids don't have auto-toxicity effects (Maighany 2003); therefore, they have a good potential for application as a natural herbicide (as mulch) in the monocotyledon crop farms.

17.5   Effects of Allelopathic Stress in Plants

Allelopathic stress is a multidimensional stress, and its effects in plants occur at molecular, biochemical, physiological, morphological, and eventually ecological levels (Gniazdowska and Bogatek 2005; Inderjit and Einhellig 1993; Kohli et al. 2001).

17.5.1 Structural and Ultrastructural Changes in Cells

The shape and structure of plant cells are affected by allelochemicals. For example, some allelochemicals (like volatile monoterpenes) can lead to nuclear abnormalities, increasing in vacuole numbers and widen or shorten root cells (Bakkali et al. 2008; Pawlowski et al. 2012). Compounds existing in plant pollen grains especially corn plants reduce mitotic activity by more than 50% not only in plant cells but also in animal cells (Cruz Ortega et al. 1988; Sunar et al. 2013). Exposure to hordenine, which is allelochemicals from barley, can lead to damage in cell walls, increases in

both the size and number of vacuoles (a marker for low metabolism), disorganization of organelles, and cell autophagy induction (Kaur and Inderjit Kaushik 2005; Liu and Lovett 1993). Cinnamic acid and its derivatives significantly deformed the ultrastructure of chloroplasts and mitochondria leading to destruction in their normal functions (Wu et al. 2004). Some allelochemicals can alter the random amplification of polymorphic DNA (RAPD) profiles of receiver plants (Kekec et al. 2013; Sunar et al. 2013). Citral as volatile essential oil of aromatic crops such as citrus tree can cause disruption of cortical microtubules in plant cells. Considering mitotic microtubules and subsequently cell divisions were affected from the cortical microtubules, eventually citral can alter cell's ultrastructure (Chaimovitsh et al. 2010, 2012; Dudai et al. 1999). Cell wall thickening, reduced intercellular communication, and change in the root hair formation are the other effects of allelopathic compounds (Grana et al. 2013).

17.5.2 Inhibition of Cell Division and Elongation

Allelopathic phenomenon not only influenced ultrastructure of cells but also affected cell growth and expansion. Allelochemicals including camphor, cineole, beta- and alpha-pinene, and camphene are affecting cell proliferation and DNA synthesis in plant meristems (Nishida et al. 2005; Sanchez-Moreiras et al. 2008). Colchicine and sorgoleone are reducing the number of cells in each cell division, damaging tubulins and resulting in polyploid nuclei that lead to production of polyploid cell lines (Hallak et al. 1999). The extracts of some allelopathic weeds inhibit primary root elongation and lateral root development, decrease root hair length and density, inhibit cell division in root tips and the regeneration of root cap cells, and finally reduce root growth (Burgos et al. 2004; Cai and Mu 2012). Roots exposed to the allelochemicals mostly have inhibited mitosis by damaging chromatin organization (Cai and Mu 2012).

17.5.3 Imbalance in the Redox State and Induction of Oxidative Stress

Generally, exposure of plants to allelochemicals leads to the generation of reactive oxygen species (ROS) and subsequently plant metabolism alteration (Bais et al. 2003, 2006; Ding et al. 2007; Sun et al. 2014). The balance of the redox state in the cell plays an important role in plant's cell homeostasis (Bais et al. 2003, 2006). Although oxidative stress is a secondary stress and appears after an initial stress, increasing the concentration of ROS and free radicals isn't done at once. The free radical production starts from the early stages of stress in plants, but antioxidant systems of plants control their concentration. By increasing cell damage, potential of cells for scavenging of free radicals is reduced, and ROS concentration reaches to critical level, and oxidative stress is induced (Giazdowska et al. 2015). Allelochemicals by inducing the free radicals' production indirectly led to

membrane damage, degradation of macromolecules such as chlorophyll and proteins, disturbance in the hormonal signal transduction pathway, and so on (Dehghani et al. 2014; Haddadchi and Gerivani 2009; Maighany 2003; Singh and Sunaina 2014). Studies show that the activity of antioxidant enzymes such as catalase (CAT) (Ahrabi et al. 2011), peroxidase (POD) (Singh and Sunaina 2014, Yu et al. 2003, Zeng et al. 2001), polyphenol oxidase (Batish et al. 2008; Haddadchi and Gerivani 2009), superoxide dismutase (SOD) (Xiao-Jun et al. 2013; Yu et al. 2003; Zeng et al. 2001), and ascorbate peroxidase (APX) (Zuo et al. 2012a, b) increases in plants under allelopathic stress. In addition, the synthesis of osmotic compatible compounds, such as proline, which prevent the production of free radicals, has been reported in a number of studies (Haddadchi and Massoodi Khorasani 2006).

17.5.4 Increasing the Permeability of Cell Membrane

Many studies have shown that allelochemicals significantly inhibit the antioxidant system activity and increase free radical levels. Free radicals attack membrane lipids, which are the most abundant macromolecules in the cell, and lead to the peroxidation of these molecules (Harun et al. 2014; Lin 2010; Lin et al. 2000; Sunmonu and Van Staden 2014; Zeng et al. 2001). Lipid peroxidation by ROS and subsequently alteration in membrane potential are the reasons of the membrane permeability increasing and electrolytes leakage into the intercellular space. As well as increasing the concentration of hydrogen peroxide and malondialdehyde (MDA) in cells, especially in the vicinity of membranes, is the other result of allelochemicals (Farhoudi and Lee 2013; Farhoudi et al. 2012; Zuo et al. 2012a, b). The high membrane permeability is an important factor involved in inducing the other allelopathic effects. On the other hand, by increasing the permeability of the membrane and destroying the integrity of it, allelochemicals easily enter into the cells and have the opportunity to increase their concentration in the cytosol and finally trigger other allelopathic effects. The famous example of this phenomenon is the decrease in the activity of cytosolic SOD and APX enzymes in potato after treatment with leaf extract of wheat. Studies show that the decrease in the activity of these enzymes can be documented after damage to the plasma membrane so that the mutant plants (for the abovementioned enzymes being silent mutants) do not show such responses (Zuo et al. 2012a, b).

17.5.5 Effect on the Plants' Hormonal System

Allelochemicals can alter the growth and development of agronomic plants due to changes in contents of plant growth regulators and induction of imbalance in hormonal system (Peterson et al. 2002; Wasternack and Hause 2013; Yang et al. 2005). It has been shown that one of the causes of allelochemicals toxicity in plants is interfering with the natural auxin activities. Most phenolic allelochemicals can stimulate IAA oxidase (a peroxidase that acts like an oxidase) activity and influence

endogenous indoleacetic acid (IAA) level (Maighany 2003; Yang et al. 2005). Some of these compounds show antihormonal behavior on gibberellic acids (GA) and abscisic acids (ABA), and some of them accelerate the effect of these hormones (Inderjit and Einhellig 1993; Kohli et al. 2001). Growth inhibition was observed in plants exposed to the high concentrations of ferulic acid. This effect is interpretable by the accumulation of IAA, GA, and cytokinin (CK), as well as simultaneous increase in endogenous ABA (Leslie and Romani 1988; Lin et al. 2001; Soltys et al. 2012). Disruption of hormonal balance is one of the inhibitory effects of allelochemicals, which indicates their effect on plant growth and development. With attention to the fact that hormones are the main factors involved in the regulation of vital genes expression in plants, the effects of allelochemicals on genes expression can be explainable (Wasternack and Hause 2013; Weir et al. 2004; Yang et al. 2005). Although probably allelochemicals have independent effect on gene expression, few studies have looked at the nature of their potential receptors, receptors location, and the components of involved signal transduction pathway. It seems that allelochemicals instead of directly affecting gene expression promote the allelopathic process by acting on macromolecules such as enzymes (through or without a physical connection) (Inderjit and Einhellig 1993; Yang et al. 2005). Plant hormones are also involved in the allelopathic activity, and their effects on this phenomenon can be examined in several general modes as follows:

1. Hormones are regulators of growth and development and can impact allelopathic phenomenon by affecting the differentiation of tissues (Maighany 2003; Yang et al. 2008). Specific cell differentiation, size, position, cell wall structures, and so on are the some results of hormonal balance, which in turn affects the type and amount of specific allelochemical effect on each tissue (Liu and Hu 2001; Soltys et al. 2012).

2. Plant hormones by affecting the biosynthesis of secondary metabolites, which are also allelochemicals produced mainly from these biosynthesis pathways, regulate the concentration of these compounds in plants. Jasmonate is an example of these hormones (Maighany 2003; Wasternack and Hause 2013). Jasmonate regulates synthesis of several compounds such as nicotine, anthocyanins, artemisinin (quinine), and glucosinolates through the COI1/JAZ pathway. More interestingly, the biosynthesis of vinblastine, an allelochemical produced in *Catharanthus roseus* L. cells, is a jasmonate-dependent pathway (Wasternack and Hause 2013).

3. A number of plant hormones are directly and without intermediation involved in allelopathic interaction. On the other hand, some hormones or their derivatives fall into the allelopathic group. Jasmonates and salicylates, especially methyl derivatives, and derivatives of brassinosteroids such as 24-epibrassinolide and 28-homobrassinolide and ethylene (Grana et al. 2013; Leslie and Romani 1988; Peterson et al. 2002; Wasternack and Hause 2013) are well-known examples.

4. Some plant hormones, such as jasmonates, affect the biosynthesis of allelochemicals as well as themselves are the allelopathic compounds as well (Maighany 2003; Wasternack and Hause 2013).

17.5.6 Effect on the Function and Activity of Enzymes

Allelochemicals can affect the synthesis, functions, contents, and activities of various enzymes (Einhellig 1995; Rice 1984; Sunar et al. 2013; Liu and Hu 2001). Many allelochemicals were introduced as inhibitor or stimulator of different enzymes such as auxin oxidase, amylase, invertase, cellulase, polygalacturonase, pepsin, succinate dehydrogenase, phenylalanine ammonia lyase (Einhellig 1995; Gu et al. 2009; Maighany 2003; Rice 1984; Sunar et al. 2013; Liu and Hu 2001), polyphenol oxidase (Haddadchi and Gerivani 2009), CAT (Ahrabi et al. 2011; Dehghani et al. 2014; Haddadchi and Gerivani 2009; Xiao-Jun et al. 2013) proteinases, SOD (Haddadchi and Gerivani 2009; Xiao-Jun et al. 2013), dehydrogenase, POD (Ahrabi et al. 2011; Dehghani et al. 2014; Haddadchi and Gerivani 2009), and decarboxylase (Maighany 2003). In some cases, some allelopathic compounds, mainly phenolic compounds, act as a cofactor for certain enzymes and by changing in the activity of the enzymes leading to physiological and morphological changes in target plants (Haddadchi and Gerivani 2009). One of the most important enzyme complexes affected by the allelopathic phenomenon is the H^+-ATPase in the plasma membrane. The remarkable point is that impairment in the function of this enzyme ultimately causes a change in the physiological pH and also affects the activity of other enzymes. In addition to cellular homeostasis, maintaining the integrity of the membrane and, consequently, transferring the nutrients from the width of the cell membrane is largely dependent to the activity of this enzyme complex (Inderjit and Einhellig 1993; Kohli et al. 2001; Maighany 2003; Singh et al. 2001). Membranes are one of the most important cellular components, and maintaining intracellular homeostasis depends on maintaining the membrane integrity of the cells. Often, allelochemicals (like phenolic compounds) cause membrane depolarization, which isn't irrelevant to the activity of the plasma membrane's H^+-ATPase pump (Ahrabi et al. 2011; Inderjit and Einhellig 1993; Maighany 2003).

Recent studies have shown that nitrate reductase enzyme activity is reduced in plants exposed to allelopathic stress (Kohli et al. 2001; Singh and Sunaina 2014; Zhou et al. 2010), which is probably one of the reasons for the decline in crop growth under such conditions. Also studies have revealed that some allelopathic compounds inhibit glutathione synthetase activity, either through effect on folding or role in reducing the substrate (ATP) of this enzyme, and led to amino acids accumulation, reduction of the redox potential of antioxidant system, and the decline nitrogen fixation at the nitrate reductase level (Ma 2005).

17.5.7 Effect on Photosynthetic Pigments

Reducing leaf chlorophyll content is a general response of crops to allelochemicals, which is, probably, the result of cell damage. It is not clear that the decrease in chlorophyll content is due to its higher degradation or the reduction of synthesis, but it is a phenomenon that occurs during the allelopathy (Borella et al. 2014; Dehghani

et al. 2014; Maighany 2003; Singh and Sunaina 2014). According to the chlorophyll pigment anchored to the membrane (with the phytol intermediation), it seems that disrupted membrane integrity accelerates its turnover. In addition, free radicals produced by allelochemical during oxidative stress can attack on macromolecules such as chlorophyll and cause them to degrade.

Plant carotenoid concentration shows a dramatic increase in response to allelopathic stress. This increase appears to be due to increased activity of the xanthophyll cycle which is involved in removing of free radicals and is one of the mechanisms involved in oxidative stress resistance (Ahrabi et al. 2011; Dehghani et al. 2014; Kohli et al. 2001). In addition to the change in the content of photosynthetic pigments, the plants' anthocyanin pigment content increases in response to the allelopathic stress. Carotenoids and anthocyanins are the antioxidant compounds with low molecular weight that exhibit increased concentrations under other stress conditions such as water stress, heavy metals toxicity, and so on (Ahrabi et al. 2011).

17.5.8 Effect on Photosynthesis

The direct impacts of allelochemicals on plant photosynthesis mainly are inhibition and/or damage to the photosynthesis apparatus and accelerating the decomposition of photosynthetic pigments. Moreover, alteration in chloroplasts' structure, decreasing in photosynthetic pigment contents, decline in energy and electron transfer due to reducing ATP synthesis activity, and decreasing in stomatal conductance and transpiration rate can indirectly influence plant photosynthesis (Meazza et al. 2002; Wu et al. 2004; Yu et al. 2003, 2006). Main effect of allelochemicals on photosynthesis is influencing the function of PSII (Wasternack and Hause 2013; Wink and Latzbruning 1995; Sunmonu and Van Staden 2014; Achigan-Dako, et al. 2014). Studies show that the D1 subunit of this photosystem is highly susceptible to the allelochemicals, which are directly or indirectly destructed by increasing the concentration of free radicals in the photosynthetic space. Given that this protein is the first electron emitter to the electron transport chain, its disruption can disrupt the entire system (Gonzalez et al. 1997; Shao et al. 2009; Uddin et al. 2012). Failure in transferring of electrons in such conditions leads to the production of ROS. Studies show that allelopathic compounds can also affect photosynthesis by interfering with the signal transduction pathways of hormones such as ABA (Inderjit and Einhellig 1993; Maighany 2003; Weir et al. 2004). Despite the decrease in photosynthesis, the concentration of soluble sugars increases under allelopathic stress, which can be due to the growth decline. Generally, growth is affected under stress conditions before photosynthesis, and its reduction leads to decline in demand for carbon skeletons, resulting in artificial increase in the concentration of soluble sugars (Dehghani et al. 2014).

17.5.9 Effect on Respiration

Allelochemicals affect plant growth by influencing various stages of respiration, such as electron transfer in the mitochondria, oxidative phosphorylation, CO_2 generation, and ATP synthesis enzyme activity. Some allelochemicals can reduce oxygen intake, prevent NADH oxidation, inhibit or reduce ATP synthesis in the mitochondria, disturb plants' oxidative phosphorylation, and ultimately inhibit respiration (Abrahim et al. 2003a, b; Cruz Ortega et al. 1988; Hejl and Koster 2004a, b; Inderjit and Einhellig 1993; Pruvis 2000). The extracts from pollen grains of grasses cause the mitochondrial electron transfer chain to be inhibited. Studies show that the specific inhibition site was most likely located upstream of cytochrome C (Cruz Ortega et al. 1988). Alpha-pinene is a compound in pine resin which inhibits the coupling between oxidative phosphorylation and electron transfer, so that electron transfer does not lead to ATP production and finally causes disruption in the respiration metabolism (Hejl and Koster 2004a, b; Rasmussen et al. 1992). Although the main effect of allelopathic compounds on respiratory metabolism is inhibition of the electron transfer chain, in some studies, the role of these compounds in inhibition of the ADP transport complex as well as the reduction of the mitochondrial membrane potential has been demonstrated (Abrahim et al. 2003a, b).

17.5.10 Effect on Water Relations and Mineral Nutrition

Almost all of the allelochemicals have an effect on the absorption of nutrients through the roots. They can induce water stress and reduce availability of water and nutrients in the agronomic plants. Studies reveal that, under allelopathic stress condition, increasing in ABA level changes the plant's water relations and, consequently, ion uptake due to decreasing in stomatal opening (Inderjit and Einhellig 1993; Maighany 2003). Allelopathic compounds affect the H^+-ATPase pump in the plasma membrane which is involved in the uptake and transport of vital ions from the membrane, resulting disturbance in the ions uptake such as K^+, Na^+, and the other ions (Kohli et al. 2001; Maighany 2003). Some allelochemicals such as ferulic acid cause interference with the uptake of phosphates, nitrates, and sulfates and stimulate the inactive outlet of phosphate from the plants' root (Ahrabi et al. 2011; Bradow and Connick 1987). In addition, certain compounds likes ferulic acid, sorgoleone, syringic, and umbelliferone disrupt Ca^{2+}, Mg^{2+}, Fe^{2+}, and Cl^- uptake (Yu and Matsui 1997; Yu et al. 2003). Studies have shown that allelochemicals affect ion uptake often by altering membrane permeability and the proton pump activity. In addition, according to involvement of active process in ion uptake, decline in the energy levels of cells under stress conditions isn't ineffective in this subject (Hejl and Koster 2004a, b; Lv et al. 2002). Allelochemicals, such as cinnamic acid and p-hydroxybenzoic, strongly inhibit the activities of root dehydrogenase, root-combined ATPase, and nitrate reductase, thus inhibiting the root uptake of K^+, NO_3, and H_2PO_4 and nitrate assimilation (Yuan et al. 1998; Lv et al. 2002). Decline in the molybdenum absorption during allelopathic stress has also been reported, which can be one of the factors leading to reduction in

nitrogen fixation in legume plants (Barros et al. 2014). It is often argued that the allelopathic compounds do not lead to accumulation of specific ions in the plants, but nitrogen accumulation in the amaranth plant is controversial (Inderjit and Einhellig 1993; Khalaj et al. 2013; Weir et al. 2004).

17.5.11   Effect on Biosynthesis and Metabolism of Proteins and Nucleic Acids

Alkaloids are the important compounds involved in the allelopathy phenomenon. Due to similarity of some alkaloids to the DNA structure, they can enter the DNA structure and increase the optimum temperature of DNA strand denaturation. Some of them can inhibit DNA polymerase I and prevent the transcription and translation of DNA, whereas other alkaloids can inhibit protein biosynthesis (Wink and Latzbruning 1995; Sunmonu and Van Staden 2014; Achigan-Dako et al. 2014). Most allelochemicals can alter the absorption and transfer of amino acids in relation to the proteins synthesis and challenge the cells' growth (Abenavoli et al. 2003). All phenolic acids have the potential to affect the integrity of DNA and RNA. This suggests that the allelopathic effects are the result of all interactions of the allelopathic compounds with their main goals in the cells such as DNA, RNA, proteins, and other processes associated with them (Xiao-Jun et al. 2013; Li et al. 2010; Mahmood et al. 2013). Investigating the gene expression profile in the plants exposed to allelopathic stress has shown that allelochemicals can be involved in one of the following pathways (Golisz et al. 2008): (1) response of plants to the environment, (2) intracellular placement, (3) in the activity of proteins as inhibitors or cofactors, (4) cell protection from toxins, (5) defensive responses, and (6) metabolism.

Generally, plants display similar responses to nonbiological and biological stresses, including allelopathic stress. This suggests that allelopathic compounds have similar cross-talking in signal transduction pathways with biotic and abiotic stresses, for example, in the production of free radicals (Baerson et al. 2005; Bais et al. 2003; Golisz et al. 2008, 2011). Recent finding shows that the allelochemical affects the expression of psbA, mcyB, prx, and faab (Shao et al. 2009). Cyanamide is an allelochemical that alters the expression of the expansin genes, LeEXPA9 and LeEXPA18, which are responsible for cell wall remodeling after cytokinesis (Soltys et al. 2012). Recent studies revealed that the role of allelochemicals in the expression of miRNAs, which have a role in plant hormone signal transduction, p53 signaling pathways, nucleotide excision repair, and the peroxisome proliferator-activated receptor (Fang et al. 2015).

In the allelopathic interactions, receiver plants' responses to allelochemicals produced by donor plants are important viewpoint. The largely receiver plants will response (or react) to the donor plants by induction of the changes in gene expressions. The upregulated expression of phenylalanine ammonia lyase (PAL), cinnamate-4-hydroxylase (C_4H), ferulic acid 5-hydroxylase (F_5H), and caffeic acid O-methyltransferases (COMT) was observed in the plants that exposed to the allelopathic stress (He et al. 2012a, b).

17.5.12   Effects on Lipids' Prevalence

Lipids are the most abundant component of the cell membranes and play a key role in the resistance of plant cells to environmental stresses. Allelopathic stress and its related compounds not only decrease the membrane integrity by lipid peroxidation but also reduce the amount of unsaturated fatty acids by decreasing the activity of desaturase enzymes. Decline in unsaturated fatty acids of the cells reduces fluidity of the membrane and increases its sensitivity to the low and high temperatures (Dos Santos et al. 2008; Rasmussen et al. 1992). Studies have shown that the prevalence of fatty acids such as palmitic, stearic, and oleic acid is increased and prevalence of linoleic and linolenic acid is reduced. It seems that the lipid saturation is targeted in the allelopathic action, which is very destructive to the activity of chloroplasts (Dos Santos et al. 2008; Maighany 2003).

17.5.13   Morphological and Anatomical Effects

Studies show that allelochemicals prevent seed germination of different species and lead to decline in seedlings' viability (Haddadchi and Massoodi Khorasani 2006; Maighany 2003; Dayan et al. 2009). Some of the allelopathic compounds, such as colchicine, cause irregularities in the process of cell division and also change the rate of division (Inderjit and Einhellig 1993). Some of them cause damage to cell walls through interruptions in the function of biosynthesis enzymes and interfering in the pathway of the hormonal signals that are involved in the biogenesis of the cell wall (Haddadchi and Gerivani 2009; Inderjit and Einhellig 1993). The loss of organelles organization, the increase in the number of vacuoles, and the appearance of fatty grains, which are the result of a decline in metabolism, are the other anatomical effects of allelochemicals at the cellular level; that final results are observable on the whole plant (Inderjit and Einhellig 1993). The plants treated with allelochemicals show varied morphological differences with the control plants from early stages of seedling growth. Most important differences include the induction of short roots with brown apexes, reduction in the growth rate of seedlings, reduction of root and shoot length, and seedlings' etiolation. Some of these effects are very intense that the plant is unable to survive and dying during the seedling stage. Some of the effects are also moderate and don't cause a quick death of the plant, but it reduces the power of survival and competition potential of the plant as well as its power for reproduction (Dayan et al. 2009; Shao-Lin et al. 2004).

17.5.14   Effect on Microorganisms and Ecological Relationships

Researchers believe this fact that there are significant relationships between crop growth and soil microbe's during allelopathic stress (Bais et al. 2006; Barazani and Friedman 1999; Mishra et al. 2013). Indirect effects of allelopathy can be

more important than its direct effects through the mediation of the soil microorganisms (Zeng 2014). After the release of allelochemicals from the donor plant, a cascade of chemical and photochemical reactions occurs that are determinant in fate of the allelopathic phenomenon. Microorganisms are the main factors of this cascade and placed downstream of allelopathic effects, and also they are the one of the main goals of the allelopathy (Huang et al. 2013; Li et al. 2002; Stinson et al. 2006; Abenavoli et al. 2003; Dayan et al. 2009). Allelopathic phenomenon can have a negative effect on the growth and development of agronomic plants as well as elements' availability in soil, indirectly by impact on soil microflora (Macias et al. 2003). The association of many soil microorganisms with crops can have positive consequences. Among them, the symbiotic relationships and increasing tolerance of environmental stresses by microorganisms can be pointed out. Allelopathic compounds, by changing the balance of microorganisms in the soil and by reducing the beneficial microflora for plants, can give opportunity to pathogenic microorganisms to act in the rhizosphere (Mishra et al. 2012). Allelochemical such as some lactones and sulfide compounds have antibacterial effects (Chadwick et al. 2013; Khan et al. 2011).

The impact on microorganisms is only a small part of the effects of an allelopathic interaction on ecosystems and ecological relationships. Allelopathic compounds by affecting on physiological and morphological traits of plants alter their responses to environment as well as their ecological behaviors (Fernandez et al. 2013). Changing in the pattern and frequency of flora is another effect of the allelopathy phenomenon on ecological level. The change in the ecological patterns of plants is one of the results of allelopathic interaction. Studies showed that the ecological effects of this phenomenon can lead to balances in the population of plants and microorganisms, the control of pests in natural and agronomic environments, and diversity in the flora, fauna, and the microflora in different regions. In fact, allelopathy is a phenomenon that has been created during evolution and was chosen through natural selection. On the other hand, allelopathy is one of the evolutionary tools of natural selection, which is more sensible about plants and affects many aspects of their evolution (Field et al. 2006; Inderjit and Einhellig 1993; Inderjit et al. 2011; Kohli et al. 2001; Weir et al. 2004; Abenavoli et al. 2003; Chou 1999; Anaya 1999; Zheng et al. 2015).

17.6 Plants' Responses and Resistance to Allelopathic Stress

Crops have mechanisms in order to resistance against allelopathic compounds that generally include toxins' tolerance or neutralizing them. In contrast to soil's phytotoxins that produce by deep roots, toxins are mostly absorbed and trapped in the surface layers of soil by colloids. By this manner, the plants will also protect themselves from their allelopathic compounds (auto-toxicity) (Chou 1999; Anaya 1999). Tolerance of plants to allelochemicals can be associated with several mechanisms as follows (Kohli et al. 2001; Maighany 2003):

1. Toxins secretion to the surface of the roots or leaves.
2. Compartmentation of toxins in the apoplasts, vacuoles, and cell walls to eliminate toxic compounds from active cell metabolism centers. If these sites are saturated, the concentration of allelochemicals in the cytoplasm increases rapidly.
3. Establishment of allelochemicals in the trichomes for secretion.
4. Establishment of allelochemicals in the cytoplasm.
5. The allelochemicals detoxification, which can be initiated or induced depending on the plant species.

All defense mechanisms of plants against allelopathic toxins have three steps. The first step is a metabolic attack on toxins, which occurs through molecular hydroxylation and dealkylation and increases the polarity of the molecules. The second step is detoxification of allelochemicals through conjugation with sugars, amino acids, and malonic acid, which increase the solubility of these compounds in the water. Finally, the third step is when the compounds are transferred to storage compartment such as vacuoles and cell walls or secreted to the plant surface. In fact, the overall goal of these three steps is to increase the solubility of toxic compounds in water for facilitation of compound secretion from the cells, which can also include excretion into the vacuoles (Chou 1999; Anaya 1999; Kohli et al. 2001; Maighany 2003).

Some crops are able to enter external allelochemicals into the secondary metabolites' pathways. This ability depends on the plant species and the type of allelopathic compounds in the environment. For example, the cucumber increases the lignin biosynthesis in the presence of ferulic acid in its growth medium. However, this plant is sensitive to other phenylpropanoids (Dos Santos et al. 2008). Ultimately, all of these pathways lead to the production of compounds that accumulate in the apoplast or vacuoles (Maighany 2003).

17.7 Soil and Fate of Allelochemicals

The amount of allelochemicals added to the soil depends on the plants' biomass and density as well as concentration of released compounds and the solubility in the soil (Maighany 2003; Vidal and Bauman 1997). Allelopathic compounds are removed from the soil by leaching, chemical processes, microorganisms decomposing, and absorption by plants. The degree of allelochemicals' influence severity depends on the distance from origin and time of transfer of these compounds in the soil. So that, reducing the distance and transfer time increases the effectiveness level, although some allelopathic compounds also become toxic for longer time (Inderjit and Einhellig 1993; Vidal and Bauman 1997). After entering of the allelochemicals into the soil, different fates are awaiting them as follows (Inderjit and Einhellig 1993; Kohli et al. 2001; Gimsing et al. 2009; Maqbool et al. 2013; Narwal 2000):

1. Maintenance on the soil due to allelochemicals' absorption by the colloids. Therefore, the content of colloids in soil is determinant factor for allelochemicals' accumulation in soil.

2. The transformation that occurs mainly by microorganisms intermediation. Initially, allelochemicals are active and toxic in soil, but that concentration and subsequently toxicity gradually reduce because of degradation by microorganisms. An example of the microorganism's intermediation effect on the allelopathic action is the absence of the allelopathic effect of benzoxazinones in the sterile soil.
3. Some allelochemicals are also reaching to receiver plant or away from it during the transfer phenomenon.

In addition to the interaction between allelochemicals and soil microorganisms, other soil characteristics also are effective on the allelopathic phenomenon (Soltys et al. 2013; Maighany 2003). In many studies, it has been observed that the allelochemicals' affectivity and toxicity are depending on soil texture. Allelopathic compounds in sandy soils show a more inhibitory effect than clay soils which is due to lower absorption rate by soil particles and higher amount in the soil solution (Kohli et al. 2001; Maighany 2003; Singh et al. 2001). pH, organic carbon, and cations' concentration also are affective on the absorption rate of allelochemicals in the soil. Accordingly, the absorption of these compounds increases with increasing the amount of organic matter and multivalent cations. In addition, higher soil organic matter generally leads to increase in soil microbial activity (Inderjit and Einhellig 1993; Kohli et al. 2001; Vidal and Bauman 1997) that can be an effect of allelopathic phenomenon.

17.8   Allelopathy and Environmental Stresses

17.8.1 Drought Stress

Studies have shown that during drought stress, allelopathic potential of plants increases. This phenomenon not only is a result of an increase in the amount of released toxins but also depends on the increase in their concentration in the soil due to lower water content and diminished activity of microorganisms. Under drought stress, the growth and development of crops is reduced, and the size of the plants becomes smaller, which is a resistance mechanism in order to reduce water wastage (Inderjit and Einhellig 1993). Studies have shown that there is an inverse relationship between plant size and allelochemicals' concentration. On the other hand, reducing the size of the plant, which is affected by the decline of plant water content, increases the concentration of allelochemicals. Generally, the drought stresses accelerate the allelopathic phenomenon from either donor or receiver plant viewpoint (Kohli et al. 2001). Allelopathy in desert ecosystems appears to be more severe due to its dryness, limited sources of nutrients, and the increased toxicity of compounds due to the low activity of microorganisms. Studies showed that in most cases, allelopathic effects are higher in dehydrated conditions and decrease with increasing water. The reason of this finding is that drought conditions increase secondary metabolites' production and accumulation in plants, while no significant increase in the concentration of these compounds was observed during flooding condition (Einhellig 1995, 1996).

There is a bilateral relationship between allelopathy phenomena and drought stress so that allelopathy can induce drought stress condition in the soil (Maighany 2003). Low soil humidity is due to the dehydration of the soil or the increasing of water absorbent compounds in the soil. The allelochemicals decrease the water potential of soil by increasing the osmotic pressure and suction power of the soil, leading to induction of pseudo-drought or physiological drought (Cheema and Khaliq 2000; Cheema et al. 2004; Maighany 2003).

17.8.2 Deficiency and Toxicity of Nutrients

The effect of nutritional deficiencies and toxicity on the phenomenon of allelopathy has been studied. Donor plants that are subjected to nutrient deficiencies, especially nitrogen, show a significant increase in allelochemicals concentration (Inderjit and Einhellig 1993). It is predictable that the lower availability of nutritional elements will enhance the allelopathic action. Donor plants increase the amount of toxic compounds as well as their releasing rate to the environment in order to control conditions in their favor such as elimination of competitors (Geng et al. 2009; Maighany 2003). Adding fertilizer to agricultural fields is a new way to reduce the allelopathic interactions, although the use of the fertilizer has its own special complexity and is associated with the considerations (Sodaeizadeh and Hosseini 2012). Studies have shown that after removing of nutrient deficiency stress, donor plants resume their growth and development faster than other plants. This is because donor plants can use allelochemicals as a nutrient chelator. Secondary compounds such as phenolic compounds are able to bind metal elements such as iron (Kohli et al. 2001).

Interestingly, under the influence of nutrient toxicity, target plants are less affected by allelochemicals. It seems that growth slows down in these conditions, and consequently decreasing demand for sinks reduces the uptake of allelochemicals from the environment (Einhellig 1995, 1996). Some allelochemicals also interfere with the nutrient uptake, causing pseudo-deficiency or pseudo-toxicity. These compounds mainly including phenolic compounds, such as chlorogenic acid, which in treated plants with this compound, nitrogen accumulation and its toxicity symptoms are observed. Nitrogen toxicity is one of the stresses rarely seen in certain environments; however, it is inducible by allelopathic action (Einhellig 1995; Inderjit and Einhellig 1993; Khalaj et al. 2013).

17.8.3 Temperature Stress

There is a direct relationship between the increase in temperature and the production of allelochemicals in plants. Temperature stress increases the amount of production and even releasing of these compounds (Maighany 2003). Studies have shown that under full sunlight in midday, growing seedlings are affected by a lower concentration of allelochemicals. Therefore, a donor plant is more successful to produce and release allelopathic compounds into the environment during this period. Significant

temperature increase in the midday and its effect on the temporary water deficit are benefits for donor plants, and these plants with the least energy go through the allelopathic phenomenon (Inderjit and Einhellig 1993; Kohli et al. 2001).

Increasing temperature is one aspect of temperature stress. However, reducing the degree of environment temperature also is another aspect of temperature stress. Reducing the temperature induces the synthesis of allelopathic compounds. For example, in response to temperature drop, the tobacco plant increases the chlorogenic acid content in its tissues up to five times. It seems that in addition to electron utilization in biosynthesis of these compounds which can reduce production of ROS, in such situations, allelochemicals' production play a protective role (Einhellig 1995, 1996).

17.8.4 Light Stress

Investigations have shown that in the adverse light conditions, receiver crops are more affected by allelopathic phenomenon (Einhellig 1995, 1996). The effect of light on the allelopathy is considered to both in terms of quantity and quality of light spectrum (Maighany 2003). Increasing of light flow increases the concentration and toxicity of allelopathic compounds (Bhowmik and Doll 1982). Studies have shown that the quality of light in the environment is much more effective than its quantity so that the treatment of seeds of donor plants such as sorghum with gamma rays considerably increases the allelopathic outflow from the mature plant roots (Einhellig 1996). The cause of this phenomenon is still unexplained. Ultraviolet rays also increase the concentration and toxicity of phenolic compounds in plants. It has been observed that in the presence of high quantity of ultraviolet in the light spectrum, more toxic phenolic compounds are produced in plants, which are likely to produce very low under normal conditions (Inderjit and Einhellig 1993; Maighany 2003). It seems that the length of the light period is also very effective, but the available reports do not give a logical and general conclusion (Kohli et al. 2001). Therefore, the conclusion in this regard requires more extensive studies.

Other abiotic stresses such as the presence of ozone molecules in the plants atmosphere, heavy metal toxicity, environmental pH changes, and flooding stress have similar effects (Einhellig 1996; Inderjit and Einhellig 1993; Kohli et al. 2001; Maighany 2003; Narwal 2000).

17.8.5 Biotic Stresses

The causes of disease in crops, such as microorganisms and insects, intensify the phenomenon of allelopathy. These factors make the agronomic plants more susceptible to allelochemicals, and allelochemicals also make the target plants more susceptible to contamination with pathogens (Einhellig 1996). Studies have shown that the presence of allelochemical residues in the environment can increase the infectivity of pathogens such as *Fusarium*, fungus responsible for root rot, and increase the duration of its activity (Odeyemi et al. 2013; Peng et al. 2004; Wu et al. 2015).

Surprisingly, the pathogens' attack increases the concentration of allelopathic compounds in the donor plants, because allelochemicals in such situation act in favor of the donor plants and reduce the damage caused by the pathogens. There are roughly similar reports about insects and herbivores (Einhellig 1995, 1996; Fang et al. 2013).

Important point in this context is the impact of allelopathic phenomenon on the symbiotic relationship between crops and microorganisms. Symbiotic microorganisms often don't show pathogenicity to host plants. The presence of donor plants in the environment of symbionts, especially the mycorrhizal symbiont, makes fungus to change their strategy and compete for nutrient sources with the host plants and subsequently act as parasitic microorganisms for the host plants. Eventually, the elimination of fungus by the host plant from the environment and the lack of this symbiosis make the host plant more susceptible (Einhellig 1995, 1996). The reason for the occurrence of such a phenomenon is still not well clear. On the other hand, there are reports that the presence of phenolic allelochemicals in the rhizosphere of leguminous plants causes a disturbance on their symbiosis with rhizobium. Studies shown that the primary response of rhizobium to plant-produced phenolic compounds is impaired (Bais et al. 2006; Cheng 2012; Zhou et al. 2010). In addition to adverse effects of the microorganisms present in the rhizosphere of receiver plants, some of these organisms have a positive effect on plants under these conditions. Some microorganisms can use allelopathic compounds as carbon sources (Mishra et al. 2012; Mishra and Nautiyal 2012); therefore, these compounds are decomposed and eliminated from the allelopathic cycle.

17.9 Allelopathy and Herbicides

Although the presence of herbicides in ecosystems in the old perspective is an abiotic stress, herbicides are not a natural ecological factor and are often artificially added into the ecosystems by human activities. Therefore, studying their impacts on the allelopathic phenomenon in a separated study field would be more appropriate.

Although allelopathic compounds and herbicides have different origins, the probability of the presence of both is very high particularly in the arable systems (Guillon 2003). Many studies have shown that allelochemicals and herbicides have synergic behavior, despite of their different physicochemical characteristics. Increasing allelopathic effects during co-application of allelochemicals and herbicides has been observed in numerous bioassays, such as synergic activity of atrazine-ferulic acid and fluraline-salicylic acid (Einhellige 1996; Guillon 2003; Nawaz et al. 2014; Ihsan et al. 2015). Therefore, if a donor plant (especially a weed) has a resistance to herbicides, the use of these toxins is not only beneficial for crops' production, but also exacerbates its allelopathic potential.

In addition to collaboration of herbicides with allelopathic compounds, studies have shown that herbicides also stimulate the production and releasing of allelochemicals from donor plants so that the treatment of donor plants with herbicides such as 2,4-D and glyphosate increases the concentration of allelochemicals in these

plants (Einhellig 1995, 1996). There are various reports of increased synthesis of secondary metabolites during treatment of plants with low concentrations of herbicides (Inderjit and Einhellig 1993; Kohli et al. 2001; Maighany 2003).

17.10 Allelopathy Genetics

Allelochemicals are produced by biological systems so that their biosynthesis is controlled by genes. Therefore, the study of allelopathy genetics in order to introduce effective varieties for allelopathic interactions is completely unavoidable (Duke et al. 2001; Haddadchi and Gerivani 2009; Maighany 2003). Unlike to the numerous challenges in assessing the allelochemicals inheritance, few studies in the field of genetics are available. Some of these challenges are as follows (Inderjit and Einhellig 1993; Kohli et al. 2001; Maighany 2003):

1. Difficulty in isolation, purification, and determination of allelochemicals due to the lack of advanced chemical techniques.
2. The difficulty of studying allelopathic inheritance due to the interference of several genes in their biosynthesis and the variation in the type of compounds as well as biochemical pathways for biosynthesis of them.
3. The absence of a linear relationship between the production of allelochemicals in a particular tissue and the tissue's allelopathic potential.
4. Control of the production and release of allelopathic compounds by regulating genes that are controlled by ecological factors. Consequently, different allelopathic behavior appears in different environments.
5. Information about molecular biology being limited for chemical structure and biosynthetic pathway of known compounds.
6. The difficulty of discovering genes associated with biosynthesis of allelochemicals due to the high specificity of these genes.
7. Complexity of identification of enzymes involved in the biosynthesis of allelopathic compounds due to the low abundance of these enzymes in the enzymatic set of plants.
8. The difficulty of sequencing and even the production of antibodies for the mentioned enzymes due to failure to isolate and purify sufficient amounts of enzymes.

Already, various methods have been tested by scientists to track the genetics of allelopathic interaction such as different mutagenic methods, the use of donor cells' mRNAs, immunoblotting techniques, and so on (Duke et al. 2001; Haddadchi and Gerivani 2009; Inderjit and Einhellig 1993; Kohli et al. 2001; Maighany 2003; Abenavoli et al. 2010; Chou 1999; Anaya 1999). Among all of these methods, mutagenesis by transposons in the donor plants tissues and, thereafter, the differential screening of mutated and wild-type cells have been effective and provide valuable results. The basis of this method is based on the existence of two cell groups that are the same in all traits and only differ in the allelopathic behavior (Duke et al. 2001).

The production and subsequently isolation of cells that are only mutant in the genes involved in the allelopathy phenomenon is a very difficult, laborious, time-consuming, and costly process, which are the major disadvantages of this method (Maighany 2003; Abenavoli et al. 2010; Chou 1999; Anaya 1999).

Today, an improvement in the practical issues of plant biotechnology has contributed to a better understanding of the allelopathy heredity. Studies have shown that the allelopathic phenomenon, like all other quantitative traits, is controlled by QTL (quantitative trait locus) genetic factors. Hence, genetic markers such as RAPDs, RFLPs, AFLPs, SCARs, and SSRs can provide beneficial information for the allelopathic traits (Kohli et al. 2001). This subject has revealed the exploring mystery of allelopathic genetics in the not too distant future. The launch of a massive plant genomic decoding program over the past few decades will undoubtedly be a great help in realizing this.

17.11 Allelopathy and Biotechnology

The yield of crop plants is very important in food production on the earth planet. Crops are always exposed to pathogens and parasites that ultimately reduce yield and lead to problems for farmers to keep them. Yearly, large quantities of poisons are used as herbicides, fungicides, insecticides, and so on in agricultural lands. Apart from the economic costs of production, these compounds are toxic substances that impose irreparable effects on the environment and are also hazardous to humans and livestock, the main consumers of crops. During the last two decades, allelopathic compounds have been regarded as biological compounds with anti-pathogen and anti-parasite effects. Studies showed that most plants have potential for allelochemicals' production, but crop plants mainly lost these characteristics during plant breeding for selection of desirable traits (Anaya 1999; Bhadoria 2011; Inderjit and Einhellig 1993; Kohli et al. 2001; Abenavoli et al. 2010; Chou 1999; Soltys et al. 2013). Nowadays, scientists tried to isolate the allelochemicals' genes from wild species or even microorganisms and inserted them into the crops by using traditional methods of plant breeding and recombinant DNA technology and genetic engineering. As a result, keeping of crops was more easily, reducing keeping costs and preventing the entering of hazardous and toxic substances to the environment (Anaya 1999; Fragasso et al. 2013; Gealy and Yan 2012; Kohli et al. 2001; Mahmoud and Croteau 2002; Kremer 2006; Maighany 2003; Soltys et al. 2013). Production of a resistant transgenic plant and its reproduction can lead to the expansion of the fields of protected crops against various pests.

In recent years, many efforts have been made to produce allelopathic effective wheat cultivars by using QTL traits (Bertholdsson 2004, 2010; Fragasso et al. 2013; Gealy and Yan 2012; Kong et al. 2011). Although no plant has been produced by these traits, it seems that in the near future, this important issue will come true.

Despite all the advantages of producing allelopathic cultivars, the actual use of these plants is accompanied by the following considerations (Cheema et al. 2013; Duke et al. 2001; Farooq et al. 2013; John et al. 2010): (1) Natural donor plants often have an auto-toxicity potential, but they also have mechanisms to avoid it.

This is because the transgenic crops have necessary genetics potential for being donor, but they lack the ability to avoid auto-toxicity and can damage themselves more than any other one. (2) It is very important to assess the potential risks to humans, especially for plants that have feed usages. Therefore, transgenic allelopathic crops must be evaluated for harm to human health and the environment before transformed. Human health issues include the toxicity of allelochemicals and their metabolism intermediates, the allergenic effects of transgenes into the crops, and their unpredictable metabolic effects, which can reduce the nutritional value of agronomic plants. Another most important risk in this regard is the horizontal transfer of wild-type species genes into crops that can make the recipient species more competitive than other endemic plants. Always must keep cautious in ecological relationship manipulation, because human beings wittingly or unwittingly are components of these relations and affected from. This apply to the use of natural tools such as allelopathic phenomenon is also true.

17.12 Application of Allelopathy in Agronomic Systems

Allelopathy is a natural ecological behavior among organisms particularly plants. It has been known and used anciently in agriculture in many civilizations such as Egyptian and Chinese (Zeng 2008, 2014). Allelochemicals can stimulate or inhibit plant germination, growth, and even development; thus it can facilitate some agronomic aims. They are suitable substitutes for synthetic herbicides because allelochemicals' efficacy and specificity are limited in the environment (Bhadoria 2011; Macias et al. 2003; Zeng 2008). Therefore, allelopathy can be used as tool in agricultural production and reduction of the chemical pesticides usage and consequently environmental pollution and as effective method for the sustainable development of agricultural production and ecological systems (Han et al. 2013; Jabran et al. 2015; Zeng et al. 2008; Macias et al. 2003). Nowadays, application of allelopathic crops in agriculture systems is regarded as components of crop rotations, for intercropping, as cover crops, or as green manure (Cheema et al. 2004; Dhima et al. 2006; Iqbal et al. 2007; Reeves et al. 2005; Singh et al. 2003; Albuquerque et al. 2010; Wezel et al. 2014; Wortman et al. 2013). The application of allelopathy for the improvement of crop productivity and environmental protection by environmentally friendly control of weeds, insect pests, and crop diseases, conservation of nitrogen in crop lands, and synthesis of novel agrochemicals based on allelochemicals has gained much attention from scientists (Haider et al. 2015; Farooq et al. 2011; Khanh et al. 2005; Xuan et al. 2005; Yildirim and Guvenc 2005). Allelochemicals are important components of plant defense mechanisms against weeds and herbivores. Accordingly, allelochemicals' modification for the production of environmentally friendly pesticides and plant growth regulators allows the effective management of agricultural production and makes less environmental problems in the soil due to the high degradability of allelochemicals (Bhadoria 2011; Ihsan et al. 2015; Uddin et al. 2014). Nitrogen leaching is a severe ecological problem in the agricultural systems. Mineralization of soil organic

nitrogen, especially during the nitrification of fertilizer nitrogen, is one of the main reasons for the enrichment of nitrogen in the soil. In recent years, studies have proven that nitrification-inhibiting substances produced by plants are the first choice for soil nitrification management. For example, allelochemicals, such as ferulic acid, p-hydroxybenzoic acid, and hydroxamic acid, can act on soil microbes to inhibit soil nitrification (Abenavoli et al. 2010; Dietz et al. 2013; Ma 2005). Breeding of allelopathic cultivars, which have great potential to minimize the pest damages and effectively control weeds in agronomic ecosystems, represents the most promising application of allelopathy (Fragasso et al. 2013; Mahmood et al. 2013; Weston and Duke 2003). Both traditional breeding methods and transgenic technology can be useful in the breeding of allelopathic cultivars (Gealy and Yan 2012). Despite all efforts, until now, a successful allelopathic crop cultivar has not been obtained, but it will be a good research subject for scientist in the future.

17.13 Conclusion

Although allelopathy has been known in agriculture since ancient times to now, scientists and farmers had less attention to allelopathy as biotic stress, and there isn't enough information about it. Allelopathy is a prevalent stress factor and can affect different aspects of crops growth, development, and yield. Furthermore, allelochemicals can act as environmentally friendly herbicides, fungicides, insecticides, and plant growth regulators and can be most important in the sustainable agriculture. With increasing reliance on organic agriculture and environmental health, increasing attention has been paid to allelopathy research, and the molecular mechanisms of allelopathy are gradually being elucidated as well. It is clear that allelopathy requires advanced techniques and more research for widespread application in agricultural system worldwide.

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Oxidative Stress in Crop Plants

18

Arun Kumar Maurya

Abstract

Abiotic stresses such as drought, cold and high temperature, heavy metals, salinity, UV and ozone exposure, mineral deficiencies, etc. induce a negative influence on the crop production and food security globally through the generation of reactive oxygen species (ROS) and reactive nitrogen species (RNS) in the cells of the crop plants. ROS is an umbrella term which encompasses radical and non-radical products generated by incomplete reduction of oxygen through the enzymatic processes like photosynthesis, respiration, and fatty acid oxidation or by non-enzymatic mechanisms. Oxidative stress shows its effect on almost all component of cell as oxidation of DNA fragment; RNA degradation; oxygenation, modification, and destruction of lipids and proteins; and leakage of ions that causes decline in the growth, development, and productivity of crop plants. Nitric oxide (NO)-derived molecules are referred to as RNS and associated with nitro-oxidative stress. NO is a small, uncharged, free radical, and lipophilic molecule acting as a protective and signaling molecule. Diverse sources are reported for NO generation in plants by enzymatic synthesis involving putative nitric oxide synthase (NOS)-like enzymes, xanthine dehydrogenase/oxidase nitrate reductase, nitrite-NO reductase, as well as non-enzymatic synthesis. Stress conditions induces ROS generation and sometime concomittant increase in NO concentration in plant cells. Both these molecules also present acooperative mechanism in plant cell to counteract the harmful effects of stress. Failing to properly coordinate and balance these two molecules in plant cells affects growth, development, yield, productivity and ultimately survival of plants.

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Abbreviations

AOX	Alternative oxidase
APX	Ascorbate peroxidase
CAT	Catalase
H_2O_2	Hydrogen peroxide
NADPH oxidase or NOX	Nicotinamide adenine dinucleotide phosphate oxidase
NO	Nitric oxide
NOS	Nitric oxide synthase
NR	Nitrate reductase
RNS	Reactive nitrogen species
ROS	Reactive oxygen species
SOD	Superoxide dismutase

18.1   Introduction

In both natural and agriculture conditions, plants are frequently exposed to various types of stress due to their sessile nature. Environmental factors such as temperature (chilling, cold, or heat) can become stressful in just a few minutes or hours, but others may take days to weeks (water/drought) or even months (mineral nutrients or heavy metals) to become stressful. Abiotic stresses such as mineral deficiency, drought, low and high temperature, and UV and ozone exposure all induce the generation of reactive oxygen species (ROS) and reactive nitrogen species (RNS). Plants started facing oxygen at least approximately 2.7 billion years, when they started generating from H_2O, and its level has been constantly rising, which has contributed in the evolution of species (Dowling and Simmons 2009).

ROS is an umbrella term which encompasses radical and non-radical products generated by incomplete reduction of oxygen; radical components include superoxide radical ($O_2{}^{\bullet-}$), hydroxyl radical ($^{\bullet}OH$), alkoxyl radical ($RO^{\bullet}$), and peroxyl radical ($ROO^{\bullet}$), while non-radical components are hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and ozone (O_3). ROS are generated in diverse metabolic pathways as a by-product or from free metals released from enzymes (Gupta et al. 2015). ROS initiates oxidative destructive processes as well as triggers various signaling pathways. Thus, maintenance of non-harmful, appropriate ROS levels might represent a healthy condition in plants.

Nitric oxide (NO)-derived molecules are referred to as RNS and associated with nitro-oxidative stress. RNS are basically a family of molecules produced via the enzymatic as well as non-enzymatic activity in plants as by-products of aerobic metabolism or in response to stress. NO is a ubiquitous intra- and intercellular messenger and one of the key RNS which interact with ROS in various ways and might serve an antioxidant function during various stress conditions (Beligni and Lamattina 1999) (Table 18.1).

Table 18.1 Different types of ROS and RNS generated in plants

Reactive oxygen species		Reactive nitrogen species	
Non-radical	Free radicals	Non-radical	Free radicals
Hydrogen peroxide (H_2O_2) hypochlorous acid (HOCl), ozone (O_3), singlet oxygen ($^1O_2$)	Superoxide ($O_2^{\bullet -}$), hydroxyl ($^\bullet OH$), hydroperoxyl (HO_2), peroxyl ($RO_2^\bullet$)	Nitrous acid (HNO_2), nitrosyl cation (NO^+), nitroxyl anion (NO^-), peroxynitrite ($ONOO^-$)	Nitric oxide ($NO^\bullet$), nitrogen dioxide ($NO_2^\bullet$), nitrate radical ($NO_3^\bullet$)

The harmful ROS molecules are removed from cell system through either enzymatic (superoxide dismutase, catalase, glutathione peroxidase (GPX), peroxiredoxin (Prx), and the ascorbate-glutathione cycle) or non-enzymatic systems (NO, ascorbic acid, glutathione (GSH), carotenoids). ROS also plays a key role in signaling for several cellular processes in response to many abiotic and biotic stresses (Mittler et al. 2011) and shows cross talk with phytohormones, Ca^{2+}, kinases (Petrov and Van Breusegem 2012), and other bioactive molecules like NO.

ROS are best-suited molecules as by-product or signaling molecules' secondary messenger because of their non-toxic levels which can be maintained within normal cell by balancing its generation and scavenging through enzymatic and non-enzymatic process (Mittler et al. 2004). Diverse sources of ROS generation, the mobile nature of forms like H_2O_2, and local as well as distant signaling have been implicated in physiological processes like programmed cell death (PCD), disease resistance, and various types of stress tolerance which are inevitable to be faced by sessile nature organisms like plants.

18.2   ROS Generation in Plants

Many pathways for ROS generation exist in plants involving enzyme-catalyzed processes like photosynthesis, respiration, and fatty acid oxidation or directly through amine oxidase, glycolate oxidase, oxalate oxidase, xanthine oxidase, peroxidases, or non-enzymatic means like excited chlorophyll and metals (Mittler 2002). Apart from these, organelles like chloroplast, peroxisome, mitochondria, and plasma membrane also contribute in ROS generation (Fig. 18.1).

18.2.1 Chloroplasts

Chloroplasts are organelles that transform kinetic energy of the sun into chemicho-potential energy in ATP and NADPH. It is carried out by a specialized subpart of chloroplast known as thylakoids which is also one of the key sources for the ROS generation (Tripathy and Oelmuller 2012). Chloroplasts are contributing a great amount of ROS in the cell in the form of $O_2^{\bullet -}$ and singlet oxygen ($^1O_2$) (Apel and Hirt 2004). In the presence of light, oxygen-evolving complex (OEC) of photosystem II causes the photolysis of water that releases oxygen. But the main site of ROS
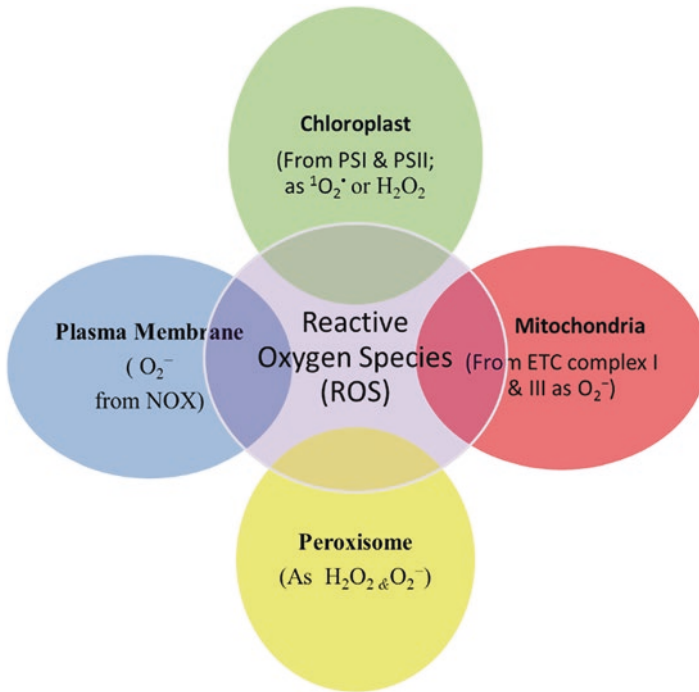
Fig. 18.1 Sources of reactive oxygen species (ROS) in a plant cell

generation is the photosystem I (PSI) because under excessively reduced ferredoxin and low NADP availability, the auto-oxidation of this iron-sulfur protein occurs with the formation of $O_2^{\cdot}$ (Asada 2006). As ROS generation is a normal phenomenon in the chloroplast, the organelle has evolved counteractive strong antioxidant system to eliminate it in normal conditions (Møller 2001). Sometimes, ROS generation in the form of $O_2^{\cdot}$ occurs, and then reduced ferredoxin reacts with $O_2^{\cdot}$ and forms hydrogen peroxide (H_2O_2), which is relatively a mobile form of ROS (Mehler 1951).

Under high light, PSII is involved in ROS production via energy transfer and electron transport. Singlet oxygen is produced by the energy transfer form triplet chlorophyll to molecular oxygen formed by the intersystem crossing from singlet chlorophyll in the PSII antennae complex or the recombination of the charge-separated radical pair in the PSII reaction center. Triplet carbonyls are also formed by lipid peroxidation that transfers energy to molecular oxygen forming singlet oxygen (Pospisil 2016). Additionally, it has been also found that biosynthetic and catabolic intermediates of chlorophyll are photosensitizers that also generate singlet oxygen (Pruzinska et al. 2005).

18.2.2 Mitochondria

In plants, mitochondria are also one of the main ROS production sites. It occurs due to electron leakage from respiratory electron transport chain (ETC) components to O_2 producing superoxide (O_2^-). The free radical (O_2^-) generation sites reside mainly in complex I and complex III of ETC. Both complexes release O_2^- to the matrix of mitochondria, while complex III may also release some O_2^- to the inter-membrane space (IMS). A matrix-localized manganese superoxide dismutase (Mn-SOD) enzyme further converts O_2^- to H_2O_2 (Rinalducci et al. 2008).

Alternative oxidases (AOX) are ubiquitous in the kingdom Plantae (Mcdonal and Vanlerbughe 2006). AOA is an interfacial membrane protein and a cyanide-insensitive metalloprotein located toward the matrix side of the inner mitochondrial membrane (IMM) and coupling the oxidation of ubiquinol to the four-electron reduction of O_2 to water (Vanlerburghe 2013). AOX gets activated when the reduction level of ubiquinone increases. It reduces ATP generation and the energy released is dissipated as heat. Thus, AOX provides a heat-dissipating mechanism useful for certain plant species showing thermogenesis and to prevent the overproduction of superoxide radicals (Gupta et al. 2018). AOX acts to prevent the over-reduction of ETC components that leads to single electron leak and also indirectly controls the synthesis of signaling molecules like H_2O_2, O_2^-, and NO. ROS generation in mitochondria is usually overcome by anti-oxidative system but when it goes beyond control leads to stress, necrosis, and programmed cell death.

18.2.3 Plasma Membrane

Plant membrane-bound nicotinamide adenine dinucleotide phosphate (NADPH) oxidase (NADPH oxidase or NOX) is a transmembrane protein, also known as respiratory burst oxidase homologue (RBOH). The molecular structure of plant NOX shows two parts: (a) membrane-bound respiratory burst oxidase homologue (M.W. 105 to 112 kDa) and (b) its cytosolic regulator Rop (Rho-like protein), which is a Rac homologue of plants. The enzyme protein also possesses regulatory components involving phosphorylation and Ca^{2+} (Ogasawara et al. 2008).

NOX transfer electrons from intracellular NADPH across the plasma membrane before they are coupled to molecular oxygen in the apoplast to produce $O_2^{\bullet-}$, and its subsequent dis-mutation product is H_2O_2. The apoplastic ROS synthesis by plants after pathogen recognition is also a membrane-bound NAPDH oxidase-induced phenomenon (Skelly and Gary 2013).

18.2.4 Peroxisomes

Peroxisomes are asubcellular organellae bound with single membrane involved in diverse functions, namely, the β-oxidation, the glyoxylate cycle, the photorespiration, the ureide metabolism, and the metabolism of ROS and RNS. The peroxisome also contains two marker enzymes catalase and H_2O_2-generating flavin oxidase involved in oxidative metabolism. The peroxisomal membrane is a potential source of ROS in the form of $O_2^{\cdot-}$ through the existence of a small electron transport chain using NADH as electron donor. It is composed of a flavoprotein NADH:ferricyanide reductase of about 32 kDa and a cytochrome b (Schrader and Fahimi 2006). Xanthine oxidase is an FAD-, molybdenum-, iron-, and sulfur-containing hydroxylase enzyme present in peroxisome that uses substrate xanthine and converts into uric acid with the concomitant formation of H_2O_2 and $O_2^{\cdot-}$ (Harrison 2002).

Thus, it is evident that the ROS production in plant cells is limited to apoplast, chloroplasts, mitochondria, and peroxisomes. The ROS level is maintained at a level which is not harmful and can be coped with by plants. But when it exceeds under certain adverse conditions which we call stress, ROS can damage all biological molecules and structures. Therefore, the ability of cells to resist oxidative damage induced by ROS is determined by the strong antioxidant molecules and system operative in plant system.

18.3   Physiological Effects of Oxidative Stress

Oxidative stress affects almost all components of cell, and effects become visible as oxidation of DNA fragment; RNA degradation; oxidation, modification, and destruction of lipids and proteins; and leakage of ions (Farmer and Mueller 2013) that ultimately may lead to necrosis and cell death. Lipid oxidation also known as peroxidation is induced by stress that causes damage of cell membranes and products of it (malondialdehyde (MDA), 4-hydroxyalkenals, etc.) that induces a mutagenic and cytotoxic effect on cell (Dubovskaya et al. 2007). High level of peroxidation causes breakdown of intigrity of cell membrane, lysis of organelles, oxidation and dysfunctions of proteins, DNA and RNA (Halliwell and Gutteridge 2015).

Proteins are modified due to ROS interaction and lose their native structure and become prone for the action of protease (Mehta et al. 1992) or inactivation or fragmentation RuBisCO (Soengas et al. 2018). Proteins are nitrosylated at tyrosine residues by RNS (Corpas et al. 2008), and such nitrosylation is responsible for inactivation of RuBisCO (Abat and Deswal 2009). The only ROS species which directly causes DNA damage is OH·, and its effects visible as oxidation of nitrogenous bases and their modification, breaking the sugar phosphate bonds that ultimately causes chromosome damage. The high levels of ROS inhibit DNA synthesis and cell division, which ultimately leads to cell death (Apel and Hirt 2004) (Fig. 18.2).
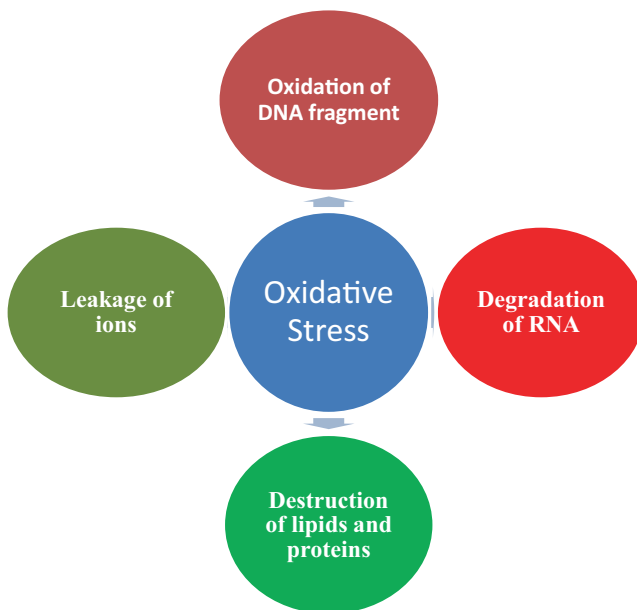
Fig. 18.2 Effects of reactive oxygen species (ROS) in a plant cell

18.4   NO Generation in Plants

NO is one of the key RNS molecules. It is a small, uncharged, free radical, lipophilic molecule acting as a protective and signaling molecule. It has very short life span due to unstable nature (less than 6 s) (Bethke et al. 2004). These features make it able to diffuse within the cell but only a short distance of about 30 microns and to cross plant membranes (Leshem 2001). Diverse sources are reported for NO generation in plants through enzymatic synthesis putative by nitric oxide synthase (NOS)-like enzymes, xanthine dehydrogenase/oxidase, nitrate reductase, and nitrite-NO reductase as well as non-enzymatic synthesis (Gupta et al. 2010) (Fig. 18.3).

18.4.1 Nitric Oxide Synthase-like Enzymes

Nitric oxide synthase (NOS; EC 1.14.13.39) was first identified and described in 1989 in an animal system, and its three isoforms were cloned and purified between 1991 and 1996 (Stuehr 1996; Stuehr et al. 1991). The first X-ray crystallographic structure of NOS domains was published in 1998 and 1999 in humans (Li et al. 1999; Raman et al. 1998). The Nobel Prize was awarded jointly to R. Furchgott, L. Iganarro, and F. Murad in 1998 for the work that led to the discovery of nitric oxide as a signaling molecule produced by mammalian cells.
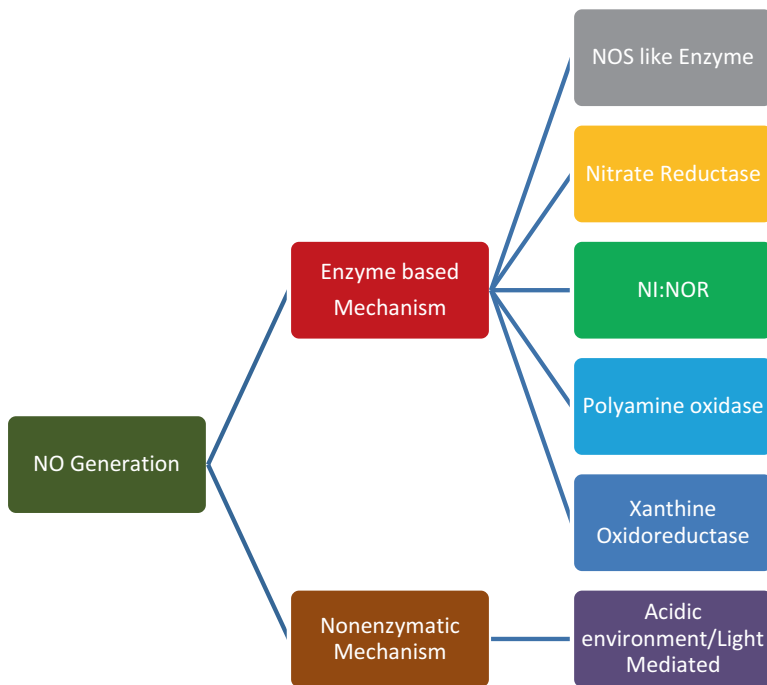
Fig. 18.3 Sources of nitric oxide (NO) within a plant cell

NOS enzyme is a dimer in the active form which contains relatively tightly bound cofactors like tetrahydrobiopterin (BH_4), FAD, FMN, and iron protoporphyrin IX (heme). NOS catalyzes a reaction of L-arginine, NADPH, oxygen to the free radical nitric oxide (NO$^•$), citrulline, and NADP$^+$ through L-hydroxyarginine as an intermediate. NADPH and oxygen act as co-substrate for the enzyme (Knowles and Moncada 1994; Marletta 1992; Nathan and Xie 1994). Electrons are donated by NADPH to the reductase domain of the NOS enzyme and move via FAD, FMN redox carrier of the heme iron, and tetrahydrobiopterin at the active site to catalyze the reaction of oxygen with L-arginine generating NO and citrulline as products.

NOS enzymes responsible for the production of NO in animal systems have an array of physiological roles. It provoked plant biologists to hunt for homologue of NOS enzyme in plants. Plant research initially used anti-NOS antibodies raised against animal NOS. Similarly using mouse anti-NOS from the brain, western blot analysis showed the presence of positive immune reactivity to this protein in yeast and wheat germ (Kuo et al. 1995). The rabbit anti-NOS from the brain used in pea embryonic axis revealed the presence of single band of 105.4 kDa, while in wheat germ, two bands 57.5 and 89.7 kDa were observed (Sen and Cheema 1995). Based on western blot analysis using antibodies raised against mouse macrophage NOS and rabbit brain NOS, a protein band about 166 KDa was detected in soluble

fraction of root tips and young leaves of maize seedling which was capable of converting [U-^{14}C] arginine to L- [U-^{14}C] citrulline.

Later on, immunofluorescence study in the maize showed that NOS protein is present in the cytosol of cells in the division zone and is translocated in the nucleus in the cells of elongation zone of the maize root tips, indicating the existence of a NOS enzyme in maize tissue with the localization of this protein depending on the phase of cell growth (Ribberio et al. 1999).

After sometime plant NOS research shifted to the use of NOS inhibitors, and radiolabelled substrate which was well established in animal system to confirm the presence of NOS activity in higher plants (Ninnemann and Maier 1996) revealed the presence of putative NOS activity in roots and nodules of *Lupinus albus* (Cuteo et al. 1996). In soybean cell extract, NOS activity was found to be calcium dependent and present primarily in cytosolic fraction which was further confirmed by using NOS inhibitor L-NNA, PBITU (Delledonne et al. 1998). NOS-like activity has also been reported in TMV-resistant tobacco, infected with TMV that was inhibited by NOS inhibitor (Durner et al. 1998).

The subcellular presence of NOS in peroxisome and chloroplast from leaves of pea using activity assay in purified intact peroxisomes, a Ca^{2+}-dependent NOS activity has been reported. It showed inhibition by mammalian NOS inhibitor, and revealed the presence of protein band of 130 kDa when immune blot analysis of peroxisome carried out with a polyclonal antibody raised against the C-terminal region of murine iNOS. Electron microscopy immune gold labeling also confirmed the subcellular localization of NOS in matrix of peroxisome as well as chloroplast (Barraso et al. 1999). The presence of NO in peroxisome was further substantiated by fluorometric analysis and EPR using Fe-MGD (Corpas et al. 2001).

Studies in *Arabidopsis* by use of NOS inhibitors suggest the presence of inducible form of NOS (Garces et al. 2001). It was found in *Arabidopsis* that a gene *AtNOS1* encodes a protein involved in NO synthesis and its presence was confirmed by activity assay, inhibitor, mutants, and fluorescent dye (Guo et al. 2003). Later on, it was demonstrated that pathogen-induced, NO-synthesizing enzyme is a variant form of glycine decarboxylase (GDC) from *Arabidopsis*. It is a Ca^{2+}- and CaM-dependent enzyme and appeared to be ~120 kDa (Chandok et al. 2003), but later on concerns about the reliability of the published data led to their retraction (Klessig et al. 2004). Presence of NOS-like protein in various plant systems has been confirmed, but it has also been shown that there is no NOS-like gene homologue in *Arabidopsis* (Butt et al. 2003).

Recently a gene encoding one functional NOS that resembles human NOSes has recently been discovered in the green alga *Ostreococcus tauri* (Mamiellophyceae, Chlorophyta) (Foresi et al. 2010). Further, in silico study has revealed that NOS-like sequences exist in two additional members of this class, *Bathycoccus prasinos* and *Ostreococcus lucimarinus* (Kumar et al. 2015). However, neither a NOS protein nor a gene has been found in embryophytes till date.

In addition, in some cases NO production was not inhibited by NOS inhibitors suggesting that some alternative forms of NOS or alternative enzymes (like NR) might be operative in plants.

18.4.2 Nitrate Reductase

Nitrate reductase (NR) is one of the oldest known enzymes for NO generation (Dean and Harper 1988). NR helps in assimilation of most of the nitrate absorbed by their roots into organic nitrogen compound through the reduction of nitrate to nitrite in the cytosol (Oakes 1994) with the help of the enzyme NR as

$$NO_3^- + NADPH + 2e^- \rightarrow NO_2^- + NAD(P)^+ + H_2O$$
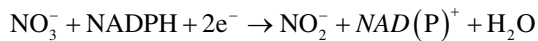
The nitrite is further converted into NH_3 that gets incorporated into amino acids or used in NO synthesis. NR-mediated NO generation is also reported in plant species like soybean, winged bean (Dean and Harper 1986), *Arabidopsis thaliana* (Seligman et al. 2008), moss *Physcomitrella patens* (Rigoberto Medina-Andrés et al. 2015), and green algae like *Scenedesmus obliquus* (Mallick et al. 2000), *Chlamydomonas reinhardtii* (Sakihama et al. 2002), and *Chlorella sorokiniana* (Tischner et al. 2004). Thus, NR-generated NO also plays a key role in protecting plants from abiotic stresses through activating antioxidant enzymes and increasing antioxidant content in plant cells.

18.4.3 Nitrite:NO Reductase (NI-NOR)

NI-NOR enzyme has been found responsible for the generation of NO. It was reported from purified plasma membrane of tobacco (*Nicotiana tobaccum* L. cv. *samsun*) roots. The root-specific succinate-dependent PM-bound nitrate reductase reduces apoplastic nitrite to NO with reduced cytochrome c as an electron donor. NI-NOR has a molecular mass which was 310 kDa in comparison to 200 kDa PM-NR and insensitive to cyanide and anti-NR IgG which makes it different from PM-NR. The enzyme is most suitable for root system because it works in low availability to oxygen, whereas NOS requires ample oxygen for NO production (Stohr et al. 2001).

18.4.4 P Protein-Induced NO Synthesis

It was reported that pathogen-inducible nitric oxide synthase (iNOS) in plants is a variant of the P protein of the GDC which is over 1300 kDa in size and present in the mitochondrial matrix of plant and animal cells and in microbes. P protein contains a 100–120 kDa pyridoxal phosphate, an L protein, and a 50–60 KDa lipoamide dehydrogenase; T protein a 40–45 kDa tetrahydrofolate-containing enzyme; and H protein an ~15 kDa lipoamide. The GDC complex, along with serine hydroxymethyl transferase, catalyzes the conversion of two glycine molecule into serine, CO_2 and NH_3 (Chandok et al. 2003); later on concerns about the reliability of the published data led to their retraction (Klessig et al. 2004).

18.4.5 Xanthine Oxidoreductase

The enzyme is peroxisome based, and the main products of enzymes are uric acid and superoxide under aerobic conditions. It also catalyzes the nitrite reduction to NO under anaerobic conditions, using NADH or xanthine as reducing substrate (Gupta et al. 2010).

18.4.6 Polyamine-Mediated NO Production

Though exact locations are not known, high levels of the polyamines spermine and spermidine induce NO release which is involved in root development and embryogenesis, cadmium toxicity, and drought stress (Gupta et al. 2010).

18.4.6.1   Non-enzymatic Sources

NO is also generated from non-enzymatic mechanisms. It was reported in human by chemical reduction of inorganic nitrite that yield NO under acidic or reducing conditions. At a low or acidic pH, the nitrite ion (NO_2) will be converted to nitrous acid and then into nitrogen oxides including NO. Reducing agents like ascorbic acid help in nonenzymatic NO generation. Here, ascorbate reacts with nitrous acid and forms NO and dehydroascorbate (Weitzberg and Lundburg 1998). The barley aleurone cells can generate a sufficient acidic apoplastic environment to support nitrite to NO conversion using ascorbate as a reductant. Under acidic pH and selected compartment of the cells, the light-mediated conversion of nitrogen dioxide to NO can be catalyzed by carotenoides (Cooney et al. 1994). NO_2 was also reported to be absorbed by rush, lawn grass and gingko leaves and released as NO. The potential reductant was fractionated and identified as a polysaccharide (Nishimura et al. 1986).

18.5   Abiotic Factors and Nitro-Oxidative Stress in Crop Plants

Abiotic stress generated on plants is a key threat that affects crop growth and production (Fancy et al. 2017). Water/drought, temperature, salt, heavy metal, mineral deficiency, and ozone are considered as main factors under abiotic stresses. The stress conditions lead to the excessive ROS production in the cell (Neill et al. 2002). Parallel to this, plant cell also shows increase in NO concentration in plants. Thus, it can be seen as a co-action mechanism existing in plant cell to counteract the harmful process. Thus, it can be seen as a cooperative mechanism existing in plant cell to counteract the harmful nitro-oxidative process. Failing to properly coordinate and balance the nitro-oxidative process affects plant growth, development and survival (Fig. 18.4).

Fig. 18.4 Generalized pathway in plants against oxidative stress to provide abiotic stress tolerance
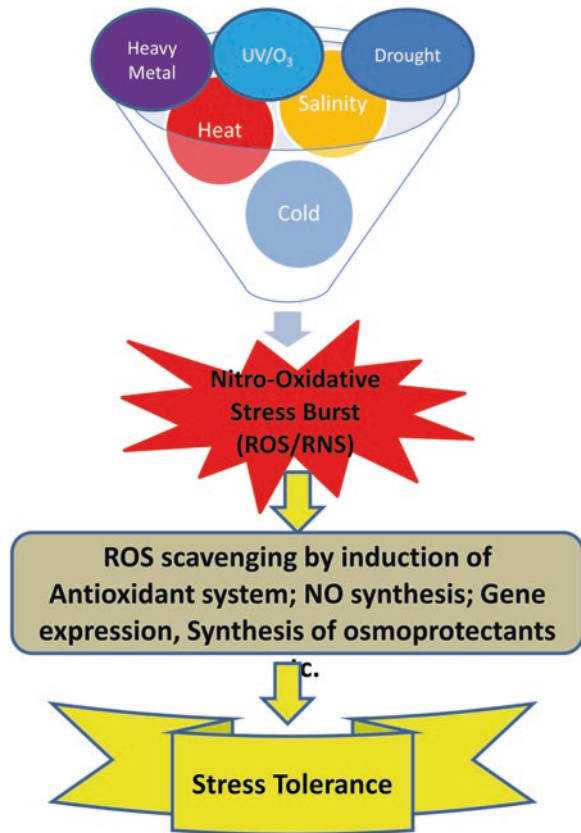
18.5.1 Oxidative Stress and Water Stress

Day by day the requirement for water is increasing, while clean water availability is decreasing, leading to drought stress in crop plants. Drought is undoubtedly one of the most important stresses having a great impact on growth and productivity of the crops. Drought stress affects seed germination and seedling establishment in early stage and significant yield losses in later stages of life in major field crops limiting crop productivity (Misra et al. 2011). NO evolution in stressed reed plants imparts osmotic tolerance through its protection against oxidative damage.

Change in osmotic stress and induction of soil drought stress are two major outcomes of water stress and later on are mostly encountered in agricultural fields (Misra et al. 2011). Drought stress is physiologically countered by plants by closure of stomata, water retention, and induction of antioxidant system in plants. Drought stress induces generation of ROS and develops oxidative stress in cells. It has been found that under abiotic and biotic stress conditions, extracellular ROS are mainly produced by plasma membrane-localized NADPH oxidases, whereas intracellular ROS are produced in multiple organelles like chloroplast, peroxisome,

mitochondria, etc. These ROS form a complex cellular signaling network. It has been observed that accumulation of apoplastic ROS is an early hallmark that help in regulating stomatal movement, ABA, CO signaling, and immunity responses. It suggests that ROS signaling is integrated in various pathways during abiotic and biotic stress in plants (Qi et al. 2018).

To cope up the physical or physiological drought condition, plants have developed counteractive mechanisms, and among them NO is playing an important role. It is found that NO works with phytohormone ABA during drought and provides drought stress tolerance but its exact role is still under investigation. ABA is synthesized following turgor loss and stimulates guard cell to synthesize NO which also causes the upregulation of the antioxidant system especially the ascorbate-glutathione cycle possibly by *S*-nitrosylation of its enzymes (Bai et al. 2011).

Leshem and Haramaty (1996) reported that wilting increased NO emission from pea plants. Possibly NO does not act alone but interacts with other signaling molecules such as H_2O_2 and ABA to effect stomatal closure, thereby reducing transpiration and conserving water. Water stress increased NOS-like activity in wheat seedling, and ABA accumulation was inhibited by NOS inhibitors (Zhao et al. 2001) and showed cross talk between ABA, ROS, and NO levels. Nitric oxide induces stomatal closure and enhances the adaptive plant responses against drought stress in wheat and various other species by application of NO donors (Garcia-Mata and Lamattina 2001). Cotton has evolved various physiological responses against drought stress apart from ROS scavenging, such as stomata closing, root development, cellular adaptations, photosynthesis, and abscisic acid (ABA) and jasmonic acid (JA) production (Ullah et al. 2017).

During drought, the mitochondrial ETC also acts as source of superoxide and H_2O_2. The ROS-inducible alternative oxidase (AOX) limits ROS production in mitochondria, which suggests that deficiency in the AOX pathway enhances drought sensitivity (Wang and Vanlerberghe 2013).

18.5.2 Oxidative Stress and Temperature

Temperature is a crucial factor that influences crop productivity. Biennial and perennial crops are exposed to face seasonal changes because of their life cycle. Extreme temperature (cold and high temperature) responses are seen as an increment in reactive oxygen species (ROS) that affects the photosynthetic activity and consequently the yield. The ROS accumulation in chloroplasts decreases the chlorophyll content and provokes photoinhibition that leads to a low fixation of CO_2 and loss of dry weight. Plants increase the antioxidant defenses and decrease the chlorophyll content as a low-temperature response in comparison with heat conditions, but dry weight losses are higher when plants are grown under heat than under cold conditions, probably because of the inactivation of RuBisCO and/or the associated enzymes as observed in *Brassica oleracea* (Soengas et al. 2018). NO production measured in the shoot apoplast of *Brassica juncea* seedlings showed non-enzymatic nitrite reduction to NO in cold stress where thiol pool enrichment, and 48 putative

Table 18.2 Impact of heat stress on certain crop plants

S. No	Plant species	Effect	References
1.	Soybean (*Glycine max*)	Damaged PSII at 42–43 °C	Li et al. (2009)
2.	Rice (*Oryza sativa*)	Decreased photosynthesis at 33 °C for 5 days	Hurkman et al. (2009)
3.	Maize (*Zea mays*)	Decreased pollen viability and pollen tube elongation at 32.5 °C	Herrero and Johnson (1980)
4.	Common bean (*Phaseolus vulgaris*)	Degeneration of tapetal cells at 33/29 °C	Suzuki et al. (2001)
6.	Wheat (*Triticum aestivum*)	Abnormal ovary development resulting in reduced pollen growth and seed set at 30 °C	Saini et al. (1983)
7.	Mustard (*Brassica napus*)	Abnormal embryo sac development at 32/26 °C	Polowich and Sahney (1988)

S-nitrosylated proteins, provided the preview of RNS-mediated cold stress signaling in the apoplast (Sehrawat et al. 2013) Low temperature-induced S-nitrosylation is responsible for significant (approximately 40%) inactivation of RuBisCO (Abat and Deswal 2009) (Table 18.2).

High temperature (HT) and light also had activating effect on the different indicators of reactive nitrogen species (RNS) metabolism in pea plants, and results suggest that low and high temperature, continuous light, and high light intensity are abiotic stress conditions that can induce nitrosative stress. Protein tyrosine nitration is a potential marker of nitrosative stress (Carpos et al. 2008). High temperature provokes inhibition of sunflower carbonic anhydrase (β-CA) activity (Chaki et al. 2013) that affects the growth and production of cucumbers (Yu et al. 2018).

High bush blueberry, PSII photochemical activity was restored and antioxidant system elevated to provide protection under high-temperature stress (Wei et al. 2010). HT stress resulted in a marked decrease in membrane thermostability and cell viability and an increase in content of lipid peroxide and activities of antioxidant enzymes, viz., superoxide dismutase, catalase, ascorbate peroxidase, guaiacol peroxidase, and glutathione reductase of two cultivars of wheat (Bavita et al. 2012). High temperature (HT) inhibits NO accumulation by guard cell protoplasts (GCPs); suppresses activation of the BA auxin-responsive effects such as expansion of protoplast 20- to 30-fold, cell wall regeneration and dedifferentiation, and cell cycle reentering and division. It also reduces the mitotic indices of primary root meristems and inhibits lateral root elongation in tobacco plant (Beard et al. 2012).

Involvement of NO in stresses such as heat and chilling has also been showed. Short-term stress caused an increase in NO production in alfalfa (Leshem 2001). Application of NO which mediates chilling resistance has been shown in tomato, wheat, and corn (Lamattina et al. 2001) reflecting the antioxidant properties of NO via suppression of the high levels of ROS that accumulates following exposure to chilling or heat stress (Neill et al. 2002b). An appropriate dosage of exogenous NO could also enhance the activity of antioxidant system and alleviated the cell injury in loquat leaves under low-temperature stress (Wu et al. 2009). NO causes polarized

pollen tube growth in *Camellia sinensis* by alterations to gene expression under low-temperature stress (Pan et al. 2016). Contrary to that NO production from NOS-like enzyme reaction decreased the cold-responsive pollen germination, inhibited tube growth, and reduced Pro accumulation, partly via cGMP signaling pathway in *C. sinensis* (Wang et al. 2012). It has been observed that CO acts as a novel regulator to improve the tolerance of recalcitrant seeds to low temperatures through NO-mediated glutathione homeostasis.

Cold-induced NO is involved in the inhibition of pollen tube growth along with disruption of the cytoplasmic $Ca^{(2+)}$ gradient, increase in ROS content, acidification of cytoplasmic pH, and abnormalities in organelle ultrastructure and cell wall component distribution in the pollen tube tip in the *C. sinensis*. In a tropical country like India, thermal stress is one of the major factors which significantly affect the productivity of crop plants.

18.5.3 Oxidative Stress and Salinity

Approximately 30 crop species provide 90% of our food, most of which display negative effects as severe yield losses under moderate salinity worldwide. Na^+, Cl^-, Mg^{2+}, SO_4^{2-}, or HCO_3^- contributes to salt salinity and toxicity. The inhibition of biochemical or physiological processes causes imbalance in metabolism and cell signaling and enhances the production of ROS interfering with cell redox and energy state. Salinity effects are seen as ion imbalance resulting in toxicity, osmotic stress, and generation, and over-accumulation of ROS results in oxidative damage of membrane lipids, proteins, and nucleic acids (Gill and Tuteja 2010).

Maize (*Zea mays*) is an economically important cereal crop affected by high salinity that induces differential oxidative stress and antioxidant responses in maize seedling organs (AbdElgawad et al. 2016). Salt stress causes reduction in sunflower (*Helianthus annuus* L.) seedling growth (Arora and Bhatla 2017), injurious to germinating *P. sativum* L. (var. Shubhra IM-9101), and reduction in growth and biomass yield, leaf relative water content (LRWC), and chlorophyll content in chickpea plants (Ahmad et al. 2016). The effects of high salinity are seen as increase in electrolyte leakage, carotenoid content, the levels of osmolytes (proline, glycine betaine, soluble proteins, and soluble sugars), hydrogen peroxide (H_2O_2), and malondialdehyde (MDA). High salinity also induces antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase in chickpea (*Cicer arietinum* L.) plants (Ahmed et al. 2016) and drastically affect redox and NO homeostasis in tomato roots (Manai et al. 2014).

The ROS decreases but increased NO was seen under salinity stress and ethylene promoted germination of *Arabidopsis* seed (Lin et al. 2013) via EIN3 protein. EIN3 (ethylene insensitive 3) is an ethylene signaling transduction transcription factor. High salt enhanced the expression of EIN3 transcripts and was largely attenuated in the NO biogenesis mutant nia1nia2 plants than in wild ones (Li et al. 2016).

Salt stress induced an increase in endogenous carbon monoxide (CO) production and the CO synthetic enzyme heme oxygenase (HO) in wheat seedling roots which

showed improved salt tolerance by nitric oxide-mediated maintenance of ion homeo-
stasis and upregulation of antioxidant defense (Xie et al. 2008). NO affected the salt-
induced changes in free amino acid levels and cadaverine levels that may be involved
in regulating the response to salt stress in maize (Simon-Sarkadi et al. 2014).

Exogenous application of NO in the form of its donor had the capability to miti-
gate the adverse effects of high salinity on chickpea plants by improving LRWC,
photosynthetic pigment biosynthesis, osmolyte accumulation, and anti-oxidative
defense system (Ahmed et al. 2016) and in *J. curcas* during seedling establishment
by inducing an effective antioxidant system and limiting toxic ion and reactive oxy-
gen species (ROS) accumulation (Gadelha et al. 2017) by increasing the accumula-
tion of proline content, total protein content, and total soluble sugar in line with
increasing antioxidant enzyme activity under salinity conditions in raspberry (*Rubus
idaeus* var. Danehdrosht) (Ghadakchiasl et al. 2017).

The cocktail of SA and NO donor (SNP) shows positive response against salinity
stress in *Pisum sativum* L. (Yadu et al. 2017). The atmospheric application of trace
amounts of nitric oxide enhances tolerance to salt stress and improves nutritional
quality in spinach (*Spinacia oleracea* L.) (Du et al. 2015).

The interaction network among nitrate reductase (NIA/NR) and NOA1-
dependent NO production and HY1 expression showed that upon salinity stress, the
majority of NO production was attributed to NIA/NR/NOA1 confirmed by use of
mutants which exhibited progressive salt hypersensitivity and was rescued by NO
donors suggesting compensatory and synergistic modes, linking NIA/NR/NOA1-
dependent NO production and HY1 expression in the modulation of plant salt toler-
ance in *Arabidopsis* (Xie et al. 2013).

Changes in S-nitrosylation of pea mitochondrial proteins (Camejo et al. 2013)
and protein carbonylation and nitration are involved in acclimation to salinity stress
in the roots and leaves of sour orange plants (*Citrus aurantium* L.) (Tanou et al.
2012). It involves caspase-like enzymatic activity, and the ascorbate-glutathione
cycle participates in salt stress tolerance of maize conferred by exogenously applied
nitric oxide (Keyster et al. 2012). NO and salt stress act as potent regulators of GST
gene and enzyme expression through both ABA-dependent and ABA-independent
pathways in soybean (*Glycine max* L.) plants (Dinler et al. 2014).

Salinity increases NO production selectively in mesophyll cells of sorghum
leaves, where photosynthetic C_4 phosphoenolpyruvate carboxylase (C_4 PEPCase) is
located, which in turn is regulated by a phosphoenolpyruvate carboxylase-kinase
(PEPCase-k), whose levels are greatly enhanced by salinity (Monreal et al. 2013).

The relationship between salinity and oxidative stress (ROS) in two cereal crops,
barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*), showed the tissue-specific
and ROS type association between flux responses of K^+ and Ca^{2+} to oxidative stress,
and salinity stress tolerance was found (Wang et al. 2018).

18.5.4 Oxidative Stress and Heavy Metals

Heavy metal (HM) presence in the soil causes toxicity. It affects the crop plant growth, development, and ultimately decline seen in productivity. Heavy metal stresses also tend to alter the hormonal balance of the roots which in turn affects the root structure. The effects of different HM on physiology of crop plants are discussed below.

18.5.4.1   Cadmium (cd)

NO is reported to be involved in the plant response to cadmium (Cd) stress (Gill et al. 2013) and counteract HM-induced ROS either by direct scavenging it or by stimulating antioxidant defense mechanism. The imbalance between ROS, NO, and antioxidant system of cell becomes visible as nitrosative and oxidative stress or a combination of both, i.e., nitro-oxidative stress. NO counteracts cadmium-induced cytotoxic processes mediated by ROS in *Brassica juncea* through cross talk between ROS, NO, and antioxidant responses (Verma et al. 2013). During HM stress the organelles such as mitochondria, chloroplasts, peroxisomes, cytoplasm, endoplasmic reticulum, and apoplast of plant cells can biosynthesize NO parallel to the ROS synthesis (Sahay and Gupta 2017). The role of NO is tested by application of NO donor (SNP) that successfully ameliorates adverse impact of silver nanoparticles (AgNps) on pea seedlings by regulating the Ag uptake, antioxidant system, oxidative stress, and anatomical structures of root and shoot (Tripathi et al. 2017).

Cadmium (Cd) is one of the very toxic metals among HMs. It inhibits the growth of the primary root by inhibiting root meristem growth involving NO-mediated repression of auxin accumulation and signaling in *Arabidopsis*. Cd exposure also causes decrease in auxin levels. It is associated with reduced PIN1/3/7 protein accumulation, and additionally Cd stabilized AXR3/IAA17 protein to repress auxin signaling. It is confirmed by use of either NO-specific scavenger or NO synthase inhibitor (Yuan and Huang 2016). Higher concentration of Cd (100 μM) markedly reduced biomass, NO production, and chlorophyll level concentration (Chl *a*, Chl *b*, and total Chl) but stimulated ROS and Cd accumulation in plants.

The NO donor (SNP, 50 μM) substantially attenuated growth inhibition, reduced hydrogen peroxide (H_2O_2) and malonyldialdehyde (MDA) levels along with stimulated ROS-scavenging enzymes/agents, and mitigated the $H^{(+)}$-ATPase inhibition in proton pumps in *Trifolium repens* L. plants. S-nitrosylation is involved in the ameliorating effect of SNP against Cd toxicity in leaves of *Boehmeria nivea* (L.) Gaud. This involvement exhibited a concentration-dependent property (Wang et al. 2016). SNP considerably upregulated the level of jasmonic acid (JA) and proline in plant tissues but downregulated the level of ethylene (ET) in both shoots and roots and the level of salicylic acid (SA) in roots only, which might be related to the elevated NO synthesis. Exogenous NO could promote the scavenging of ROS, keep the mineral nutrition in balance, and alleviate the damage of Cd stress to the leaf photosynthetic apparatus, making the tomato seedlings preserve their photosynthetic efficiency (Zhang et al. 2010).

NO modulates protein changes in the plasma membrane. A quantitative proteomics approach showed 66 differentially expressed protein, among which phospholipase D (PLD) was altered substantially after the treatment of Cd or Cd and NO suggesting that NO signaling is associated with the accumulation of antioxidant enzymes, glutathione and PA, which increases cadmium tolerance in rice via the antioxidant defense system (Yang et al. 2016).

Alleviation of Cd toxicity by NaCl treatment contributed to reduction of NO accumulation in plants where root number was reduced in plants exposed to Cd and increased by the addition of NaCl and reduced by the addition of SNP (Zhang et al. 2014). SNP exerted an advantageous effect on alleviating the inhibitory effect of Cd on rice seed germination and seedling growth, which might interact with NO in rice (*Oryza sativa* L.) (He et al. 2014).

Cd exposure caused a significant decrease in total phenolic, GSH, and nitric oxide (NO) levels at the highest concentration tested when compared with control in maize plants (Akinyemi et al. 2017). GSH regulates tolerance to cadmium (Cd) stress confirmed by inhibition of GSH biosynthesis by buthionine sulfoximine (BSO) which aggravated Cd toxicity by increasing accumulation of ROS and reducing contents of NO and S-nitrosothiol (SNO) in tomato roots. GSH modulated the cellular redox balance through maintaining increased GSH:GSSG and AsA:DHA ratios and also increased phytochelatin contents. Thus, GSH increases Cd stress tolerance not only by promoting the chelation and sequestration of Cd but also by stimulating NO, SNO, and the antioxidant system through a redox-dependent mechanism (Hasan et al. 2016).

NO promotes Cd^{2+}-induced PCD by promoting MPK6-mediated caspase-3-like activation in *Arabidopsis* (Ye et al. 2013) and in roots and signaling response of yellow lupine plants. These changes were accompanied by the NADPH oxidase-dependent superoxide anion (O_2^-) production (Arasimovicz et al. 2012). Gibberellic acid (GA) involved in alleviation of Cd toxicity which is mediated through the reduction of the Cd-dependent NO accumulation and expression of Cd^{2+} uptake-related gene IRT1 in Arabidopsis (Zhu et al. 2012). On the other hand, Ca may alleviate Cd toxicity via endogenous NO with variation in the levels of non-protein thiol, protein thiol, and matrix polysaccharides (Zhang et al. 2012). Thus, it seems that nitrogen (N) management is a promising agronomic strategy to minimize cadmium (Cd) contamination in crops.

18.5.4.2 Zinc (Zn)

Heavy metal such as Zn can induce oxidative stress by generation of ROS and reactive nitrogen species (RNS), which can reduce growth and yield in crop plants. NO via SNP ameliorates zinc oxide nanoparticle-induced phytotoxicity in rice seedlings (Chen et al. 2015). Nine-day-old hydroponically grown *Brassica juncea* (Indian mustard) and *B. napus* (oilseed rape) seedlings were treated with $ZnSO_4$ that showed *B. juncea* is more tolerant to Zn stress than *B. napus* in terms of ROS, and RNS parameters suggested that the oxidative components are predominant compared with the nitrosative components in the root system of both species (Feigl et al. 2015).

Role of GSNO is like a NO donor that help in the modulation of Zn uptake and in root-to-shoot translocation during the transition from deficient to sufficient levels of Zn supply in hydroponically cultured wheat plants (*Triticum aestivum* cv. Chinese Spring) (Buet et al. 2014). Zn-induced NO production promoted an increase in ROS accumulation in *Solanum nigrum* roots by modulating the expression and activity of anti-oxidative enzymes, and programmed cell death (PCD) was observed in primary root tips. These events are favorable for the *S. nigrum* seedling response to long-term Zn toxicity by modulating root system architecture and subsequent adaptation to Zn stress (Xu et al. 2010). NO-activated hydrogen sulfide is essential for cadmium stress response in Bermuda grass (*Cynodon dactylon* (L). Pers.) (Shi et al. 2014).

The use of zinc oxide nanoparticles (ZnO NPs) is rapidly increasing in agriculture and consumer products. The impact has been evaluated on crops like wheat, maize, radish, bean, lettuce, tomato, pea, cucumber, and beet which showed that soil pH and plant species are key factors affecting the Zn availability and phytotoxicity of ZnO NPs (García-Gómez et al. 2018).

18.5.4.3   Iron (Fe)

It was observed that *Arabidopsis* HY1 confers cadmium tolerance by decreasing nitric oxide production and improving iron homeostasis (Han et al. 2014). Wild-type and iron uptake-inefficient tomato (*Solanum lycopersicum*) mutant (T3238fer) plants were grown in pH-buffered hydroponic culture which showed the upregulation of the Fe uptake system was responsible for NO_3^--facilitated Cd accumulation in plants (Luo et al. 2012).

Fe deficiency triggered significant accumulation of NO in the root system predominantly in the outer cortical and epidermal cells of the elongation zone of in *Malus xiaojinensis* (Zhai et al. 2016), and various dicots increase their root branching which contributes to the enhancement of ferric-chelate reductase activity (Jin et al. 2011). The deficiency of P, Fe, or both increased the cluster root number and cluster zones and also enhanced NO accumulation in pericycle cells and rootlet primordia at various stages of cluster root development with the expression of LaSCR1 and LaSCR2. These two genes are crucial in cluster root formation in white lupin (Meng et al. 2012).

Fe deficiency leads to an increase in the expression of ferritin during the senescence of *Lotus japonicus* nodules (Chungopast et al. 2017). Glutathione plays an essential role in nitric oxide-mediated iron deficiency signaling and iron deficiency tolerance in *Arabidopsis* (Shanmugam et al. 2015). The interplay of three factors, namely, auxin, ethylene, and NO, is crucial in the regulation of Fe deficiency responses by Strategy I plants (non-leguminous). Here, auxin acts upstream of ethylene and NO, and ethylene is probably the last activator (Romera et al. 2011) evidenced by the fact that NOS-generated, rather than NR-generated, NO acts downstream of auxin in regulating this Fe deficiency-induced response, which enhances the plant tolerance to Fe deficiency (Jin et al. 2011). NO and glutathione impact the expression of iron uptake- and iron transport-related genes as well as the content of metals in *A. thaliana* plants grown under iron deficiency (Koen et al. 2012).

GSH threshold requirement for NO-mediated expression of the *AtFer1* ferritin gene is seen in response to iron in *Arabidopsis* (Tauraine et al. 2012). NO is involved in regulating the synthesis of cell wall. Root apoplast is the main reservoir for iron. The iron deficiency elevated NO level in tomato (*Solanum lycopersicum*) roots. However, application of S-nitrosoglutathione, a NO donor, significantly enhanced iron retention in root apoplast of iron-deficient plants, accompanied with a decrease of iron level in xylem sap of shoots. It is accompanied with increased pectin methylesterase (PME) activity and decreased degree of pectin methylation in root cell wall of both iron-deficient and iron-sufficient plants, and it causes iron retention in pectin fraction and increased binding capacity of iron to the extracted cell wall (Ye et al. 2015).

18.5.4.4 Copper (Cu)

Increasing concentrations of Cu resulted in increase in cellular damage and nitro-oxidative stress, with an induction in activity of ROS and RNS metabolism enzymes (SOD, CAT, APX, NR) with an increased concentration of the allergenic protein profiling production in basil plants. The increasing concentrations of Cu and Zn led to a decrease in the concentration of total proteins and antioxidant capacity, and severe Cu stress resulted in the accumulation of specific proteins related to transpiration and photosynthetic processes. In comparison to Cu and Zn, Ni stress appears to be less damaging and with lower allergenic potential (Georgiadou et al. 2018).

NO contributes to copper tolerance by influencing ROS metabolism in *Arabidopsis* (Peto et al. 2013). The main effect of Cu^{2+} was seen as lipid peroxidation, reduction in root and nitrate reductase (NR) activity, and Cu accumulation. NO alleviated negative effects and made the biomass of tomato seedlings recover and increased root activity (Wang et al. 2016). Exogenous NO mediated GSH-PC synthesis pathway in tomato under copper stress (Wang et al. 2014) and differently affected the sub cellular distribution of Cu. An NR-mediated early NO production in the shoots of hulless barley plays an important role protecting from Cu toxicity through enhanced antioxidant enzyme activities and antioxidant pools (Hu et al. 2015).

Copper (Cu^{2+}) at a concentration of 50 μm resulted in a large reduction in cotyledon area and hypocotyl and primary root lengths, accompanied by an increase in auxin levels. In cotyledons, a low $Cu^{(2+)}$ concentration promoted NO accumulation, negativated by NOS or NR inhibitors, and inhibition of auxin transport resulted in an increase in NO levels suggesting that auxin and NO negatively regulate each other's level and NO intensifies the metal-induced cotyledon expansion but mitigates elongation processes under $Cu^{(2+)}$ exposure (Peto et al. 2011). Copper-induced cross talk among calcium, H_2O_2, and NO and a calcium-dependent activation of gene expression involving calmodulins and calcium-dependent protein kinases are involved in management in *Ulva compressa* (Gonzalez et al. 2012).

18.5.4.5 Lead (Pb)

Pb exposure significantly decreased in vivo NO level, and exogenous NO partially ameliorated Pb toxicity, but could not restore the plant growth on prolonged Pb exposure (Kaur et al. 2015). It was found that NR was responsible for the

Pb-triggered NO burst and played a critical role in Pb uptake by *P. crinitum* root cells (Yu et al. 2012).

18.5.4.6   Manganese (Mn)

NO participates in tolerance to Mn stress, but negative effects of the highest SNP dose were also observed in *Matricaria chamomilla* (Kovacik et al. 2014). NO alleviates aluminum (Al) toxicity when the exogenous NO treatments are given in plants through activating anti-oxidative capacity to eliminate reactive oxygen species (He et al. 2012).

18.5.5 Oxidative Stress, UV, and Ozone

The incoming solar radiation (insolation) coming from the sun to earth also consists of UV radiation. The UV radiation is subdivided into UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm). The UV-C radiation is completely absorbed by atmospheric gases; UV-B radiation is partially absorbed by stratospheric ozone, while UV-A radiation is hardly absorbed by ozone (Frohnmeyer and Staiger 2003). The adverse effects of UV-B on plants involve oxidative stress, increased ion leakage and H_2O_2 content, and thylakoid membrane protein oxidation in bean (*Phaseolus vulgaris*) leaves (Shi et al., 2005). Heme oxygenase (HO) has antioxidant properties and is upregulated by ROS in UV-B-irradiated plants (Yannarelli et al. 2006). It has been observed that UV-B triggers an increase in ABA concentration in maize leaves (Tossi et al. 2009) followed by H_2O_2 generation and an enhancement of NO production through NOS-like enzymes or by NR in guard cells and involves multifaceted pathway mediated by ABA, UVR8, COP1, HY5, NADPH oxidase, and H_2O_2 (Tossi et al. 2014). It is found that tomato plants use non-enzymatic antioxidant pathways to cope with moderate UV-A/B irradiation inducing oxidative stress that could be used in protected tomato horticulture systems (Mariz-Ponte et al. 2018).

The secondary metabolites like flavonoids and anthocyanins are important actors in protecting plants from UV-B effects. The induction of *Chs* by UV-B appears to be meditated by NO. Two compounds known to generate NO, GSNO and SNAP, were found to lead to an increase in *Chs* transcript levels in the absence of UV-B, suggesting the importance of NO in regulating gene expression in response to UV-B radiation (Mackerness et al. 2001). NO and ROS have also been implicated in UV-B-induced ethylene production in maize seedlings (Wang et al. 2006). The effect of UV-B exposure on chili pepper (*Capsicum annuum* cv. 'Coronel') associated with response to subsequent drought stress showed that when both are applied combinedly, it induced a reduction both in stem length, stem dry weight, and number of floral primordial and induced mitochondrial Mn-SOD gene expression to cope with the oxidative stress but flavonoids were increased only with UV-B treatment suggesting that the UV-B treatment alone did not induce significant tolerance in plants toward drought stress under the conditions used (Rodríguez-Calzada et al. 2018).

Rapid industrialization has led to releases of chemical precursors of ozone; therefore, the ozone concentration has risen and given rise of ozone pollution. It affects the yield of many ozone-sensitive crops such as winter wheat. It has been found that the accumulation of endogenous NO in wheat leaves was found to increase in response to ozone mitigating the adverse effect induced by ozone (Li et al. 2018).

18.5.6 Oxidative Stress and Mineral Deficiency

Soil acidity associated with aluminum (Al) toxicity and low phosphorus (P) availability is considered the most important problem for agricultural production. Oxidative stress induced by Al toxicity and P deficiency activates antioxidant systems and upregulates expression of phosphate transporters gene in ryegrass (*Lolium perenne* L.) plants (Parra-Almuna et al. 2018).

In the Krebs cycle, aconitases are the major NO targets in animals (Mott et al. 1997) and directly affect the aconitase functionality (Gardner et al. 1998). Aconitase is an iron-sulfur (4Fe-4S)-containing enzyme that catalyzes the reversible isomerization of citrate to isocitrate. This inactivation of aconitase decreases cellular metabolism and may have protective effect against additional oxidative stress by acting as a reversible circuit breaker. Inactivation results in reduced electron flow through the mitochondrial electron transport chain and thereby decreases the generation of ROS, the natural by-product of respiration. Conversely, aconitase inactivation has been proposed to increase ROS generation due to the accumulation of reduced metabolite, a condition termed "reductive stress" (Yan et al. 1997).

An additional role for aconitase in animals was found when the iron regulatory protein (IRP), a protein that controls iron homeostasis, was determined to be the cytosolic isoform of aconitase (Klausner et al. 1993). IRP binds to mRNAs containing a specific iron-responsive element (IRE) consensus sequences and thereby regulates their translatability and/or stability. NO converts the cytosolic aconitase into an IRP by promoting the loss of the iron-sulfur cluster which otherwise prevents IRE binding. Thus, aconitase in addition to being a key NO sensor in animals also regulates iron homeostasis. The tobacco aconitase-like animal counterparts were inhibited by NO donors. A tobacco cytosolic aconitase gene (*NtACO1*) whose deduced amino acid sequence shared 61% identity and 76% similarity with the human IRP-1 was cloned. Furthermore, residues involved in mRNA binding by IRP-1 were conserved in *NtACO1*. These results reveal additional similarities between the NO signaling mechanisms used by plant and animals (Navarre et al. 2000).

Iron deficiency impairs chlorophyll biosynthesis and chloroplast development in both dicotyledon and monocotyledon species; therefore, iron availability maintains direct correlation with plant productivity. When the strategies for iron acquisition fail, stress symptom becomes evident. NO is involved in iron homeostasis in plants, and most of the leaf iron (80%) is located in chloroplast. NO donors completely prevented leaf interveinal chlorosis in maize plants growing with an iron concentration as low as 10 μM Fe-EDTA in the nutrient solution. In NO-treated maize plants,

mesophyll chloroplast appeared completely developed. NO treatment did not increase iron content in plant organs when expressed in a fresh matter basis, indicating that root iron uptake was not enhanced. Under iron-deficient growth condition, NO treatment increases the chlorophyll content of leaves. These increases are accompanied by the accumulation of transcript encoding both the D1 protein of PS II and the RuBisCO large subunit (LSU). D1 protein was more sensitive to oxidative stress than the LSU (Giardi Masojidek and Godde 1997). Oxidative stress causes cross-linking of RuBisCO large subunit and protein degradation (Mehta et al. 1992). An iron-storing protein known as ferritin is found in bacteria, plants, and animal cells. Its level, which is regulated by NO in *Arabidopsis*, was found by treating *Arabidopsis* cell suspension culture with NO donors which showed the accumulation of ferritin at both mRNA and protein levels. Iron is not necessary for this NO-mediated ferritin transcript accumulation. Ferritin regulation though the IRDS sequence of the *Atfer* 1 promotor was responsible for transcriptional repression under low iron supply, suggesting that NO, by acting downstream of iron in the induction of ferritin transcript accumulation, is therefore a key signaling molecule for regulation of iron homeostasis in plants (Murgia et al. 2002).

18.6 Conclusions

After the abundance of oxygen in earth atmosphere, it led to evolution a life based on aerobic respiration and other oxygen-based reactions. Simultaneously, it also gave birth of many harmful processes that force and threaten to end cellular process and ultimately affect life, if not managed properly. Oxidative stress (ROS) is one of the phenomena that have negative impact on cellular systems of organisms. Plants including crop plants are also severely affected by oxidative stress and poses great threat for sustainable food production. Apart from ROS, RNS (NO) is also another cellular factor that gets induced. NO acts as a signaling molecule and helps in counteracting the ROS effects generated in plant systems. ROS and NO involvement has been observed in most of the abiotic stresses like drought or water stress, salinity, high and low temperature, heavy metal, UV and ozone, and mineral deficiency. There is a great need to minimize impact of ROS to achieve the optimum yield from crop plants. It can be overcome by either minimizing the impact of stress factors or augmenting the crop plants (biochemical or genetic level) so that they can generate enough antioxidants, protective metabolite, or protein to cope up the bad effects of stress.

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Herbicide Resistance in Crops and Weeds

19

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Abstract

Weeds have been proved as the ultimate pests of crop plants. Use of herbicides has become one of the best solutions to control weeds on a large scale. Due to ignorance, less diversity in herbicides, and their availability in local markets and cost affordability etc. The farmers use only one or a few major herbicides for long time, and it causes the herbicide résistance in weeds. Genetically modified (GM) herbicide-resistant (HR) crops have been blindly cultivated by farmers throughout the world, especially in the United States. GE crops have been blamed for increased problems with HR-weeds. Due to adoption of GM, herbicide-resistant cultivars substantially reduced herbicide diversity in maize, cotton, and soybean. Intensive use of glyphosate in these crops largely displaced herbicides that were likely to be selected for HR-weeds and the impact of reduced herbicide diversity has been mitigated. It has been expected that if the same pattern of use of herbicides continues, more HR-weeds will develop and the need for developing more HR-crops will increase.

Keywords

Weeds · Herbicide-resistance · Genetically modified crops · Maize · Market

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19.1   Introduction

In the 1950s, the first case of herbicide resistance was found in the United States, and field bindweed resistant against 2,4-D was listed in Kansas in 1964, as common groundsel resistant to the herbicide "triazine" was reported in Washington in 1970. The number of discovered bio-types in the beginning of the 1980s was noted with a rapid increase in the United States, and all over the world; resistance to more than 1 of the 25 herbicides has been reported in more than 65 weed species in the United States. In India, *Phalaris minor* developed resistance to isoproturon during 1992–1993 in N-W wheat belt mainly in Punjab and Haryana. Herbicide resistance in the crops is the main trait that has been engineered into crops. Weed resistance problem to herbicides is the key factor to provide information for scientists to develop crop resistance against previously nonselective herbicides. Herbicide-resistant crops (HRCs) can be categorized as non-transgenic and transgenic. Non-transgenic HRCs are the traditional genetic methods of selection for resistance character, while transgenic HRCs are the genetic engineering methods. Non-transgenic HRCs were made through the techniques of conventional breeding. In 1984, the first crop canola was developed as a resistant crop against triazine through breeding program. After that many other methods introduced, e.g., pollen mutagenesis, microspore selection, tissue culturing, seed mutagenesis, cell selection, and transfer through a weed relative, have been used for producing a non-transgenic HRCs.

19.2   Definitions

19.2.1 Weed

Weed is a valueless wild plant which is growing at a cultivated land or an unwanted plant at an improper place that has no economic value.

19.2.2 Herbicide

Herbicides can be defined as chemical substances used to control weeds in the field crops.

19.2.3 Resistance

Resistance is defined as a change in the sensitivity of a pest population to a pesticide, resulting in the failure of a correct application of the pesticide to control the pest.

19.2.4 Herbicide Resistance

Herbicide resistance is the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide that would normally be lethal to the wild type.

19.2.5 Weed Resistance

Weed resistance is the decreased response of the population of a weed species to an herbicide because of long and continued application of the same herbicide.

19.2.6 Susceptibility

Susceptibility is defined as the extent to which a plant has to face injury or death by a particular herbicide.

19.2.7 Herbicide Tolerance

Tolerance is the inherent ability of the weed species to survive and reproduce after herbicide treatment.

19.2.8 Dormancy

Seed dormancy is a survival mechanism by which seeds can delay germination until the right environmental conditions for seedling growth and development.

19.3   Resistance Types

19.3.1 Multiple Resistance

The phenomenon in which a weed is resistant to more than one herbicide having different modes of actions. Resistant plants possess more than one distinct resistance modes, e.g., first developed in *Lolium rigidum* against PS-II inhibitors, ALS inhibitors, ACCase inhibitors, mitotic inhibitors, glyphosate, etc. Continuous use of single herbicide until population of weed shows resistance, and then another single herbicide is used again and again without proper management, and the same weeds become resistant to the second herbicide and so on. One of the other sources of multiple resistance can also take place by the movement of pollens in cross-pollination between sexually companionable plants having different resistant genes.

19.3.2 Cross-Resistance

The phenomenon of cross-resistance occurs when the gene that made it resistant to the single herbicide makes it resistant for the others by the same mode of action. In cross-resistance, a weed biotype is resistant to more than one herbicides due to the single mode of action, e.g., *Phalaris minor* resistant to isoproturon has also gain cross-resistance against clodinafop-propargyl, diclofop-methyl, and sulfosulfuron. More common type of resistance is cross-resistance than multiple, but multiple resistance is of great concern potentially because it decreases the used number of herbicides to control weeds.

19.3.2.1 Target Site–Based Resistance
Resistance to two or more herbicides due to a similar target site, e.g., triazines, phenylureas, and uracil, which inhibit PS-II.

19.3.2.2 Metabolic-Based Resistance
Resistance to two or more herbicides due to similar mechanisms of degradation of herbicides, e.g., in *Phalaris minor* showing resistance to isoproturon and diclofop-methyl.

19.4   Mechanism of Herbicide Resistance

19.4.1 Altered Target Site

Every herbicide has a specific targeted site of action where it disrupts by acting to a specific plan process or function. Somewhat alteration in the target site resulted in no longer binding of herbicide to the site of action, and hence, it becomes unable to put its phytotoxic effects. This type of mechanism of herbicide resistance is more common. More number of examples of resistance to herbicide "triazine," like as "atrazine" and "simazine," are due to an alteration in the target site.

19.4.2 Enhanced Metabolism

Plants use mechanism of metabolism to detoxify outsider compounds such as herbicides. A weed plant having quickly degrading ability to herbicides can actively inactivate the herbicides prior to reaching its target site within the plants, e.g., resistance to propanil in *E. colona* is due to enhanced enzyme activity of aryl-acylamidase that detoxifies propanil.

19.4.3 Sequestration or Compartmentalization

Some plants have restricting ability to the movement of outsider herbicidal compounds within their tissues or even cells to stop cause of harmful effects of that compound. In this situation, herbicides are inactivated through binding (e.g., to a molecule of plant sugar) or removed through metabolically active region to inactive region like glyphosate resistance in *Lolium rigidum* and paraquat resistance in *Hordeum glaucum.*

19.4.4 Over-Expression of Target Protein

If the target protein, on which the herbicide acts, can be produced in large quantities by the plant, then the effect of the herbicide becomes insignificant.

19.5   Guidelines for Prevention and Management of Herbicide Resistance

19.5.1 Where Resistance Has Already Cropped up

Make awareness, training, and participatory approach among farmers. Abandon the herbicide to which weeds are showing resistance. Stop sale/purchase/borrowing or exchange of crop seed from area under resistance to other areas where resistance is not reported. Prevent its spread and seed bank enrichment in soil. Clean tillage and harvest equipment. Rogue for prevention of contamination of crop harvest.

19.5.2 Cultural Approaches

  (i) Competitive and high-yielding variety.
 (ii) Pure and certified crop seed.
(iii) Stale seed bed technique.
 (iv) Closer row spacing.
  (v) Proper time, method, and rate of sowing.
 (vi) Crop rotation.
(vii) Crop residue management.

19.5.3 Mechanical and Manual Options

  (i) Tillage practices.
 (ii) Soil solarization.
(iii) Harrowing.
(iv) Manual weeding.

19.5.4 Biological Control of Resistance

Trichoderma viride are the biological agents which are helpful in controlling *Phalaris minor* selectively by making colonies in roots of the plants.

19.5.5 Reducing the Risks of Herbicide Resistance

The steps in reducing the risks of herbicide resistance are given below:

  (i) Evaluation of alternative herbicides by using suitable doses and time to control flushes of resistant weed.
 (ii) Use of herbicide mixtures with different sequences and rotation to delay/avoid the development of cross- or multiple resistance in the previously resistant weeds.
(iii) By the use of crop safeners/protectants and synergists.
(iv) Well knowledge about spraying techniques and equipment.
 (v) By the use of different agronomic practices like as field fallowing, manual weeding, and also sterilization/fumigation.
(vi) Proper monitoring.
(vii) Integrated weed management (IWM).

19.6 Selection by Herbicide

19.6.1 Characteristics of Cropping System

  (i) No or little crop rotation.
 (ii) No or little pre-plant tillage.
(iii) Less competition of crop.
(iv) No or little rotation of modes of action (MOA) of herbicides.

19.6.2 Characteristics of Weed

  (i) Annual growth pattern.
 (ii) High rate of seed production.
(iii) Less extent of seed dormancy.
(iv) Longevity of some seeds in seed bank.
 (v) Greater frequency of resistance mutations or alleles.
(vi) More generations per year.
(vii) Trends of gene flow, e.g., pollen or seed.
(viii) No fitness consequence for resistance trait.
(ix) High susceptible species to the herbicides.

19.6.3 Characteristics of Herbicide

  (i) Single action's site.
 (ii) High rate of efficacy.
(iii) High rate of usage relative to need amount (favors selection of target-site resistance).
(iv) Less or marginally effective use rates (favors selection of non-target-site resistance).
 (v) Long residual activity of soil.
(vi) Higher use frequency.

19.6.4 Other Factors

19.6.4.1   Resistance Inheritance

Nuclear inheritance is the key factor to determine resistance in most classes of herbicides whereby offspring get resistance genes by both pollen and ovules. In most weeds in which the resistance inheritance has been studied, single and major nuclear genes control the resistance. Additionally, in the majority of species, a dominant or partially dominant allele conferred the resistance. Through mathematical models it has been shown that a single conferred resistance, dominant allele consequences as more quick evolution of resistance in out crossing weeds as compared to recessive allele. It is rare that when a resistance mutation earliest appears in a weed population. In recessive mutation, only homozygotes will be resistant, while, in the case of dominant resistance, homozygotes and heterozygotes both will be resistant and able to survive under herbicide treatment.

19.6.4.2   Fitness in the Absence of Herbicide Treatment

Some time resistant plants have been found to have lower fitness in the survival, growth, and successes of seed production as compared to susceptible plants in the lack of herbicidal treatment. The decreased fitness of resistant plants in the periods of herbicides which are not applied will cause slow resistance evolution process and spread as well, in addition to by increasing effectiveness of herbicide rotations by cultural practices in the management of resistance. If equal fitness is found in resistant and susceptible plants, then there is no increase or decrease in the relative frequency of resistant plants, but it also remains constant throughout the periods in which herbicides are not used. On the other hand, if resistant plants have lesser fitness as compared to susceptible plants in the lack of herbicide treatment, the decreased fitness causes a reduction during herbicide-off periods in resistant individuals among population.

19.6.4.3   Mating System and Life Span

Evolution rate and spread of resistance are influenced by the mating system and life span of a weed species. In a new arisen resistance as mutation or immigrant, gene will be present initially in heterozygotes due to mostly presence of such individuals in the population for susceptible homozygotes for that gene. Heterozygous plants

will survive the herbicide treatment if the mutation is dominant. But in the case of recessive mutation, heterozygous plants will be susceptible and will not survive in the herbicide treatment.

On the other hand, in the case of highly self-fertilized weeds, e.g., plants that pollinate their own ovules like green foxtail, recessive resistance mutations can readily become established and disperse. Frequency of homozygotes is rapidly increased by selfing, at the cost of heterozygotes then exposing recessive resistance alleles to herbicide selection and decreasing the chances of loss of a new homozygous recessive mutation. In highly self-fertilized species, recessive resistance mutations disperse at generally the same rate as dominant resistance mutations.

19.7 Current Status of Herbicide Resistance in Weeds

19.7.1 Herbicide Resistance

Herbicide-resistive ant weeds are a common problem throughout the world, but greater than herbicide-resistant weed problem with resistance found in those countries which are using highly mechanized agriculture cropping systems due to the higher reliance on herbicides. At least in 60 countries, biotypes of herbicide-resistant weeds were reported which included about 400 distinctive combinations of species-herbicide groups. Due to a highly intensive cropping system, the United States has a higher number of resistant biotypes (144) as compared to other countries followed by Australia 62; Canada 59; China, France, Germany, Spain, and Brazil 31–35; and California having 21 distinctive cases of herbicide-resistant weeds in which there are 15 grasses or sedges and 6 broadleaf species.

Resistance to photosystem-II inhibitors and ALS inhibitors is dominant over herbicide-resistant weeds in the whole world and the United States due to extensive use of unlike herbicides in broader areas of cereal and grain crops. Multiple resistant biotypes are more problematic than others, for example, in Australia, a single population of rigid ryegrass is reported with resistance to nine different modes of action, while in California, ALS inhibitor resistance is dominant over herbicide-resistant biotypes, mostly due to intense pressure of selection in rice cropping systems.

Even though herbicide resistance has been reported in most of the weedy species, a few genera have been documented to dominate. There are 17 genera that have been presented to have biotype resistance with 4 or more herbicide mode of action groups. These weeds tend to be more problematic species among the most widespread weed species, and herbicide resistance is becoming more complicated for effective management.

19.7.2 Mechanism of Resistance in Weeds

In crop plants herbicide resistance is mostly conferred by mechanisms which cause herbicide resistance in weeds (Fig. 19.1). At first, lack of herbicide activity can
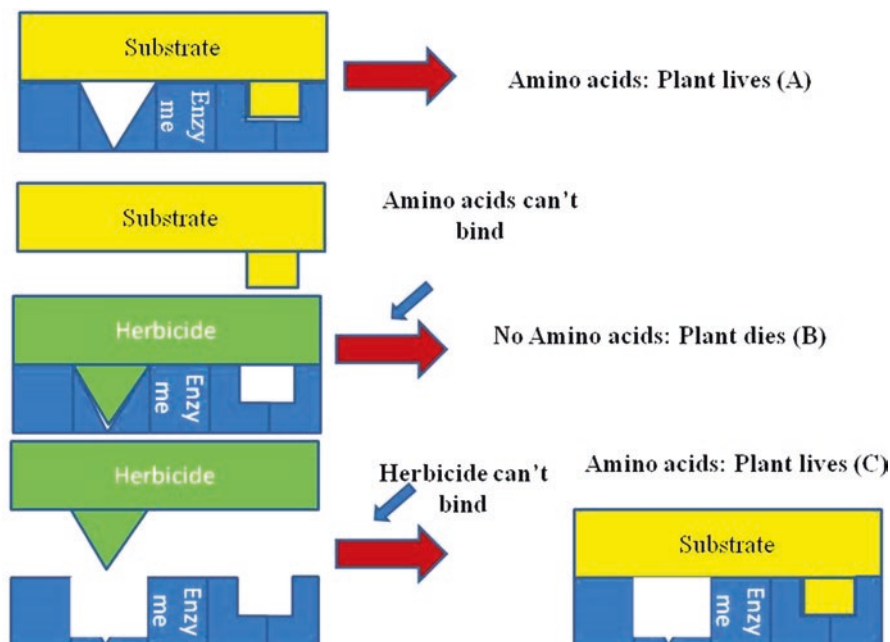
Fig. 19.1 Herbicide resistance mechanism in plants

cause resistance at the action site, e.g., target site absent, present the target site but binding site of herbicide is absent, extreme amount of target enzyme related to the herbicide amount. Mutation of non-target sites like fast metabolic detoxification of herbicide is another process that keeps the plants live with less or no non-reversible effects of herbicidal applications. Plant growth stages and environmental conditions influence the metabolic rates. This is one of the reasons that weed control and crop safety are more different dramatically in cool environment than ideal growing conditions (Fig. 19.1).

When any herbicide is applied, a selective pressure is exerted on a weed in a field by killing all S-biotype plants and not injuring the R-biotype plants. Selection of pressure intensity can be enhanced:

- If an herbicide acts on a single site of action, e.g., ALS inhibiting herbicides act on a particular single enzyme in the plant. Herbicide substrate binds to the enzyme and does not permit to further function in the S-biotype plant, while in the R-biotype plant, due to change in enzyme structure, a herbicide cannot remain bind for longer time, and enzyme functions normally. (Fig. 19.1).
- If the herbicide is highly effective (>95% control), the R-biotype will be able to flourish, and there is no competition since few, if any, S-biotypes survived.
- Soil activity provided by herbicides for longer period of time can control weeds that characteristically emerge late in the season, and so it continues to remove S-biotypes and permits R-biotypes to survive after emergence.

19.7.3 Conventional Method

Almost all species of plants are resistant to some herbicides and susceptible to others at the same time naturally. Conventional techniques of breeding mostly consist of identification of parental lines of potential variety by screening with the interested herbicide. One of the methods is to survey the germplasm of crop species, because some varieties and breeding lines may show more resistance than a cultivar. Identification of higher resistant lines and introgression the gene of resistance by traditional crossing and used to transfer the resistance genes into the commercial cultivars. The second method is exposing the crop species to sublethal doses of related herbicide and then selecting the best performed survivors after many of the generations and spray regimes.

Induced mutation is the conventional approach used by breeders by ionizing radiation, mutagenic chemicals, etc. for alteration of genetic makeup of a plant for producing resistance to a variety of herbicides. This one is the simplest method in which breeders first of all take seeds in a large amount and then expose them to the mutagen, sow and grow them and then spray the progeny with the herbicide, and select any survivors as prospective resistant mutants. By using mutagenesis, several herbicide-resistant crop cultivars are developed, in which wheat cultivars are described which were based on a mutagenized hard red wheat line (FS-4) with novel resistance to imidazolinone herbicides.

19.7.4 Molecular Method

Methods of genetic engineering in the late 1980s had become advanced. According to these methods, genes of specific traits transferred into various species of crops. In the first experiment, traits (which opposed to experimental marker) were herbicide resistant which were used as single genes conferring resistance to particular herbicides and had been passing through the processes of isolation, cloning, and then characterization. The first herbicide resistance genes were conferred to the glyphosate and glufosinate, of which examples are Rely™, Liberty™, and Basta ™ herbicides. After that, initially genes were utilized as in vitro selective marker (still in use as such) being developed for the control of weeds in transgenic herbicide-resistant crops. At the same time, herbicide-resistant genes came into being to develop crop resistance against other herbicides like bromoxynil, sulfonylurea, and imidazolinone herbicides. With these genes in the early crop species were canola, soybean, corn, flex, and cotton. In spite of advanced research and development, few crop cultivars have been evolved by genetic engineering commercially. However, transgenic modified crops are getting popular in the farmer community.

19.8   Concerns Related to Herbicide-Resistant Crops

19.8.1 Selection for Herbicide-Resistant Weeds

Evolution and selection of herbicide-resistant weeds are the issues having largest concerns associated with adoption of herbicide-resistant crops. Attributes that make herbicide-resistant crops attractive to growers (i.e., broad weed control spectrum, low application cost, fewer non-target or negative environmental effects) can lead to reliance on a single herbicide mode of action and impose tremendous selection pressure for resistant weeds. For example, although glyphosate has been used in North America since the early 1970s, glyphosate-resistant weeds were not reported until 2001, several years after the commercialization of the first Roundup Ready crop. In the years since the first report, 21 unique cases of glyphosate-resistant weeds have been reported, and many appear to have been selected in glyphosate-resistant cropping systems. Among the most dramatic examples of this include glyphosate-resistant cotton, soybean, and corn systems in the Midwestern and Southeastern United States afflicted with glyphosate-resistant pigweeds (*Amaranthus palmeri*, *A. rudis*, *A. tuberculatus*) and horseweed/marestail to the point of almost total failure in some regions.

19.8.2 Managing Herbicide-Resistant Crop Volunteers

Herbicide-resistant crop volunteers that emerge in subsequent crops can be a significant agronomic concern and may require alternate management practices compared to susceptible crop volunteers. Herbicide-resistant crop volunteers may become more problematic and difficult to control if another crop resistant to the same herbicide is planted in rotation. For example, volunteer soybean in cotton became a problem in the Southeastern United States with the commercialization of glyphosate-resistant soybean and cotton.

19.8.3 Effects on Rotational Crops

Herbicides differ in both their residual activity and recommended plant-back intervals for different crops. One of the benefits to farmers using herbicide-resistant crops is a decrease in the rotation time between the harvest of one crop and the planting of the next because a sensitive crop cannot be rotated into a field until a residual herbicide has dissipated to the point that the rotational crop will not be affected. Herbicide-resistant crops, which share an herbicide resistance trait, would allow farmers to rotate crops promptly; however, this practice is likely to encourage monoherbicide application which is detrimental to resistance management.

19.8.4 Gene Flow

Gene flow is important in the maintenance of genetic variation in populations as well as in the spread of new traits among populations and across species boundaries. Gene flow can occur by pollen movement or by direct movement of seed or in some cases by vegetative propagules, but within an agronomic system, these pathways often are linked. Global expansion in cultivation of herbicide-resistant crops has increased concerns regarding pollen- and seed-mediated gene flow from herbicide-resistant crops to conventional and organic crops. Although gene flow is not unique to herbicide-resistant crops, it has been suggested consistently and repeatedly as an environmental concern. The primary areas of concern are that unexpected gene flow could cause changes in food safety, harm markets, and lead to changes in biodiversity of agricultural or natural areas.

19.8.5 Pollen-Mediated Gene Flow

Pollen-mediated gene flow is the transfer of genetic information between plant populations resulting from cross-pollination. Gene flow between populations of the same species is known as *intra-specific* gene flow, whereas gene flow among different species (e.g., between domesticated crops and wild relatives) is known as *inter-specific* gene flow. A number of factors determine the likelihood and extent of intra-specific pollen-mediated gene flow among plant populations. These include the reproductive biology of a species or cultivar within a species, flowering phenology, sexual compatibility, pollen load, and environmental conditions at specific vegetative or reproductive stages of plant development, spatial and temporal distribution of pollen donors and recipient plants, and also size of the pollen donor and recipient plant populations.

19.8.6 Seed-Mediated Gene Flow

Seed-mediated gene flow primarily occurs through seed dispersal within and among agricultural fields but may also be facilitated by seed spill during transport, admixture of seed used for planting, and co-mingling of seeds within the seed handling system. Seed-mediated gene flow may occur by natural dispersal mechanisms via animals, wind, or water or by human actions such as tillage and transport. Unlike natural seed-mediated gene flow, seed movement by human results in a limitless dispersal capability. Due to the "permeable" nature of the supply chain, seed-mediated gene flow can occur at most stages of production. Although seed-mediated gene flow is a large source of transgene input into the environment and the agricultural supply chain, it has received relatively little attention in the scientific literature compared to pollen-mediated gene flow from herbicide-resistant crops.

19.8.7 Environmental Issues

There are environmental issues related to herbicide-resistant crop use, which, although not unique to genetically engineered cultivars, are still relevant. Herbicides are widely used at present, and most areas where farmers will use herbicide-resistant crops are already treated with herbicides as part of a weed control program. The herbicides for which herbicide-resistant crops are being developed are, in general, low-use-rate, low-mammalian-toxicity herbicides with short soil half-lives; therefore, the use of these herbicide-resistant crops should result in lower environmental impact than occurs at present with higher-impact herbicides.

19.8.8 Herbicide Use

The existence of herbicide-resistant crops does not necessarily translate into an increased use of herbicides. If industry succeeds in making herbicide-resistant crops cost-effective, the herbicides to which tolerance is being engineered will almost certainly increase in sales. An increase in sales does not necessarily mean that farmers are applying more herbicide per acre, but may simply mean that the acreage being treated using these herbicides has been increasing and/or that the older herbicides are being replaced by those used with the transgenic cultivars. While herbicide-resistant crops do encourage continued use of herbicides, they also offer farmers alternatives at a time when the development and registration of new herbicides or other effective weed management strategies have been slowed by market, economic, and regulatory issues.

19.8.9 Water and Environmental Quality

Most herbicide-resistant crops are based on glyphosate, glufosinate, imidazolinone, and sulfonylurea herbicides. The specific herbicides and application rates used in these crops usually have acceptable persistence in soil, low mammalian toxicity, and fewer issues with leaching than compounds such as simazine and diuron which are commonly found in California groundwater. Rotation of cropping systems with herbicide-resistant crops and non-engineered varieties of the same crop species should encourage the rotation of herbicides, thereby reducing environmental buildup.

19.8.10   Economic Issues

The additional cost of herbicide-resistant crops, coupled with the cost of the herbicides, imposes some additional economic burdens on farmers; however, indiscriminate use of herbicides will never be cost-effective, nor would it be permissible based on US Environmental Protection Agency (EPA) policy. In order to be adopted in the

marketplace, herbicide-resistant crops must lead to weed control strategies that provide an economic and/or managerial benefit to growers and be acceptable to the consumers of the end products. Attaining this goal is time-consuming; estimates of the time required for the identification and introduction of a tolerance trait are 6 years or more. Acceptance and establishment of the HRC cultivars in the marketplace could take several more years.

19.8.11   Effects on the Herbicide Industry

Cropping systems developed to rely on only a few nonselective herbicides can be expected to affect the development and commercialization of new alternative herbicides. The development of herbicide-resistant crops has already led to a global restructuring of private-sector agrochemical research, development, and marketing systems. Certainly, in the near term, development activity will continue to focus on herbicide-resistant crop strategies, but the effect of this on the development of other agrichemical approaches is not known.

19.8.12   Labeling

Labeling foods as being derived from genetically modified (GMO) crops has been a controversial issue. The call for such labeling has been resisted in the United States and Canada because mandatory labels in those countries are based on the composition and features of the final food, rather than on the particular method of breeding or processing. Not least of the problems is that there is no standard definition of a "GMO" food. Every jurisdiction, from the United States to Canada to the European Union (EU), has different definitions of what would need to be labeled. For example, the EU already has a process trigger for food labels, such that any food made "with" GMOs requires a label. However, foods made "from" GMOs do not. To avoid any confusion that may arise in distinguishing between food made "from" GMOs and those made "with" GMOs, the United States and Canada use an objective compositional trigger for mandatory labels, so only foods with a measurable nutritional compositional change or changes to levels of substances normally present (including allergens or other anti-nutritional substances) are required to carry labels.

19.8.13   Export Markets

The term "adventitious presence" refers to the unintentional and incidental commingling of trace amounts of one type of seed, grain, or food product with another. When used in relation to herbicide-resistant crops, the term describes the inadvertent presence of herbicide-resistant crop seeds or other materials in conventional or organic crop seeds. Low levels of impurities are inherent in commodity crops due to

the nature of the supply chain; herbicide-resistant crops are grown in close proximity to other crops, and common equipment is frequently used to plant, harvest, transport, and store grains.

19.8.14 Mechanism of Resistance in Crops

Herbicide resistance mechanisms can be classified into two groups: exclusionary resistance and site of action resistance (Dekker and Duke 1995).

19.8.14.1 Exclusionary Resistance
Those that excludes the herbicide molecule from the site in plants where they induce toxic response. In exclusionary resistance mechanism, the herbicide is excluded from the site of action in many ways.

19.8.14.1.1 Differential Herbicide Uptake
In resistant biotypes, the herbicides are not taken up readily due to morphological uniqueness like overproduction of waxes, reduced leaf area, etc.

19.8.14.1.2 Differential Translocation
In resistant biotypes the apoplastic (cell wall, xylem) and symplastic (plasma lemma, phloem) transport of herbicide is reduced due to different modifications.

19.8.14.1.3 Compartmentation
Herbicides are sequestered in many locations before they reach the site of action. For example, some lipophilic herbicide may become immobilized by partitioning into lipid-rich glands or oil bodies (Stegink and Vaughn 1988).

19.8.14.1.4 Metabolic Detoxification
Herbicide is detoxified before it reaches the site of action at a rate sufficiently rapid that the plant is not killed. The biochemical that detoxifies herbicides can be grouped into four major categories: oxidation, reduction, hydrolysis, and conjugation. Three enzyme systems are known to be involved in resistance due to increased herbicide detoxification. Resistance to atrazine in some population of *Abutilon theophrasti* is due to increased activity of glutathione *S*-transferase that detoxifies atrazine.

19.9 Weed Control Spectrum of Selective Herbicides and Population Shift Factors

1.1 Plant factors and herbicide selectivity.
   (i) Plant age and growth rate.
  (ii) Morphology.
 (iii) Physiological and biochemical processes.
  (iv) Genetic inheritance.

1.2 Herbicides and edaphic factors.
1.3 Factors related to weed resistance and dormancy, avoidance, and weed density.
1.4 Factors enhancing herbicide resistance.

19.10 Conclusions

Resistance mitigation seeks to diversify weed control methods in order to delay the evolutionary process by reducing the selection pressure exerted by herbicides. Target-site resistance is conferred by an alteration causing loss of plant sensitivity to herbicides with a specific mechanism of action. It is, therefore, clear that one way of dealing with the problem is by switching to another herbicide effective on the same weed species, but having a different mechanism of action. The use of herbicide mixtures or sequences involving herbicides with different mechanisms of action can protect the herbicides and delay the evolution of resistance to each, since mutants with resistance to one herbicide would be controlled by the other herbicide and vice versa. The recurrent use of the same herbicide mixture could theoretically select for biotypes with resistance to both herbicides (multiple resistance).

From this discussion of resistance mechanisms in herbicide-resistant weeds, it should be clear that resistance cannot be mitigated only by switching or combining herbicides in production systems that rely solely on the intensive use of selective herbicides for weed control. Instead, herbicide resistance management requires the integrated diversification of chemical and non-chemical weed control methods to reduce selection pressure for resistant weed biotypes. Herbicides are one of the most effective tools for weed management; however, they must be used judiciously. They should be "one of the many tools" in a weed management toolbox rather than the only tool, or else we are at risk of losing effective herbicides due to the evolution of herbicide-resistant weeds.

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Improving Crop Health and Productivity: Appraisal of Induced Mutations and Advanced Molecular Genetic Tools

20

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Abstract

Food security and crop improvement has become one of the foremost challenges faced by the world today. The production of both food and economic crops is compromised due to different man-made activities that affect the environment adversely, including abiotic and biotic factors. So, the agriculture around the world is under pressure to increase the food production by 70% by 2050 in order to cope with the ever-increasing population's requirement. Thus, there is a need to improve agronomic traits of the crops by enhancing their nutritional value and also increasing resistance with a better chance of survival. A range of approaches including the utilization of additional land and water resources or agrochemicals are being adopted to achieve improved crop productivity. The idea of conventional breeding, frequently applied for crop improvement, is not so successful since the gene pool of elite trait is quite restricted that requires other state-of-the-art techniques. Thus, this paper (a) overviews induced mutations and major molecular crop improvement techniques; (b) appraises recent works on the strategies for mutation induction and approaches for their detection; (c) critically reviews reports on the major molecular genetic approaches for crop improvement; (d) highlights the role of bioinformatics in crop improvement; and finally (e) concludes the major outcomes of the discussion and highlights the major aspects so far unexplored in the present subject.

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20.1 Introduction

Mutation breeding is based on selfing mutants until the induced character has a stable expression in the advanced mutant generations. It is a way of creating variations in the existing germplasm or genetic resources which are phenotypically screened or are present in the genome. It helps the plant breeders to make decision on utilizing these variations for increasing the food productivity so as to overcome the future challenges (Sikora et al. 2011a). The most common variations are due to point mutations. Mutation breeding has advantages of being cost-effective, quick, proven, and robust apart from being non-hazardous and environmentally friendly. There are more than 3200 mutant varieties officially released for commercial use (FAO/IAEA 2016).

For decades forward genetic approach was used by breeders and geneticists for studying variations and their functions, but it was based on defective mutants of our interest. Today, the use of reverse genetics has made possible to study any gene by disrupting it (Belhaj et al. 2013). Random mutagenesis is a naturally occurring phenomenon. Genome editing has evolved from the use of chemical and physical mutagenic agents to biological tools including sequence-specific nucleases and oligonucleotide-directed mutagenesis (Songstad et al. 2017). Induction of mutation has been an important tool for crop breeding since the release of first-ever mutant variety of tobacco in the 1930s (Jankowicz-Cieslak et al. 2017).

Mutation breeding serves as a platform for breeders to showcase their varieties to a global audience and at the same time to stimulate germplasm transfer for cultivation, breeding, or genomic studies.

A mutant variety is a new plant variety that is bred through:

1. Direct use of a mutant line that is developed through physical and chemical mutagenesis or somaclonal variation and activation of endogenous transposable elements.
2. Indirect use of a mutant line/lines, which is/are used as a parental variety/varieties in crossbreeding (cross between mutant lines or with a commercial variety/varieties).

Use of wild species' genes translocated into plant genomes through irradiation facilitated translocations, e.g., genes of wheat wild relative species (FAO/IAEA 2016). Molecular biotechnology tools such as of the genetic engineering and the marker-assisted breeding by utilization of QTL techniques have led to increased understanding of the complex traits responsible for decline in crop productivity. The present paper (a) appraises recent works on the strategies for mutation induction and

molecular approaches for their detection of induced mutations using molecular crop improvement techniques; (b) critically reviews reports on the major molecular genetic approaches for crop improvement; (c) highlights the role of bioinformatics in crop improvement; and finally (d) highlights the major aspects so far unexplored in the present subject.

20.2   Mutagens: Tools for Inducing Genetic Variability

Several types of mutagenic agents are used extensively to create genetic variation for use in genetics and crop improvement. Muller (1928) was the first to discover the mutagenic properties of X-rays (Fig. 20.1). Since then, several physical and chemical mutagens have found their application and contributed in induced mutagenesis. Living cells quickly respond to DNA damage caused by physical and chemical mutagens and further kill the damaged cell or repair DNA lesions. Ionizing radiations cause single- and double-strand breaks and also produce chemically reactive species that interact with the cellular and molecular environment of the cell (Suprasanna et al. 2015). Mutations have been induced to enhance the nutrient contents of crops. Mutations were induced in red pepper to enhance the production of beta-carotene (a precursor of vitamin A). It was observed that the induced mutation had no detrimental effects on the concentration of mineral elements and secondary metabolites in the fruits (Tomlekova et al. 2017; Table 20.1).

Mutation is a spontaneous change that is caused due to point mutation during the replication of DNA or during cell division. Though the rate of natural mutation is very low in nature but can be increased artificially by exposure to chemical

Fig. 20.1 LET curves for Ne and C ion beam penetration in water. Water can be used as surrogate for soft tissue penetration in plants. A beam of high energy penetrates a plantlet and/or plant tissue with rather low and uniform LET (FAO/IAEA)
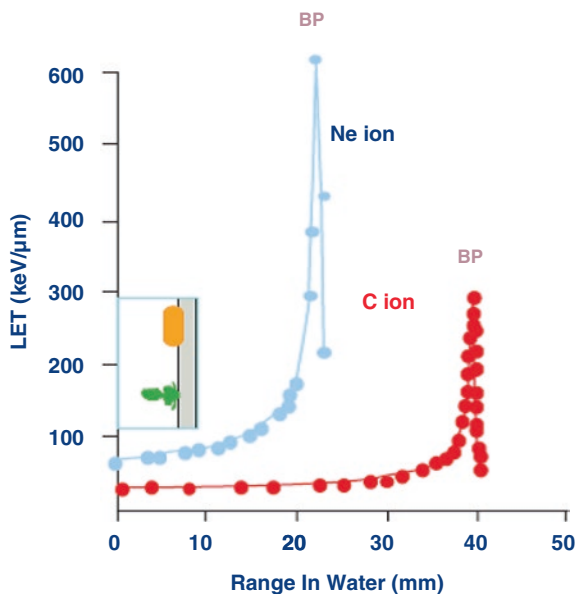
Table 20.1 Penetrating effect of different radiations on plant tissues (Suprasanna et al. 2015)

Type of radiation	Property description	Penetration in plant tissue	Energy
X-rays	Electromagnetic radiation	A few mm to many cm	50–300 keV
Gamma rays	Electromagnetic radiations similar to X-rays	Through whole parts	Up to several MeV
Neutron (fast, slow, and thermal)	Uncharged particle, slightly heavier than proton, observable only through interaction with nuclei	Many cm	From less than 1 eV to several MeV
Alpha particles	A helium nucleus, ionizing heavily	Small fraction of a mm	2–9 MeV
Beta particles, fast electrons, or cathode rays	An electron (− or +) ionizing much less densely than alpha particles	Up to several cm	Up to several MeV
Protons or deuterons	Nucleus of hydrogen	Up to many cm	Up to several GeV
Low-energy ion beams	Ionized nucleus of various elements	A fraction of mm	Dozens of keV
High-energy ion beams	Ionized nucleus of various elements	A fraction of cm	Up to GeV

mutagens, ionizing radiation, etc. The induced mutations enhance the process of evolution by modifying and exploiting a single or few characters of a superior cultivar (Jain et al. 2013). Induced mutagenesis produces macromolecular changes in plants, which may lead to alteration in biophysiology and morphology of crop genotypes (Laskar et al. 2018).

Induction of mutation has been successfully used in a range of economically important crops including barley, rice, wheat, cowpea, cotton, and peanut (Gottschalk and Wolff 2012). The types of mutations differ with relevance to plant type, mutagen used, and its dosage and time applied. The mutations bring changes in phenotype due to modifications in transcriptome and structural and numerical changes in chromosome (Gill et al. 2015). Mutation that occurs at a single point due to transitions or transversions can cause frame shifting and gives rise to new codons and new proteins. Genome editing or targeted mutation has a promise for molecular breeding (Ma et al. 2017).

20.3 Strategies for Mutation Induction

The initial step for introducing mutations in a crop plant is the identification of the plant part followed by selecting the mutagen. The γ-ray bombardment is less destructive causing point mutations and small deletions, whereas fast neutron bombardment causes translocations, chromosome losses, and large deletions (Suprasanna et al. 2015). Ion beam that has been successfully used on rice in China and Thailand against disease resistance, has obtained high grain quality and a shorter growth cycle (Huang and Han 2014). Mutagenesis was induced in groundnuts using EMS

Table 20.2 Mutagens

Name	Abbreviation	Molecular weight[a]
Ethyleneimine	EI	43.07
Dimethyl sulfate	DMS	126.13
Diethyl sulfate	dES (DES)	154.19
Ethyl methanesulfonate	EMS	124.2
N-ethyl-N-nitrosourea	ENU (ENH)	117.11
N-methyl-N-nitrosourea	MNU (MNH)	103.08
N-methyl-N1-nitro-N-nitrosoguanidine	MNNG	147.09
Sodium azide	NaN3	65.01

Note: [a]Data from Haussman and Parzies (2009)

and gamma rays. It was observed that the mutants possess desirable agronomic characters and favorable oil chemistry (Kavera 2017).

Chemical mutagens provide high mutation rates and induce mostly point mutations. These include base analogues, acridine dyes, nitrous acid, hydroxylamine, etc. (Haussman and Parzies 2009) (Table 20.2). Lestari (2012) has detailed various plant chemical mutagens and their action. Alkylating agents, such as ethyl methanesulfonate (EMS), react with guanine or thymine by adding an ethyl group which causes the DNA replication machinery to recognize the modified base as an adenine or cytosine, respectively (Table 20.3).

20.3.1 Mutation Discovery

A variety of molecular techniques are available for the identification and study of mutants. Both forward and reverse genetics are applied to investigate the change (Table 20.4). Forward genetics is a classical method in which a particular phenotypic change that is brought about by mutation is compared to a wild-type variety of the same plant to characterize the mutated gene (Mba 2013). However, plants which are genetically polyploids have much variation in some genes, and the change is difficult to detect via a phenotypic change. When such a problem arises, reverse genetics needs to be applied that studies the genotype of the plant and then the phenotype. With the discovery of PCR and sequencing techniques, it has now become quite easy to detect the genomic changes of a plant directly.

20.3.2 Mutation Detection by TILLING

Target-induced local lesions in genomes (TILLING) is a high-throughput, non-transgenic molecular technique that applies reverse genetics and facilitates high-throughput study of

Table 20.3 Effect of different concentrations of alkylating agent on different plant species for different exposure time (Shu 2012)

Alkylating agent	Plant species	Plant material	Concentration (mM)	Exposure	References
MNU (MW 103.08)	*Begonia*	Leaf explants (in vitro)	0.2–10	1 h	Bouman and De Klerk (2001)
	Lathyrus sativus	Pre-soaked seeds (12 h)	0.5–1.4	3 h	Rybinski (2003)
	Lens culinaris	Seeds	0.49–3.88	6 h	Sharma and Sharma (1986)
	Nicotiana glauca	Pre-soaked seeds (16 h)	1	2 h	Marcotrigiano and Hackett (2000)
	Oryza sativa	Panicles	1	45 min	Suzuki et al. (2008)
	Pisum sativum	Seedlings	1	1–4 h	Pereira and Leitão (2010)
ENU (MW 117.11)	Var. botrytis	Pieces of curd (in vitro)	0.3	Days	Deane et al. (1995)
	N. plumbaginifolia	Protoplasts	0.1	Days	Rey et al. (1990)
	Phaseolus vulgaris	Seeds	1.5–6.2	8 h	Svetleva (2004)
	P. sativum	Seedlings	5	1–4 h	Pereira and Leitão (2010)
	Zea mays	Callus	1–30	4–8 h	Moustafa et al. (1989)
EMS (MW 124.16)	*Glycine max*	Embryogenic cultures	1–30	4 h	Hofmann et al. (2004)
	G. max	Seeds	18	24 h	Wilcox et al. (2000)
	Helianthus annuus	Pre-soaked seeds (4 h)	80	5–12 h	Nehnevajova et al. (2007)
	O. sativa	Panicles	94.2	(injected)	Lee et al. (2003)
	P. vulgaris	Seeds	6.2–25	8 h	Svetleva (2004)
	Trigonella foenum-graecum	Pre-soaked seeds (4 h)	10–300	2–24 h	Saikat et al. (2008)

point mutations in specific genes (Figs. 20.2 and 20.3). The technique compares the enzymatic cleavage of mismatches among wild and mutant types of the crop plants (Mba 2013). This technique detects mutations in a small population of plants rather than producing large amounts of mutants with considerable mutation. TILLING saves a lot of time and hence increases the efficiency of mutation breeding. TILLING has been used on a variety of plant species including maize, barley, tomato, banana, etc. (Chen et al. 2014; Esfeld et al. 2013).

TILLING combines chemical mutagenesis which can be detected by a sensitive mutation detection instrument. DNA from a collection of EMS-mutagenized plants can be pooled and then subjected to PCR amplification. The product was screened

Table 20.4 Identification of mutants in target genes for target traits in different crops (Martin et al. 2009)

Crop	Target trait	Target gene	Amplicon length	Lines screened	Mutants identified	References
Rice	Leaf emergence	PLA1	1327 bp	767	10	Suzuki et al. (2008)
Sorghum	Forage digestibility	COMT	1013 bp	768	2	Xin et al. (2008)
Barley	Grain hardness	Hin-a	420 bp	4608	4	Caldwell et al. (2004)
	Virus resistance	eIF4E	525 bp	3148	5	Talamè et al. (2008)
Bread wheat	Starch quality	Wx-A1	2114 bp	1152	106	Slade et al. (2005)
	Plant height	GA20ox1A	1289 bp	1152	17	King et al. (2015)
Durum wheat	Photosynthesis	RCA-A1	1435 bp	480	13	Martin et al. (2009)
Oil seed rape	Oil quality	FAE1	852 bp	930	15	Wang et al. (2000)

for mutations using denaturing HPLC (DHPLC). DHPLC detects mismatches in heteroduplexes created by melting and annealing of heteroallelic DNA. TILLING is suitable for any organism that lacks genetic tools.

Uauy et al. (2009) suggested a modified TILLING approach for wheat of which mutations were screened using non-denaturing polyacrylamide gel. TILLING is a high-throughput method to detect point mutations in crop plants, the plants under study are required to be free of chimeras, and a large population of mutants is required. Recently, Serrat et al. (2014) reported a new method that enables one to rapidly obtain TILLING mutant population from rice. The raw material used was seed-derived rice calli and mutation induced by ethyl methanesulfonate (EMS). The screening of in vitro regenerated plants showed a high rate of desirable mutations in the population. Using reverse genetic strategies like TILLING, mutations have been induced in *Arabidopsis*, wheat, barley, tomato, and soybean (Jankowicz-Cieslak et al. 2017).

Another modified TILLING system using non-labeled primers and fast capillary gel electrophoresis was applied in *O. sativa* by Suzuki et al. (2008). This method proved to be very efficient and convenient in screening the mutant population. The same method was used in the detection of single nucleotide substitution mutations. The mutation rate was as high as 7.4×10^{-6} per nucleotide representing one mutation in every 135 kb genome sequence (Fig. 20.4). Suzuki et al. (2008) developed mutant populations of *O. sativa japonica* cv. Taichung 65, by treating single zygotic cells with *N*-methyl-*N*-nitrosourea (MNU). Mutagenesis in single zygotes created mutations at a high frequency and rarely formed chimeric plants. A modified TILLING system using non-labeled primers and fast capillary gel electrophoresis was applied for EcoTILLING.
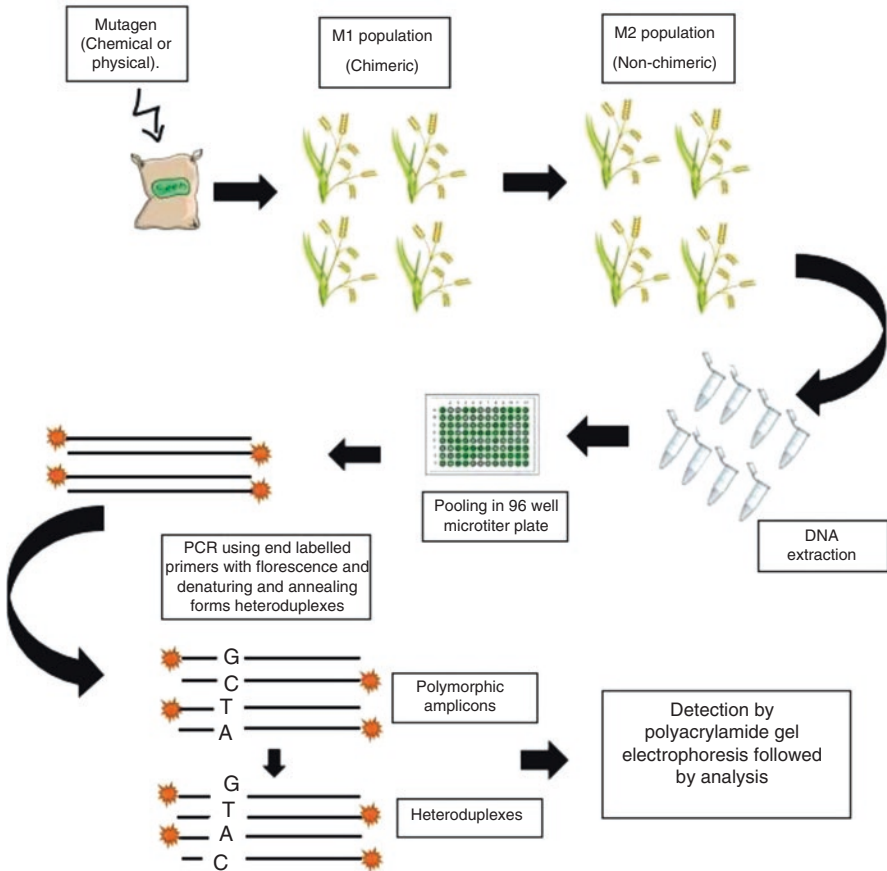
Fig. 20.2 Basic approach for TILLING. The seeds of the selected plants are mutated using mutagen (physical/chemical) to induce choice of mutation (point, chromosomal mutation). The first generation (M1) is chimeric (i.e., different mutations occur in different cells of the plant). TILLING cannot be performed on chimeric population. Thus, it is eliminated in M2 generation which is created by crossing only mutagenized population from M1 population. The DNA is extracted and pooled in a 96-well plate for PCR using end-labeled primers with fluorescence. Mutation is screened using enzymatic cleavage which forms heteroduplexes detected by polyacrylamide gel electrophoresis. Different fragments are used for molecular weight analysis for characterization of mutation

20.3.3 EcoTILLING

EcoTILLING, a modified version of TILLING, has been used as an efficient tool to detect SNPs in natural populations and also to identify polymorphisms in large populations (Kong et al. 2014). The DNA pooling in EcoTILLING is conducted by mixing the genomic DNA of the test plant with the control genotype in 1:1 ratio. It is a quick, accurate, and economical method to recover a wide range of haplotype
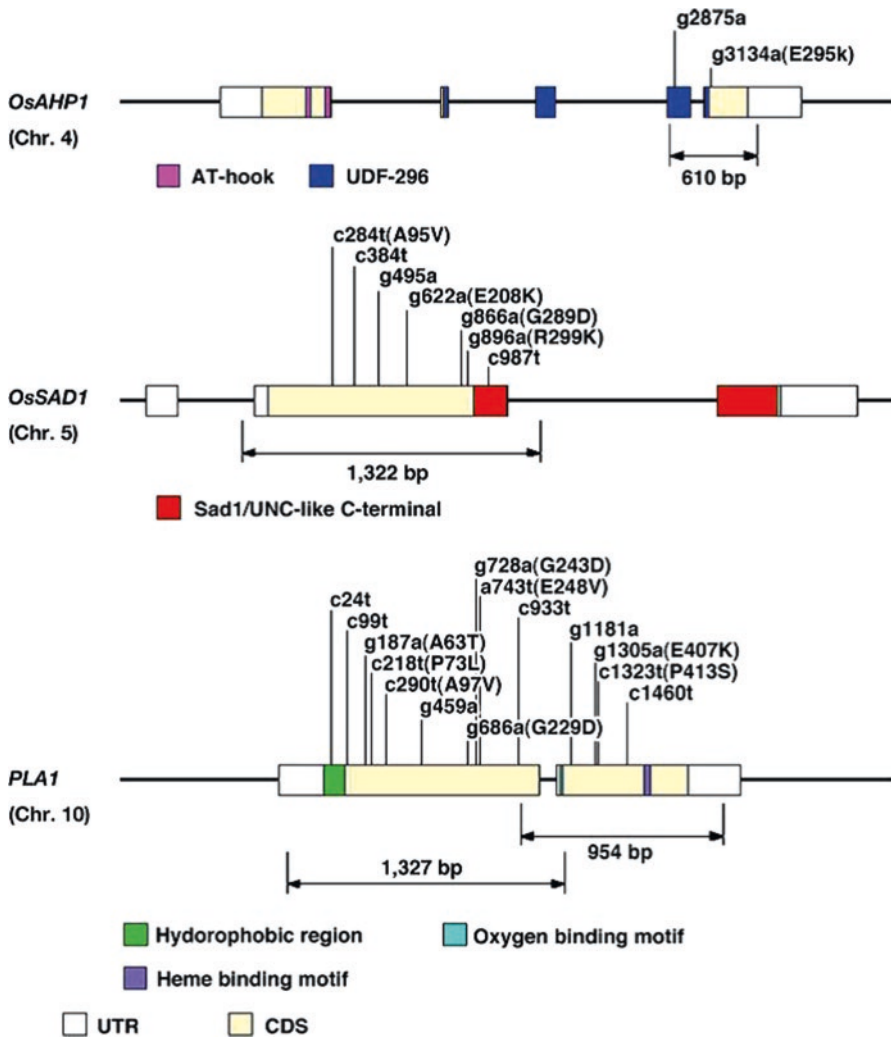
Fig. 20.3 Mutations with and without amino acid changes detected in four gene fragments in three genes, *OsAHP1*, *OsSAD1*, and *PLA1*. Nucleotide substitutions and their locations are shown in the schematic gene and domain structures. The beginning, indicated by the letters a, t, g, or c in each, was the original nucleotide in T65 followed by the nucleotide number from the translation start point and ends with one of four nucleotides substituted. *Letters* and *Figures* in parentheses indicate the same for amino acid changes. DNA fragments amplified by PCR are shown by arrowhead lines with their bp length at the bottom of each gene (Suzuki et al. 2008)

diversity in target genes in natural populations. The method has been exploited for a number of applications that include population diversity studies in different crops. Xia et al. (2013) has applied EcoTILLING technique in barley to detect SNPs unique haplotypes. Similarly, Negrao et al. (2013) genotyped 392 rice varieties by EcoTILLING to study the genotypic differences in 5 key salt-related genes.
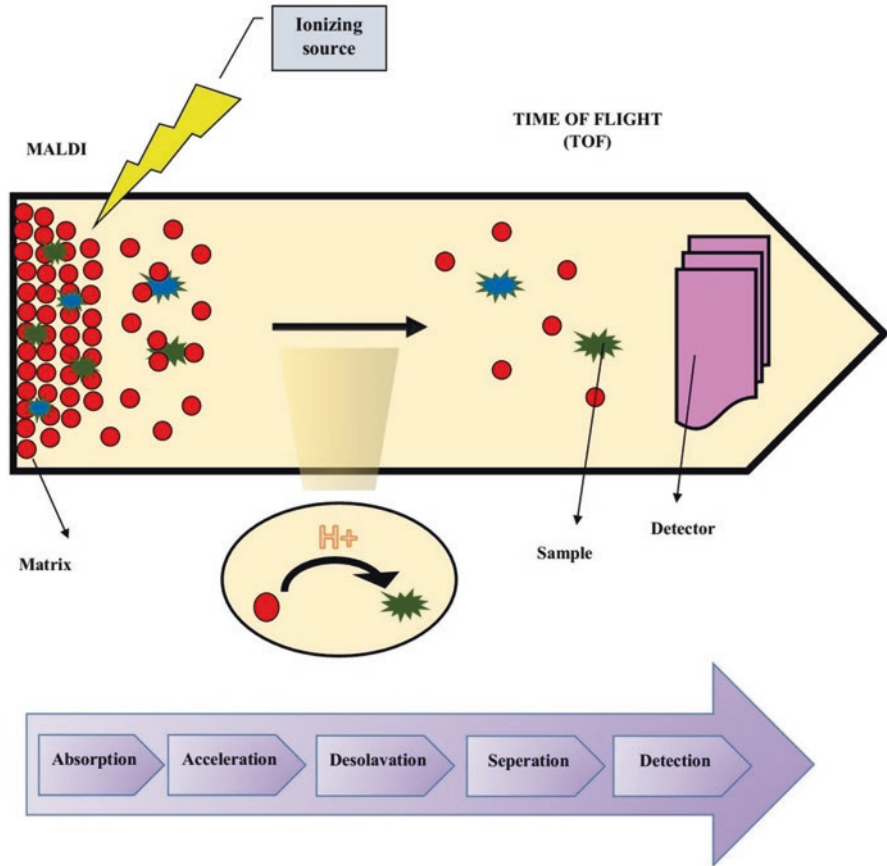
Fig. 20.4 Basic principle of MALDI-TOF. There are two parts to the apparatus, the first being MALDI and the second which measures the time of flight of the excited particle (TOF). The matrix consists of organic molecules that are mixed with the sample (e.g., a mutated plant sample). The ionizing source which is a pulsed laser ionizes the matrix and sample mixture converting them to high-energy ions. The excited ions (matrix+ sample) are accelerated in the chamber and allowed to move in a specific direction. After a short distance, the matrix separates from the sample donating a proton to it (desolvation). The separated sample ion moves to the detector, and its time of flight is detected in the form of peaks on a display. The time of flight is proportional to mass to charge ratio of the ions

Similarly, Frerichmann et al. (2013) studied polymorphisms in BvFL1 gene, associated with winter hardiness in beetroot. Nowadays, EcoTILLING identifies the role of genetic polymorphism in phenotypic variations with the help of computer programs such as TASSEL. This coupling with computer programs allows EcoTILLING to be more feasible in crop improvement programs (Kong et al. 2014).

20.3.4 High-Resolution Melt Analysis

Another approach known as high-resolution melt analysis (HRM) is used to screen the population from TILLING procedures. The process involves the use of fluorescently labeled DNA which is subjected to thermal denaturation, while the fluorescence is lost in the process. The results are displayed as temperature to fluorescence graphs. Graphs of mutated lines are compared with those of wild-type varieties (Sikora et al. 2011b). Close control of temperature and monitoring of fluorescence allow the single-base mutations as mismatches in amplicons of about 500 bp length (Simko 2016). Though, the efficiency of HRM is limited by the length of the amplicons and GC content but it is most useful when the sequence under study has many short exons.

20.3.5 Matrix-Assisted Laser Desorption/Ionization Time-of-Flight Spectroscopy

Matrix-assisted laser desorption/ionization time-of-flight spectroscopy (MALDI-TOF) has been widely used for proteomics studies but is also used for screening mutations in a TILLING population. The method is very sensitive and accurate in the detection of homozygous mutations (Sikora et al. 2011b).

A mass spectrometry usually possesses an ionizing chamber where the sample is ionized, a mass analyzer in which the ionized sample particles move toward the detector in a controlled pathway, and a detector where the analysis of sample's mass to charge ratio is calculated and presented on the screen (Fig. 20.5). In MALDI-TOF, the matrix is able to crystallize the sample and allows it to absorb light at a specific wavelength. The matrix is usually composed of organic molecules. The sample is excited in the MALDI-TOF by a pulsed laser which is absorbed by the matrix. The sample is excited by the laser absorption of the matrix, and it covers a short distance after leaving the surface and taking the matrix along with it. The sample is prepared for analysis by the TOF. This happens because during desolvation, a proton is transferred to the sample from matrix-forming ions. The TOF measures the time of flight of the ion which is proportional to the mass to charge ratio. The results are displayed on the monitor attached to the apparatus (Katam et al. 2015). The principle of MALDI-TOF for mutation detection is based on analysis of base-specific fragments which are generated by using PCR prior to MALDI-TOF application. A primer with a transcription site present at 5′ end is used for PCR. Once the transcripts are achieved; fragments are produced using RNAses. Gut (2004) used an alternate approach where DNA polymerase which attaches NTPs was used in the PCR. The NTP substrate was supplied in the PCR recipe, and any of the dNTPs were replaced by an NTP, and fragments were obtained by alkali backbone cleavage at NTP points.

Kamal et al. (2009) applied MALDI-TOF mass spectrometry to study cultivar-specific proteins in wheat. The different concentrations of proteins which were related to pathogen-related proteins, abiotic and biotic stress proteins, proteins
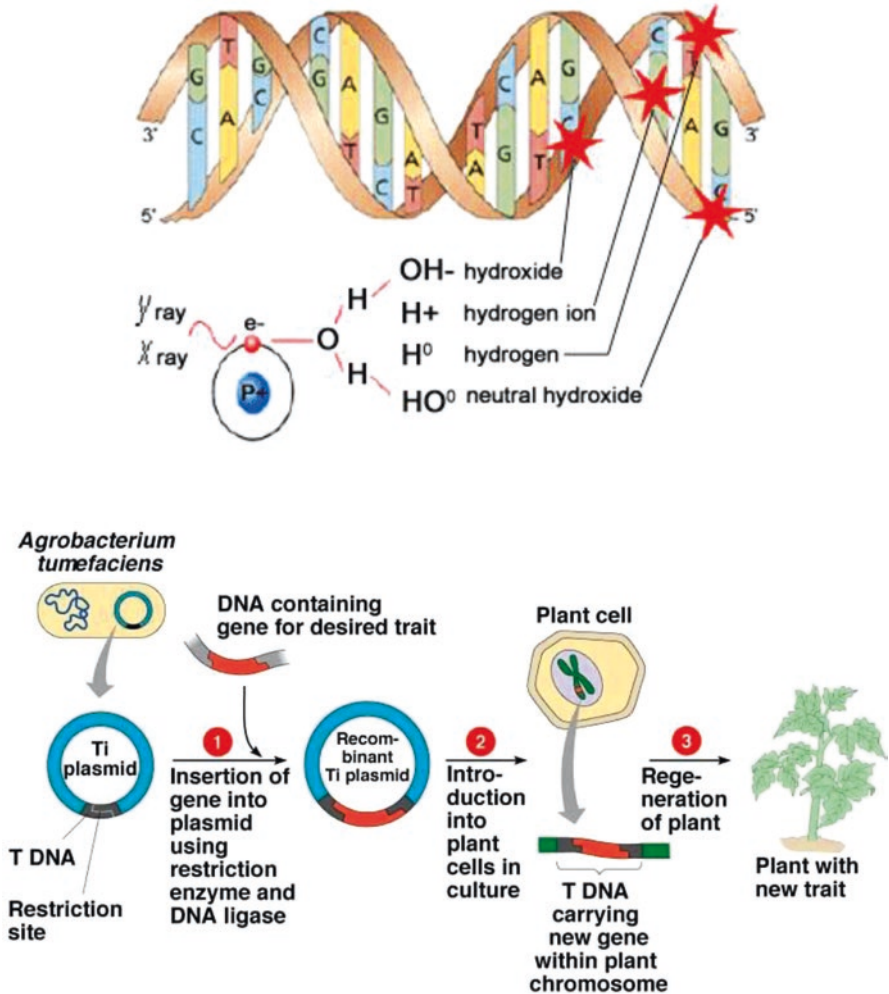
Fig. 20.5 Agrobacterium-mediated gene transformation. The agrobacterium-mediated gene transformation is carried out in vitro via tissue culture technique. The plant cell (target plant) is subjected to transformation. The T-DNA of Ti plasmid is modified by engineering the target gene into the plasmid. The virulence gene of the agrobacterium is removed and allowed to clone. The transformation is done by co-inoculating the bacterial cell and the plant cell in a media. The T-DNA is transferred into the host pant with the help of proteins. Once in the host cell, the T-DNA carrying the gene of interest integrates into the host cell genome. If transformation is successful, the gene begins to express. The transformed cells are grown by tissue culture into a callus and into a plantlet. The plantlet is subjected to hardening which forms into a transformed plant. The transgenic plant may be taken for field trials

responsible for roughness and viscoelasticity of wheat, proteins responsible for causing allergies in consumers, proteins responsible for grain textures, and other proteins responsible for antimicrobial and toxin activity were observed. Westphal et al. (2010) screened cell wall mutants which could be used for further analysis in *Arabidopsis* using MALDI-TOF.

20.3.6 MutMap

The latest developments in genome sequencing technologies have eased the scientists and breeders to study phenotypic changes and associate them with different genome sequences. A recent technique, MutMap is now applied to study the casual nucleotide changes in plant genome. MutMap accelerates the genetic improvement of many crop plants significantly rice. In MutMap a recessive mutant having the phenotype of interest is crossed with the parental line used for the mutagenesis. The DNA of several individuals of mutant F2 progeny is sequenced. The short reads obtained are aligned with reference sequences which are constructed using the parental lines. The resulting alignment is used to infer the genomic location of the casual mutation that was responsible for the change in phenotype (Abe et al. 2012). The reference sequence should contain the genomic fragment spanning causative mutation which is unfortunately not guaranteed. This is because the reference sequence is constructed using the reference genome of a representative cultivar or line of the species, for instance, cv. Nipponbare in rice (*Oryza sativa*) and the Col ecotype in *Arabidopsis thaliana.* The parental line will be resequenced, and the nucleotides of the reference genome will be replaced with those of the parental line at all available SNPs. MutMap is particularly useful for crop species because it minimizes the number of genetic crosses and mutant F2 progeny that is required. Abe et al. (2012) applied MutMap to seven mutants of a Japanese elite rice cultivar. They successfully identified the unique genomic positions that most probably caused the mutations that lead to pale green leaves and semi-dwarfism. Fekih et al. (2013) further enhanced the MutMap technique calling it MutMap+. Through this method, it is not necessary to cross mutants and the wild-type parental line artificially, and thus it is useful in detecting mutations that cause lethality or sterility during early developmental stages. It is also a good approach for isolation of genes in plants that are recalcitrant to artificial crosses.

Despite its efficiency, the MutMap cannot identify gaps when comparing with the reference sequences. For this purpose, a new technique which is a combination of MutMap and de novo assembly of gap regions called the MutMap-Gap has been applied.

The MutMap-Gap technique involves delineating a region of interest that carries the required mutation using the MutMap method and followed by de novo assembly, alignment, and identification of the mutation within genome gaps. Takagi et al. (2013) successfully applied the MutMap-Gap method to isolate the blast-resistant gene Pii from cv. Hitomebore in rice mutant lines that have nonfunctional Pii gene. It is inferred that MutMap-Gap method will further value the application of

whole-genome sequencing in isolating novel plant genes using forward genetic approaches.

20.3.7 In Vitro Mutagenesis

In vitro mutagenesis also known as cell culture mutagenesis is used to produce somaclonal variation in plants which are later screened concerning a particular condition such as for drought tolerance, disease resistance, or resistance against other abiotic stress (Lestari 2012). Mutation induction during tissue culture enhances the effectiveness of mutation. It is easier to differentiate between mutated and non-mutated varieties as tissue culture also allows a variety of parts to be used for inducing mutation. It also encourages the use of large population to be subjected to mutagens and also selection and cloning of mutated variants (Jain et al. 2013). Tissue culture also solves the problem of heterozygosity and absence of a phenotype due to the existence of mutation as predominantly recessive. To obtain homozygous alleles, several cycles of regeneration are required in the conventional method, while tissue culture saves capital and time that is utilized in the regeneration of cycles by producing double haploids (Suprasanna et al. 2015).

Mutations cannot only be induced blindly, but in the era of molecular biology and genomics, they can be applied, modified, and detected by using various new techniques. These techniques may not necessarily involve the use of traditional mutagenesis to induce mutations in plants; rather, they are focused on introducing mutations at the molecular level.

20.3.8 Transposable Element Insertion and RNAi Mutants

Transposable elements are either introduced or are activated in genes and cause such changes in the genotype that are easily detected in the phenotype. This technique can be characterized as both forward and reverse genetics because these elements allow one to study specific gene sequences on the basis of a specific phenotype (Azman et al. 2014). On the other hand, in order to create mutants in crop varieties, techniques such as RNAi or antisense RNA suppression technique are applied although RNAi mutants produced have a very low range of allele varieties.

20.3.9 Gene-Targeted and Transcriptome Mutations

Specific genes of interest are targeted for modifications so as to achieve maximum desired results. A gene can be modified by either completely inactivating it, or a novel sequence appears suddenly due to successful repair of the DNA. This also gives the opportunity to introduce a gene of interest in the DNA break (Peer et al. 2015). Gamma ray mutation brings about modifications in the transcriptome. Batista et al. (2008) observed 11,000 affected genes in rice after exposure to gamma

radiations. These changes give an opportunity to study the expression of many genes and then tailor them for novel traits and characteristics as per requirement in different crop plants. Using this technique, even the silent mutations can be detected easily.

20.4   Other Advanced Molecular Techniques and Crop Improvement

With the advancement of molecular biology, many sophisticated techniques are now being practiced for the improvement of various crop plants. The need for producing a large amount of food grains and economically important crops has led to much research in the field of molecular biology. The early techniques of enhancing the food grains were based on Mendelian genetics. Later the release of new semi-dwarf varieties of rice and wheat for increasing food production resulted in "Green Revolution." Finally many of the breeding programs were based on the modern tools and techniques of cell and molecular biology. The latter was equipped with other techniques of identifying the useful loci carrying the gene of interest known as quantitative gene loci (QTL) which led to a new era of plant breeding that made use of genomics. The last two decades have witnessed a remarkable activity in the development and use of molecular markers in plant systems that revolutionized the crop breeding methods (Gupta et al. 2008). Next-generation sequencing and array-based assays have further added to the revolutionary process, and the technology has now become high throughput with the effective use of bioinformatic tools (Kage et al. 2015). Many techniques can be carried out in silico that makes the process and progress of crop improvement cost-effective, fast, and accurate. Nowadays, the crop improvement has been taken to a much greater level without using traditional breeding approaches. These new techniques include the tissue culture applications especially those involved in genetic transformation of the crops and also the latest technique of RNA interference.

20.4.1 RNA Interference

RNA interference (RNAi) has immense potential in opening a new vista for crop improvement as it interferes with the expression of genes in a specific mechanism that degrades its complementary mRNA. It has been employed successfully to alter the gene expression in plants for better quality traits like nutritional improvement in terms of bio-fortification and bio-elimination and also in overcoming the biotic and abiotic stresses (Saurabh et al. 2014). For gene silencing, miRNAs are extensively used. Many aspects of the plant growth including floral differentiation, leaf morphogenesis, transition from the vegetative stage to reproductive growth, hormonal changes, defensive mechanisms against pathogen invasions, and responses toward environmental stress are controlled by miRNA (Saurabh et al. 2014).

One of the main limitations of RNAi occurs when siRNA-based RNAi plays a role in antiviral defense mechanism as plant viruses encode proteins that suppress silencing (Alvarado and Scholthof 2009). Also, suppressors of silencing from unrelated viruses involve a variety of mechanisms to block silencing, thereby making it difficult to persuade broad-spectrum protection. Another major limitation is that post-transcriptional silencing in plants is mobile which once induced locally can then spread throughout the plant. Thus, siRNA-based RNAi strategies might not be suitable for applications where tissue-specific silencing of genes is required.

20.4.2 Plant Tissue Culture and Genetic Engineering

Tissue culture is the method of clonal propagation that consists of a set of in vitro techniques and strategies. These methods have been exploited to create genetic variability for crop improvement. Crop improvement is achieved by producing gameto-clonal and somaclonal variation in the plant.

Tissue culture helps in improving the state of health of the planted material and also increases the number of desirable germplasms available to the plant breeder. Tissue culture techniques in combination with molecular techniques have been successfully used to incorporate specific traits through gene transfer.

It is believed that for decades to come, genetic engineering will be the answer to the rising problems of the world. Genetic engineering tools produce plants with superior traits that are incorporated into the genome as well as engineered to produce high nutritional value crops (bio-fortification) and also modify plant products such as starch, oil, etc. for industrial or commercial use (Zhu et al. 2013). Genetic engineering improves crops by improving quality of plant products, increasing yield and productivity, and producing plants resistant to biotic and abiotic factors. Useful genes are incorporated in the plants from bacteria, animals, or other organisms by chemical, mechanical, or biological (via biological organism) method.

Genetic transformation can be carried both by direct method and indirect method. In the direct method of gene transformation, the gene is transferred using methods like electroporation, liposome-mediated transformation, microinjections, biolistics, and microprojectile bombardment or through chemical method usually using polyethylene glycol. On the other hand, in the indirect method, the transformation of the gene of interest is carried by a biological vector which is generally *Agrobacterium tumefaciens* or *A. rhizogenes* or vectors of viral origins. This pathogenic bacterium transfers its DNA segment known as T-DNA found in the Ti plasmid (extrachromosomal DNA) into the host cell. Once this T-DNA is incorporated into the host cell genome, the desired trait is expressed in the cell (Fig. 20.3). Transgenics for useful traits have been studied in many crop plants (Datta 2012, 2013).

20.4.3 QTL Mapping and MAS

Basically, breeding is giving rise to a progeny that is better than its parent by crossing the best varieties together. Many of the traits that are of economic value are controlled by many loci at a time, and each locus has a positive or negative effect upon the trait. These loci are termed as QTLs (quantitative trait loci) which are tightly linked with one or groups of genes that inherit together. The progeny with elite traits is usually backcrossed many times with its elite parents so as to make the trait stable and to introgress a single gene. With each generation of backcross, the gene of interest is selected, and recovery of plants with superior genotype is done. Gene pyramiding is done in the same way by crossing and introgressing more than one gene for the same trait followed by selection. Another breeding known as pedigree breeding is done to make elite varieties in which parents with the elite genotype are crossed and their F1 generation is then self-pollinated to make the plant genotype stable. The identification of QTL associated with a complex trait is difficult and requires a closely linked DNA marker called as marker-assisted selection (MAS). MAS has become important for the traits governed by both major and minor genes. It can also be used to exploit and introgress the desirable traits that are present in the wild type. This approach is an important technique to identify useful traits that can be scrutinized and can be used toward crop improvement. The success of a breeding project mainly depends upon the choice of the parents that need to be crossed, the size of the population, and the individuals chosen for phenotypic and molecular analysis.

Gene pyramiding phenomenon works well to cumulate the superior trait genes present in the parents in a single plant against resistance to biotic and abiotic stress. Gene pyramiding has been applied successfully in wheat, against powdery mildew and rust diseases, and in barley against yellow mosaic virus and against soybean mosaic virus (Suzuki et al. 2015). Gene pyramiding gives the elite variety in just two subsequent generations (Joshi and Nayak 2010). Gene pyramiding, when applied along with genetic markers (biological features), is very efficient and can make the screening of desirable traits much faster. Since the genetic markers are close to the gene of interest on a chromosome, they are passed from generations to generations. This phenomenon is known as genetic linkage.

The possible advantage of MAS over conventional breeding is that these markers will only be useful and effective for every trait, if a huge investment is made in time, money, and resources required for their development. These do not have much role for those traits where effective phenotypic screening methods already exist and the traits where their genetic control is known or understood.

Many markers of desirable traits and disease resistance traits are now available for the majority of the important crops (Ibitoye and Akin-Idowu 2015). These markers includes (a) restriction fragment length polymorphism (RFLP), (b) random amplification of polymorphic DNA (RAPD), (c) amplified fragment length polymorphism (AFLP), (d) sequence-characterized amplified regions (SCAR), (e) sequence-tagged sites (STS), and (f) simple sequence repeat (SSR).

RFLP are hybridization-based markers which are probed with specific DNA sequence as their restriction sites are changed in the target DNA. Different restriction enzymes may be used to detect polymorphism, and these fragments are separated on agarose gel. This method is time-consuming and has the involvement of radioactivity for detection purposes due to which it has been replaced by other PCR-based markers like RAPD, AFLP, SCAR, STS, SSRs, and SNPs. Of these, SSRs are the "markers of choice" due to the high rate of polymorphism, no prior genome information, and low cost of production. Nowadays, SNP markers are considered to be a high-throughput marker that can be used for screening of crops. These are based on point mutations, and their main limitation is that they are biallellic. SNPs are only restricted to major food crops but have been identified in silico from EST database or genomic databases.

In the urge of speeding up the process of selection and in turn breeding process, the development of microarrays on DNA chips was introduced. Microarrays have several spots of microscopic DNA that are immobilized over a solid surface that may be of nylon, glass, or silicon. These DNAs act as probes for its complementary mRNA. These are SNP-based markers which are used to transcript profiling of a cultivar by measuring the differences in hybridization signals. The level of polymorphism is detected by the amount of hybridized mRNA to it respective probes (Akpınar et al. 2013).

20.4.4 Next-Generation Sequencing

Few years ago, sequencing was very expensive and laborious. The problem is solved by the new array of sequencing technologies such as Roche/454 FLX Pyrosequencer, Illumina/Solexa sequencing, SOLiD sequencing, HeliScope single molecule sequencing, single molecule real-time (SMRT) sequencing, massively parallel signature sequencing, DNA nanoball sequencing, Ion Torrent semiconductor sequencing, and polony sequencing. Roche/454 FLX Pyrosequencing was one of the first methods introduced as the NGS. It uses the measurement of light that is produced proportionally to the number of nucleotides incorporated by DNA polymerase enzyme in the chain. In Illumina/Solexa sequencing, the nucleotide bases are labeled with a specific fluorescent dye and a special DNA polymerase for them. The read length is from both the paired ends.

20.4.5 Diversity Arrays Technology

The research of new SNP markers and then finding of more and more efficient assays to analyze or genotype SNPs is a very expensive and tiring work. A new promising technology of Diversity Arrays Technology (DArT) is able to discover many markers at a time and does not demand for an assay to detect them. This had been developed as a powerful tool for whole-genome fingerprinting tool (Kilian et al. 2012). DArT makes use of a complexity reduction step similar to the AFLP

marker that is used both for the generation of arrayed probe sequences and production of labeled target DNA. DArT has been applied to a wide range of crop species because no prior genomic or DNA sequence is required. Since the markers are derived from a random library, the map position of each marker has to be determined experimentally. DArT technology is a good technique for species with large and complex genomes where sequence-based markers are difficult to obtain. There is currently a growing potential for the increased use of microarrays in crop research. A greater range of technological platforms will become available for more crops as sequencing efforts will proceed and as new resequencing methods will provide large number of new potential molecular markers (Galbraith and Edwards 2010).

DArT assay has been developed for about 16 crops including rice being the first one, wheat, barley, and sugarcane (Castillo et al. 2013).

20.4.6 Genome-Wide Association Studies and Genomic-Wide Selection

Finding the genetic basis of agronomic traits has been one of the major scientific challenges in the process of crop improvement. Most of the agronomically important traits are quantitative in nature, and hence finding the discerning genetic differences underlying the phenotype of interest is a difficult task. More recently the use of genome-wide association studies (GWAS) and wide genomic selection (GS) is applied for plant breeding. This technology covers the whole genome so that all the genes are expected to have a linkage disequilibrium and also the population of unrelated individuals.

A number of unbiased set of common SNPs were studied in rice by Huang et al. (2011) to identify strong associations between genetic loci and different agronomic traits like heading date, grain size, and starch quality.

In genome-wide association studies, the traits that are strongly confounded reduce the power of the analysis and can lead to false negatives. Traits such as flowering time and cold tolerance, which are governed by environmental gradients, reduce the association signals around major adaptive genes (Bergelson and Roux 2010). Also rare alleles that are involved in natural variation are not detected.

20.5   Molecular Cytogenetics

Molecular cytogenetics of plants is a field of molecular biology that includes techniques that are applied to identify the physical position of a known gene on a chromosome.

The power of cytogenetics has increasingly focused on two related aspects of the genomic in situ hybridization (GISH) and fluorescence in situ hybridization (FISH) technique Advances in microscopic sensitivity, signal increase, and noise reduction have all contributed to improved detection limits. The use of cytogenetic tools to

guide genome sequencing efforts in tomato and potato has been a milestone to study synergy between plant genomics and cytogenetics (Figueroa and Bass 2010).

FISH and GISH are frequently used for chromosome mapping in plants, to identify the chromosomes using species-specific genes or ribosomal genes. Using this physical technique, mapping of many crops has been carried out. GISH is also used in characterization of hybrid plants and recombinant breeding lines. GISH can elucidate the relationship between wild and cultivated plants to identify their ancestry that can be identified in terms of phylogeny and taxonomy. The FISH patterns of a tissue culture regenerated population can be useful in identifying the somaclonal variation occurrence in the individuals. These results are useful specially when inducing mutations in the plants for crop improvement. GISH and FISH help in the detection of an alien chromosome in new plant varieties that may have segregated along with the desirable trait during the crossing (LU and Ellstrand 2014).

20.6   Bioinformatics and Crop Improvement

Progress in plant genomics based on omics research has led to significant discoveries. This has modernized the methods of crop improvements. The high-throughput methods of analyzing the immense amount of genomics and proteomics data have made it possible for scientists to sequence the genomes of model plants like *Arabidopsis* and rice and construction of large-scale EST libraries for large-scale comparative analysis (Chuang et al. 2015). Compared to the conventional methods of crop improvement, the latest techniques of molecular breeding like QTL and MAS have greatly increased the efficiency of the breeding process. MAS has limited role, when it comes to the selection of complex traits which are controlled by many genes and also genes with discrete phenotypes (Bosquet et al. 2012). The availability of genomic tools and resources has facilitated the study of the relationship between the genotype and its phenotype, particularly for complex traits.

The mass sequencing of genomes and transcriptomes using NGS is producing vast data, and thus the genomes can be tailored as per breeders' needs. This has helped us to understand the complexity of the genome of an organism and their role in evolution. Even the resequencing of genomes is useful for genome-wide discovery of markers (Perez-de-Castro et al. 2012; Barabaschi et al. 2016). The advent of NGS has unhidden all the valuable genes which were once hidden in landraces and wild cultivars and also their current diversity present in the gene pool.

Even an in silico paleogenomic study which is based on a deep comparison of monocot and eudicot genomes has allowed the reconstruction of ancestral protochromosome segments and has provided the description of the evolutionary dynamics which lead to the present-day genomes, their organization, and regulation (Salse 2012).

20.7   Conclusion and Prospects

Crop improvement is a fundamental process that needs to be performed rapidly and efficiently so as to meet the requirement of commercial and industrial crops in today's time. This paper emphasized on the molecular techniques and techniques applied to induce mutations to produce better crops in respect to yield, productivity, resistance against biotic and abiotic stress, and enhanced production of secondary metabolites. Induced mutation has been seen to be an effective, safe, cheap, and successful technique for introducing new and improved crop varieties. Techniques such as TILLING and EcoTILLING have greatly contributed toward the improvement of this method. However, these techniques are not frequently applied for the concerned purpose mainly due to the large population size of putative mutants that needs to be handled and repeated crossing of the plants to many generations in order to eliminate the presence of chimeras. Moreover, the mutations are usually recessive and require repeated crosses to achieve viable homozygous plants.

Induced mutation is not only a useful technique in crop improvement but also overcomes the regulatory restrictions imposed on GMOs. It involves screening approaches along with the reverse genetic selection of useful mutations that could result in a major impact on crop breeding in the near future. It is frequently applied for functional genomics, and new genes are exploited for their new functions, thereby indirectly contributing toward crop improvement. Gene editing through induced mutations has allowed improvement in nutrition, plant breeding procedures, seed oil composition, weed protection, and disease resistance in polyploidy food crops including wheat, citrus, potato, peanut, cotton, apple, and *Brassica* oils including rapeseed, *Camelina*, and canola (Weeks 2017).

Recent techniques in inducing and screening mutations allow the identification of novel alleles of target genes within existing germplasm collections and mutagenized populations, thereby assessing the candidate genes for future crop improvement. Researchers are adopting plant gene editing techniques including CRISPR-Cas genome editing tools, which have potentials in work on model organisms, evolutionary studies, and improvement of food crops (Carroll 2017).

Although molecular biology is now much advanced and new techniques are available to speed up the process of crop improvement at low cost, still much work is required in the field to achieve the required target of crop production. One such hindrance is the identification of desirable traits. Not many elite traits are available for manipulation in the gene pool that can give improved crops. This can be achieved by extensive knowledge of functional genomics which is possible by the integration of various fields such as bioinformatics, biotechnology, molecular biology, and biochemistry toward identifying useful traits. Another challenge faced in plant breeding for crop improvement especially in MAS of QTLs is of analyzing the data and scoring methods available to do so especially when a large size of population is under study. Improved scoring methods and screening tests need to be developed to make screening of bred plants more efficient and make it possible to breed useful traits effectively.

It will be advantageous if other fields of biology also contribute toward crop improvement along with molecular biology. More focus needs to be given to cash crops and food crops such as rice, wheat, potato, cassava, cotton, etc. Utilization of genome-wide approaches, such as genome sequencing, is helping to design the new plant with selected traits for all the loci in the genome, in a cost-effective manner. This would eliminate the need for extra multi-location field trials at each generation but would only require some phenotyping to maintain and increase the accuracy of the prediction models. With newer techniques being introduced in the field of molecular biology and their use in plant breeding, novel alleles will not be impeded from the crops, and this will assure a continuous supply of food grains, and the problem of food shortage as foreseen can be avoided.

The development of mutated crops will lead to the satisfaction of high demand of consumers, nutrient-rich crops, food safety and security, and production of high value-added crops in the future (Ilahy et al. 2018). These improved crops are expected to produce pharmaceutically important compounds and show resistance to biotic and abiotic stresses. However, there is a long way to go to achieve success in commercialization of mutated plants (Dawkar et al. 2018).

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Use of Biostimulants to Improve Salinity Tolerance in Agronomic Crops

21

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Abstract

The world population is exceeding 7.63 billion, resulting in more than quadrupled compared to that of 1915 (1.8 billion), and according to the United Nations most recent predictions, we may reach 9.7 inhabitants by the year 2050. This exponential growth, along with the shift from rural to urban life, the increase in per capita food consumption, and the changes in diet in developing countries, due to the rise in income, are driving up the global food demand, which is expected to increase worldwide from 59% to 98% in the next 30 years. However, it will be hard to square the twin challenge of reconciling a maximization of agricultural production with environmental sustainability. Indeed, in the last 50 years, mechanization and new management techniques based on the massive use of fertilizers and irrigation have increased agricultural production also in arid and semi-arid areas, but they have also exacerbated the problems of soil salinity and pollution. In fact, one of the most serious effects of these unsustainable practices has been the salinization of at least 20% of all irrigated and productive lands. Therefore, the main objective of modern agriculture is to increase crop yield production and potential, also in marginal and salinized areas, through innovative farming systems and/or products with an eco-friendly approach. Among the new products which have favorable effects both on soil and cultivated crops, even under environmental constrains like salinity, are biostimulants. They include substances, metabolites, or mixtures of metabolites and/or microorganisms which, when applied to plants or soil, increase the nutrient availability, uptake, and assimilation while reducing the use of agrochemicals in agriculture

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and improving food resources, preventing leaching of nutrients, and increasing the response to stress in an eco-friendly perspective. Biostimulants do not replace fertilizers or pesticides but represent a complement to the action of both fertilizers and crop protection products, allowing enhancing crop performance even under stress. We will consider the biostimulants derived from plants or animals like seaweed extracts, humic substances, protein hydrolysates, microbial inoculations, etc. and will describe their beneficial effects on plants, especially nutrient use efficiency and plant fitness to abiotic stresses and in particular to salinity.

Keywords

Biostimulants · Salinity · Abiotic stress tolerance · Resource use efficiency · Seaweed extracts · Humic substances · Protein hydrolysates · Microbial inoculations

Abbreviations

APX	ascorbate peroxidase
CAT	catalase
EBIC	European Biostimulants Industry Council
GMOs	genetically modified organisms
GR	glutathione reductase
HS	humic substances
MF	mycorrhizal fungi
PGPR	plant growth-promoting rhizobacteria
PHs	protein hydrolysates
ROS	reactive oxygen species
RUE	resource use efficiency
SOD	superoxide dismutase
SWEs	seaweed extracts

21.1 Introduction

Agriculture is an essential component of the economic and productive system of many countries. Since the last century and in particular over the past five decades, conventional agriculture has spread all over the world, replacing the traditional one. Thanks to the green revolution, the possibility to use high-yielding variety seeds, chemical fertilizers, and pesticides together with mechanization has oriented farmers toward the objective to maximize production and profits. Over time, it has

allowed tripling the cereal crop production increasing only of 30% the cultivated land area and to cope with the doubling of world's population (Wik et al. 2008). However, this agricultural model has required not only large public investment in crop engineering and technologies, mainly by developed countries, but has also entailed the use of intensive agricultural practices critical for the ecology of the agricultural system as well as for the environment in general and directly or indirectly on human health (Pingali 2012). The use of high-yielding varieties has brought about, in fact, high inputs of fertilizers, water, and pesticides and at the same time intensive tillage. These practices, disturbing soil microorganisms' biological activity and diversity, have led to soil erosion, runoff, and loss of soil organic matter (Annunziata et al. 2013). Moreover, they have determined accumulation of pollutants in soil and water, nonselective toxicity on fauna, induced resistance by pests, reduction of biodiversity, and presence of potentially harmful chemicals in food products (Pingali 2012 and references therein).

In order to limit these negative effects, various agricultural production systems with a lower environmental impact have been introduced, like integrated agriculture, eco-compatible agriculture, sustainable agriculture, and biodynamic and organic farming. All of these agricultural systems imply a sustained crop production without relying on chemical synthesis products in the field and/or invasive practices, like intensive tillage and monoculture, for preserving natural resources and environment (De Pascale et al. 2012; Tal 2018; Muller et al. 2017; Bullock 1992).

In recent years, expectations and demands of consumers for good-quality and healthier food and government policies focused on eco-friendly agriculture practices have both boosted organic farming system (Dornburg et al. 2010). Between 2008 and 2016, organic horticulture has almost doubled, with about 3.5 million hectares cultivated following this production system, practiced in more than 87 nations (Willer and Lernoud 2016). Organic farming, according to the European Union Organic Regulation 834/2007, is a global system of "farm management and food production" relying on the beneficial interaction between eco-friendly practices, preservation of natural resources, conservation and protection of plant and animal biodiversity, and crop production obtained with natural substances and processes.

However, the main disadvantage of organic farming compared to the conventional one is the lower yield that makes it necessary to increase the surface area of the soil to obtain the same amount of product and therefore to deforest a larger area to be used for agriculture, limiting the environmental benefits of biological system (Seufert et al. 2012). Recent studies conducted on the productivity of the nonconventional systems have shown that the decrease in yield of organic farming can range between 5% and 34%. This decrease can be mainly attributable to reduced availability of nutrients such as N and P and to a greater biotic pressure that is expressed in the increase in fungal, bacterial, or parasitic diseases in general (Seufert et al. 2012; Orsini et al. 2016; and references therein). These aspects are in contrast with the need to increase crop production to meet the growing food demand from the rapidly expanding human world population. The predictions based on recent studies conducted in the United Nations estimate a population of almost ten billion by 2050, increasing the agricultural demand by 50%, at least, compared to 2013.

The better per capita incomes in developing countries would imply higher consumption of meat, fruits, and vegetables compared to that of cereals, boosting the pressure on soil, water, and already heavily depleted ecosystems (FAO 2017).

Nowadays, agriculture is responsible for the 69% of freshwater withdrawn worldwide, and in the coming decades, the share of this resource accessible on Earth may not be sufficient to meet the anthropic demands (UN 2018). In addition, agricultural lands, particularly in arid or semi-arid regions, which require more frequent irrigation, undergo secondary salinization that reduces productivity. Today, around 15–20% of irrigated soils are characterized by an increase in salinity that hinders the development of most crops (Carillo et al. 2011a; Machado and Serralheiro 2017).

Allocating new areas of the land surface for agricultural use to support global food needs would result in a significant increase in costs in ecological terms due to the consequent increase in CO_2 emissions and loss of biodiversity. Therefore, the most satisfactory alternatives are those that aim to increase the yield per unit of land area in a sustainable way.

A very important approach is that of genetic engineering, which could allow obtaining transgenic lines of some species of crops able to grow and develop even in environmental conditions characterized by high salinity or low water availability. However, the use of genetically modified organisms (GMOs) creates concern over potential unintended effects and new risks to food security and environmental and human health and therefore implies numerous ethical, political, and social implications (Maghari and Ardekani 2011).

On the contrary, a promising and sustainable alternative that is attracting global interest is the use of natural substances and microorganisms, called biostimulants, that can improve the resource use efficiency by plants and increase their ability to tolerate and react to biotic or abiotic stresses(du Jardin 2015). Biostimulants represent a valuable tool that can help to reduce the yield gap between the organic production system and conventional agriculture with more efficient and environmentally sustainable use of natural resources. Their use can respond to the increasing global food demand and at the same time meeting the requirements of food security and quality of products (Colla and Rouphael 2015; Van Oosten et al. 2017).

21.2 Salinity Stress

Soil salinity is one of the most widespread threats limiting the yield potential of agricultural crops, which affects all climatic regions, mostly in arid and semi-arid regions(Hasanuzzaman et al. 2014). Agricultural losses caused by this abiotic stress are difficult to evaluate, but it has been estimated that it jeopardizes the food production of about 6% of the worldwide cultivated lands and 20% of all irrigated lands (Aslam et al. 2017; Munns and Tester 2008; Hasanuzzaman et al. 2013). Climate changes will exacerbate this phenomenon; predictive models have estimated that irrigated soils affected by salinity may reach 50% in the coming years (Pitman and Läuchli 2002).

Soil salinity can be caused by many natural or anthropogenic factors. Primary salinization is mostly due to the intrinsic characteristics of the soil and natural factors, while secondary salinization is mainly due to human activities. The main factors liable for primary soil salinization are weathering of rocks, capillary rise from shallow brackish groundwater, intrusion of seawater in fresh aquifers along the coast, salt-laden sand blown by sea winds, hindered drainage, and last, but not the least, seasonal rainfall variability. While the human activities that cause secondary soil salinization are the deleterious practices in agricultural management, in particular the introduction of irrigation without proper drainage system, excessive use of fertilizers, removal of natural plant cover, flooding with salt-rich waters, and use of poor-quality groundwater for irrigation (Rasool et al. 2013; Carillo et al. 2011a).

On the basis of their different ability to tolerate salinity, plants can be classified into glycophytes and halophytes. Halophytes are plant species able to complete their life cycle even under conditions of high salt concentration in the soil. Most of the terrestrial plants including agricultural crops are, instead, salt-sensitive glycophytes, and their growth is strongly inhibited by high levels of salt which cause osmotic stress and ion toxicity (Cheeseman 2015; Munns and Tester 2008; Gorham et al. 2010). In alkaline soils, the excess of sodium ions interacts with the negative charges present on the surface of the soil particles, hindering their interaction with other particles. In this way, the soil is more compact, less permeable, and aerated, with resulting problems soil hypoxia (Keren 2003). Moreover, if evapotranspiration exceeds the amount of irrigation and rainfall, the excess of Na^+ and Cl^- in the soil solution causes a lowering of its osmotic potential and consequently a reduction of root water uptake ability, stomatal aperture, and transpiration and therefore an alteration of all plant water relations (Zhu 2003; Munns 2002; Läuchli and Epstein 1990; Flowers et al. 2015; Annunziata et al. 2017). In particular, when sodium is present at high concentration in the plant cells, it is able to substitute potassium in key enzymatic reactions inhibiting enzymes, affecting metabolic processes, and inducing plant nutritional imbalance and oxidative stress. These effects further impair processes like protein synthesis, enzyme activities, and photosynthesis, reducing plant growth and development (Carillo et al. 2011b; Hasegawa et al. 2000; Munns and Tester 2008) (Fig. 21.1). Germination and seedling stages are particularly sensitive to salt toxicity (Ferchichi et al. 2018).

However, plants try to limit stress damages and restore growth by sequestrating toxic ions (mainly sodium and chloride) in the vacuole, as cheap osmotica, and synthesizing and accumulating compatible osmolytes in the cytosol to prevent toxicity and osmotically adjust the cell (Annunziata et al. 2017). The synthesis of these compatible compounds is energy-consuming (50–70 moles ATP for mole) (Raven 1985; Shabala and Munns 2012), but they, in addition to their supposed role as osmolytes, can scavenge reactive oxygen species (ROS), osmoregulate the cytosolic compartments, stabilize membranes, buffer redox potential, and induce salt-responsive genes (Carillo 2018).
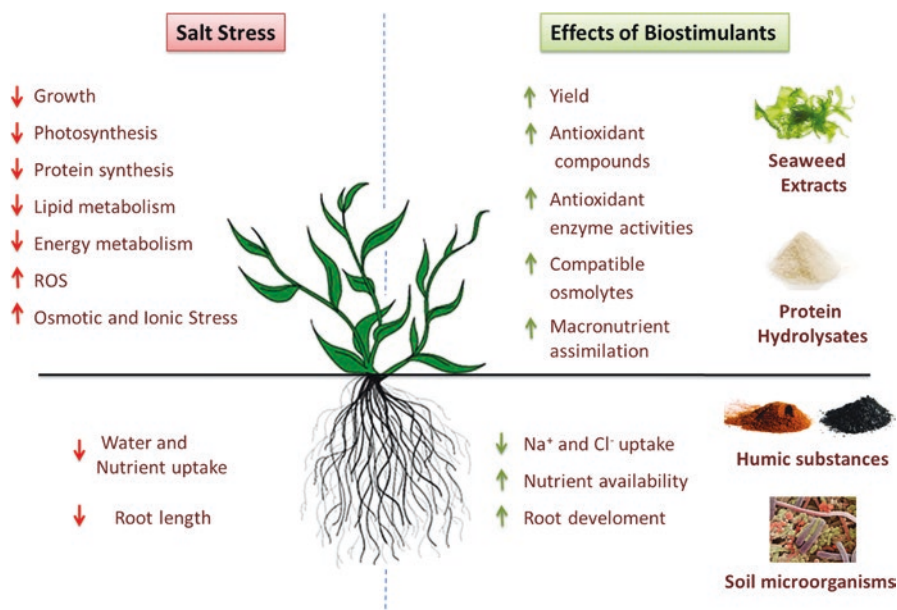
Fig. 21.1 Overview of the effects of salinity stress and biostimulant application on plants

21.3   Biostimulants

Plant biostimulants are substances or microorganisms that when introduced into the plant growing environment may have positive effects on growth and tolerance to biotic and abiotic plant stresses. Biostimulants increase the availability, uptake, and assimilation of nutrients, as well as the resistance to environmental stresses such as the presence of parasites or pathogens, water deficit, soil salinization, and exposure to suboptimal growth temperature (du Jardin 2015) (Fig. 21.1). Biostimulants are not nutrients and do not have direct effects on parasites and pathogens, so they cannot be considered as fertilizers or pesticides (Colla and Rouphael 2015). On the contrary, they are a category of products that includes different types of materials and substances, similar to each other for the effects they have on crops, but with a very different chemical or biological composition (du Jardin 2015). They often are mixtures of complex compounds or aggregates that make it difficult to determine which of the specific components make positive contributions (Van Oosten et al. 2017). The improvement of the nutritional status of plants, contextual to the use of biostimulants, may be due to synergistic and additive effects regarding the (i) improvement of biological nitrogen fixation processes, (ii) higher mineralization of dead organic matter by microorganisms,(iii) better mobility and solubility of nutrients, (iv) structural changes of roots which increase the volume of soil accessible by the root system itself, and (v) upregulation of transporters and enzymes involved in uptake and assimilation processes in various tissues (De Pascale et al. 2018) (Fig. 21.1).

Usually, in the soil, less than 5% of total nitrogen is present as inorganic nitrogen compounds (i.e., NH_4^+, NO_2^-, and NO_3^-), although it is essential for the normal growth of the plant and the main form of the element absorbed (Brady and Weil 2008). In agriculture, the maintenance of soil fertility to meet the nutritional requirements of crop plants is guaranteed by the application of organic and inorganic fertilizers (Hartz 2003). However, not all the fertilizers applied to soil are absorbed and available to the plants, since most are lost by leaching, volatilization, and denitrification (Brady and Weil 2008). In particular, losses of nitrogen fertilizers from the soil/plant system can not only decrease soil fertility and crop yield but also severely impact on the environment, causing eutrophication, greenhouse effect, and acid rains (Cameron et al. 2013; Gastal and Lemaire 2002). Moreover, the consumption of contaminated water or crops containing high amounts of nitrates and nitrites can be very dangerous for animal and human health (Cockburn et al. 2013). Biostimulants can improve the nutrient uptake and assimilation efficiency in plants while reducing the use of agrochemicals in agriculture and improving food resources, preventing leaching of nutrients, and increasing the response to stress (Meena et al. 2015; de Wit 1992).

The use of pesticides is regulated by European Union regulations. For this reason, targeted research is necessary in order to be able to find suitable substances that are not harmful to the environment and, at the same time, to humans. The use of chemical products in agriculture could be drastically reduced by the use of plant biostimulants, which are completely safe and do not damage the environment.

In Europe, in order to promote the growth and development of the European biostimulant industry and overcome regulatory differences between member states, the European Biostimulants Industry Council (EBIC) was legally recognized in 2013. The EBIC represents a platform for interaction and exchange of information between the various stakeholders such as farmers, industrialists, investors, scientists, and consumers. In 2012, the European Commission supported a study carried out internationally by Patrick du Jardin, which made it possible to identify and list many substances with biostimulant properties. The list includes humic substances, complex organic materials, beneficial chemical elements (e.g., silicon), inorganic salts (e.g., bicarbonates), algae extracts, chitin and chitosan derivatives, antiperspirants (e.g., kaolin), amino acids, and other nitrogen compounds. EBIC defined biostimulants as "Products containing substances and/or micro-organisms that, when applied to the plant or the rhizosphere, stimulate natural processes that improve the efficiency of absorption and assimilation of nutrients, the tolerance to abiotic stress and/or product quality regardless of their nutrient content" (du Jardin 2015). More recently, Yakhin et al. (2016) have given a more detailed definition of biostimulants to discriminate between them and the already existing product categories, among which are fertilizers, pesticides, and plant hormones. This definition describes biostimulants as "a formulated product of biological origin that improves plant productivity because of the novel or emergent properties of the complex of constituents and not as a sole consequence of the presence of known essential plant nutrients, plant growth regulators, or plant protective compounds."

Many studies have highlighted the numerous positive effects of the diverse animal- and plant-derived biostimulants on plant growth and metabolism even under environmental stresses and in particular under salinity (Table 21.1).

Table 21.1 Summary of the effects exerted by different animal- and plant-derived biostimulants on plants under salinity stress

Biostimulant	Crop	Effect related to salinity tolerance	References
Seaweed extracts	*Solanum melongena*	Increase of phenols, tannins, total soluble sugars, activity of SOD and APX, and potassium to sodium ratio	Hegazi et al. (2014)
	Triticum aestivum	Increase of antioxidant enzyme activity (SOD, CAT, APX, and GR)	Ibrahim et al. (2014)
	Triticum durum	Increase of seed germination, growth, and antioxidant enzyme activities	Latique et al. (2017)
	Triticum durum	Increase of leaf pigments, total phenolics, carotenoids, and antioxidant enzymatic activities	Chernane et al. (2015)
	Persea americana Mill.	Improve growth parameters. Increase potassium and calcium content in leaves	Bonomelli et al. (2018)
Humic substances	*Solanum lycopersicum*	Increase root growth and decrease membrane damages	Türkmen et al. (2004) and Paksoy et al. (2010)
	Phaseolus vulgaris	Increase proline levels	Aydin et al. (2012)
	Capsicum	Increase mineral nutrient uptake efficiency in shoot and root. Reduce sodium content in shoot and root	Çimrin et al. (2010)
	Lepidium sativum	Increase germination.	Masciandaro et al. (2002)
	Zea mays	Improve growth parameters	Masciandaro et al. (2002)
Protein hydrolysates	*Diospyros kaki*	Increase the synthesis of compatible osmolytes	Visconti et al. (2015)
	Lactuca sativa	Increase root dry weight, total length, and macronutrient uptake and assimilation	Lucini et al. (2015)
	Zea mays	Increase plant biomass and proline content in leaves. Stimulate nitrogen metabolism and antioxidant defense	Ertani et al. (2013)
Microbial inoculations	*Lactuca sativa*	Increase germination and fresh and dry weight	Barassi et al. (2006)
	Zea mays	Increase of uptake of potassium and phosphorus and nitrogen availability, exclusion of sodium	Rojas-Tapias et al. (2012)
	Triticum aestivum	Increase biomass, N content, and grain yield	Chaudhary et al. (2013)
	Cicer arietinum, *Vicia faba*	Increase nodulation and root and shoot development	Hamaoui et al. (2001)
	Hordeum vulgare	Reduce ethylene emission and root surface sodium uptake. Increase root and shoot dry weight and water content in the root system	Suarez et al. (2015)

21.3.1 Seaweed Extracts

In agriculture, the use of seaweeds as fertilizer is a very old practice, known in Roman times and also adopted in Britain, France, Spain, Japan, and China for centuries (Nedumaran and Arulbalachandran 2015). Seaweeds contain all the elements and the hormones required for plant growth. The extracts are rich in minerals like nitrogen, phosphorus, and potassium and growth hormones like auxins, cytokines, and gibberellins, as well as vitamins, fatty acids, amino acids, antibiotics, and micronutrients (Blunden 1972; Booth 1965). Carbohydrates and other organic substances present in algae can change the nature of the soil and improve its ability to retain moisture (Zodape 2001). Often, seaweed material is even more efficient than chemical fertilizers (Craigie 2011). Several studies, in many species, have highlighted the positive effects on the growth of plants favored by seaweed extracts (SWEs). However, the nature of seaweeds is very mutable and complex; this makes it difficult to determine which constituents are responsible for this activity (Di Stasio et al. 2018; Van Oosten et al. 2017). The SWEs can also improve the tolerance to salinity, heat, cold, and drought (Latique et al. 2014; Shukla et al. 2018; Di Stasio et al. 2018). Many studies have shown that SWEs have excellent activities against salt stress (Chernane et al. 2015). In particular, their positive effects are due to the induction of synthesis of antioxidant molecules and bioactive compounds which could improve plant growth and stress resistance (Cardozo et al. 2007). Hegazi et al. (2014) showed that SWE application to eggplants under salinity could increase phenol, tannin, and total soluble sugar content and superoxide dismutase (SOD) and ascorbate peroxidase (APX) enzymatic activities, promoting higher potassium to sodium ratio. In *T. aestivum* seedlings under salinity, the increase in the concentration of applied SWEs from 1% to 10% can determine a significant rise in plant fresh and dry weight and the increase of activity of APX and glutathione reductase (GR) at 1% SWEs and SOD and catalase (CAT) at higher concentration of algal extracts (Ibrahim et al. 2014). *Ascophyllum nodosum*-based SWEs increased the accumulation of minerals, antioxidants, and essential amino acids in tomato fruits under salinity, improving the fruit growth and nutritional value (Di Stasio et al. 2018).

21.3.2 Humic Substances

Humic substances (HS) are natural substances produced by chemical and biological transformations of organic residues and by microbial metabolism during the decomposition process (du Jardin 2015; Canellas et al. 2015). Humic substances represent about 80% of the organic fraction of the soil and affect its physicochemical properties, in particular helping soil to retain water in a very efficient way than does sand and to reduce water needs in agriculture. Humic substances are polymeric compounds with inconstant composition depending on their genesis, without specific chemical formula, dark, colloidal, partially aromatic, acidic, hydrophilic, and able to retain water and cations. Humic substances have a high molecular weight and are very resistant to degradation. They are mainly composed of humic acids, fulvic

acids, and humin. These molecules differ from each other because of the degree of solubility, the molecular weight, and the functional groups. Fulvic acids have a higher oxygen content and a lower molecular weight compared to humic acids (Bulgari et al. 2015).

The stimulation of root growth and the improvement of the nutritional status of plants, mainly linked to the increase of resources' (nutrients plus water) availability in the soil, are the principal biostimulant effects of HS. They improve the availability of nutrients by increasing the cation exchange capacity and the buffering power of the soil (du Jardin 2015; Canellas et al. 2015). Furthermore, the HS form soluble complexes with micronutrients (e.g., iron), which improve the nutrients' availability for plants preventing their leaching (Chen et al. 2004; García-Mina et al. 2004). The micronutrients complexed with fulvic acids can also be absorbed directly from the plant cells, because of the low molecular weight of fulvic acid which can easily reach the plasma membrane. Humic acids can interact only with the cell wall because of its larger size (Nardi et al. 2009).

Humic substances show significant effects also on plant secondary metabolism, promoting tolerance to environmental stresses. For example, the hydroxyl, carboxylic, and phenolic groups of humic substances are the main binding sites for herbicides and heavy metals. In particular, humic acids enhance the photolysis and therefore the detoxification of atrazine (Zeng et al. 2002). Moreover, they form complexes with free Pb^{2+} ions in solution limiting their absorption and translocation in plants and their entry into the food chain (Santos et al. 2014). Furthermore, there are numerous examples showing the potential of these substances to improve the tolerance to salinity stress in plants. Tomato studies have shown that the application of HS can induce salt tolerance by increasing root growth and decreasing membrane damage (Paksoy et al. 2010; Türkmen et al. 2004). Application of humic acids to the common bean (*Phaseolus vulgaris* L.) in conditions of high salinity (120 mM NaCl) resulted in increased levels of endogenous proline (Aydin et al. 2012).

21.3.3 Protein Hydrolysates

Plant- and animal-derived protein hydrolysates (PHs), defined as mixtures of polypeptides, oligopeptides, and amino acids, produced from plant or animal protein sources through partial hydrolysis, are applied as biostimulants on numerous crops (Colla et al. 2015a). Chemical reactions (acid or alkaline hydrolysis) and thermal and enzymatic hydrolysis of many animal wastes and plant biomass are principally used for the production of PHs (Colla et al. 2017; du Jardin 2015). The innovative use of plant and animal biomass, which represents a largely available and cheap raw material, could be a valid eco-friendly solution for producing these bio-products while reducing the need for their disposal in landfills, which could adversely impact the environment (Carillo et al. 2012; Carillo and Morrone 2017; Baglieri et al. 2014). The chemical composition of PH commercial products can highly differ in dependence on the source of proteins (animal or plant residual biomass) and synthesis process (chemical and/or enzymatic hydrolysis) (Ertani et al. 2009, 2013; Colla

et al. 2017). Anyhow, the major components are represented by free peptides and amino acids (Calvo et al. 2014). Other compounds may also be found, such as carbohydrates and trace amounts of mineral elements, phenols, phytohormones, and other organic compounds (Ertani et al. 2014; Colla et al. 2015a).

Protein hydrolysates are having a fair success in agriculture because of their ability to increase germination, productivity, and quality of a wide range of horticultural and agronomic crops. They can indirectly affect plant growth by increasing the availability of nutrients in the soil and the absorption and use efficiency of nutrients as well as stimulating the growth of microorganisms in the rhizosphere and phyllosphere (Colla et al. 2015b). Protein hydrolysates can directly stimulate carbon and nitrogen metabolism, regulating key enzymes involved in the N uptake and assimilation process and interfering with hormonal activity (Colla and Rouphael 2015; Colla et al. 2015a; du Jardin 2015; Nardi et al. 2016).

Their application can also alleviate the negative effects of salinity, drought, and heavy metals on the plant (Rouphael et al. 2017). Several studies on the mechanisms underlying their beneficial effects show the ability of small peptides and other amino acid derivatives to induce plant defense responses, thus increasing plant tolerance to abiotic stresses (Tuteja 2007). According to Visconti et al. (2015), the application of PHs and calcium was able to reduce Cl^- uptake, leaf necrosis, and leaf water potential in persimmon trees grafted on *Diospyros lotus* under salinity, even if soil salinity and Cl^- concentration increased upon treatment. The increase of compatible osmolytes like glycine betaine and proline and salt stress response proteins in the PH-treated plants (Visconti et al. 2015) suggests that these biostimulants can activate an alternative plant defense mechanism. As also seen in plants under the combined application of multiple stresses, PHs probably induce new transcription factors able to modify gene expression programs and create new genetic traits for salinity stress adaptation (Woodrow et al. 2011, 2017). Accordingly, Lucini et al. (2015) found that the application of plant-derived PHs on roots and/or leaves of lettuce plants under salinity improved the nitrogen assimilation and photosynthesis efficiency in treated plants. The authors related the improved lettuce crop tolerance to salinity to a PH-dependent phenomenon of oxidative stress mitigation, due to the increase of osmolyte and glucosinolate synthesis and accumulation and changes in sterol and terpene composition.

21.3.4 Microbial Inoculations

The plant microbiota consists of a complex microbial consortium including bacteria, fungi, protists, and viruses, many of which are able to create a beneficial, neutral, or harmful interaction with the host. In particular, beneficial interactions with microorganisms like mycorrhizal fungi or nitrogen-fixing symbiotic bacteria play a crucial role in availability and acquisition of nutrients by crop plants indirectly influencing their growth and development (Jacoby et al. 2017; Philippot et al. 2013), even under abiotic stress conditions (Bulgarelli et al. 2013). These

microorganisms have co-evolved with their hosts and are significant for crop growth and for ecosystem functioning (Turner et al. 2013; Marin et al. 2017; Bona et al. 2018). Their cell number highly exceeds that of plant cells, and their genome is also generally defined as the second genome of the plant or its microbiome (Berendsen et al. 2012). Several studies have shown that phylogenetically not related plants present a radical microbiome dominated only by a few phyla of bacteria, principally belonging to proteobacteria, actinobacteria, bacteroidetes, and to a lesser extent firmicutes (Berg et al. 2016). The fungal communities, on the other hand, are more numerous and assorted, and their composition varies according to biogeography, the host plant species, and the plant compartment (Shakya et al. 2013).

Most of the interactions between microorganisms and plants occur in the rhizosphere, a confined area of soil that surrounds and is influenced by plant roots, as well as in the phyllosphere which covers the surface of the leaves. The rhizosphere is rich in root mucilage, exudates, and sloughed cells (Bertin et al. 2003). Plant and cultivar species influence the composition of root exudates (Micallef et al. 2009), which are mainly composed of organic acids and sugars but also amino acids, fatty acids, vitamins, growth factors, hormones, and antimicrobial compounds (Bertin et al. 2003). Cellulose and pectins, instead, predominate in mucilage and sloughed cells (Dennis et al. 2010) and are degraded by cellulolytic bacteria, in particular *Bacillus*, *Pseudomonas*, *Streptomyces*, and *Clostridium* (Carillo et al. 2012), and fungi present in soil and operate via a two-stage process that at the end forms glucose that can be rapidly used as a carbon source by heterotrophic soil microorganisms (Killham and Prosser 2015).

Plant growth-promoting rhizobacteria (PGPR) are of particular interest since they are able to bring beneficial effects to plant growth, making nutrients available and favoring their absorption (Bloemberg and Lugtenberg 2001). They can fix atmospheric nitrogen, synthesize several compounds like amides or phytohormones, solubilize phosphorus-containing minerals, as well as transfer nutrients, trace elements, and water directly into the roots and promote the process of decomposition of the organic matter of the soil. Many PGPR may also influence plant growth indirectly by acting as antagonists to plant pathogens through the production of antimicrobials (Rezzonico et al. 2005). In particular, actinomycetes are very common in soil and in the rhizosphere and produce many antibacterial substances but also antifungal, antiviral, nematocide, and insecticide compounds (Turner et al. 2013). Similar to PGPR, the association between mycorrhizal fungi (MF) of the soil and the roots of the plants is also beneficial. Fungi can also improve the availability of phosphate, ammonium, nitrate, calcium, zinc, and iron in conditions of nutrient deficiency or low availability, since the dense network of external hyphae, which extend the surface of absorption of nutrients and production of secretions of organic substances, are able to bind and/or solubilize nutrients (Marschner 1986).

Symbiotic microorganisms can also improve the plant's tolerance to abiotic stresses. Bacteria potentially able to act as biostimulants belong to different genera such as *Rhizobium*, *Bradyrhizobium*, *Azotobacter*, *Azospirillum*, *Pseudomonas*, and *Bacillus* (Selvakumar et al. 2009; Upadhyay et al. 2009). One of the strategies these microorganisms adopt is the production of a protective biofilm layer on the root surface, thanks to the greater accumulation in the cell wall of exopolysaccharides, proteins-lipopolysaccharides, and lipids-polysaccharides. Moreover, they are able to reduce the concentration of the solutes in the surrounding solution by accumulating them inside the cells. These mechanisms allow plants to improve water retention and therefore promote greater tolerance to salt-induced osmotic and ionic stresses (Paul and Lade 2014). Improved stress tolerance and growth-promoting effects after treatment with microorganisms have been observed in several species. In fact, a study of Barassi et al. (2006) showed that the inoculation of lettuce seeds (*Lactuca sativa* L. cv. Mantecosa) with *A. brasilense* increased germination and tolerance to high salinity and allowed to obtain even plants with higher fresh and dry weight. In maize plants under salinity, inoculation with *Azotobacter* increased potassium and phosphorus uptake and nitrogen availability while excluding sodium; moreover, it increased the polyphenol content, with a protective function against ROS (Rojas-Tapias et al. 2012). The inoculation with salinity-tolerant *Azotobacter* strains of wheat plants under salinity improved the tolerance to stress by increasing biomass, nitrogen content, and grain yield (Chaudhary et al. 2013).

21.4   Conclusion

Many obstacles stand in the way of the efforts to maximize agricultural production. The massive uses of synthetic fertilizers and pesticides and repeated irrigations to improve crop yields have had a very negative impact on the environment and are no more usable. One of the most serious problems has been the reduction of irrigated lands, which supply more than 40% of the food produced worldwide, mainly due to the increase in soil salinization (FAO 2017). Therefore, a major goal of agricultural research and innovation is to improve the resource (mainly nitrogen and water) use efficiency (RUE) and the salt tolerance/resistance in crop plants, to obtain higher yields without affecting the environment. The use of biostimulants can improve RUE combining economic development, food security, and environmental sustainability even in conditions of salinity. However, plants treated with animal- or plant-derived biostimulants show tailored responses completely different from non-treated plants, probably due to the biostimulant induction of changes in plant genome and the consequent specific metabolic modifications. Therefore, exploring the molecular mechanisms underlying the global responses of plants to biostimulants is of capital importance to maximize their action and allow targeted interventions, with the creations of new formulations, able to improve crop yields even under salinity.

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Abiotic Stress Tolerance in Wheat and the Role of Silicon: An Experimental Evidence

22

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Abstract

Silicon (Si) has beneficial effect on crop growth and development under water stress condition. The study about the effect of silicon application on growth and water relation of wheat under water-limited conditions was carried out in pots at PMAS Arid Agriculture University, Rawalpindi, Pakistan. Seeds of two cultivars, i.e., NARC-2009 and Chakwal-50, were taken from the National Agricultural Research Center (NARC). In this experiment, as the source of silicon, silicic

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acid, sodium silicate, and silica gel were used in the silicon-applied treatments. The effect of silicic acid, sodium silicate, and silica gel at rate of 0.5%, 1.0%, and 1.5% solution was investigated for germination, physiological, and yield traits, and it was compared with control. Physiological parameters like leaf membrane stability index, epicuticular wax, crop growth rate, relative water content, stomatal conductance, transpiration rate, photosynthetic rate, leaf area, leaf area index, chlorophyll contents, leaf succulence, relative leaf water contents, silicon concentration in leaves, and proline contents were measured. The results depicted that different silicon rates and application levels have a significant impact upon crop growth and development. Wheat crop responded well to silicon priming treatments. Maximum grain yield was obtained for silica gel with 1.5% silicon application level, whereas minimum grain yield was obtained by control treatment. Similarly, genotypes responded significantly to silicon priming treatments for grain production. Cultivar NARC-2009 performed well under different silicon regime of the rainfed zone of pothwar, while cultivar Chakwal-50 gave less seed production. Silicon priming could be a good viable option in the future to cope abiotic stress.

22.1 Introduction

A decline in quality and productivity of crops due to water scarcity is sufficiently severe enough to reduce crop yield and a common problem of arid and semiarid regions. Drought is the prolonged dry weather condition because of little rain and high temperatures. It can take a week, a month, and even years. Whereas if soil moisture availability to plants has dropped to such a level that it adversely affects the crop yield and hence agricultural profitability, then it is called an agricultural drought. This kind of drought could be evaluated by the soil water time series framework. The dry year has been observed in 4–10 years instead of 3 out of 10 years. About 25% of the GDP is affected due to drought because the crop yields are affected. The drought has directly or indirectly affected the social, environmental, and economic aspects of the world, and some can be handled or managed, whereas others are not. The drought has led to unemployment in the field of agriculture and other industries as well.

Plant growth and development even under drought could be optimized by the use of silicon (Si). It is the element which can boost agricultural crop productions under abiotic stresses (Ahmed et al. 2011). Silicon can increase drought tolerance in crops by maintaining water potential (Hattori et al. 2005a, b). Water economy and dry matter yield of water have been improved due to the application of Si (Gong et al. 2003). Silicon can also help to improve salinity tolerance in plants (Romero-Arnada

et al. 2006). The stimulation of antioxidant system and alleviation of specific ion effect by reducing Na uptake were also drought tolerance mechanisms in plants exposed to Si application (Liang et al. 2005). Silicon is next to oxygen in abundancy and is taken up directly as silicic acid (Ma et al. 2001). Its main accumulation is in leaves, and in dried plant parts, the silica bodies are located in silica cells below the epidermis and in epidermal appendices (Dagmar et al. 2003). Growth effects of silicon, including increased dry mass and yield, enhanced pollination, and most commonly increased disease resistance, were concluded earlier. Silicon can also alleviate imbalances between zinc and phosphorus supply (Rodrigues et al. 2004).

Silicon is not considered as essential plant nutrient, but it has beneficial effects on the growth and production of plants. It can mitigate environmental stresses and build resistance in plants against fungal and bacterial pathogens. Silicon and plant-pathogen interactions have been reported by various authors in which they concluded Si-induced biochemical/molecular resistance during plant-pathogen interactions. It can act as a modulator influencing plant defense responses and interacting with key components of plant stress signaling systems leading to induced resistance (Ye et al. 2013). Abiotic stress in the form of diseases is a major threat to agricultural production which can be mitigated using Si as it can control fungal and bacterial diseases (Rodrigues and Datnof 2015). Regulation of Si in plant diseases has been summarized in Table 22.1. Meanwhile, activities of defense-related enzymes have been boosted by the application of Si (Ye et al. 2013). The detail has been presented in Table 22.2. Application of Si helps the plant to build resistance against pathogens as Si accumulates beneath the cuticle and forms cuticle-Si double layer (Fig. 22.1).

Water stress is a common problem in the rainfed regions of the world nowadays, which have caused deviation of plant functions from normal to abnormal. It is a major environmental issue which can limit the growth and production of crops. Silicon application improves the plant hydraulic properties by promoting root water uptake and decreased water loss under water stress conditions (Chen et al. 2018). The mechanism of plant root water uptake under water stress due to the application of Si involves (1) osmotic adjustment, (2) improvement in transport activity of aquaporin, and (3) increased root-shoot ratio by modification in root growth (Fig. 22.2).

Furthermore, water stress problem can be solved by using seed priming. Silicon has the potential to be used as priming material as it can improve germination percentage and seedling vigor under stress (Janmohammadi and Sabaghnia 2015). It can augment plant defense against biotic and abiotic pressures. Silicon application by seed priming helped to improve growth of stressed plants by enhancement in LRWC (leaf relative water content) and levels of photosynthetic pigments, soluble sugars, soluble proteins, total free amino acids, and K^+, as well as activities of SOD (superoxide dismutase), CAT (catalase), and POD (peroxidase) enzymes. These findings indicated that Si plays a pivotal role in removing the negative effects of stress. The authors further concluded that seed priming with Si is an efficient strategy that can be used to boost the tolerance of crop plants to abiotic stress (Latef and Tran 2016). Different scientists reported new panorama of Si research involves seed priming (exposing seeds to Si for only few hours) to

Table 22.1 Effects of silicon on plant disease and related resistance mechanisms

Hosts	Diseases	Pathogens	Effects	Resistance mechanisms
Arabidopsis	Powdery mildew	*Erysiphe cichoracearum, Agrobacterium tumefaciens*	+	Physical, biochemical, and molecular
Banana	Black sigatoka	*Mycosphaerella fijiensis*	+	Physical and biochemical
	Fusarium wilt	*Fusarium oxysporum* f. sp. *cubense*	+	Physical and biochemical
	Root rot	*Cylindrocladium spathiphylli*	+	Biochemical
	Xanthomonas wilt	*Xanthomonas campestris*	+	Physical and biochemical
Barley	Powdery mildew	*Blumeria graminis*	+	Physical
Bean	Angular leaf spot	*Pseudocercospora griseola*	+	Physical
Belle pepper	Phytophthora blight	*Phytophthora capsici*	+	Physical
Bent grass	Dollar spot	*Sclerotinia homoeocarpa*	+	Physical and biochemical
Bitter gourd	Powdery mildew	*Erysiphe* sp.	+	Biochemical
Capsicum	Anthracnose	*Colletotrichum gloeosporioides*	+	Physical and biochemical
Cherry	Fruit decay	*Penicillium expansum, Monilinia fructicola*	+	Biochemical
Chinese cantaloupe	Fusarium root rot	*Fusarium* spp.	+	Physical and biochemical
	Postharvest pink rot	*Trichothecium roseum*	+	Physical and biochemical
Coffee	Leaf rust	*Hemileia vastatrix*	+	Physical
	Root-knot nematode	*Meloidogyne exigua*	+	Biochemical
Common bean	Anthracnose	*Colletotrichum lindemuthianum*	+	Biochemical
Cotton	Fusarium wilt	*Fusarium oxysporum* f. sp. *vasinfectum*	+	Physical and biochemical
Creeping, turf grass	Brown patch	*Rhizoctonia solani*	+	Physical and biochemical
Cucumber	Crown and root rot	*Pythium ultimum*	+	Biochemical
	Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	+	Physical and biochemical
	Powdery mildew	*Sphaerotheca fuliginea, Podosphaera xanthii*	+	Physical and biochemical
Gerbera daisy	Powdery mildew	*Erysiphe cichoracearum, Podosphaera fusca*	/	/

(continued)

Table 22.1 (continued)

Hosts	Diseases	Pathogens	Effects	Resistance mechanisms
Hami melons	Decay	*Alternaria alternata, Fusarium semitectum, Trichothecium roseum*	+	Biochemical
Lettuce	Downy mildew	*Bremia lactucae*	+	Physical and biochemical
Melon	Bacterial fruit blotch	*Acidovorax citrulli*	+	Biochemical
	Powdery mildew	*Podosphaera xanthii*	+	Biochemical
Muskmelon	Pink rot disease	*Trichothecium roseum*	+	Biochemical
	Powdery mildew	*Sphaerotheca fuliginea*	+	Physical and biochemical
Oil palm	Basal stem rot	*Ganoderma boninense*	+	Physical
Pea	Brown spot	*Mycosphaerella pinodes*	+	Biochemical
Pearl millet	Downy mildew	*Sclerospora graminicola*	+	Physical and biochemical
Perennial ryegrass	Fusarium patch	*Microdochium nivale*	+	Physical
	Gray leaf spot	*Magnaporthe oryzae*	+	Biochemical
Potato	Dry rot	*Fusarium sulphureum*	+	Biochemical
Pumpkin	Powdery mildew	*Podosphaera xanthii*	+	Physical and biochemical
Rice	Blast	*Pyricularia oryzae, Magnaporthe grisea, Magnaporthe oryzae*	+	Physical, biochemical, and molecular
	Brown spot	*Bipolaris oryzae, Cochliobolus miyabeanus*	+	Physical, biochemical, and molecular
	Grain discoloration	*Bipolaris oryzae*	+	Molecular
	Leaf scald	*Monographella albescens, Microdochium oryzae*	+	Physical and biochemical
	Sheath blight	*Rhizoctonia solani*	+	Physical and biochemical
Rose	Powdery mildew	*Podosphaera pannosa*	+	Physical
Sorghum	Anthracnose	*Colletotrichum sublineolum*	+	Physical and biochemical
Soybean	Phytophthora stem and root rot	*Phytophthora sojae*	+	Molecular
	Rust	*Phakopsora pachyrhizi*	+	Biochemical
St. Augustine grass	Gray leaf spot	*Magnaporthe grisea*	+	Physical and biochemical
Strawberry	Powdery mildew	*Sphaerotheca aphanis*	+	Physical and biochemical
Sugarcane	Brown rust	*Puccinia melanocephala*	+	Physical and biochemical

Table 22.1 (continued)

Hosts	Diseases	Pathogens	Effects	Resistance mechanisms
Tall fescue	Brown patch	*Rhizoctonia solani*	−	/
Tobacco	Viral infection	Tobacco ringspot virus	+	Molecular
		Tobacco mosaic virus	/	/
Tomato	Bacterial speck	*Pseudomonas syringae*	+	Biochemical
	Bacterial wilt	*Ralstonia solanacearum*	+	Molecular
	Fusarium crown and root rot	*Fusarium oxysporum* f. sp. *radicis-lycopersici*	+	Physical
Tomato, bitter gourd	Root rot	*Pythium aphanidermatum*	+	Biochemical and molecular
Wheat	Blast	*Pyricularia grisea*	+	Physical and biochemical
	Leaf blast	*Pyricularia oryzae*	+	Biochemical
	Leaf streak	*Xanthomonas translucens*	+	Physical and biochemical
	Powdery mildew	*Blumeria graminis*	+	Physical, biochemical, and molecular
	Spot blotch	*Bipolaris sorokiniana*	+	Physical and biochemical
Zucchini squash	Powdery mildew	*Erysiphe cichoracearum, Podosphaera xanthii*	+	Physical and biochemical

Wang et al. (2017)
Positive (+), negative (−), or no effect (/) of Si on plant resistance to diseases

protect plants against future stress events (van Hulten et al. 2006; Conrath 2011; Van Bockhaven et al. 2013; Azeem et al. 2015; Coskun et al. 2016). Based upon the above review related to the importance of Si, present study was conducted to evaluate the response of two wheat varieties under different levels of silicic acid, sodium silicate, and silica gel as priming materials. The specific objectives of the proposed study were as follows:

- To evaluate the effect of wheat seed priming for drought stress tolerance.
- To compare various silicon sources for their priming effect on wheat seed.

22.2   Review of Literature

The application of silicon is known to enhance crop tolerance against various environmental stresses. Recent studies on water uptake and transport in crops revealed that silicon affected these traits and the effects differed among species. Other recent studies have shown relationships between silicon and dehydration tolerance at cell or tissue levels. Water stress is a severe environmental constraint to plant productivity. The loss in crop yield due to water scarcity probably exceeds losses from all other causes. Plants cannot survive without water. Water deficiency has adverse

Table 22.2 Defense-related enzymes regulated by silicon in plant-pathogen interactions

Hosts	Diseases	Pathogen	Defense-related enzymes
Bean	Anthracnose	*Colletotrichum lindemuthianum*	Superoxide dismutase, ascorbate peroxidase, glutathione reductase
Cucumber	Crown and root rot	*Pythium* spp.	Chitinase, peroxidases, polyphenol oxidases
	Powdery mildew	*Podosphaera xanthii*	Peroxidases, polyphenol oxidases, chitinases
Melon	Pink rot	*Trichothecium roseum*	Peroxidase
	Powdery mildew	*Podosphaera xanthii*	Chitinases, superoxide dismutase, β-1,3-glucanase
Chinese cantaloupe	Pink rot	*Trichothecium roseum*	Peroxidases, phenylalanine ammonia-lyase
Pea	Leaf spot	*Mycosphaerella pinodes*	Chitinase, β-1,3-glucanase
Perennial ryegrass	Gray leaf spot	*Magnaporthe oryzae*	Peroxidase, polyphenol oxidase
Rice	Blast	*Magnaporthe oryzae, Pyricularia oryzae*	Glucanase, peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase, superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, lipoxygenase
	Brown spot	*Bipolaris oryzae*	Chitinase, peroxidase
	Sheath blight	*Rhizoctonia solani*	Phenylalanine ammonia-lyases, peroxidases, polyphenol oxidases, chitinases
Soybean	Target spot	*Corynespora cassiicola*	Chitinases, β-1-3-glucanases, phenylalanine ammonia-lyases, peroxidases, polyphenol oxidases
Wheat	Blast	*Pyricularia oryzae*	Chitinases, peroxidases

Wang et al. (2017)

effects on a number of physiological parameters of plants. Drought caused a more pronounced inhibition growth and photosynthetic rates in the more sensitive cultivars Adamello compared with the relatively tolerant cultivars Ofanto. Drought also affects transpiration efficiency of plants. To confirm this, a field experiment was designed using wheat, and less transpiration rate was recorded which resulted in a decrease in productivity compared to the irrigated field. Carbon dioxide assimilation and chlorophyll content were also influenced from drought (Monneveux et al. 2006). Similarly, Younis et al. (2000) applied water stress at vegetative or at the reproductive stage in three sorghum cultivars. Water stress was found to reduce relative growth and net assimilation rates. Short-term water stress in the vegetative phase improved the chlorophyll content in leaves, while long-term stress in the vegetative and reproductive phases reduced chlorophyll content (Chang-juan 2006). Many studies have suggested the positive effects of silicon on plant growth under stress. Effect of silicon on growth under water stress is getting reputed because of the good response of Si fertilization. Gong et al. (2005) stated that application of
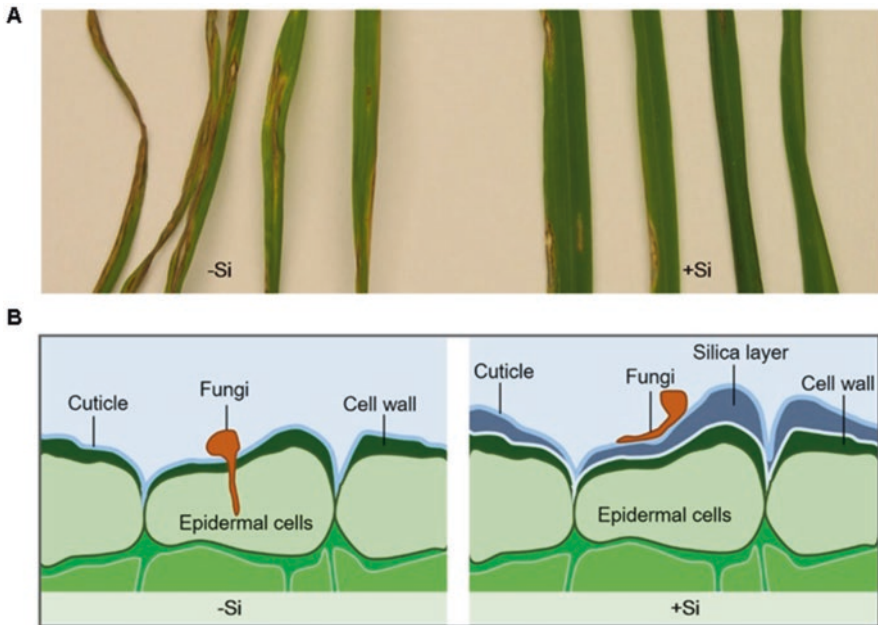
Fig. 22.1 Silicon application and fungal disease (Wang et al. 2017)

silicon increased the contents of photosynthetic pigments and soluble proteins under drought. In this experiment, wheat (*Triticum aestivum* L.) plants were grown in pots applied with or without silicon under drought stress. The results showed that application of silicon improved the water status of drought-stressed plants compared with the non-silicon treatment.

Plant biomass and yield of crops are severely affected by drought stress due to its impact upon various physiological and agronomical parameters. In an experiment, Humayun et al. (2010) investigated the influence of fertilization on various plant growth attributes including shoot length and plant fresh and dry weight. The effect of fertilization with Si compounds on accumulation of Si in wheat (*Triticum aestivum* L.) has been studied by Joanna et al. (2007) in which wheat plants were grown under identical growing conditions but subjected to fertilization with various Si compounds (pyrolitic fine silica particles, sodium silicate, silica gel), and the Si content of the aboveground plants was analyzed via X-ray microanalysis (EDX) and atomic absorption spectroscopy (AAS). Silicon under different water regimes was evaluated on wheat crop. Si was added in soil at 50 mg/kg and 150 mgkg^{-1} of soil. Three levels of water contents (50%, 75%, and 100% of field capacity) were maintained (Ahmad et al. 2007). Growth performance, relative water contents (RWC), and mineral nutrition were studied by Mali and Aery (2008) in *Triticum aestivum* L. treated with different concentrations of silicon (25, 50, 100, 200, 400, and 800 ppm). Lower administrations of silicon (25–200 ppm) resulted in an enhancement in relative yield, relative water contents, and calcium and potassium contents. Shoots were significantly richer in silicon content than roots.
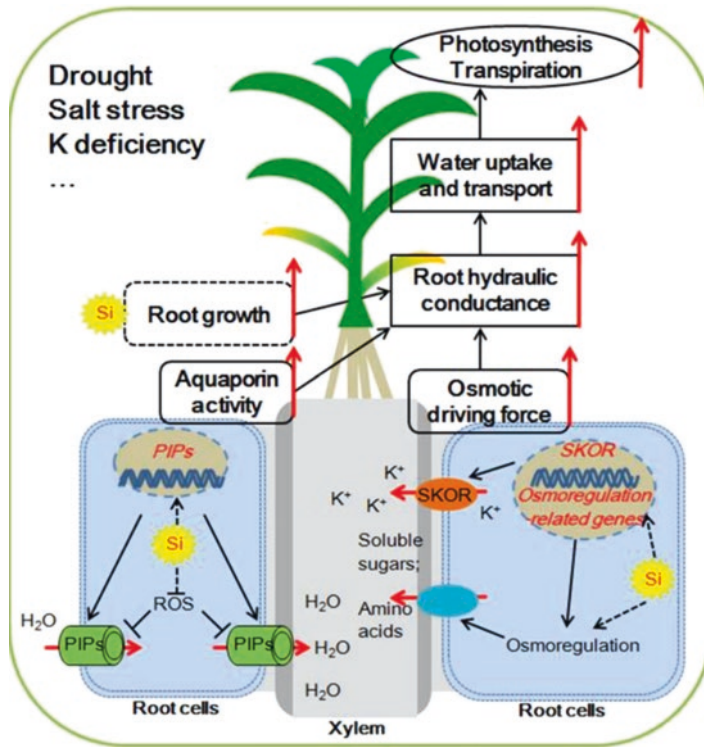
Fig. 22.2 Si mediated water balance of plants (Chen et al. 2018)

22.3 Methodology

The experiment relating to the effect of silicon on wheat growth, development, and drought resistance index was conducted in a crop physiology laboratory, Department of Agronomy, Arid Agriculture University, Rawalpindi, Pakistan. Seeds of two cultivars, viz., NARC-2009 and Chakwal-50, were primed with T1 = control (distilled water only), T2 = silicic acid (0.5%, 1.0%, 1.5%), T3 = sodium silicate (0.5%, 1.0%, 1.5%), and T4 = silica gel (0.5%, 1.0%, 1.5%). The experiment was laid out as CRD, and pots of uniform size were covered with aluminum foils to prevent an increase in soil temperature caused by solar radiation. Pots were irrigated before adding soil. Each pot was filled with 10 kg of well-pulverized soil. Fertilizer was added on the rate of N:P as 100:50 on the basis of soil weight in the pots. Two wheat cultivars primed in T2, T3, and T4 with three replications were used as plant material in the present study. Ten seeds of each cultivar were sown per pot. Plastic sheets coated with aluminum film were placed on the soil surface to prevent evaporation from the pots. Evaporation data was taken from Meteorological Observatory, and it correlated with all treatments. Data for the silicon concentration of the fully expanded flag leaves was measured according to Lux et al. (2002). Physiological

parameters like photosynthetic rate (An), transpiration rate (E), and stomatal conductance (gs) were measured at flag leaf stage by infrared gas analyzer (IRGA) (Long and Bernacchi 2003). Leaf membrane stability index (LMSI) was determined according to the method described by Chandrasekar et al. (2000). Leaf succulence (LS) and relative water content (RWC) were calculated by the following formulae:

LS = fresh leaf weight – dry leaf weight/leaf area
RWC (%) = [(fresh leaf weight – dry leaf weight) / (turgid leaf weight – dry leaf weight)] × 100

Epicuticular wax was measured by the procedure proposed by Silva et al. (1964). Chlorophyll content was measured by SPAD chlorophyll meter by taking three readings from the flag leaf and then taking the average. Drought resistance index (DRI) was calculated by using the following formulae:

DRI = DC × (Ya/Y′a)
DC = drought resistance coefficient = Ya/Ym

where:

Ya is the average yield of all the varieties with no irrigation.
Y′a is the yield of the variety without irrigation.
Ym is the maximum yield of variety under irrigation.

Proline content was estimated spectrophotometrically following the ninhydrin method (Bates et al. 1973) using pure proline. At maturity, plant height (cm), spike length (cm), number of spikelet per spike, number of grains per spike, hundred grain weight, biological yield (g m^{-2}), and grain yield (g m^{-2}) were calculated from five randomly selected plants.

22.3.1 Statistical Analysis

The observations collected were analyzed for variance by STATISTICA version 8. Means were compared by the LSD test at the 5% level of probability.

22.4   Results and Discussions

22.4.1 Silicon Concentration in Plants

Results depicted significant variation for silicon accumulation of different silicon priming treatments on wheat at three-leaf stage (Appendix 22.1). Silicon priming treatments differed significantly for silicon accumulation at three-leaf stage (Z-13) for wheat crop (Table 22.3). Maximum silicon was recorded for silica gel

(0.0279 μg g⁻¹), whereas minimum silicon was recorded for control treatment (0.0034 μg g⁻¹) at three-leaf stage. Meanwhile, silicon application rates differed significantly for silicon accumulation in the wheat plant. Maximum silicon was accumulated for 1.5% application rate (0.0165 μg g⁻¹); however, minimum silicon contents were accumulated for 0.5% application rate (0.0157 μg g⁻¹) at three-leaf stage. Similarly, wheat genotypes differed significantly for silicon accumulation. Genotype NARC-2009 accumulated maximum silicon contents (0.0181 μg g⁻¹) at three-leaf stage; however, genotype Chakwal-50 accumulated minimum silicon contents (0.0143 μg g⁻¹). The interactive effect G × T and T × L were highly significant. Considerable variation was observed among wheat genotypes at varying silicon priming rates and different chemicals at anthesis stage (Appendix 22.2). Priming by silicon chemicals differed significantly for silicon accumulation in wheat plants at anthesis stage (Z-60). The highest silicon contents were accumulated for silica gel (0.0718 μg g⁻¹), while the lowest silicon contents (0.0086 μg g⁻¹) were accumulated for control treatment (Table 22.3). Similarly, different silicon levels varied greatly for silicon accumulation at anthesis stage of wheat. The highest silicon contents were accumulated (0.0426 μg g⁻¹) for 1.5% silicon application levels, whereas the lowest silicon contents were accumulated (0.0397 μg g⁻¹) for 0.5% application. The percentage difference among the highest and lowest level was 7. In the same way, wheat genotypes differed significantly for silicon accumulation at anthesis stage. Maximum silicon (0.0426 μg g⁻¹) was accumulated by cultivar NARC-2009, whereas minimum silicon (0.0401 μg g⁻¹) was accumulated by cultivar Chakwal-50. The percentage difference among both genotypes for silicon accumulation at anthesis stage was 6%.

The effect of different silicon priming by different silicon application rates on wheat genotypes at maturity stage (Z-92) was elaborated by ANOVA table (Appendix 22.3). Silicon priming chemicals varied considerably in depicting silicon accumulation in wheat crop at maturity stage. The highest silicon was accumulated (0.1026 μg g⁻¹) for silica gel, whereas the lowest silicon (0.0123 μg g⁻¹) was accumulated for control silicon priming treatment. Meanwhile, silicon application rates differed greatly for silicon accumulation at maturity stage. Maximum silicon was accumulated (0.0609 μg g⁻¹) for 1.5% silicon application levels, whereas minimum silicon (0.0568 μg g⁻¹) was accumulated when silicon application level was 0.5%. The percentage difference among the highest and lowest silicon application levels was 7. Similarly, wheat cultivars varied greatly for silicon accumulation at maturity stage. Cultivar NARC-2009 accumulated maximum silicon contents (0.0608 μg g⁻¹), while minimum silicon contents (0.0572 μg g⁻¹) were accumulated for cultivar Chakwal-50. The percentage difference among two cultivars was 5.

Silicon contents increased by increasing silicon application rates. Different chemicals behaved differently for uptake of silicon in wheat. Silica gel dissolved predominantly frequently than other chemicals, viz., sodium silicate and silicic acid. However, various studies have demonstrated that Si application increased plant growth significantly (Alvarez and Datnoff 2001). The highest silicon was accumulated for 1.5% silicon application rate, while the lowest silicon was accumulated for 0.5% silicon application rates. The results of current study were as per

with Hattori et al. (2005a, b) who testified that silicon concentration in leaf was increased by Si application regardless of soil water regime. Our results were also in accordance with Hodson and Sangster (1988) and Mecfel et al. 2007 who stated that silicon deposition in wheat plant leaves can be enhanced by silicon chemicals in the soil.

22.4.2 Photosynthetic Rate (An)

The effect of different silicon priming compounds by different silicon application rates and levels on wheat genotypes were elaborated by ANOVA (Appendix 22.4). Silicon priming compounds have significant effect on photosynthesis of wheat crop (Table 22.4). The highest net photosynthesis was calculated (25.87 μ mole m^{-2} sec^{-1}) for silica gel, whereas the lowest net photosynthesis was calculated (22.8 μ mole m^{-2} sec^{-1}) for control silicon priming treatment. There was 13% difference among the highest and lowest silicon compounds. Meanwhile, silicon application rates did not differ for net photosynthesis. On the other hand, wheat cultivars varied greatly for net photosynthesis at flag leaf stage. Maximum net photosynthesis was calculated for cultivar NARC-2009 (24.38 μ mole m^{-2} sec^{-1}), while minimum net photosynthesis (22.87 μ mole m^{-2} sec^{-1}) was calculated for cultivar Chakwal-50. The percentage difference among two cultivars was 7%. The interaction among G × L was significant at 5% P level, and T × G was significant at 1% P level. Net photosynthesis is reduced in drought conditions. Different silicon compounds behaved differently for photosynthesis during current study. The variation among different compounds was due to their solubility. With the addition of silicon as seed priming treatment, photosynthesis increases. Our results were in line with Liang et al. (2003) who reported that silicon enhances different metabolic activities in plants like photosynthesis and transpiration. Also Matichenkov et al. (2001) stated that silicon enhanced photosynthetic activity in wheat.

22.4.3 Transpiration Rate (E)

Significant difference was observed for transpiration rate among two wheat cultivars for all silicon treatments and application levels (Appendix 22.5). Silicon application compounds varied significantly for transpiration rate. The highest transpiration rate (9.78 mole m^{-2} sec^{-1}) was recorded for silica gel, whereas the lowest transpiration rate (6.21 mole m^{-2} sec^{-1}) was calculated for control treatment. There was 36% difference among silica gel and control treatment for transpiration rate. Similarly, there was a significant difference among the highest and lowest silicon application levels. Maximum transpiration rate was calculated for 1.5% silicon application level (8.50 mole m^{-2} sec^{-1}), whereas minimum transpiration rate was calculated for 0.5% silicon application level (7.69 mole m^{-2} sec^{-1}). There was 10% difference among 1.5% and 0.5% silicon application levels. In the same way, wheat cultivars due to

their genetic behavior differed considerably for transpiration rate. The highest transpiration rate (8.86 mole m^{-2} sec^{-1}) was calculated for cultivar NARC-2009, whereas the lowest transpiration rate (7.35 mole m^{-2} sec^{-1}) was calculated for cultivar Chakwal-50. Both the cultivars differed 17% for transpiration rate. All the interactions for transpiration were non-significant (Table 22.4). Silicon remains in the leaves of crop plants which reduces the water losses through stomatal transpiration (Agarie et al. 1998; Savant et al. 1999). The leaves applied with silicon were thicker than control silicon treatment, so it is assumed that silicon reduces transpiration in wheat plants. Our results were in line with Gong et al. (2003) who stated that by applying silicon, water losses reduce by decreasing transpiration rate. Silicon is also known to increase drought tolerance in plants by maintaining plant water balance, photosynthetic activity, erectness of leaves, and structure of xylem vessels under high transpiration rates (De Melo et al. 2003; Hattori et al. 2005a, b). Shu and Liu (2001) also found that by adding silicon, transpiration rate increased by increasing plant water potential.

22.4.4 Stomatal Conductance (g_s)

The effect of different silicon priming compounds by different silicon application rates and levels on wheat genotypes for stomatal conductance (g_s) was expressed by ANOVA table (Appendix 22.6). Silicon application treatments varied significantly for stomatal conductance. Maximum stomatal conductance was calculated for silica gel treatment (0.7806 mole m^{-2} sec^{-1}), whereas minimum stomatal conductance (0.4772 mole m^{-2} sec^{-1}) was calculated for control silicon treatment. Similarly, different silicon application rates varied significantly for stomatal conductance. Maximum stomatal conductance (0.6637 mole m^{-2} sec^{-1}) was calculated for 1.5% silicon application level, while minimum stomatal conductance (0.5979 mole m^{-2} sec^{-1}) was recorded for 0.5% silicon application level. There was 11% difference for stomatal conductance among maximum and minimum silicon application levels. In the meanwhile, wheat cultivars varied noticeably for stomatal conductance. Cultivar NARC-2009 accumulated the highest stomatal conductance (0.6978 mole m^{-2} sec^{-1}), whereas cultivar Chakwal-50 accumulated the lowest stomatal conductance (0.5644 mole m^{-2} sec^{-1}). The percentage difference among both genotypes for stomatal conductance was 19. However, all interactions remained non-significant for stomatal conductance (Table 22.4). Stomatal conductance reduces in drought conditions to save water losses. By reducing stomatal conductance, photosynthesis reduces which results in less biomass production. In the current study by adding silicon, stomatal conductance increased which led to enhanced biomass production. Stomatal conductance increased by enhancing silicon application levels. Our results were in accordance with Yeo et al. (1999) who stated that by adding silicon, stomatal conductance enhanced in drought conditions that might be because of maintenance of water in the leaf of crops.

22.4.5 Stomatal Resistance (r$_s$)

Significant variation was observed for stomatal resistance (r$_s$) among two wheat cultivars for all silicon treatments and application levels (Appendix 22.7). Silicon application led to significant difference in stomatal resistance. Maximum stomatal resistance (0.7833 m^2 s mole^{-1}) was observed for control treatment, whereas silica gel gave minimum (69.12 m^2 s mole^{-1}) stomatal resistance. There was 58% difference among silica gel and control treatments. Meanwhile, silicon application levels varied significantly for stomatal resistance. Maximum stomatal resistance (0.7417 m^2 s mole^{-1}) was calculated for 0.5% silicon application level, whereas minimum stomatal resistance (0.5375 m^2 s mole^{-1}) was recorded for 1.5% silicon application level. On the other hand, wheat cultivars did not vary significantly for stomatal resistance. The interaction among G × L was significant at 1% P level (Table 22.4). Stomatal resistance causes reduction in physiological activities of the plant. For control silicon application treatment, the highest stomatal resistance was recorded during current study. However by adding silicon, stomatal resistance reduced. Minimum stomatal resistance was recorded by the highest silicon application level. Several researchers supported that the silicon was involved in physiological activities under drought and reduces stomatal resistance (Liang et al. 2003; Zhu et al. 2004).

22.4.6 SPAD Chlorophyll Contents

Silicon priming chemicals and application levels varied extensively for chlorophyll contents (Appendix 22.8). Silicon application treatments varied significantly for chlorophyll contents. Maximum SPAD chlorophyll contents were calculated for silica gel treatment (55.35), whereas minimum chlorophyll contents (37.85) were calculated for control silicon treatment. The percentage difference among the highest silicon application treatment and control treatment for chlorophyll contents was 32%. Similarly, there was a significant difference among the highest and lowest silicon application levels. Maximum chlorophyll contents (47.83) were calculated for 1.5% silicon application level, whereas minimum chlorophyll contents (44.85) were calculated for 0.5% silicon application level. There was 6% difference among 1.5% and 0.5% silicon application levels. Similarly, wheat cultivars varied considerably for chlorophyll contents. Cultivar NARC-2009 accumulated the highest chlorophyll contents (48.537), whereas cultivar Chakwal-50 accumulated the lowest chlorophyll contents (44.13). The percentage difference among both genotypes for chlorophyll contents was 9%. However, the interactions remained non-significant (Table 22.4). Chlorophyll contents are the direct measures of photosynthesis. Under drought conditions, the number of chlorophyll contents decreased. In the current study, maximum chlorophyll contents were recorded for silica gel with 1.5% application level, while minimum chlorophyll contents were recorded for control treatment. Our results were in line with Paknejad et al. (2007) who found that chlorophyll contents in different wheat cultivars could be reduced more than 25% due to drought stress.

22.4.7 Drought-Resistant Index (DRI)

Significant variation was observed for drought-resistant index (DRI) among two wheat cultivars for all silicon treatments and application levels (Appendix 22.9). Silicon application chemicals varied significantly for drought-resistant index (Table 22.5). The highest DRI (0.53) was recorded for silica gel, whereas the lowest DRI (0.43) was calculated for control treatment. There was 22% difference among silica gel and control treatment for drought-resistant index. Similarly, there was a significant difference among the highest and lowest silicon application levels. Maximum DRI was calculated for 1.5% silicon application level (0.4864), whereas minimum DRI was calculated for 0.5% silicon application level (0.4719). There was 3% difference among 1.5% and 0.5% silicon application levels. In the same way, wheat cultivars due to their genetic behavior differed considerably for drought-resistant index. The highest DRI (0.521) was calculated for cultivar NARC-2009, whereas the lowest DRI (0.439) was calculated for cultivar Chakwal-50. Both the cultivars differed 19% for drought-resistant index. Drought-resistant index is the key factor to determine better crop growth under drought conditions. Different silicon compounds behaved differently for drought-resistant index. Silica gel enhanced drought-resistant index to cope with different types of stresses. Wheat cultivar NARC-2009 accumulated more silicon contents and higher DRI. The results of the current study were in line with the findings of Zhao et al. (2007) who calculated the DRI values for wheat cultivars grown under different moisture regime and silicon conditions and found that cultivars applied with higher silicon concentrations had more DRI values and were more resistant to drought.

22.4.8 Epicuticular Wax (ECW)

Silicon priming chemicals and application levels varied considerably for epicuticular wax (Appendix 22.10). Silicon compounds differed greatly for epicuticular wax accumulation. Maximum ECW was accumulated for silica gel (7.6459 mg), whereas control treatment accumulated minimum epicuticular wax (6.2852 mg). There was 22% difference among the highest and lowest silicon application treatments. On the other hand, silicon application levels did not fluctuate for epicuticular wax accumulation. Meanwhile, wheat cultivars due to genetic makeup differed significantly for epicuticular wax accumulation. Cultivar NARC-2009 accumulated maximum EW (7.7732 mg), while Chakwal-50 accumulated minimum epicuticular wax (6.2048 mg). There was 25% difference among both cultivars for epicuticular wax accumulation. Silicon enhances epicuticular wax to overcome drought. Silicon compounds on the basis of their solubility enhanced epicuticular wax on the leaves. Our findings were in accordance with Avestan et al. (2019) who documented that cuticle wax accumulation enhances the drought tolerance in plants and silicon holds a vital place under such circumstances.

22.4.9 Relative Water Content (RWC)

The effect of different silicon priming chemicals by different silicon application rates on wheat genotypes for relative water contents (RWC) were elaborated by the ANOVA (Appendix 22.11). Silicon application treatments varied significantly for relative water contents (Table 22.5). Maximum relative water contents were calculated for silica gel treatment (83.88%), whereas minimum relative water contents (74.10%) were calculated for control silicon treatment. The percentage difference among the highest silicon application treatment and control treatment was 13. However, different silicon application rates did not vary significantly for relative water contents. On the other hand, wheat cultivars varied considerably for relative water contents. Cultivar NARC-2009 accumulated the highest RWC (83.19%), whereas cultivar Chakwal-50 accumulated the lowest relative water contents (75.14%). The percentage difference among both genotypes for RWC was 10.

Relative water content is directly related to plant physical status. Relative water content is the measure of crop physical conditions. Application of Si enhanced relative water content in wheat crop. The findings of Ma et al. (2006) supported our results as they thought that silicon improved crop relative water potential. Relative water contents also enhance silicon concentration in the leaves as silicon enters through transport chain. Similar to our results, Dehghanipoodeh et al. (2018) also described that Si uptake enhances with an increase in moisture contents as it is impassively absorbed via mass flow.

22.4.10 Leaf Succulence (LS)

The chemicals used for silicon priming and application levels varied considerably for epicuticular wax (Appendix 22.12). Silicon priming chemicals differed significantly for leaf succulence (Table 22.5). Maximum leaf succulence was recorded for silica gel (15.13 mg/m^2), while minimum leaf succulence (12.44 mg/m^2) was recorded for control treatment. There was 22% difference among silica gel and control treatment for leaf succulence. Meanwhile, silicon application levels did not differ significantly for leaf succulence. Whereas, wheat cultivars due to variation in their genetic makeup varied considerably for leaf succulence. Maximum leaf succulence (15.42 mg m^{-2}) was recorded for cultivar NARC-2009, while minimum leaf succulence (12.25 mg m^{-2}) was recorded for Chakwal-50. There was 26% difference for leaf succulence among both wheat cultivars. The interaction among all the treatments was not significant at 5% P level. Leaf succulence represents the activity of plant leaves. Less leaf succulence denotes stunted plant growth. Leaf succulence increased with the increase in silicon application. Silicon-enhanced leaf water potential ultimately increased leaf succulence. Zhu et al. (2019) also found that silicon increases water potential which increased leaf succulence value.

22.4.11 Leaf Membrane Stability Index (LMSI)

Significant variation was observed for leaf membrane stability index (LMSI) among two wheat cultivars for all silicon treatments and application levels (Appendix 22.13). Silicon priming chemicals differed potentially for leaf membrane stability index (Table 22.5). The highest leaf membrane stability index (78.90%) was observed for silica gel, whereas control silicon application treatment observed the lowest (69.12%) leaf membrane stability index. There was 14% difference among silica gel and control treatments. However, silicon application levels did not differ significantly for leaf membrane stability index. In the meanwhile, wheat cultivars varied significantly for leaf membrane stability index accumulation. Maximum LMSI (77.82%) was calculated for cultivar NARC-2009, whereas Chakwal-50 accumulated minimum leaf membrane stability index (70.54%). Both the cultivars varied 10% for leaf membrane stability index. All the interactions remained non-significant at 5% P level. Leaf membrane stability index is the ability of plant to be alive in drought conditions. Silicon increased leaf membrane stability index. Minimum leaf stability index was recorded for control treatment, whereas, by the addition of silicon, the membrane stability index increased. The findings of the current study were in accordance with Maghsoudi et al. (2016) who reported that silicon played a significant role in maintaining membrane stability.

22.4.12 Proline Content

The chemicals used for silicon priming and application levels varied considerably for proline contents (Appendix 22.14). Silicon application treatments varied significantly for proline contents. Maximum proline contents were calculated for silica gel treatment (54.90 µg g^{-1}), whereas minimum proline contents (45.12 µg g^{-1}) were calculated for control silicon treatment. Similarly, there was a significant difference among the highest and lowest silicon application levels. Maximum proline contents (50.85 µg g^{-1}) were calculated for 1.5% silicon application level, whereas minimum proline contents (49.34 µg g^{-1}) were calculated for 0.5% silicon application level. There was 3% difference among 1.5% and 0.5% silicon application levels. Similarly, wheat cultivars varied considerably for proline contents. Cultivar NARC-2009 accumulated the highest proline contents (53.82 µg g^{-1}), whereas cultivar Chakwal-50 accumulated the lowest proline contents (46.54 µg g^{-1}). The percentage difference among both genotypes for proline contents was 16% (Table 22.3). Silicon priming increased proline contents with an increase in drought. Similar findings have been documented that proline contents reduced under increased stress; however, it increased in resistant cultivars which led to higher yield (Mamrutha et al. 2019).

Table 22.3 Silicon concentration in plants at three-leaf (Z13), anthesis (Z-60), and maturity (Z92) stage

Treatments	Si-Z13	Si-Z-60	Si-Z92
Genotype (G)			
NARC-2009	0.0181a	0.0426a	0.0608a
Chakwal-50	0.0143b	0.0401b	0.0572b
Treatments (T)			
Control	0.0034d	0.0086d	0.0123d
Silicic acid	0.0136c	0.0343c	0.049c
Sodium silicate	0.0199b	0.0505b	0.0722b
Silica gel	0.0279a	0.0718a	0.1026a
Application level (L)			
0.50%	0.0157b	0.0397c	0.0568c
1%	0.0164a	0.0416b	0.0594b
1.50%	0.0165a	0.0426a	0.0609a
Interactions			
C × T	***	***	***
C × L	NS	NS	NS
T × L	***	***	***
C × T × L	NS	NS	NS

Any two means not sharing a common letter in a column differ significantly at 5% probability level. (***significant at $P < 1\%$ level, *NS* non-significant)

22.4.13 Plant Height

The effect of different silicon priming compounds on plant height by different silicon application rates on wheat genotypes was elaborated by ANOVA (Appendix 22.15). Silicon priming compounds varied considerably on plant height at maturity stage (Table 22.4). The highest plant height (85.05 cm) was recorded for silica gel, whereas the lowest plant height (75.27 cm) was recorded for control silicon priming treatment. The percentage difference among the highest and lowest priming treatments for plant height was 13%. Meanwhile, silicon application rates differed greatly for plant height at maturity stage. Maximum plant height (81.00 cm) was recorded for 1.5% silicon application levels, whereas minimum plant height (79.49 cm) was recorded when silicon application level was 0.5%. The percentage difference among the highest and lowest silicon application levels for recording plant height was 13%. Similarly, wheat cultivars varied greatly for plant height at maturity stage. Maximum plant height (85.19 cm) was recorded for cultivar NARC-2009, while minimum plant height (75.47 cm) was recorded for cultivar Chakwal-50 (Table 22.5). The percentage difference among two cultivars was 2. Plants reduce their height under drought conditions. Drought can be mitigated by applying silicon nutrients to plants. In the current study, minimum plant height was recorded for control treatment where drought was at its peak, whereas, by adding silicon through seed priming, drought was mitigated, and maximum plant height was recorded. Gong et al. (2003) observed that silicon increased plant height, leaf area,

Table 22.4 Physiological parameters among two wheat cultivars for different silicon priming chemicals and levels

Treatments	An	E	g_s	r_s	SPAD
Cultivar (C)					
NARC-2009	24.3a	8.8a	0.71a	0.63^{NS}	48.5a
Chakwal-50	22.8b	7.3b	0.56b	0.65	44.1b
Treatments (T)					
Control	22.8b	6.2d	0.47d	0.78a	37.8d
Silicic acid	23.2b	7.7c	0.59c	0.63ab	43.3c
Sodium silicate	22.5b	8.6b	0.67b	0.65ab	48.8b
Silica gel	25.8a	9.7a	0.78a	0.49b	55.3a
Application level (L)					
0.50%	23.0^{NS}	7.6c	0.60c	0.74a	44.8c
1%	24.2	8.1b	0.63b	0.64ab	46.3b
1.50%	23.5	8.5a	0.66a	0.54b	47.8a
Interactions					
C × L	**	NS	NS	***	NS
T × C	***	NS	NS	NS	NS
L × T	NS	NS	NS	NS	NS
C × T × L	NS	NS	NS	NS	NS

Any two means not sharing a common letter in a column differ significantly at 5% probability level (***significant at $P < 1\%$ level, **significant at $P < 5\%$ level, *NS* non-significant)

Table 22.5 Physiological parameters among two wheat cultivars for different silicon priming chemicals and levels

Treatments	DRI	ECW	RWC	LS	LMSI	Proline
Genotype (G)						
NARC-2009	0.52a	7.77a	83.19a	15.42a	77.82a	53.82a
Chakwal-50	0.44b	6.20b	75.14b	12.25b	70.54b	46.54b
Treatments (T)						
Control	0.43d	6.28c	74.11d	12.44c	69.12d	45.12d
Silicic acid	0.47c	6.80b	77.81c	13.46bc	72.83c	48.87c
Sodium silicate	0.50b	7.22ab	80.85b	14.29ab	75.87b	51.87b
Silica gel	0.53a	7.64a	83.88a	15.13a	78.90a	54.90a
Application level (L)						
0.50%	0.47b	6.87^{NS}	78.32^{NS}	13.60^{NS}	73.34^{NS}	49.34b
1%	0.48a	7.01	79.33	13.88	74.34	50.35a
1.50%	0.48a	7.08	79.84	14.01	74.85	50.85a
Interactions						
L × T	NS	NS	NS	NS	NS	NS
G × L	NS	NS	NS	NS	NS	NS
T × G	NS	NS	NS	NS	NS	NS
G × T × L	NS	NS	NS	NS	NS	NS

Any two means not sharing a common letter in a column differ significantly at 5% probability level. (*NS* non-significant)

and dry mass of wheat even under drought. Sundahri et al. (2001) showed positive effects of silicate on the wheat grown under stressed conditions in increasing plant height and biological yield.

22.4.14 Grains per Spike

Priming silicon application compounds and application levels varied extensively for number of seeds per spike (GS) (Appendix 22.16). Silicon application treatments varied considerably for number of seeds per spike (Table 22.5). Maximum number of seeds per spike was calculated for silica gel (47.11), whereas minimum number of seeds per spike (37.13) was calculated for control silicon treatment. There was 27% percentage difference among the highest silicon application treatment and control treatment. Similarly, there was a major difference among the highest and lowest silicon application levels for calculating the number of seeds per spike. Maximum number of seeds per spike (42.94) was calculated for 1.5% silicon application level, whereas minimum number of seeds per spike (41.35) was calculated for 0.5% silicon application level. There was 4% difference among 1.5% and 0.5% silicon application levels for number of seeds per spike. Similarly, wheat cultivars varied noticeably for number of seeds per spike. Cultivar NARC-2009 accumulated the highest number of seeds per spike (45.86), whereas cultivar Chakwal-50 accumulated the lowest number of seeds per spike (38.61). The percentage difference among both genotypes for number of seeds per spike was 19%. The interactions were non-significant. Drought can decrease seeds per spike on wheat plant. Silicon as seed priming chemical reduces drought and enhances seeds per spike. Our results were in line with the findings of Tamai and Ma (2008) who reported an increase in yield due to silicon application.

22.4.15 Spike Length

Significant variation was observed for spike length among two wheat cultivars for all silicon priming compounds and their application levels (Appendix 22.17). Spike length differed significantly for all Silicon application treatments (Table 22.5). The highest spike length (15.70 cm) was observed for silica gel, whereas control silicon application compound observed the lowest (12.38 cm) spike length. There was 27% difference among silica gel and control compounds for spike length. Similarly, there was significant difference among the highest and lowest silicon application levels. Maximum spike length (14.31 cm) was calculated for 1.5% silicon application level, whereas minimum spike length (13.78 cm) was calculated for 0.5% silicon application level. There was 4% difference among 1.5% and 0.5% silicon application levels for spike length. In the meanwhile, wheat cultivars varied expressively for spike length. Maximum spike length (15.29 cm) was recorded for cultivar NARC-2009, whereas Chakwal-50 accumulated minimum spike length (12.87 cm). Both the cultivars varied 10% for spike length. The interactions were non-significant

at 5% P level. Birsin (2005) supported our results, as he was of the opinion that spike length was significantly affected under stressed conditions and ultimately impacted grain yield. The highest spike length attributed toward good source-sink relationship as more photoassimilates translocated from source to sink efficiently.

22.4.16 Spikelet per Spike

Significant variation was observed for spikelet per spike (SLS) among two wheat cultivars for all silicon priming compounds and application levels (Appendix 22.18). Silicon application chemicals varied significantly for spikelet per spike (Table 22.5). The highest spikelet per spike (17.91) was calculated for silica gel, whereas the lowest spikelet per spike (14.59) was calculated for control treatment. There was 23% difference among silica gel and control treatment for spikelet per spike. In the same way, there was a major difference among the highest and lowest priming silicon application levels. Maximum spikelet per spike (16.52) was calculated for 1.5% silicon application level, whereas minimum spikelet per spike (15.99) was calculated for 0.5% silicon application level. There was 3% difference among 1.5% and 0.5% priming silicon application levels. Meanwhile, wheat cultivars due to their genetic behavior differed considerably for spikelet per spike. The highest spikelet per spike (17.50) was calculated for cultivar NARC-2009, whereas the lowest spikelet per spike (15.08) was calculated for cultivar Chakwal-50. Both the cultivars differed 19% for spikelet per spike. This variation might be due to the length of spike because of efficient utilization of available water and temperature and efficiently accumulation of photoassimilates. Similar results had been documented, demonstrating that cultivars differed among themselves regarding spikelets/spike under various silicon applications (Arif et al. 2016).

22.4.17 Hundred Grain Weight

Substantial difference was observed among wheat genotypes at varying silicon priming rates and different compounds for hundred grain weight (Appendix 22.19). Priming different silicon compounds diverged significantly for hundred grain weight in wheat plants (Table 22.5). The highest hundred grain weight was accumulated for silica gel (4.468 g), while the lowest hundred grain weight (3.2826 g) was calculated for control treatment (Table 22.5). Similarly, different silicon levels varied greatly for hundred grain weight. The highest hundred grain weight was recorded (3.9739 g) for 1.5% silicon application levels, whereas the lowest hundred grain weight was recorded (3.8025 g) for 0.5% application levels. The percentage difference among the highest and lowest level was 7%. In the same way, wheat cultivars differed significantly for hundred grain weight. Maximum hundred grain weight (4.3934 g) was accumulated by genotype NARC-2009, whereas minimum hundred grain weight (3.3934 g) was accumulated by genotype Chakwal-50. The percentage difference among both genotypes for silicon accumulation at anthesis stage was 6%.

Hundred grain weight varied due to droughts, and this variation might be due to an increase in temperature and moisture stress during later growth stages of wheat crop, and ultimately it had marked influence on grain yield of crop. Results were in line with the findings of Aggarwal (2008). Ultimately grain yield is the most important entity for farmer. Varieties having more grain weight under stressed conditions can be considered as drought-resistant varieties. So the selection of drought-resistant varieties may be based on 100 grain weight for optimum production under stressful environment.

22.4.18 Biological Yield

Priming silicon application compounds and application levels varied extensively for biological yield (BY) (Appendix 22.20). Silicon application treatments varied considerably for biological yield (Table 22.5). Maximum biological yield was calculated for silica gel (13,938 kg ha^{-1}), whereas minimum biological yield (9384 kg ha^{-1}) was calculated for control silicon treatment. There was 48% difference among the highest silicon application treatment and control treatment. Similarly, there was a major difference among the highest and lowest silicon application levels for calculating biological yield. Maximum biological yield (12,555 kg ha^{-1}) was recorded for 1.5% silicon application level, whereas minimum biological yield (11,471 kg ha^{-1}) was recorded for 0.5% silicon application level. There was 9% difference among 1.5% and 0.5% silicon application levels for biological yield. Similarly, wheat cultivars varied prominently for biological yield. Cultivar NARC-2009 accumulated maximum biological yield (12,239 kg ha^{-1}), whereas cultivar Chakwal-50 accumulated minimum biological yield (11,880 kg ha^{-1}). The interaction among T × L was significant at 1% P level. Silicon priming increased biological yield with the addition of silicon. By adding silicon, drought was reduced. Similar to our findings, Singh et al. (2006) suggested that the increased dry matter and yield by adding silicon. Sundahri et al. (2001) also observed positive effects of silicate on the wheat grown under stressed conditions in increasing plant height and biological yield.

22.4.19 Grain Yield

The effect of different silicon priming compounds by different silicon application rates and levels on wheat genotypes for grain yield was expressed by ANOVA table (Appendix 22.21). Silicon application treatments varied significantly for grain yield. Maximum grain yield was calculated for silica gel treatment (3010 kg ha^{-1}), whereas minimum grain yield (2404 kg ha^{-1}) was calculated for control silicon treatment. The percentage difference among the highest silicon application treatment and control treatment was 25% for grain yield. Similarly, different silicon application rates varied pointedly for grain yield. Maximum grain yield (3213 kg ha^{-1}) was calculated for 1.5% silicon application level, while minimum grain yield (2575 kg ha^{-1}) was recorded for 0.5% silicon application level.

Table 22.6 Yield and yield parameters among two wheat cultivars for different silicon priming chemicals and levels

Treatments	GS	SL	SLS	HGW	PH	GY	BY
Genotype (G)							
NARC-2009	45.86a	15.29a	17.50a	4.39a	85.19a	3381a	12239a
Chakwal-50	38.61b	12.87b	15.08b	3.39b	75.47b	2295b	11880b
Treatments (T)							
Control	37.13d	12.38d	14.59d	3.28d	75.27d	2404b	9384d
Silicic acid	40.76c	13.59c	15.80c	3.73c	78.98c	2974a	11286c
Sodium silicate	43.94b	14.65b	16.86b	4.09b	82.02b	2965a	13630b
Silica gel	47.11a	15.70a	17.91a	4.47a	85.05a	3009a	13938a
Application level (L)							
0.50%	41.35b	13.78b	15.99b	3.80b	79.49^{NS}	2575b	11471c
1%	42.41a	14.14a	16.35a	3.90a	80.497	2726b	12153b
1.50%	42.94a	14.31a	16.52a	3.97a	81.003	3213a	12555a
Interactions							
L × T	NS	NS	NS	NS	NS	NS	NS
G × L	NS	NS	NS	NS	NS	NS	NS
T × G	NS	NS	NS	NS	NS	NS	***
G × T × L	NS	NS	NS	NS	NS	NS	NS

Where *GS* grains per spike, *SL* spike length, *SLS* spikelets per spike, *HGW* hundred grains weight, *PH* plant height, *GY* grain yield, and *BY* biological yield

Any two means not sharing a common letter in a column differ significantly at 5% probability level. (***significant at $P < 1\%$ level, *NS* non-significant)

There was 24% difference for grain yield among maximum and minimum silicon application levels. In the meanwhile, wheat cultivars varied noticeably for grain yield. For cultivar NARC-2009, maximum grain yield (3381 kg ha^{-1}) was recorded, whereas cultivar Chakwal-50 accumulated minimum grain yield (2295 kg ha^{-1}) (Table 22.6). The percentage difference among both genotypes for grain yield was 47%. All the interactions remained non-significant. Grain yield can be reduced by drought. Silicon reduced drought and increased grain yield. Similar to our findings, Mukkram et al. (2006) also found that silicon increased growth and yield due to decreased stress. Many studies have suggested the positive growth effects of silicon, including increased dry mass and yield and enhanced pollination (Korndörfer and Lepsch 2001).

22.5 Summary

Silicon has beneficial effect on crop growth and development under water stress condition. The effect of silicic acid, sodium silicate, and silica gel at rate of 0.5%, 1.0%, and 1.5% solution was investigated for germination, and it was compared with control. The present study revealed that different silicon rates and application levels have significant impact upon crop growth and development. Wheat crop responded well to silicon priming treatments. Maximum grain yield was obtained

for silica gel with 1.5% silicon application level, whereas minimum grain yield was obtained by control treatment. Similarly, genotypes responded significantly to silicon priming treatments for grain production. Silicon priming could be future priming strategy to cope abiotic stress.

Appendices

Appendix 22.1: Analysis of Variance for Silicon Concentration in Plants at Three-Leaf Stage Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	2.57E-04	2.57E-04	620.76	***
Treatments (T)	3	0.0058	0.00193	4669.49	***
Application level (L)	2	1.08E-05	5.39E-06	13	***
C × T	3	6.15E-05	2.05E-05	49.46	***
C × L	2	8.79E-07	4.40E-07	1.06	NS
T × L	6	1.57E-05	2.62E-06	6.32	***
C × T × L	6	2.98E-06	4.96E-07	1.2	NS
Error	48	1.99E-05	4.14E-07		
Total	71	0.00617			
CV	3.97				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.2: Analysis of Variance for Silicon Concentration in Plants at Anthesis Stage Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	1.13E-04	1.13E-04	78.13	***
Treatments (T)	3	0.03835	0.01278	8818.93	***
Application level (L)	2	1.03E-04	5.15E-05	35.5	***
C × T	3	4.27E-05	1.42E-05	9.82	***
C × L	2	8.58E-07	4.29E-07	0.3	NS
T × L	6	1.60E-04	2.66E-05	18.37	***
C × T × L	6	3.34E-06	5.56E-07	0.38	NS
Error	48	6.96E-05	1.45E-06		
Total	71	0.03884			
CV	2.91				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.3: Analysis of Variance for Silicon Concentration in Plants at Maturity Stage Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	2.31E-04	2.31E-04	78.13	***
Treatments (T)	3	7.83E-02	2.61E-02	8818.93	***
Application level (L)	2	2.10E-04	1.05E-04	35.5	***
C × T	3	8.72E-05	2.91E-05	9.82	***
C × L	2	1.75E-06	8.75E-07	0.3	NS
T × L	6	3.26E-04	5.44E-05	18.37	***
C × T × L	6	6.81E-06	1.13E-06	0.38	NS
Error	48	1.42E-04	2.96E-06		
Total	71	7.93E-02			
CV	2.91				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.4: Analysis of Variance for Photosynthetic Rate Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	40.95	40.951	5.08	**
Application level (L)	2	18.81	9.403	1.17	NS
Treatment (T)	3	125.27	41.756	5.18	***
G × L	2	67.33	33.665	4.17	**
T × G	3	414.79	138.265	17.14	***
L × T	6	64.19	10.698	1.33	NS
G × T × L	6	56.23	9.372	1.16	NS
Error	48	387.11	8.065		
Total	71	1174.68			
CV	12.02				

$**p \leq 0.01$, $***p \leq 0.001$, and NS = Non-significant

Appendix 22.5: Analysis of Variance for Transpiration Rate Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	41.299	41.2989	146.66	∗∗∗
Application level (L)	2	7.796	3.8982	13.84	∗∗∗
Treatment (T)	3	123.364	41.1212	146.02	∗∗∗
G × L	2	0.013	0.0066	0.02	NS
T × G	3	0.588	0.1961	0.7	NS
L × T	6	1.589	0.2648	0.94	NS
G × T × L	6	0.085	0.0141	0.05	NS
Error	48	13.517	0.2816		
Total	71	188.251			
CV	6.55				

∗∗∗$p \leq 0.001$ and NS = Non-significant

Appendix 22.6: Analysis of Variance for Stomatal Conductance Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	0.32	0.32	216.14	∗∗∗
Application level (L)	2	0.05202	0.02601	17.57	∗∗∗
Treatment (T)	3	0.87983	0.29328	198.09	∗∗∗
G × L	2	0.00068	0.00034	0.23	NS
T × G	3	0.00974	0.00325	2.19	NS
L × T	6	0.00736	0.00123	0.83	NS
G × T × L	6	0.00021	0.00004	0.02	NS
Error	48	0.07107	0.00148		
Total	71	1.34091			
CV	6.1				

∗∗∗$p \leq 0.001$ and NS = Non-significant

Appendix 22.7: Analysis of Variance for Stomatal Resistance Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	0.005	0.005	0.05	NS
Application level (L)	2	0.50083	0.25042	2.46	*
Treatment (T)	3	0.75278	0.25093	2.47	*
G × L	2	1.08583	0.54292	5.34	***
T × G	3	0.34833	0.11611	1.14	NS
L × T	6	0.68139	0.11356	1.12	NS
G × T × L	6	0.50083	0.08347	0.82	NS
Error	48	4.88	0.10167		
Total	71	8.755			
CV	49.69				

$*p \leq 0.05$, $***p \leq 0.001$, and NS = Non-significant

Appendix 22.8: Analysis of Variance for Chlorophyll Contents Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	350.46	350.463	326.22	***
Application level (L)	2	106.22	53.1093	49.44	***
Treatment (T)	3	3030.77	1010.26	940.38	***
C × L	2	0.24	0.12043	0.11	NS
T × C	3	6.87	2.29083	2.13	NS
L × T	6	8.91	1.48531	1.38	NS
C × T × L	6	0.02	0.00337	0	NS
Error	48	51.57	1.07431		
Total	71	3555.07			
CV	2.24				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.9: Analysis of Variance for Drought-Resistant Index Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	0.00262	0.00131	6.1	***
Treatments (T)	3	0.0864	0.0288	134.14	***
Cultivar (C)	1	0.12083	0.12083	562.76	***
T × L	6	0.00112	1.87E-04	0.87	NS
C × L	2	9.93E-06	4.97E-06	0.02	NS
C × T	3	3.28E-04	1.09E-04	0.51	NS
C × T × L	6	4.26E-06	7.10E-07	0	NS
Error	48	0.01031	2.15E-04		
Total	71	0.22161			
CV	3.05				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.10: Analysis of Variance for Epicuticular Wax Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	0.5548	0.2774	0.49	NS
Treatments (T)	3	18.3074	6.1025	10.75	***
Cultivar (C)	1	44.2765	44.2765	77.99	***
T × L	6	0.2378	0.0396	0.07	NS
C × L	2	0.0044	0.0022	0	NS
C × T	3	0.1446	0.0482	0.08	NS
C × T × L	6	0.0019	0.0003	0	NS
Error	48	27.2494	0.5677		
Total	71	90.7767			
CV	10.78				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.11: Analysis of Variance for Relative Water Content Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	28.65	14.3247	1.76	NS
Treatments (T)	3	945.43	315.143	38.71	***
Cultivar (C)	1	1166.94	1166.94	143.32	***
T × L	6	12.28	2.04638	0.25	NS
C × L	2	0.07	0.03454	0	NS
C × T	3	2.28	0.75989	0.09	NS
C × T × L	6	0.03	0.00493	0	NS
Error	48	390.82	8.14209		
Total	71	2546.5			
CV	3.6				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.12: Analysis of Variance for Leaf Succulence Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	2.173	1.087	0.44	NS
Treatments (T)	3	71.714	23.905	9.57	***
Cultivar (C)	1	181.341	181.341	72.62	***
T × L	6	0.931	0.155	0.06	NS
C × L	2	0.018	0.009	0	NS
C × T	3	0.599	0.2	0.08	NS
C × T × L	6	0.008	0.001	0	NS
Error	48	119.863	2.497		
Total	71	376.647			
CV	11.42				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.13: Analysis of Variance for Leaf Membrane Stability Index Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	28.65	14.325	1.15	NS
Treatments (T)	3	945.43	315.143	25.37	***
Cultivar (C)	1	955.29	955.293	76.91	***
T × L	6	12.28	2.046	0.16	NS
C × L	2	0.07	0.035	0	NS
C × T	3	2.28	0.76	0.06	NS
C × T × L	6	0.03	0.005	0	NS
Error	48	596.24	12.422		
Total	71	2540.27			
CV	4.75				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.14: Analysis of Variance for Proline Content Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	28.65	14.325	6.25	***
Treatments (T)	3	945.43	315.143	137.4	***
Cultivar (C)	1	955.29	955.293	416.5	***
T × L	6	12.28	2.046	0.89	NS
C × L	2	0.07	0.035	0.02	NS
C × T	3	2.28	0.76	0.33	NS
C × T × L	6	0.03	0.005	0	NS
Error	48	110.09	2.294		
Total	71	2054.12			
CV	3.02				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.15: Analysis of Variance for Plant Height Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	28.65	14.3247	1.23	NS
Treatments (T)	3	945.43	315.143	26.96	***
Cultivar (C)	1	1700.04	1700.04	145.44	***
T × L	6	12.28	2.04638	0.18	NS
C × L	2	0.07	0.03454	0	NS
C × T	3	2.28	0.75989	0.07	NS
C × T × L	6	0.03	0.00493	0	NS
Error	48	561.08	11.6891		
Total	71	3249.86			
CV	4.26				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.16: Analysis of Variance for Grain Per Spike Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	31.3	15.652	6.57	***
Treatments (T)	3	987.4	329.133	138.07	***
Cultivar (C)	1	945.91	945.909	396.82	***
T × L	6	13.42	2.236	0.94	NS
C × L	2	0.08	0.038	0.02	NS
C × T	3	1.01	0.338	0.14	NS
C × T × L	6	0.03	0.005	0	NS
Error	48	114.42	2.384		
Total	71	2093.57			
CV	3.66				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.17: Analysis of Variance for Spike Length Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	3.478	1.739	6.57	***
Treatments (T)	3	109.711	36.57	138.07	***
Cultivar (C)	1	105.101	105.101	396.82	***
T × L	6	1.491	0.248	0.94	NS
C × L	2	0.008	0.004	0.02	NS
C × T	3	0.113	0.038	0.14	NS
C × T × L	6	0.004	0.001	0	NS
Error	48	12.713	0.265		
Total	71	232.619			
CV	3.66				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.18: Analysis of Variance for Spikelet Per Spike Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	3.478	1.739	6.57	***
Treatments (T)	3	109.711	36.57	138.07	***
Cultivar (C)	1	105.101	105.101	396.82	***
T × L	6	1.491	0.248	0.94	NS
C × L	2	0.008	0.004	0.02	NS
C × T	3	0.113	0.038	0.14	NS
C × T × L	6	0.004	0.001	0	NS
Error	48	12.713	0.265		
Total	71	232.619			
CV	3.16				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.19: Analysis of Variance for Hundred Grain Weight Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Application level (L)	2	0.35622	0.17811	7.64	***
Treatments (T)	3	13.8041	4.60137	197.32	***
Cultivar (C)	1	18	18	771.89	***
T × L	6	0.06434	0.01072	0.46	NS
C × L	2	1.58E-31	7.90E-32	0	NS
C × T	3	7.41E-31	2.47E-31	0	NS
C × T × L	6	2.57E-31	4.29E-32	0	NS
Error	48	1.11932	0.02332		
Total	71	33.344			
CV	3.92				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.20: Analysis of Variance for Biological Yield Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	2,321,931	2,321,931	17.61	***
Treatment (T)	3	2.48E+08	8.25E+07	625.76	***
Application level (L)	2	1.44E+07	7,199,275	54.6	***
T × C	3	59000.3	19666.8	0.15	NS
C × L	2	4844.28	2422.14	0.02	NS
L × T	6	9,146,901	1,524,483	11.56	***
C × T × L	6	797.112	132.852	0	NS
Error	48	6,328,712	131,848		
Total	71	2.80E+08			
CV	3.01				

$***p \leq 0.001$ and NS = Non-significant

Appendix 22.21: Analysis of Variance for Grain Yield Among two Wheat Cultivars for Different Silicon Chemicals and Different Application Levels

SoV	DF	SS	MS	F	P
Cultivar (C)	1	2.12E+07	2.12E+07	131.53	***
Treatment (T)	3	4,541,380	1,513,793	9.38	***
Application level (L)	2	5,333,167	2,666,584	16.52	***
T × C	3	166,185	55,395	0.34	NS
C × L	2	195,159	97579.6	0.6	NS
L × T	6	1,584,736	264,123	1.64	NS
C × T × L	6	57,991	9665.17	0.06	NS
Error	48	7,745,683	161,368		
Total	71	4.09E+07			
CV	14.15				

$***p \leq 0.001$ and *NS* = Non-significant

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Molecular Mechanisms Associated with Drought and Heat Tolerance in Plants and Options for Crop Improvement for Combined Stress Tolerance

23

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Abstract

Plant responses to biotic and abiotic stresses have been extensively studied in isolation. But, in their natural environments, plants are frequently exposed to combination of stresses. The recent studies using model as well as non-model systems indicate that plant responses to combined stresses are often unique and cannot be completely deduced from their responses to individual stresses. These responses are regulated by complex and distinct regulatory pathways, mediated by diverse genes, proteins, and metabolites, which might vary with plant species and with the intensity of stress experienced. A thorough understanding of these mechanisms is essential for improving crop tolerance to combined stresses. Drought and heat stress cause severe impact on crop growth and productivity, independently, and are more likely to coexist in field conditions, especially in the changing climate scenario. This chapter aims to brief the relevance of combined drought and heat stress, elucidate the underlying mechanisms under individual stresses as well as in combination, and highlight the options for crop improvement under combination of stresses.

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23.1 Introduction

Plants are constantly exposed to unfavorable growth conditions caused by various types of abiotic stresses such as drought, high or low temperatures, salinity, flooding, high or low light, deficient or excess nutrients, heavy metals, pollutants, etc. Among these, drought is the most prevalent one, as water is one of the most limiting resources for agriculture in many parts on the globe (Basu et al. 2016). In nature, most of the stresses occur concurrently and hence crop plants are often subjected to combination of stresses in field conditions (Mittler 2006; Suzuki et al. 2014). Many times, drought is accompanied by or associated with high temperature (heat), another important stressor, critically affecting agriculture worldwide (IPCC 2014). This condition is common among crops growing in tropical or subtropical regions which are characterized by erratic rainfall and high temperature (Hamidou et al. 2013). Independent studies have shown around 50% reduction in crop yield under drought and heat stresses (Lamaoui et al. 2018), and combined stresses can have more impact (Rollins et al. 2013; Awasthi et al. 2017). The impact of drought would be further intensified by rise in global temperature due to climate change (Fang and Xiong 2015; Basu et al. 2016). The predicted 0.2 °C increase in global temperature per decade (Sita et al. 2017), coupled with the limiting water resources would have an alarming impact on crop growth and productivity.

Most often, the effect of drought and heat on crop plants has been assessed independently (Wahid et al. 2007). Since these stresses are considered to occur simultaneously, they may have different synergistic and antagonistic effects on plant stress responses. Therefore, the understanding of plant's responses to combined stress is highly important to design strategies for mitigation (Dreesen et al. 2012). Plant stress responses can be comprehended only if we understand the underlying cell tolerance trait associated and the molecular manifestation of that response. There are novel approaches and technologies that have been instrumental in identifying key genetic partners involved, thereby unraveling signaling modules and crucial signaling cross-talk (Parvathi and Nataraja 2016; Nataraja et al. 2017). This chapter presents an overview of the plant responses under combined drought and heat stress.

23.2 Plant Responses to Drought and Heat Stress: A Generic View

Plants respond to environmental cues through well-coordinated physiological trait manifestations. Cell tolerance trait is a sum effect of molecular-level regulations of a specific signaling cascade module. There exists a tightly regulated signaling network starting from stress signal perception to downstream functional gene/protein activation and regulation (Nataraja and Parvathi 2016). A general signal cascade starts from the stress-specific receptor-mediated signal perception followed by signal amplification by secondary messengers, and further transmission through either protein kinase/phospholipid signaling leading to activation/disruption of regulatory protein activity. The regulatory protein governs functional or final effector gene

Table 23.1 Typical stress-specific signaling module in plant stress responses

Stress signaling module component	Cascade partner	Representative candidate groups
Signal perception	Signal receptors	Receptor-like kinases (RLKs), Receptor-like cytoplasmic kinases (RLCKs), Histidine kinases
Signal amplification	Secondary messengers	Calcium, reactive oxygen species (ROS), Inositol 1, 4, 5-trisphosphate (IP3), Diacylglycerol (DAG)
Signal transduction	Protein kinases/ phospholipid signal transducers	Mitogen-activated protein kinases (MAPK), calcineurin B-like (CBL)-interacting protein kinase (CIPK) pathway, Ca-dependent protein kinases (CDPK) pathway
Activation of upstream regulatory proteins	Transcription factors/regulons	AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor) regulon; MYC/MYB regulon; CBF/DREB (cold-binding factor/ dehydration-responsive element binding) regulon; NAC regulon; ZF-HD (zinc finger homeodomain) regulon
Downstream effectors	Functional genes/ proteins	Compatible solutes, metabolite biosynthesis genes, transporters, Water channel proteins/ Aquaporins, ROS scavengers/homeostasis, wax biosynthesis/ deposition

activation and/or expression involved in stress response (Nataraja and Parvathi 2016). An overview of a typical signaling module in plant stress response and its representative components is presented in Table 23.1. As mentioned above, plants perceive drought and heat stress signals through cell-surface receptors, and many molecules such as inositol trisphosphate, inositol hexaphosphate, diacylglycerol, and reactive oxygen species (ROS) act as stress signals, which might increase intracellular Ca^{2+} levels (Hirayama and Shinozaki 2010). Such a complex network of signaling activates the synthesis of many primary and secondary metabolites required for plant acclimation responses (Fraser and Chapple 2011; Zandalinas et al. 2017). Specific molecular mechanisms associated with stress response pathways, specific to drought and heat stress, are presented in Tables 23.2 and 23.3, respectively. An overall summary of plant responses to drought and heat stress has been summarized in Figs. 23.1 and 23.2, respectively.

23.3   Plant Responses to Combined Drought and Heat Stress

At the whole plant level, most of the abiotic stresses induce a cascade of biochemical and molecular events leading to, in some cases, similar responses. The effect of the combination of drought and heat stress is more severe than when these stresses are taken individually (Dreesen et al. 2012). In wheat, barley, and tobacco, the combination of drought and heat results in similar physiological responses, with severe intensity, when compared to individual stress-induced effects (Keles and Oncel 2002; Rizhsky et al. 2002; Rollins et al. 2013). Plant responses, as well as their ability to withstand individual and combined stress, vary with plant species. For example, C_4 crops like maize and sorghum have better tolerance to combined

Table 23.2 Drought stress-specific molecular mechanisms in plants

	Signaling partner/ component/ physiological trait	Stimulus and molecular mechanism	References
A	*Signal receptor*		
1	ARCK1 (*Arabidopsis thaliana*) (*Arabidopsis* receptor like cytosolic kinase 1)	ABA- and osmotic stress-inducible; Interacts with cysteine-rich receptor-like kinase 36 (CRK36)	Tanaka et al. (2012)
2	GsCBRLK (*Glycine soja*) (Calcium/calmodulin-binding receptor-like kinase)	High salinity and ABA inducible; Calcium-binding RLCK	Yang et al. (2010b)
3	PSTOL1 *Pup1*-specific protein kinase gene	Phosphate-deficit soil; Improved root growth and grain yield of rice and drought response	Gamuyao et al. (2012)
4	OsRLCK253 (Rice) (*Oryza sativa* receptor like cytoplasmic kinase 253)	Interacts with stress-associated proteins (OsSAP1/11) to mediate drought and salt stress responses	Giri et al. (2011)
5	OsGUDK (*Oryza sativa* growth under drought kinase)	Drought stress signaling by activation of stress genes by OsAP37 (APETALA2/ETHYLENE RESPONSE FACTOR OsAP37)	Ramegowda et al. (2014)
B	*Signal Amplification: Secondary Messengers*		
		Calcium, ROS, Inositol 1, 4, 5-trisphosphate (IP3), Diacylglycerol (DAG)	Nataraja and Parvathi (2016)
C	*Signal Transduction: Protein Kinases/Phospholipids*		
1	Protein Kinases		
a	CDPK (Calcium-dependent protein kinase)	Dependent upon Ca^{2+} binding; Activated CDPKs relay signals through phosphorylation of specific substrates	Ray et al. (2007)
b	CBL-CIPK (Calcineurin B-like protein-interacting protein kinase)	SOS pathway: In the presence of Ca^{2+}, SOS3/CBL4 interacts physically with the regulatory domain, SOS2/CIPK24.	Martinez-Atienza et al. (2007)
c	MAPK (Mitogen-activated protein kinase)	Sequential phosphorelay by MAPK kinase kinase (MAPKKK), a MAPK kinase (MAPKK), and a MAPK	
	AtMEKK1 (*Arabidopsis thaliana* MAP kinase or ERK kinase kinase 1)	In addition to dehydration, the protein is responsive to cold and salinity	Mizoguchi et al. (1996), Moustafa et al. (2008) and Teige et al. (2004)
	AtMPK1 (*Arabidopsis thaliana* mitogen-activated protein kinase 1)	Cold, dehydration, hyperosmolarity, salinity	Ichimura et al. (2000), Droillard et al. (2002) and Yu et al. (2010)
	AtMKK7 (*Arabidopsis thaliana* MAP kinase kinase 7)	Dehydration, hyperosomolarity, salinity	Moustafa et al. (2008)

<div style="text-align: right">(continued)</div>

Table 23.2 (continued)

| Signaling partner/ component/ physiological trait	Stimulus and molecular mechanism	References
OsMPK3 (*Oryza sativa* mitogen-activated protein kinase 3)	Drought, temperatures, salinity	Agrawal et al. (2002, 2003)
OsMKK6 (*Oryza sativa* mitogen-activated protein kinase 6)	Cold, drought, salinity	Kumar et al. (2008) and Wen et al. (2002)
OsMPK4/OsMAP1 (*Oryza sativa* mitogen-activated protein kinase 4)	Cold, drought, salinity	Xiong and Yang (2003)
DSM1 (Drought hyper-sensitive mutant 1)	Drought	Ning et al. (2010)
MMK4 (mitogen-activated MAP kinase 4)	Cold, drought	Jonak et al. (1996)
ZmMPK3 (*Zea mays* mitogen-activated protein kinase 3)	Cold, drought, salinity	Wang et al. (2010)
GhMPK2 (*Gossypium hirsutum* mitogen-activated protein kinase 2)	Cold, drought, salinity	Wang et al. (2007)
GhMPK16 (*Gossypium hirsutum* mitogen-activated protein kinase 16)	Drought	Shi et al. (2011)
2 Phospholipids	Phospholipase C, phospholipase D (PLD), phospholipase A2 (PLA2), diacylglycerol pyrophosphate (DGPP), and phosphatidylinositol 3,5-bisphosphate (PI(2, 3)P2)	Nataraja and Parvathi (2016) and Lata et al. (2015)
D *Transcription factors/regulons*		
AREB/ABF regulon (ABA response element binding/ABRE-binding factor)	ABA-dependent; ABA-responsive element-binding protein/ABA-binding factor	Saibo et al. (2009), Hirayama and Shinozaki (2010), Lata and Prasad (2011) and Lata et al. (2015)
MYC/MYB regulon	ABA-dependent	
CBF/DREB (C repeat binding factor/ dehydration response element binding) regulon	ABA-independent; Cold-binding factor/dehydration-responsive element binding	
NAC (NAM-ATAF-CUC) and ZF-HD (zinc finger homeodomain) regulon	ABA-independent; NAM-ATAF-CUC; zinc finger homeodomain	

Table 23.2 (continued)

	Signaling partner/ component/ physiological trait	Stimulus and molecular mechanism	References
E	*Trait-associated functional genes*		
	Water mining	GmNAC, V-H$^+$ Ppase (Vascular H$^+$ pyrophosphatase), ThVPVH$^+$ Ppase, TaVP (*Triticum aestivum* vascular H$^+$ pyrophosphatase), AtAVP1 (*Arabidopsis* vascular H$^+$ pyrophosphatase); Aquaporin (NtAQP7)	Liu et al. (2014), Pei et al. (2012), Li et al. (2014a), Pasapula et al. (2011) and Zhou et al. (2012)
	Water conservation	EsWAX1 (*Eutrema salsugineum* wax 1) DEWAX; AtSHN1 (*Arabidopsis thaliana* SHINE 1)	Zhu et al. (2014), Go et al. (2014) and Sajeevan et al. (2017)
	Water relations	OsLEA3-2 (*Oryza sativa* late embryogenesis abundant protein 3-2), HVA1 (*Hordeum vulgare* late embryogenesis abundant protein 1)	Duan and Cai (2012) and Chen et al. (2015)
	Osmoregulation	Trehalose- OsTPS1 (Trehalose-6-phosphate synthase 1), AtTPPD (*Arabidospsis* trehalose 6 phosphate phosphatase D); Proline- P5CS (Pyrroline 5 carboxylase synthase), PvP5CS (*Phaseolus vulgaris* pyrroline 5 carboxylase synthase); Mannitol- mltD; Glycine betaine-codA	Li et al. (2011), Krasensky et al. (2014), Ghanti et al. (2011), Chen et al. (2013), Hema et al. (2014) and Goel et al. (2011)
	ROS scavenging	Ec-APX1	Bhatt et al. (2012)
	mRNA and protein turnover	OsRDCP1 (*Oryza sativa* ring domain containing protein 1), OSRIP18 (*Oryza sativa* ribosome-inactivating protein 1), CspA/B (Cold shock domain protein A/B), AtCSP3 (*Arabidopsis thaliana* cold shock domain protein 3), OsSUV3 (*Oryza sativa* SUV3 helicase), p68 helicase	Bae et al. (2011), Jiang et al. (2012), Castiglioni et al. (2008), Kim et al. (2013), Tuteja et al. (2013) and Tuteja et al. (2014)
	ER stress response	Endoplasmic reticulum (ER)-resident molecular chaperone BiP (binding protein)- OsBiP	Valente et al. (2009)
	ABA biosynthesis-stomatal regulation	OsNCED2	Xiao et al. (2009)
	Membrane integrity	CaXTH3 (xyloglucan endo-transglucosylase/hydrolase)	Choi et al. (2011)

stress compared to C$_3$ crops like wheat and sunflower (Machado and Paulsen 2001; Killi et al. 2017). Generally, one of the most affected physiological processes under combined drought and heat stress is the photochemistry and biochemistry of photosynthesis. The combined stress is known to disrupt PS-II function, Rubisco activity, and hence drastically reduce photosynthetic activity (Sainz et al. 2010; Awasthi

Table 23.3 Heat stress-specific molecular mechanisms in plants

	Signaling partner/ component/ physiological trait	Stimulus and molecular mechanism	References
A	*Signal receptor*		
	PhyB (Phytochrome B)	Heat, light	Song et al. (2017)
B	*Signal transduction: protein kinases/phospholipids*		
	MAPK	Heat	Link et al. (2002)
	SlMPK1 (*Solanum lycoersiocn* mitogen-activated protein kinase 1)	Heat	Ding et al. (2018)
C	*Transcription factors/regulons*		
	DPB3-1(DNA polymerase II subunit 3-1)/DREB31	Specifically active under stressful condition to impart heat tolerance	Sato et al. (2016)
	MBF1C (Multiprotein bridging factor 1)	Regulates the expression of 36 different transcripts during heat stress, including the important transcriptional regulator DRE-binding protein 2A (DREB2A), two heat shock transcription factors (HSFs), and several zinc finger proteins	Suzuki et al. (2011)
	HSFA2 (heat shock factor A2)	Heat inducible, HSP expression, thermotolerance	Charng et al. (2007)
	OsHSF7	Functions as a high-temperature receptive and responsive factor	Liu et al. (2009)
	AtDREB1A	Tolerance to heat stress	Hong et al. (2009)
	HSFA6b	Tolerance to heat stress	Huang et al. (2016)
	SNAC3 (Stress responsive NAC3)	Tolerance to heat stress, drought and oxidative stress	Fang et al. (2015)
D	*Trait-associated functional genes*		
	ROS scavenging	TaFER-5B (*Triticum aestivum* ferritin 5B)	Zang et al. (2017)
	Protein turnover	OsHTAS (*Oryza sativa* heat tolerance at seedling stage), OsHCI1 (*Oryza sativa* heat and cold induced 1), SlSIZ1 (*Solanum lycopersicon* SIZ1 E3 ligase)	Lim et al. (2013), Liu et al. (2016) and Zhang et al. (2017)
	Membrane integrity	sHSP17.7 (small heat shock protein 17.7)	Hu et al. (2010)
	Chaperon activity; Protection of RNA and proteins	Ef-Tu, AtP3B (ribosomal protein 3), OsHSP18.6; UBP1y (oligouridylate-binding protein 1b)	Fu et al. (2008), Ji et al. (2017), Wang et al. (2015) and Nguyen et al. (2016)
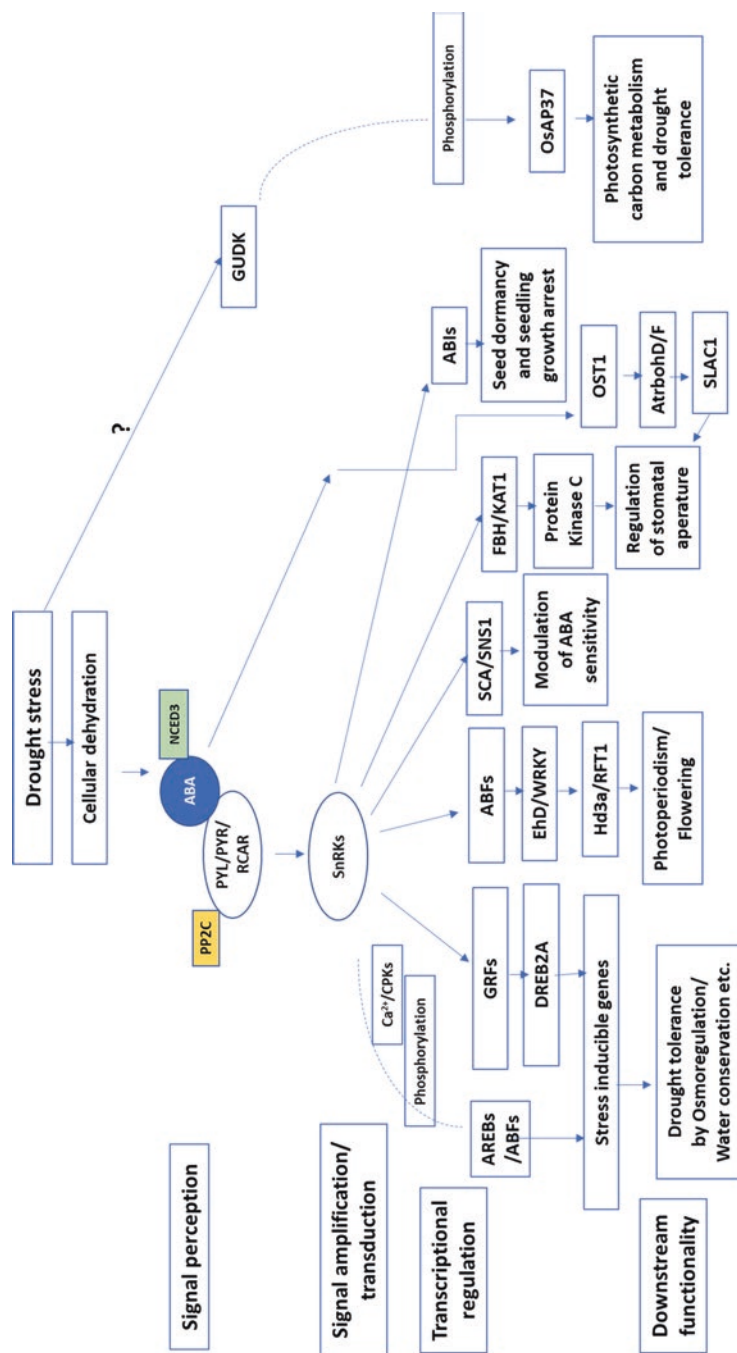
Fig. 23.1 Schematic model of different response pathways under drought stress: ABA-dependent pathway operates through PP2C-PYR/PYL/RCAR complex which positively regulates AREB/ABF-SnRK2 pathway. SnRK2s further activate/regulate other TFs downstream by phosphorylation cascades. These TFs are responsible for the expression of target functional genes in response to dehydration stress. GRF7 suppresses the expression of DREB2A, which is a key TF in ABA-independent gene expression. Abbreviations: *PP2C-PYR/PYL/RCAR* pyrabactin resistance1/PYR1-like/regulatory components of ABA receptors, *PP2C* protein phosphatase 2C, GRF7-targeting cis element, *GUDK* growth under drought kinase (Adapted from Ramegowda et al. 2014 and Joshi et al. 2016)

Note: Arrows do not essentially indicate positive/negative regulation
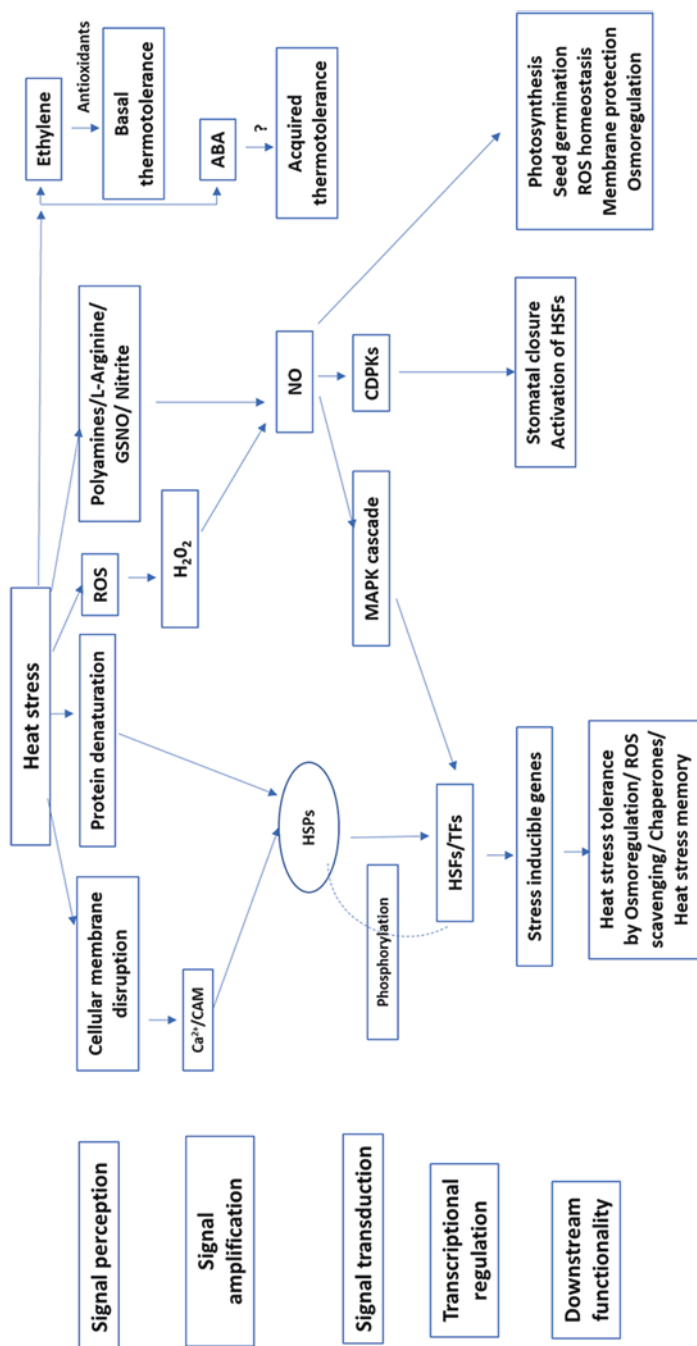
Fig. 23.2 **Schematic model of different response pathways under heat stress:** Heat stress induces Ca^{2+} influx, thereby triggering MAPK cascade leading to gene expression. Secondary signals like ROS, H_2O_2, NO, and ABA are other modes leading to heat stress tolerance. Abbreviations: *CaM* calmodulin, *CDPKs* calcium-dependent protein kinases, *MAPKs* mitogen-activated protein kinases, *NO* nitric oxide, *HSFs* heat shock factors, *HSPs* heat shock proteins, *TFs* transcription factors (Adapted from Awasthi et al. 2015; Guo et al. 2016 and Parankusam et al. 2017). *Note: Arrows do not essentially indicate positive/negative regulation*

et al. 2014). Drought, high temperature, and their combination affect ultrastructure of chloroplasts and mitochondria in wheat leaves, and the defective phenotypes are more pronounced in combined drought and heat stress conditions (Grigorova et al. 2012). Chloroplasts have also been recently referred to as the center of stress perception and regulation. Understanding the remodeling of the chloroplast proteome during abiotic stress acclimation both under individual and combined stresses involving both anterograde (from the nucleus to the chloroplast) and retrograde (from the chloroplast to the nucleus) signaling events is the current focus (Bechtold and Field 2018). Another notable impact of combined stress is on stomatal responses. Combined stress leads to a reduction in stomatal conductance that prevents plant evaporative cooling, which ultimately leads to an increase in leaf temperature (Rizhsky et al. 2002; Rizhsky et al. 2004; Zandalinas et al. 2016a). This increase in leaf temperature is a common response under heat stress (Carmo-Silva et al. 2012). In tobacco, a 2–3 °C increase in leaf temperature was observed under combined stress (Rizhsky et al. 2002). Combination of drought and heat stress also influences plant developmental processes. Combined stress can limit viable leaf area (Shah and Paulsen 2003), increase stomatal density (Vile et al. 2012) and influence grain growth (Shah and Paulsen 2003). Reproductive tissues are the most sensitive to the individual as well as combined stress effects, although the processes affected are different (Barnabas et al. 2008; Prasad et al. 2011). For example, the heading to maturity stage of wheat cultivation in Mediterranean climate encounters combined stress, which has a critical impact on kernel filling and hence grain yield (Wardlaw 2002).

The most common responses to any abiotic stress are the stress-dependent generation of ROS and activation of ROS detoxification system. Combined drought and heat stress also trigger oxidative stress and associated cellular responses. Photorespiration accounts for a major metabolic pathway generating ROS under combined stress (Zinta et al. 2014). For this reason, a C_3 crop like sunflower has more impact of combined stress compared to maize, a C_4 plant (Killi et al. 2017). The ROS deactivation system in *Arabidopsis* involved alternative oxidase (AOX), glutathione peroxidase (GPX), glutathione reductase (GR), copper/zinc superoxide dismutase (Cu/Zn-SOD), and glutathione-*S*-transferase (GST) (Rizhsky et al. 2002). In chickpea, higher levels of ascorbate peroxidase (APX), GR, ascorbate, and glutathione were induced in seeds and leaves to reduce the stress effect (Awasthi et al. 2017). Stress-induced activation of heat shock proteins (HSPs) is another important response under combined stress, which is also similar to heat stress (Ashoub et al. 2015; Zhao et al. 2016). Combined stress can influence carbohydrate metabolism, leading to altered starch and sucrose content due to reduced activity of their respective synthesizing enzymes as evidenced in chickpea, lentil, and *Arabidopsis* (Awasthi et al. 2014; Sehgal et al. 2017; Zinta et al. 2018). Accumulation of osmolytes and compatible solutes is a common stress-adaptive strategy in plants (Krasensky and Jonak 2012). Proline is crucial for stress adaptation in barley under combined drought and heat stress (Templer et al. 2017). However, proline accumulation is absent in *Arabidopsis* and tobacco under combined drought and

temperature stress suggesting that some of the stress responses are unique and might vary with crop species (Rizhsky et al. 2002).

Phytohormones have a crucial role in plant adaptation to stressful conditions (Wani et al. 2016). Under drought, abscisic acid (ABA) has long been acknowledged as a major chemical signal associated with root-to-shoot communication (Schachtman and Goodger 2008). However, the relevance of hormones and their interactions is not completely understood under heat stress. Accumulation of 9-cis epoxycarotenoid dioxygenase (NCED) protein required for ABA synthesis has been upregulated under drought and heat combination (Li et al. 2014b). Abscisic acid is also required for the accumulation of proteins APX1 and multiprotein bridging factor 1c (MBF1c), required for survival under a combination of drought and heat stress in *Arabidopsis* (Zandalinas et al. 2016b). Antagonistic to ABA, salicylic acid is known to play a role in stress signaling in citrus (Moeder et al. 2010). In *Arabidopsis*, jasmonic acid was highly accumulated as compared to salicylic acid (Caarls et al. 2015). This suggests that hormonal responses under a combination of stresses vary with crop species.

23.4   Plant Responses to Combined Drought and Heat Stress Are Also Unique

Studies on plant responses to the combination of diverse abiotic and/or biotic stresses have revealed that several of these responses are unique and cannot be inferred from the plant responses to their respective individual stresses (Pandey et al. 2015). This is evidenced by the identification of specific transcript profiles and a combination of metabolites and proteins that are unique to the combination of drought and heat stresses (Zandalinas et al. 2018). Several of such responses induce partially opposing physiological changes compared to its individual effects (Rizhsky et al. 2002; Prasch and Sonnewald 2013). For example, drought and heat stress in combination alters photosynthesis, respiration, stomatal conductance, and leaf temperature, distinctly from heat or drought alone (Rizhsky et al. 2002). Drought suppresses photosynthesis and respiration while heat enhances respiration without significantly affecting photosynthesis. However, the combination suppresses photosynthesis and enhances respiration, distinct from the individual stress effect. The combination also leads to stomatal closure similar to drought leading to enhanced leaf temperature. Another feature of combined drought and heat stress is the replacement of proline with sucrose in *Arabidopsis* (Rizhsky et al. 2002).

The uniqueness in plant responses to combined stress effect is also reflected in global transcriptome analysis (Rizhsky et al. 2004; Pandey et al. 2015; Jia et al. 2017). These responses seem to differ among plant species, and are complex, regulated by multiple genes and pathways, which might interact and/or inhibit each other (Prasch and Sonnewald 2013; Rasmussen et al. 2013; Suzuki et al. 2014). This transcriptional level response is also quite different from other stress conditions (cold, salt, or pathogen) (Rizhsky et al. 2002). Transcriptomic studies in different plant species like *Arabidopsis* (Rizhsky et al. 2004), tobacco (Rizhsky et al. 2002),

durum wheat (Rampino et al. 2012), and sorghum (Johnson et al. 2014) and tree species like poplar (Jia et al. 2017), have identified a unique transcript profile that is activated under combined stress when compared to individual drought and heat stress, and the transcripts also vary with plant type, duration, and severity of stresses (Suzuki et al. 2014; Pandey et al. 2015). The transcripts identified code for different protein kinases, transcription factors (TFs), heat shock proteins (HSPs), proteins involved in ROS detoxification, and proteases and enzymes involved in lipid bio-synthesis and starch degradation (Rizhsky et al. 2004). In sorghum, TFs like MYB8 and ATAF1, chaperons including heat shock proteins, LEAs (late embryogenic abundant proteins) and metabolic pathways including polyamine biosynthesis were specific to combined stress (Johnson et al. 2014). The higher expression levels of WOX1 (WUSCHEL related homeobox 1), a TF involved in polyamine biosynthesis is also unique to the combined stress response in sorghum (Johnson et al. 2014). In wheat seedlings, 17–36% of the differentially expressed transcripts were specifi-cally induced under a combination of drought and heat (Liu et al. 2015). Majority of these transcripts exhibited alternative splicing (AS) events unique to a combina-tion of drought and heat stress (Liu et al. 2018). AS events have been observed in several stress-responsive genes like TGN-localized SYP41-interacting protein (TNO1), WD repeat like 50 superfamily protein (WRD5A), Alfin-like 5(AL5), etc. Glutathione biosynthetic process and DNA methylation-associated transcripts were significantly enriched among these AS genes, suggesting the relevance of these responses under combined stress (Liu et al. 2018).

Proteomic studies have identified diverse types of proteins specific to combined stress, which involve enzymes associated with malate metabolism, Calvin cycle, and detoxification of ROS, while cytosolic APX is the key player in response to combined stress (Koussevitzky et al. 2008). The most abundant proteins in poplar, *Carissa,* and potato under combined stress were HSPs (Zhang et al. 2010; Li et al. 2014b; Sprenger et al. 2016). However, the metabolic profiles under combined drought and heat stress have been contradictory to transcriptomic profiles, with their similarity to heat stress response (Zandalinas et al. 2017). In a drought-toler-ant *Eucalyptus globulus* clone, drought-specific responses and trait manifestations were interestingly similar or different (Correia et al. 2018). But the shikimic acid pathway was activated under heat stress, strikingly different from that under drought. A combined stress treatment wherein drought-stressed *Eucalyptus* plants were subjected to a heat shock resulted in a decrease in photosynthesis and jas-monic acid with alterations in glutathione pool in relation to control. A noticeable response triggered by the combined stress alone was the accumulation of cinna-mate (Correia et al. 2018). The combined heat and drought stress responses in cereals indicated massive induction of HSPs and the sugar starvation phenotype in anthers (Lawas et al. 2018).

Stress tolerance in plants needs to be evaluated by simulating field conditions where multiple abiotic stresses occur simultaneously, and a lot of cross-talk exists among multiple stress situations (Chinnusamy et al. 2004; Shinozaki and Yamaguchi-Shinozaki 2007). A good number of genes that play a role in drought tolerance also

confer some degree of tolerance to salt and cold stresses. However, drought cum heat-tolerant crops will be the major targets of attention in the event of the drastic global climate change in tropical and subtropical regions (Battisti and Naylor 2009). The challenge shortly will be to identify the signaling elements that are missing in the current models/pathways and increasing our understanding of the cross-talk between pathways, as our knowledge about stress signaling networks remains gray (Yang et al. 2010a). An attempt has been made to compile the various pathways and the associated molecular mechanisms/ cascade patterning in case of both drought (Fig. 23.1) and heat (Fig. 23.2) stresses. It is very interesting to note the commonality in the stress response pathway construction with common secondary messengers like ROS and calcium and phosphorelay transduction events. For example, soybean DREB1/CBF-type TFs function in heat and drought as well as cold stress-responsive gene expression (Kidokoro et al. 2015), but it is unclear as to whether similar pathways operate upstream and downstream of these key regulatory moieties.

23.5   Options for Manipulation of Traits to Improve Stress Tolerance Under Stress Combinations

Concerted efforts are being made to improve the tolerance levels of both food and feed crops since abiotic stresses cause more than 50% yield loss in major crops worldwide (Bray et al. 2000; Lobell et al. 2011; Shao et al. 2009). Better understanding of the combined stress effects would be useful for targeted manipulation of traits contributing to tolerance in crops. Traditional crop breeding has had limited success in desired trait manipulation and mitigating the effects of abiotic stress. Genes/gene products regulating multiple molecular mechanisms are to be carefully identified and combined by novel gene stacking approaches to alter multiple traits required for combined stress tolerance in crop plants (Vemanna et al. 2013). There are options now to manipulate certain cellular tolerance traits such as protein synthesis and protein turnover, ROS detoxification, osmoregulation, etc., using transgenic approaches. Such attempts can be made by employing upstream regulatory proteins like stress-specific or basal transcription factors, which would improve the inherent tolerance capacity of crop plants (Pruthvi et al. 2014; Parvathi et al. 2015). There have been case studies where such conceptual approaches have rendered tolerance to both drought/osmotic stress as well as temperature induced stresses (Babitha 2012; Ramu et al. 2016). Multiple trait manipulation can result in multi-stress tolerant genotypes, which can be achieved by identifying and manipulating a super-regulatory gene capable of coordinating multiple trait-related gene/s expression (Parvathi and Nataraja 2017). As mentioned earlier, manipulating specific master regulatory genes such as TFs in transgenic crops has been demonstrated to be effective in engineering a broad-spectrum stress tolerance (Karaba et al. 2007; Pruthvi et al. 2014). In addition to stress-specific genes, microRNAs (miRNAs) which are small regulatory RNAs that act at the posttranscriptional level (Bartel 2004; Beauclair et al. 2010) have been found to be useful to impart stress tolerance

(Zhao et al. 2018). An increasing number of studies on plant miRNAs, such as miR393, have demonstrated that they are promising candidates for imparting multiple stress tolerance in plants and hence can be good candidates for crop genetic engineering (Rhoades et al. 2002; Shriram et al. 2016; Zhao et al. 2018).

In recent years, there are reports on the targeted DNA sequence modifications or editing using DNA sequence-specific nucleases. The zinc finger (ZF) nucleases, transcription activator-like effector nucleases (TALENs), and clustered, regularly interspaced, short palindromic repeats (CRISPR) have been employed in plants for genome editing (Voytas 2013). Now, CRISPR-cas9 technology has been used to specifically edit wheat genome (Liang et al. 2017). This can be extended for targeted manipulation of drought and heat tolerance. Better understanding of the crop genome, genes associated with the traits, and the optimization of genome editing technology in crops would advance our abilities towards the development of crops tolerant to combined drought and heat stresses. Similarly, as another approach to mitigate abiotic stresses, endophytes have been used, and endophytic microbiome research offers opportunities for improving biotic and abiotic stress tolerance in crops (Sangamesh et al. 2018). It is now well established that plant mechanisms to combat drought and/or heat stresses can be mediated by the microbes within and surrounding a plant (Lata et al. 2018). In wheat, grain yield and second-generation seed viability have been improved by fungal endophytes under drought and heat stress (Hubbard et al. 2014). These types of new-generation technologies would help in sustaining crop production under fast-changing climate.

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Abiotic Stress Tolerance in Field Crops: Integration of Omics Approaches

24

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Abstract

The development, growth, and productivity of field crops are negatively influenced by abiotic stresses resulting in significant losses in crop yield. Therefore, understanding tolerance of agronomic crops to abiotic stress factors like drought, salinity, heat, and chilling is of paramount importance for plant scientists for effective management. However, due to the complexity of abiotic stress response and tolerance, initial efforts through gene-based approaches were not enough to understand whole level mechanisms. Recently, tremendous developments made in the field of omics (genomics, transcriptomics, proteomics, metabolomics, and phenomics) have opened new avenues to understand and investigate the complex mechanisms of abiotic stress tolerance in plants, although integration of data collected from omics studies with such traits is still a challenging one. This chapter will emphasize the significance of omics field in understanding crop responses to different abiotic stresses, focusing on the recent developments made in field of omics with future prospects to overcome the major drawbacks of omic approaches.

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Abbreviations

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2D-PAGE	2-dimensional polyacrylamide gel electrophoresis
ABA	abscisic acid
CE-MS	capillary electrophoresis mass spectroscopy
EGFP	enhanced green fluorescent protein
FT-ICR-MS	Fourier transform ion cyclotron resonance mass spectroscopy
G x E	genotype–environment interaction
GBS	genotyping by sequencing
GC-MS	gas-chromatography mass spectroscopy
GWAS	genome-wide association study
ICP-MS	inductively coupled plasma mass spectrometer
ICP-OES	inductively coupled plasma-optical emission spectrometry
LA-ICP-MS	laser ablation inductively coupled plasma mass spectroscopy
LC-MS	liquid-chromatography mass spectroscopy
MALDI-TOF	matrix-assisted laser desorption/ionization time-of-flight
MAS	marker-assisted selection
mQTL	metabolite quantitative trait locus
MS	mass spectroscopy
MW	molecular weight
NAA	neutron activation analysis
NGS	next-generation sequencing
NMR	nuclear magnetic resonance
pI	isoelectric point
QTL	quantitative trait loci
ROS	reactive oxygen species
SNP	single-nucleotide polymorphism
XAP	X-ray absorption spectroscopy
XRF	X-ray fluorescence

24.1 Introduction

Yield losses due to abiotic stresses including drought, salt, heat, and chilling are still the main concern in agriculture in a world of increasing population and decreasing water resources. Plants frequently encounter abiotic stress conditions during their lifetime and they have developed three main approaches to either avoid the harmful effects of these unfavorable conditions or at least ensure the fate of their offspring. They can "escape" or "avoid" the abiotic stress by seeding earlier or by severe morphological changes, both of which lead to yield loss in terms of agriculture, or they can "tolerate" the stress conditions up to a certain level, which also cause yield loss, but usually to an acceptable level. As can be expected, among these approaches, plant's ability to tolerate abiotic stress conditions has been extensively studied to understand the key factors and ultimately to transfer them to field crops to prevent

yield loss due to unfavorable environmental conditions. However, years of scientific research showed that plant's response to abiotic stress conditions is a very complex mechanism with changes in transcription, translation, and posttranslation, causing an extensive alteration in both metabolic and biochemical levels, leading to physiological and morphological adaptation.

Omic technologies simply mean the determination of all genes, transcripts, proteins, or metabolites in a biological sample using high-throughput technologies. The Latin suffix "-ome" was first used by Professor Hans Winkler as "genome" to express all hereditary material in different chromosomes (Winkler 1920). The same suffix was used to identify all cellular activities such as transcriptome, proteome, and metabolome in the following years and became "-omics" expressing whole data obtained by high-throughput technologies. The development of new technologies enlarged the omic technologies from transcriptomics, proteomics, and metabolomics to different levels including lipidomics, ionomics, and phenomics. All data obtained by omic technologies have recently started to be integrated into systems biology through bioinformatics approaches (Fig. 24.1).

Considering the complexity of the changes in cellular metabolism, development of omic technologies led to new insights into understanding the abiotic stress response of plants. It is safe to say that all levels of omic technologies were effectively used in this scientific area and generated massive amount of data in genomics, transcriptomics, proteomics, and recently, metabolomics, that still need to be integrated to identify the key factors increasing abiotic stress tolerance of field crops. In this chapter, we will try to summarize different omic approaches to understand abiotic stress response and tolerance of several field crops by focusing on the recent

Fig. 24.1 Omic technologies
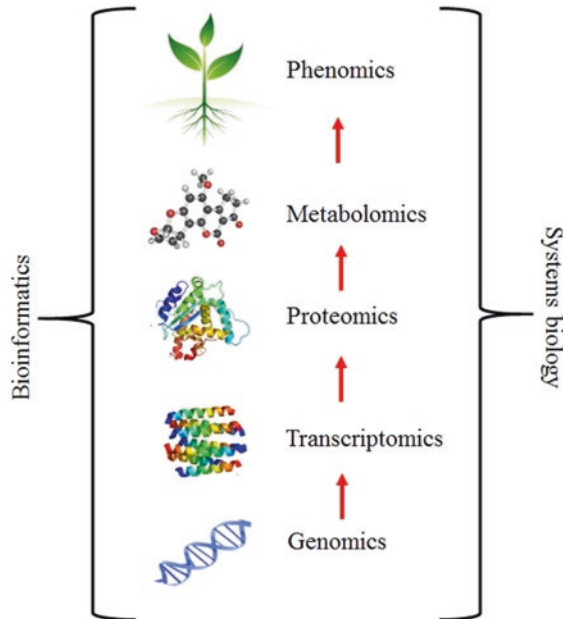
developments with future prospects and approaches to overcome major drawbacks of these high-throughput technologies.

24.2   Genomics Approach to Abiotic Stress Tolerance

Genomics is the use of high-throughput technologies to understand the complex biological functions of the genetic material of a cell, the genome. Development of next-generation technologies, including 454 Life Sciences (Roche), SOLiD (Applied biosystems), and Illumina (Solexa) platforms, enabled the sequencing of the whole plant genomes (Mochida and Shinozaki 2011; Unamba et al. 2015). With the decrease in the cost of sequencing by the use of high-throughput technologies and the increase in the effectiveness of bioinformatics analyses for the assembly of genome from thousands of contigs, currently the whole genomes of over 50 plant species have been sequenced and almost wholly assembled (Hamilton and Buell 2012; Michael and Jackson 2013; Unamba et al. 2015). The availability of whole genome sequences also enables the identification of all the potential genes and regulatory elements on the genome by bioinformatics approaches. Genomics data can further be used to find the function(s) of the gene(s) identified through functional genomics, checking the genome structure in different organisms or different organs through comparative genomics, and finding the location of gene(s) on the genome by genetic and physical mapping through structural genomics.

Functional genomics is important to reveal and prove the functions and roles in cellular metabolism of all the genes identified on the genome (Rhee and Mutwil 2014). Although the genome can be sequenced and the potential genes and regulatory elements can be identified, the function of the protein, its subcellular localization, its transcription, and the change in the transcription in different organs, in different developmental stages, and under a wide array of environmental conditions, considering the possibility of potential alternative splicing products, have to be investigated to assign a functional role in cellular metabolism. In this respect, functional genomics is the most important approach to understand the plant genome functionally.

In terms of agriculture, genomics is widely used to find single-nucleotide polymorphisms (SNPs) through comparative genomics approach. The ultimate goal is to find SNPs or quantitative trait loci (QTLs) associated with a desired phenotype. However, SNPs are very common on the genome and do not usually cause a detectable phenotype due to strong environment pressure on plants. This is especially important for abiotic stress studies which necessitate the observation of the desired phenotype, in this case the tolerance to abiotic stresses, under different environmental conditions to eliminate the changes in the desired trait due to genotype x environment (G x E) interaction. Genome-wide association studies (GWAS) and genotyping by sequencing (GBS) approaches are, therefore, commonly used to identify SNPs associated with tolerance to abiotic stresses of field crops, through which, when there is a strong relationship between tolerance and SNP(s), a marker can be

developed to be used for selection in large-scale breeding studies with marker-assisted selection (MAS) (He et al. 2014; Unamba et al. 2015; Kang et al. 2016).

Both GWAS and GBS have been used for several field crops to identify SNPs or QTLs possibly related to tolerance to a wide array of abiotic stresses (Table 24.1). Most of these studies reported several, generally at least around a hundred, SNPs and

Table 24.1 Examples of GWAS and GBS approaches used in field crops in response to major abiotic stresses

Plant	Abiotic stress	References
Aegilops tauschii	Drought	Qin et al. (2016)
Brassica napus (rapeseed)	Drought, salinity	Tan et al. (2017)
Glycine max (soybean)	Drought	Kaler et al. (2017)
	Salinity	Zeng et al. (2017)
Gossypium hirsutum (cotton)	Drought	Baytar et al. (2018)
	Drought	Lu et al. (2016)
	This study specifically focused on GWAS analyses of stress-responsive long noncoding RNAs	
	Salinity	Du et al. (2016) and Cai et al. (2017)
Hordeum vulgare (barley)	Drought	Elwafa (2016), Tavakol et al. (2016), and Merchuk-Ovnat et al. (2018)
	Salinity	Hazzouri et al. (2018)
Medicago sativa (alfalfa)	Drought	Yu (2017)
	Salinity	Yu et al. (2016) and Liu and Yu (2017)
Medicago truncatula (caliph medic)	Salinity	Yaish et al. (2018)
Oryza sativa (rice)	Drought	Ereful et al. (2016), Ma et al. (2016), Pantaliao et al. (2016), Li et al. (2017), Deshmukh et al. (2018), and Guo et al. (2018)
	Salinity	Shi et al. (2017), Yu et al. (2017), Batayeva et al. (2018), Frouin et al. (2018), Naveed et al. (2018), and Patishtan et al. (2018)
	Chilling	Pandit et al. (2017) and Schläppi et al. (2017)
Sesamum indicum (sesame)	Drought, salinity	Li et al. (2018)
Sorghum bicolor (sorghum)	Drought, chilling, salinity, heat, ABA, ROS	Woldesemayat et al. (2018)
Triticum aestivum (wheat)	Drought	Mwadzingeni et al. (2017)
Triticum aestivum (wheat)	Drought, heat, drought and heat	ElBasyoni et al. (2017)
Triticum durum (durum wheat)	Drought, heat	Sukumaran et al. (2018)

Table 24.1 (continued)

Plant	Abiotic stress	References
Triticum turgidum ssp. *dicoccoides* (wild emmer wheat)	Salinity	Feng et al. (2017)
	This study specifically focused on GWAS analyses of stress-responsive miRNAs	
Zea mays (maize)	Drought	Li et al. (2016), Wallace et al. (2016), Wang et al. (2016), Zhang et al. (2016), Shikha et al. (2017), and Wang et al. (2017)
	Chilling	Hu et al. (2017)

in some cases QTLs associated with the abiotic stress tolerance. However, the confirmation of SNPs and QTLs has been performed in independent genotypes only in a few studies. It is almost clear that GWAS, when used in identification of SNPs associated with tolerance to abiotic stresses, demonstrates changes in nucleotide sequence of genes or regulatory regions that might have a role in increasing the strength of the plant under unfavorable environmental conditions. The main drawback for these SNPs and QTLs to be used as reliable markers in breeding approaches for increasing abiotic stress tolerance is the changes in the observed phenotype due to strong environmental interaction which can hinder the demonstration of the same SNPs or QTLs to be functional in the selection of tolerant genotypes in independent plants.

It is important to realize that the expected effect of global climate change is the occurrence of multiple abiotic stresses together; for example, decrease in water availability will eventually force field crops to deal with high salinity, and increase in temperature will cause decreased water availability due to accelerated evaporation. That means, even though you have a drought-tolerant crop, if it is sensitive to heat, the yield loss will still be a concern in terms of agriculture. Therefore, the research in finding SNPs or QTLs should focus on the combination of abiotic stresses, and maybe even on the possible scenarios of effects of climate change on the cultivation area, since the expected results are very diverse depending on the region. There are two interesting studies that consider multiple abiotic stresses together on oil content of sunflower (Mangin et al. 2017) and the effects of increase in temperature and decrease in water availability based on climate change scenarios in maize cultivation in Europe (Millet et al. 2016). Both of these studies are pioneers in the use of GWAS in genomics approach to increase the tolerance of field crops to abiotic stresses, and more such studies with other field crops are required to ensure the sustainability of agriculture in the future.

24.3 Transcriptomics Approach to Abiotic Stress Tolerance

Transcriptome represents all the RNA molecules having transcription or expression from the genome in a cell at a certain time point. Transcriptomics stands for sequencing, profiling, and counting all the RNA molecules from the genome, which enables

the detailed and/or comparative analyses of gene expression quantitatively. The genome of an organism contains all the necessary genes for all developmental stages, for every tissue and for all environmental stimuli, and represents what the plant is capable of doing at a certain condition. The gene expression, or transcriptome, on the other hand, changes depending on the developmental stage, tissue, and even cells of the same tissue. Therefore, transcriptomics represents what the plant is metabolically doing at that developmental stage, at that tissue, or upon the environmental conditions at a certain time point.

Transcriptomics studies are mostly performed with microarray or next-generation sequencing (NGS) platforms, both of which provide high-throughput data representing all the transcripts depending on the availability of the whole genome sequence in microarray platform and on the sequencing depth in the next-generation sequencing approach (Unamba et al. 2015). With respect to understanding the plant's response and/or tolerance to abiotic stresses, transcriptomics is the most widely used approach (over 25,000 articles according to Google Scholar) and there is no easy way to summarize or mention all the findings related to the field crops (Agarwal et al. 2014; Imadi et al. 2015). Therefore, this chapter will mainly focus on the common approaches, critical factors, and future perspectives.

Transcriptomics studies to reveal factors related to understanding the response or factors increasing the tolerance to abiotic stresses of field crops mainly involve the comparison of gene expression of the plants with or without environmental stress conditions. The studies to understand the plant's response to abiotic stress conditions simply involve the growth of the plants and treatment with the stress. The studies aiming to investigate the factors causing the increase in tolerance or sensitivity, on the other hand, require an initial experiment or knowledge to identify the plants with increased tolerance or sensitivity to the abiotic stress worked on. In both cases, there are some critical factors to consider in experimental design to reveal all the changes in the metabolic activity upon environmental stress: RNA instability and the appropriate control group. RNA is not a stable molecule and since transcriptomics enables the quantification of gene expression, plant samples should be frozen in liquid nitrogen or stored in other means that prevents degradation. Samples should further be stored at −80 °C with or without RNA isolation, bearing in mind that several thawing of the same RNA sample or melting of the tissue sample will lead to erroneous conclusions due to severe degradation. The second factor, the appropriate control group, is very critical since the gene expression profile is highly depended on the developmental stage and growth conditions. The plants to be used as a reliable control should be grown under the same conditions, with the same treatments, except the stress, and be kept alive and healthy to obtain only the changes related to the abiotic stress conditions by comparison of transcriptomes. The tissues from stress-treated and control plants should be collected at the very same time and from the very same tissues considering the gene expression profile depends not only on the tissue and/or developmental stage but also on the daytime point. This is especially important to reveal the gene expressions of the photosynthesis-related genes whose expression changes even with the availability of sunlight.

All of these factors are reliably considered by the scientists working on the abiotic stress tolerance of field crops. As stated before, there are huge amount of data on transcriptomics in response to a certain abiotic stress condition; however, the integration of all these data to obtain a "big picture" is still a challenge. First of all, the metabolism is interconnected and should be considered as a whole to find the key factors involved in the response or tolerance. The most effective approaches to this problem so far are the use of heat maps or MapMan program (Thimm et al. 2004). Both of these approaches, especially MapMan, enable the correct visualization of cellular metabolism, which is very important considering that in most cases, an increase in gene expression of a single gene in a metabolic pathway does not necessarily mean the increase in the whole pathway, since its product can also function as a substrate of another metabolic pathway, so that it can lead to starting up or increase in the efficiency of another pathway. The main problem with integrating all the knowledge on the responses of plants to abiotic stress in the transcriptomic level is the differences in the plant, genotype, growth conditions, pretreatments, age of the plant at the stress treatment, and the time period of the stress. All these factors depend on the experimental design, which somehow differs from study to study, and considering the transcriptome is highly variable on the factors mentioned before, it appears that most of these data can never be efficiently integrated into a "big picture." Therefore, it is important to revolutionize the abiotic stress treatments into a more common way to make use of data obtained from one study to be compared with the data from another study.

Most of the literature on the transcriptomics of abiotic stress tolerance states the response upon a single treatment, drought, salinity, cold, or heat. However, the climate change scenarios, as stated before, estimate multiple stresses to affect the production of field crops. Therefore, the changes in transcriptomes upon combined stress treatments are becoming the main approach in transcriptomics studies. Another perspective to consider is the understanding of the changes in gene expression profiles upon priming, which might have clues to find the key factors on increasing the tolerance of the plant to abiotic stress conditions. Priming is simply using chemical agents such as hydrogen peroxide or sodium hydrosulfide to the seeds, which increases their tolerance to abiotic stresses during their lifetime (Savvides et al. 2016; Ashraf et al. 2018). Both of these approaches are important to get new insights into transcriptomics studies to increase the abiotic stress tolerance of field crops. However, in all cases, it is important to not to neglect the fact that the presence of the transcript does not necessarily mean the presence of the active protein functional in the response metabolism.

24.4   Proteomics Approach to Abiotic Stress Tolerance

Proteome represents all the proteins present in the tissue or the cell, and considering that not all transcripts become a functional protein, is possibly the most correct way of understanding the changes in cellular metabolism depending on growth conditions, developmental stage, or environmental stimulus. Proteomics involves the
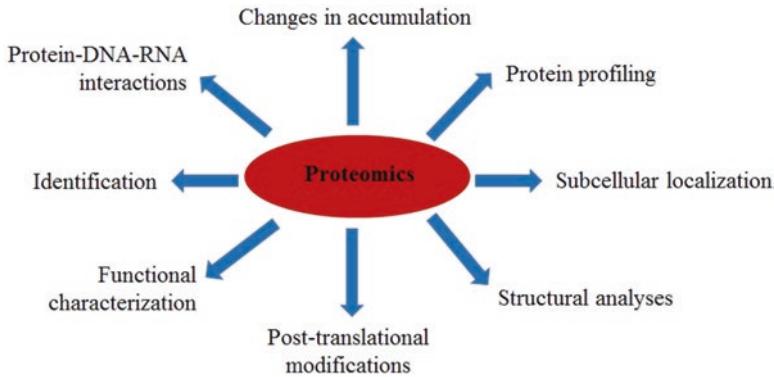
Fig. 24.2 Proteomics analyses

identification and investigation of proteins, possible posttranslational modifications, structures, functions, and interactions with other proteins or subcellular elements to understand the cellular metabolism using high-throughput technologies (Fig. 24.2). As such, it involves several other omic approaches including localisome studies for subcellular localization, interactomics for protein-protein interactions, kinomics for protein with kinase activity to understand signal transduction, and secretomics for proteins functional after secretion to extracellular space (Agarwal et al. 2012).

Proteomics studies on understanding the response and/or tolerance of field crops to abiotic stresses mainly focused on 2-dimensional polyacrylamide gel electrophoresis (2D-PAGE) and further identification and characterization of the protein spots obtained. The first dimension in 2D-PAGE differentiates proteins according to their isoelectric point (pI) and the second dimension according to their molecular weight (MW). Theoretically, two proteins in a cell cannot have the same pI and MW, which enables a separation at high resolution, that is, each spot on the gel represents a different protein. It is important to note that a cell can contain 10,000–20,000 proteins at any time; therefore, even at the highest resolution possible, 2D-PAGE cannot represent the whole proteome. The next step in proteomics analyses is the recovery and purification of the protein spots obtained and identification with techniques most common of which is matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF) mass spectroscopy. After the proper isolation and identification of the proteins, interactions with other proteins, DNA, or RNA can be investigated through yeast two hybrid system or protein microarrays, structural analyses by nuclear magnetic resonance (NMR), or X-ray crystallography, and subcellular localization through fluorescent proteins like EGFP or X-ray tomography can be investigated (Fields and Song 1989; Moreno-Risueno et al. 2010). Although all these techniques are available, except 2D-PAGE, they cannot deliver high-throughput data and there are still many drawbacks in the use of these techniques in proteomics (Abreu et al. 2013; Uhrig and Moorhead 2013; Vanderschuren et al. 2013; Jorrin-Novo 2016). Therefore, proteomics still has a long way to identify all

the cellular proteins and changes in their functions, structures, and interactions with other molecules in response to abiotic stresses.

Nonetheless, proteomics has been widely used to understand the response of abiotic stress conditions in several field crops, especially rice, wheat, and maize (Table 24.2). These studies have mostly shown the involvement of defense, energy metabolism, protein synthesis, protein degradation, protein folding, photosynthetic metabolism, and carbohydrate metabolism-related proteins, heat shock proteins, and detoxifying enzymes in abiotic stress response along with many proteins with an unknown function (Abreu et al. 2013; Barkla et al. 2013; Gong et al. 2014; Kim et al. 2014; Komatsu et al. 2014). The main drawback here is that all the proteins identified by the proteomics studies to understand the plant's response or tolerance to abiotic stress conditions mainly prove the presence of the protein of the transcript or the gene already found by genomics or transcriptomics approaches. The key factors associated with the increase in tolerance might probably be in the proteins of unknown function, which cannot be purified or identified due to technical problems associated with the technology used in proteomics approaches. It is rather clear that proteomics, compared to genomics and transcriptomics, is more promising to provide useful background information for understanding and development of abiotic stress-tolerant field crops, and improvement of technical advances is certainly required for this approach to achieve these goals.

24.5   Metabolomics Approach to Abiotic Stress Tolerance

Metabolome stands for all the biochemical, that is the small molecules, present in a cell or a tissue, and metabolomics for analysis of all metabolic byproducts, hormones, signaling molecules, and secondary metabolites present in a biological sample with techniques like mass spectroscopy (MS), gas-chromatography-MS (GC-MS), liquid-chromatography-MS (LC-MS), capillary electrophoresis-MS (CE-MS), Fourier transform ion cyclotron resonance-MS (FT-ICR-MS), and NMR (Oliver et al. 1998; Hong et al. 2016; Samota et al. 2017; Tian et al. 2017; Alseekh and Fernie 2018). Although metabolomic profiling is very important to understand complex phenotypic responses of plants to changes in environmental conditions, metabolomics is probably the hardest of the omic approaches, since metabolome is extremely varied with developmental stage and growth factors, like availability of nutrients and water, not only between the tissues but also between the cells composing the tissue, and it is almost impossible to identify secondary metabolites of complicated structure which probably have an important role in abiotic stress response (Fuhrer and Zamboni 2015; Nakabayashi and Saito 2015). Therefore, it is safe to say that metabolomics has not been effectively used in studies related to abiotic stress tolerance of field crops (Table 24.3).

Although it does not provide definitive results as genomics, transcriptomics, and even proteomics approaches, metabolomics provides a reliable metabolite quantitative locus (mQTL) data that appear to be used as a marker for breeding studies for increasing tolerance of field crops to abiotic stresses (Mochida and Shinozaki 2011).

Table 24.2 Examples of proteomics studies on understanding abiotic stress response of field crops

Plant	Abiotic stress	References
Allium cepa (onion)	Chilling	Chen et al. (2013)
Brassica juncea (Indian mustard)	Salinity	Yousuf et al. (2017)
Brassica napus (canola)	Salinity	Alagoz and Toorchi (2018) and Yin et al. (2018)
Glycine max (soybean)	Salinity	Ma et al. (2012); Fercha et al. (2016); Ji et al. (2016)
	Heat	Ahsan et al. (2010)
	Flooding	Komatsu et al. (2009, 2010), Yin et al. (2014), and Oskuei et al. (2017)
Gossypium hirsutum (cotton)	Salinity	Li et al. (2015) and Peng et al. (2018)
Hordeum vulgare (barley)	Salinity	Witzel et al. (2009) and Gao et al. (2013)
	Chilling	Longo et al. (2017)
Lolium multiflorum (ryegrass)	Drought	Pan et al. (2018)
Medicago sativa (alfalfa)	Drought	Zhang and Shi (2018)
	Salinity	Ma et al. (2017)
Oryza sativa (rice)	Drought	Agrawal et al. (2016), Wang et al. (2017), and Wade et al. (2002)
	Salinity	Fukuda et al. (2003), Chen et al. (2009), Liu and Bennett (2011); Song et al. (2011), Liu et al. (2013), Damaris et al. (2016), and Chintakovid et al. (2017)
	Chilling	Hashimoto and Komatsu (2007), Lee et al. (2009), Hashimoto et al. (2009), and Ji et al. (2017)
Pennisetum glaucum (pearl millet)	Drought	Ghatak et al. (2016)
Phaseolus vulgaris (common bean)	Drought	Zadraznik et al. (2013)
Pisum sativum (pea)	Drought	Wang et al. (2012)
Solanum lycopersicum (tomato)	Salinity	Chen et al. (2009) and Manaa et al. (2011)
	Chilling	Sanchez-Bel et al. (2012)
Solanum tuberosum (potato)	Salinity, chilling	Evers et al. (2012)
Triticum aestivum (wheat)	Drought	Ford et al. (2011), Kang et al. (2012), Alvarez et al. (2014), Faghani et al. (2014), Zhang et al. (2014), Ding et al. (2017), and Ullah et al. (2017)
	Salinity	Peng et al. (2009), Guo et al. (2012), Jacoby et al. (2013), Capriotti et al. (2014), and Fercha et al. (2014)
	Heat	Wang et al. (2015)
	Chilling	Vitamvas et al. (2012) and Kosova et al. (2013)
Zea mays (maize)	Drought	Zhao et al. (2013)
	Salinity	Zorb et al. (2010), Farooq et al. (2015), and Guo et al. (2017)

Table 24.3 Metabolomics studies on understanding abiotic stress response of field crops

Plant	Abiotic stress	References
Brassica napus (rapeseed)	Salinity	Hasanuzzaman et al. (2011)
Cicer arietinum (chickpea)	Salinity	Dias et al. (2015)
Glycine max (soybean)	Drought	Silvente et al. (2012)
	Salinity	Lu et al. (2013)
	Heat	Chebrolu et al. (2016)
	Flooding	Komatsu et al. (2011)
Hordeum vulgare (barley)	Salinity	Widodo et al. (2009) and Wu et al. (2014)
Lens culinaris (lentil)	Drought, salinity	Muscolo et al. (2015) and Skliros et al. (2018)
Lolium multiflorum (ryegrass)	Drought	Pan et al. (2018)
Lotus japonicas (legume)	Drought	Sanchez et al. (2012)
Pisum sativum (pea)	Drought	Charlton et al. (2008)
Oryza sativa (rice)	Salinity	Ghosh et al. (2011)
	Chilling	Maruyama et al. (2014)
	Drought, salinity	Fumagalli et al. (2009)
Zea mays (maize)	Drought	Sun et al. (2016)
	Salinity	Gavaghan et al. (2011) and Guo et al. (2017)

Combined with phenotypic studies such as GWAS in response to abiotic stress conditions, mQTL can be used as metabolite markers as long as the change in the concentration of the metabolite governs the change in the phenotype. Such a use of metabolomics can also give information on the mQTLs responsible for the adaptation to unfavorable environmental conditions of plants, which can further be used to improve the tolerance of field crops to abiotic stress conditions.

24.6   Ionomics Approach to Abiotic Stress Tolerance

Ionomics is the omics approach for identification and quantification of all low molecular weight inorganic molecules and their roles in plant metabolism in a particular developmental stage and physiological condition with the techniques like inductively coupled plasma mass spectrometer (ICP-MS), inductively coupled plasma-optical emission spectrometry, X-ray fluorescence (XRF), X-ray absorption spectroscopy (XAP), neutron activation analysis (NAA), and laser ablation inductively coupled plasma mass spectroscopy (LA-ICP-MS) (Satismruti et al. 2013; Singh et al. 2013). Inorganic molecules are known to be important for inter- and intracellular signal transduction and regulation of enzyme activities for the balance of cellular metabolism. In this respect, ionomics is rather important for agricultural perspective, especially in intelligent agriculture approaches, to find out if plants can make efficient use of soil minerals and correct adjustment of fertilization regime. Ionomics can also give information on the changes in the functional state of the plant due to abiotic stress conditions.

There are only a few reports of plant ionomics in literature proving its usefulness in finding functions of novel genes, altering nutritional profile of field crops by intelligent agriculture approaches and understanding the changes in ionome profile of plants in response to different environmental conditions (Baxter 2015; Huang and Salt 2016; Watanabe et al. 2016). However, integration of data on individual inorganic molecules considering their interaction with each other and other subcellular molecules in changing the phenotype of the plant with changes in environmental conditions is still required to make effective use of data obtained by ionomics studies. It is clear that ionomics approach by itself has not been helpful in understanding the key factors enabling field crops to tolerate abiotic stress conditions, yet more studies are still required to reveal the role of the trace elements in abiotic stress response and tolerance.

24.7 Lipidomics Approach to Abiotic Stress Tolerance

Lipidomics aims to profile lipids in a cell with mass spectroscopy-based approaches to identify lipid molecules, their concentrations, and modifications to reveal their functions in membrane structure and generation (Tenenboim et al. 2016; Gross 2017). Lipids not only form membrane structures but also have roles in subcellular transportation and signal transduction. Thus, in terms of agriculture, lipidomics offer the manipulation of lipid composition to enhance the tolerance of field crops to abiotic stresses, as long as the roles and characteristics of all the lipid molecules changing in response to environmental stress conditions in the plants are well characterized. However, lipidomics studies have mainly focused on *Arabidopsis thaliana* and still has a long way to go to solve the problems related to standardization of isolation of lipidome, selection of appropriate internal standards, development of a reliable data processing system, and a broad use of high-throughput technologies (Welti et al. 2007; Tenenboim et al. 2016).

24.8 Phenomics Approach to Abiotic Stress Tolerance

All omics studies summarized before are performed to understand plant's response to find out key elements for enhancing their tolerance to abiotic stress conditions. Yet, all these studies are mostly performed under controlled conditions with minimizing G x E interaction, a factor that certainly defines the biochemical and physiological changes in plants under natural growth conditions, i.e., in field. Therefore, most of the findings of the other omics approaches are not applicable to field or not reliable in nature (Alexandersson et al. 2014).

The base of breeding is defining the phenome in field conditions. Phenomics aims at the integration of the phenotypic data collected with the use of high-throughput technologies in field trials with other omics approaches to select the candidate genotypes having the desired characteristics using noninvasive, computer-based visualization techniques for the detection of even the small changes in, for

example, leaf area, leaf temperature, and root length (Furbank and Tester 2011; Alexandersson et al. 2014; Li et al. 2014; Fahlgren et al. 2015; Humplik et al. 2015; Poland 2015; Ubbens and Stavness 2017). In short, it integrates G x E interaction to data obtained with genomics, transcriptomics, proteomics, and metabolomics. Phenomics have been successfully used for selection of field crops tolerant to abiotic stresses, especially drought (Furbank and Tester 2011; White et al. 2012; Humplik et al. 2015). Therefore, compared to other omics approaches widely used to understand plant's response to abiotic stress conditions, phenomics gives the most promising results in terms of achieving sustainability in agriculture. The main disadvantage of phenomics not being widely used in increasing abiotic stress tolerance of field crops is the cost of establishing a phenomics field research area with several sophisticated visualization systems such as hyperspectral cameras and equipment like tractors, drones, and even some robotic systems allowing remote control.

24.9 Integration of Omics Data on Abiotic Stress Tolerance of Field Crops: Is it Possible?

The area of omics technologies is diversified with the development of high-throughput technologies on other research areas. There are omics approaches including epigenomics, glycomics, hormoneomics, cytomics, metallomics, ribonomics, and regulomics, each having a great potential to generate data for enhancement of abiotic stress tolerance of field crops. Integration of data obtained from genomics, transcriptomics, proteomics, and metabolomics is performed by systems biology approach (Fig. 24.3). Systems biology basically aims to understand the organism as a whole at all metabolic levels to generate interactome of cellular molecules (Mochida and Shinozaki 2011; Rhee and Mutwil 2014; Yugi et al. 2016).

However, integration of data obtained by different omics approaches upon different abiotic stresses using different plants and/or genotypes is still the major problem
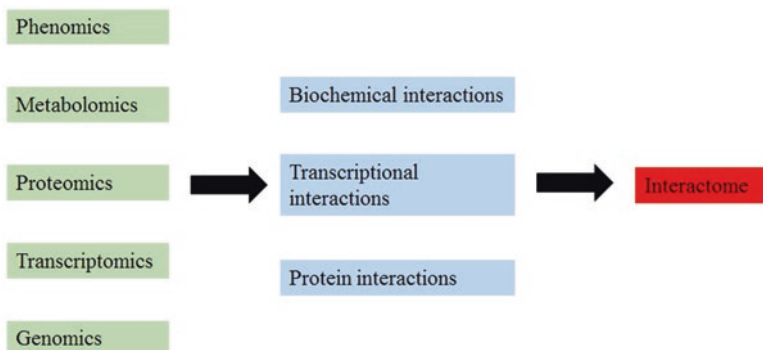
Fig. 24.3 Integration of omics approaches for systems biology to generate interactome

on making beneficial use of huge data already generated. The problem here is not just the use of different genotypes of the same plant, but also using different developmental stages and different strategies or time period for abiotic stress treatment. That is to say, almost each laboratory generates an omics data on genomic, transcriptomic, proteomic, or metabolomics levels that can be used or repeated only for that particular plant with the very same treatment design used by that laboratory. This approach makes the data integration for omics approaches a very hard, almost impossible, task for finding the key factors behind the abiotic stress tolerance. In systems biology approach, researchers mostly integrate omics data they have generated in their own laboratories with phenotypic data they have collected in field trials. As long as a unified stress treatment design depends on the plant and the abiotic stress, considering each plant species requires a particular dosage of stress to show the effect, the integration of all data available on literature seems to be beneficial to the use of one group of researchers only.

24.10 Conclusion

It is quite clear that to feed rapidly increasing human population in this changing climate, agriculture requires development of abiotic stress-tolerant field crops. Use of omics technologies is very promising and widely used in understanding plants' response to abiotic stresses and in generating field crops with increased tolerance to unfavorable environmental conditions and there are excellent reviews summarizing the findings in literature (Debnath et al. 2011; Gupta et al. 2013; Hayward 2014; Zhuang et al. 2014; Kumari et al. 2015; Van Emon 2016). Therefore, the main aim of this chapter was to lay emphasis on drawbacks and problems associated with the outcomes already reviewed.

More studies are still required to integrate data from omics studies to understand complex abiotic stress tolerance traits. First of all, the climate change scenarios estimate the presence of multiple abiotic stresses that occured together. Therefore, genomics, transcriptomics, proteomics, metabolomics, and especially phenomics, studies should be more focused on the response to combined stresses together. The comparison of abiotic stress-tolerant and sensitive genotypes is also very promising with respect to finding the key factors related to tolerance and/or sensitivity; however, the problem here is the characterization of the genotype having more tolerance or sensitivity to another genotype. In this respect, wild-type plants already adapted to unfavorable environmental conditions, such as halophytes for salinity stress or extremophiles for cold stress, can be used to enhance abiotic stress tolerance of field crops (Kumari et al. 2015; Barrero-Sicilia et al. 2017; Shen et al. 2018). Finally, omics analyses of increasing tolerance to abiotic stresses with priming need to be investigated which can provide insights of metabolic adaptation to environmental stimulus. New perspectives are definitely required in omics analyses. For example, rather than looking at cellular metabolism as a whole, the omics profiling of mitochondria or chloroplast, having an important role in initiating signaling cascades and regulation of photosynthesis in response to abiotic stress conditions, can

provide knowledge on decreasing yield loss due to environmental stresses (Watson et al. 2018).

Nevertheless, it is quite clear that omics perspective of abiotic stress tolerance of field crops is a very wide topic with huge data already available on every valuable field crop which needs to be further studied and analyzed to achieve the primary goal of agriculture: sustainability of human nutrition in global climate change.

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Use of QTL in Developing Stress Tolerance in Agronomic Crops

25

Ali Fuat Gökçe and Usman Khalid Chaudhry

Abstract

Stress is any external factor that interferes with the normal functioning and growth of crops. Abiotic stress has been extensively studied for causing devastating loss to agronomic crop yield across the globe. These problems were worse than they are today. Currently, we have contemporary genomic tools to find the root cause of problems and we have to broaden our horizon in understanding stress tolerance. Current advancement in genomics has paved our path for a more precise and comprehensive description of quantitative trait loci (QTLs) that regulate a specific trait. QTLs enable researchers to study genes that are responsible for even a single phenotypic trait. In other words, they help to study which sets of genes are responsible for making crops tolerant to stress. Numerous studies have been conducted to describe QTL mapping a significant tool for finding traits against stress tolerance. QTL mapping enables to evaluate the numbers, locations, and gene action pattern. Polygenes affect controlling a trait. Moreover, QTL has provided ease to dissect complex traits. Phenotypic analysis of QTL is done by observing numerous plants from the same segregating population for finding loci for a trait. The QTL tolerance trait so far has been accomplished in major agronomic crops, which include wheat, rice, maize, cotton, etc. In conclusion, we can say that QTL mapping is a crucial technique to elucidate specific components that allow direct assessment of stress tolerance. Therefore, in this chapter, we tried to explicate different QTL studies exploited for trait improvement of various agronomic crops for stress tolerance.

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25.1   Introduction

Plants being sessile have to survive under existing environmental conditions, and due to this, they are exposed to harsh environments (Suzuki et al. 2014). Stresses either biotic or abiotic are the major external factors that impede with the normal functioning of the plant throughout the course of its growth until harvesting (Tester and Langridge 2010). Major biotic and abiotic stresses include drought stress, salinity problem, heat episodes, and bacterial, viral, fungal, and insect attack that are lethal for agronomic crops (Agrios 2005; Mittler and Blumwald 2010; Naika et al. 2013). Salinity problem exists on almost 10% of the dry land zone, and 50% of the irrigated agricultural land zone is facing this issue (Ruan et al. 2010). Development of high-yielding crop cultivars is the prime goal of modern-era plant breeding. A significant example of green revolution is shown by producing semidwarf varieties of wheat and rice that have fed a lot of population until now (Alexandratos and Bruinsma 2012). However, it is an alarming situation that we have to increase the production of food for the burgeoning world population, as it is predicted that population will increase to 9.3 billion by 2050 (Brown and Funk 2008; Smith et al. 2010). Some agronomic crops are so sensitive to deviation from their normal environmental habitat (Pasha et al. 2015). Change in global environment is also contributing to adverse conditions favoring the environmental stress conditions for crops (Atkinson and Urwin 2012; Shabala 2013).

Drought is a condition when there is limited or no water available for normal growth of the crop. In a field, somehow, plants suffer from water-deficit conditions having detrimental yield losses (Bartels and Sunkar 2005). Plants immediately signal after detecting dry soil conditions and activate different mechanisms to cope with the harsh environment, and they have to survive under existing conditions (Duan et al. 2007; Shahzad et al. 2016). Moreover, less water availability in the vicinity of roots forces plants to develop a larger root system, higher stomatal activity, increased antioxidant activity, and accumulation of osmolyte to cope with water-deficit conditions for better yield (Manschadi et al. 2006).

Quantitative trait loci (QTL) mapping is a complex phenotypic trait that has enabled researchers to understand the diverse genetic basis of plant traits by separating phenotypic components (Bo et al. 2015). The major step is to identify QTLs affecting stress tolerance for developing stress-tolerant cultivars. It is known that QTL is an indirect procedure for controlling heritable variations of traits (Collins et al. 2008). The old conventional breeding tools were also fruitful for generating stress-tolerant cultivars (Duvick 2005; Cooper et al. 2009), but they require much time as compared to modern-era techniques that provide most accurate genotypic makeup for dissecting stress-tolerant cultivars within a short period of time (FAO 2009). In this regard, QTLs have been extensively studied to dissect stress-tolerant agronomic crops (Hammer et al. 2006). QTL is a technique to identify loci giving varying phenotypic traits under stress or any deviation from normal environmental factors. QTLs have broadened our horizon for improving crop performance under stress conditions (Collins et al. 2008). The first successful report of QTL mapping in plants was done approximately 20 years ago (Bernardo 2008), and since then, it

has been exploited in the analysis of complex traits specifically for biotic and abiotic tolerance. The genetic variance can occur even by loci; therefore, it was principally employed for breeding for stress resistance in numerous crops, that is, resistance against salinity and submergence in rice and fungal leaf diseases in maize and wheat (Crossa et al. 2014).

Drought tolerance is a quantitative trait with polygenic control (McWilliam and Baker 1989). Currently, identification of polygenic effect related to drought tolerance is the point of interest for improved cultivars having increased drought tolerance (Ribaut et al. 1996). Genomic regions are correlated with the phenotype of the plants to create accurate markers and, later on, the identification of QTLS associated with that specific trait. Root structure also has a pivotal role under drought stress conditions, as it can take water from deeper soil layers (Uga et al. 2015). Plant breeders have studied genetic loci to determine drought stress-related QTLs (Kalladan et al. 2013). Up to now, numerous studies have been documented for overcoming stress tolerance (Ravi et al. 2011). Functional genomics has aided in this situation to correlate phenotypic variations with the genotypic changes by observing the genome, and by this way, QTL is given importance (El-Soda et al. 2015).

25.2   The Procedure of QTL Mapping

Phenotypic variation in crops commonly shows a quantitative variation in their phenotypes, similar to a normal distribution, unlike that of qualitative variation falling into discrete categories. Continuous phenotypic variation is considered polygenic and/or QTL traits, which are usually modified by environments as well as internal genetic interactions. For instance, yield, biomass, quality, and tolerance to abiotic stress are considered major quantitative traits among agricultural crop plants. Similar to simple Mendelian genetic variation at a locus, any marker with allelic patterns that is separating mean values of a trait with a continuous phenotypic variation into two or more groups that are significantly different from each other is said to be linked and/or associated with QTL marker to the trait of interest. With the detection of variable molecular markers, it became as easy as simple Mendelian inheritance to understand complex phenotypic variation, to construct genetic maps, and to locate QTLs for copious traits in many economically important crops.

Correct estimations of the mean phenotypic values are the most crucial points during QTL identifications. Therefore, any environment-affected phenotypic value estimation is approved by replicated trials in different years and environments with known plant genotypes, such as clonally reproduced genotypes and/or mapping populations. Mapping populations can be created by crossing two divers' parents and then producing segregating populations, such as F_2 families, back cross lines (BCLs), doubled haploid lines (DHLs), recombinant inbred lines (RILs), or nearly isogenic lines (NILs). Lately, QTL also can be associated with a trait of interest using unrelated individuals in a population if linkage disequilibrium still exists for the trait of interest and the marker

used. Thus, it is called association mapping since this technique is based on the association between quantitative phenotypic trait and marker genotypes.

Here is the illustration of QTLs similar to regular Mendelian genes to explore the genetic basis of continuous phenotypic values using hypothetical data for F_2 segregating families developed from a cross with high- x low-yielding tomato genotypes. Let us assume that two tomato genotypes are having mean fruit yields of 30.2 and 11.5 kg/plant (Table 25.1). These two parents (maternal P_1 and paternal P_2) are crossed to get hybrid (F_1). Then, the F_1 is selfed to create segregating F_2 lines. Genotypes of the parents are symbolized as maternal (A) and paternal (B). Thus, hybrid (F_1) genotype is symbolized as heterozygous (H). Three molecular markers are named as M_1, M_2, and M_3. After evaluating the F_2 segregating lines with the three molecular markers, individual F_2 line is genotyped as A if only maternal marker alleles are present, as B if only paternal alleles are present, and as H if both maternal and paternal alleles are present. Mean fruit yields of the parents and segregating F_2 families are determined after replicated field trials and are provided in Table 25.1.

Figure 25.1 shows the variation of mean yield/plant values plotted against F_2 segregating families. The mean yields range from 9.0 to 34.4 kg/plant among 128 segregating families. When data are sorted from the lowest to highest yield value, variation shows no discrete groups (Fig. 25.2). Therefore, this type of variation is considered continuous (quantitative) variation. Please consider that there are also some environmental effects on yield along with the genetic effects.

Yield values are sorted and plotted against 128 segregating F_2 families along with the three marker genotypes given in Fig. 25.3. The marker alleles from the low-yielding paternal genotypes (B) tend to place with the low-yielding F_2 families on the left side of the figure, while the marker alleles from the high-yielding maternal genotypes (A) tend to place with the high-yielding F_2 families on the right side of the figure (Fig. 25.3). Thus, the markers with heterozygous (H) genotypes are placed within the central areas. For any one of the three molecular markers, it is possible to separate 128 segregating F_2 families into three genotypic (A, B, and H) groups. Marker allelic and trait value association is determined by testing the means of these three groups. If there is a significant difference between any of the pair-wise comparison, then there is a linkage and/or association between the molecular marker and traits of interest, which is called QTL.

Statistical analysis of the molecular markers allelic positions and the trait values of the 128 segregating F_2 families can be done using any suitable statistical test methods to determine if there are any significant differences. For the above tomato yield data, there are three markers (M_1, M_2, and M_3), each of which has three genotypic classes or levels (A, B, and H). Analysis of variance table for the markers and yield data is provided, and it is seen that all the markers and interactions have a significant effect on the yield of tomato plants (Table 25.2).

The three markers and the tomato yields are determined to be linked (associated) after statistical analysis, while the markers are not linked to each other. They are either located far from each other on the same chromosome or located on

Table 25.1 Two tomato parent genotypes (maternal P_1 and paternal P_2), their hybrid (F_1), and 128 F_2 families with three molecular markers (M_1, M_2, M_3), genotypes (A maternal, B paternal, and H heterozygous), and mean fruit yields (kg/plant)

No	M_1	M_2	M_3	Yield	No	M_1	M_2	M_3	Yield	No	M_1	M_2	M_3	Yield
P_1	A	A	A	30.2	42	H	B	H	14.2	86	H	A	H	29.4
P_2	B	B	B	11.5	43	H	B	H	14.0	87	H	A	H	29.2
F_1	H	H	H	21.5	44	H	B	H	13.8	88	H	A	H	29.0
1	B	B	B	9.2	45	H	B	A	24.0	89	H	A	H	28.8
2	B	B	B	9.0	46	H	B	A	23.8	90	H	A	H	28.6
3	B	B	H	11.6	47	H	B	A	23.6	91	H	A	H	28.4
4	B	B	H	11.4	48	H	B	A	23.4	92	H	A	H	28.2
5	B	B	H	11.2	49	H	H	B	13.6	93	H	A	A	34.0
6	B	B	H	11.0	50	H	H	B	13.4	94	H	A	A	33.8
7	B	B	A	17.6	51	H	H	B	13.2	95	H	A	A	33.6
8	B	B	A	17.4	52	H	H	B	13.0	96	H	A	A	33.4
9	B	H	B	10.8	53	H	H	B	12.8	97	A	B	B	12.0
10	B	H	B	10.6	54	H	H	B	12.6	98	A	B	B	11.8
11	B	H	B	10.4	55	H	H	B	12.4	99	A	B	H	19.2
12	B	H	B	10.2	56	H	H	B	12.2	100	A	B	H	19.0
13	B	H	H	17.2	57	H	H	H	23.2	101	A	B	H	18.8
14	B	H	H	17.0	58	H	H	H	23.0	102	A	B	H	18.6
15	B	H	H	16.8	59	H	H	H	22.8	103	A	B	A	28.0
16	B	H	H	16.6	60	H	H	H	22.6	104	A	B	A	27.8
17	B	H	H	16.4	61	H	H	H	22.4	105	A	B	B	18.4
18	B	H	H	16.2	62	H	H	H	22.2	106	A	H	B	18.2
19	B	H	H	16.0	63	H	H	H	22.0	107	A	H	B	18.0
20	B	H	H	15.8	64	H	H	H	21.8	108	A	H	B	17.8
21	B	H	A	25.6	65	H	H	H	21.6	109	A	H	H	27.6
22	B	H	A	25.4	66	H	H	H	21.4	110	A	H	H	27.4

(continued)

Table 25.1 (continued)

No	M_1	M_2	M_3	Yield	No	M_1	M_2	M_3	Yield	No	M_1	M_2	M_3	Yield
23	B	H	A	25.2	67	H	H	H	21.2	111	A	H	H	27.2
24	B	H	A	25.0	68	H	H	H	21.0	112	A	H	H	27.0
25	B	A	B	15.6	69	H	H	H	20.8	113	A	H	H	26.8
26	B	A	B	15.4	70	H	H	H	20.6	114	A	H	H	26.6
27	B	A	H	24.8	71	H	H	H	20.4	115	A	H	H	26.4
28	B	A	H	24.6	72	H	H	H	20.2	116	A	H	H	26.2
29	B	A	H	24.4	73	H	H	A	31.2	117	A	H	A	33.2
30	B	A	H	24.2	74	H	H	A	31.0	118	A	H	A	33.0
31	B	A	A	31.6	75	H	H	A	30.8	119	A	H	A	32.8
32	B	A	A	31.4	76	H	H	A	30.6	120	A	H	A	32.6
33	H	B	B	10.0	77	H	H	A	30.4	121	A	A	B	26.0
34	H	B	B	9.8	78	H	H	A	30.2	122	A	A	B	25.8
35	H	B	B	9.6	79	H	H	A	30.0	123	A	A	H	32.4
36	H	B	B	9.4	80	H	H	A	29.8	124	A	A	H	32.2
37	H	B	H	15.2	81	H	A	B	20.0	125	A	A	H	32.0
38	H	B	H	15.0	82	H	A	B	19.8	126	A	A	H	31.8
39	H	B	H	14.8	83	H	A	B	19.6	127	A	A	A	34.4
40	H	B	H	14.6	84	H	A	B	19.4	128	A	A	A	34.2
41	H	B	H	14.4	85	H	A	H	29.6					
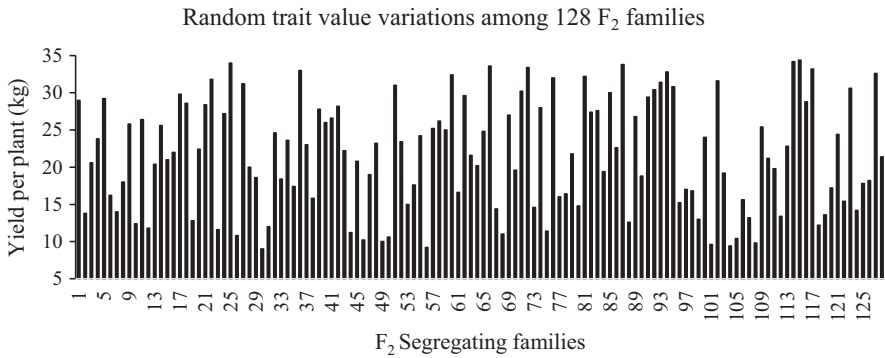
Fig. 25.1 Yield (kg/plant) values for 128 segregating F_2 families
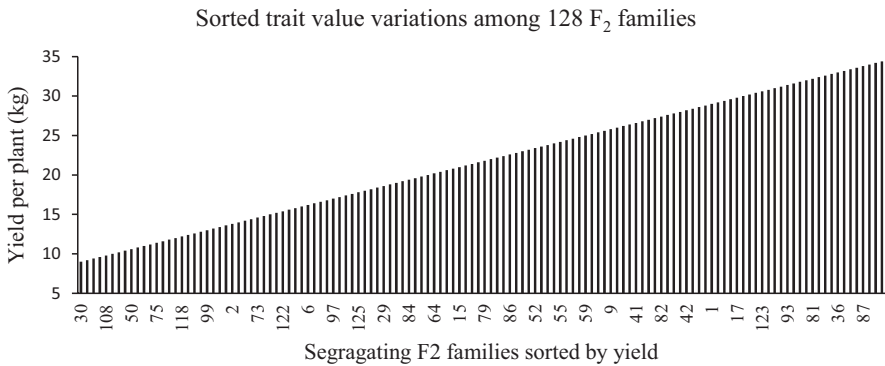
Fig. 25.2 Yield (kg/plant) values for 128 segregating F_2 families sorted by yield from the lowest to the highest
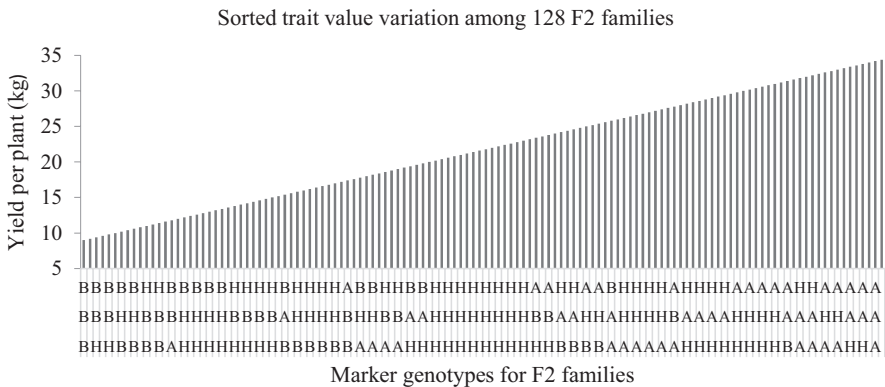
Fig. 25.3 Yield (kg/plant) values for 128 segregating F_2 families sorted by yield from the lowest to the highest along with molecular marker genotypes

Table 25.2 Analysis of variance for yield, using adjusted sum of squares (SS) for tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
M_1	2	1036.84	722.53	361.27	1390.55	0.000
M_2	2	2284.84	1651.61	825.80	3178.59	0.000
M_3	2	3433.96	2460.16	1230.08	4734.68	0.000
M_1*M_2	4	15.44	9.47	2.37	9.11	0.000
M_1*M_3	4	35.60	25.60	6.40	24.63	0.000
M_2*M_3	4	93.20	74.24	18.56	71.44	0.000
$M_1*M_2*M_3$	8	63.96	63.96	7.99	30.77	0.000
Error	101	26.24	26.24	0.26		
Total	127	6990.08				

different chromosomes. It is left for the readers to figure out why molecular markers are not linked.

As seen in Table 25.3, high-yielding plant genotypes can be selected using these markers singly, any of two, or three of them together. If M_1 is used, then the selected high-yielding genotypes would have a mean yield of 25.43 kg/plant, while if M_2 or M_3 is used, then the selected high-yielding genotypes would have mean yields of 27.34 or 28.59 kg plant^{-1}, respectively. Hence, M_3 has the biggest effects on the yield among the three markers. If the two markers M_1 and M_2 are used together, then the selected high-yielding genotypes would have a mean yield of 30.77 kg plant^{-1}, while if M_1 and M_3 or if M_2 and M_3 are used, then the selected high-yielding genotypes would have mean yields of 31.70 or 33.17 kg plant^{-1}, respectively. Hence, the M_2 and M_3 combination has the biggest effects on the yield among the two marker combinations. However, the highest yielding genotypes with a mean yield of 34.30 kg/plant can be selected using three markers together (Table 25.3) since each of the three markers has effects on the yield and shows quantitative variations. However, one should consider that, most often, the time markers are not the gene controlling the traits. Therefore, crossover may occur any time between the QTL loci and the gene controlling the traits of interest. It is advised to breeders to check QTL marker alleles and traits of interest if they are still at linkage disequilibrium in the genetic resources in hand before the marker-assisted selection is applied.

25.3   QTL Mapping for Stress Tolerance in Wheat

Hexaploid bread wheat is important for being the third largest-grown crop globally with 600 million tons produced annually (Green et al. 2012; Edae et al. 2014). It is cultivated on irrigated, arid, and semiarid climate zones of the world (Raza et al. 2015). It is one of the top lists of the most-traded crop in the world (Curtis and Halford 2014). It is the sole source of provision of 19% grain production compared to other cereal crop family, and it constitutes 55% carbohydrate consumption by human population globally (Gupta et al. 2002; Bagge et al. 2007). The yield of the crop is at risk due to unusual harsh environments (Xin et al. 2010). Climatic changes

Table 25.3 Least square means of three markers singly and with two- and three-way interactions for the yield

M_1	Mean	SE mean	M_1 x M_2 x M_3	Mean	SE mean
A	25.43	0.10	A A A	34.30	0.36
B	17.97	0.10	A A B	25.90	0.36
H	21.70	0.07	A A H	32.10	0.25
M_2	Mean	SE mean	A B A	27.90	0.36
A	27.34	0.10	A B B	11.90	0.36
B	16.06	0.10	A B H	18.90	0.25
H	21.70	0.07	A H A	32.90	0.25
M_3	Mean	SE mean	A H B	18.10	0.25
A	28.59	0.10	A H H	26.90	0.18
B	14.81	0.10	B A A	31.50	0.36
H	21.70	0.07	B A B	15.50	0.36
M_1 x M_2	Mean	SE mean	B A H	24.50	0.25
A A	30.77	0.19	B B A	17.50	0.36
A B	19.57	0.19	B BB	9.10	0.36
A H	25.97	0.13	B B H	11.30	0.25
B A	23.83	0.19	B H A	25.30	0.25
B B	12.63	0.19	B H B	10.50	0.25
B H	17.43	0.13	B H H	16.50	0.18
H A	27.43	0.13	H A A	33.70	0.25
H B	15.97	0.13	H A B	19.70	0.25
H H	21.70	0.09	H A H	28.90	0.18
M_1 x M_3	Mean	SE mean	H B A	23.70	0.25
A A	31.70	0.19	H B B	9.70	0.25
A B	18.63	0.19	H B H	14.50	0.18
A H	25.97	0.13	H H A	30.50	0.18
B A	24.77	0.19	H H B	12.90	0.18
B B	11.70	0.19	H HH	21.70	0.13
B H	17.43	0.13			
H A	29.30	0.13			
H B	14.10	0.13			
H H	21.70	0.09			
M_2 x M_3	Mean	SE mean			
A A	33.17	0.19			
A B	20.37	0.19			
A H	28.50	0.13			
B A	23.03	0.19			
B B	10.23	0.19			
B H	14.90	0.13			
H A	29.57	0.13			
H B	13.83	0.13			
H H	21.70	0.09			

are contributing to impediment in growth and yield. Significant factors responsible are drought and salinity (Shanker et al. 2014). Moreover, the population is increasing day by day, and we have more mouths to feed currently which are expected to increase in the coming years, so food security is at risk because we are using the potential of arable lands to get high yield. Therefore, it is need of the hour to increase the yield with existing situations (Yang et al. 2012); therefore, the prime aim of breeder is to increase the yield of wheat by combining traits (Ashfaq et al. 2014). QTLs for drought tolerance were studied in wheat (Hamada et al. 2012).

25.3.1 QTLs Associated with Root Traits for Stress Tolerance

Roots play a crucial role in the growth of wheat because they are the sole source of taking water from the soil and absorbing nutrients as well as providing adjustment to stress conditions (Manschadi et al. 2006; Reynolds et al. 2007). Therefore, roots have been extensively studied to observe their functions under water-limited environment in wheat (Manschadi et al. 2008, Wasson et al. 2012). Genetic control of root traits has been given importance for understanding the root architecture of wheat (Christopher et al. 2013; Zhang et al. 2014). QTLs for root traits were observed that assist in coping with drought condition for a future breeding program such as QTLs being responsible for root length, number, volume, and dry weight (Christopher et al. 2013; Bharti et al. 2014).

25.3.2 QTLs Responsible for Physiological Characteristics Under Stress Conditions

Drought severely affects physiological processes of wheat; therefore, there is a dire need to protect its chlorophyll content disruption and other reactive oxygen species produced in response to drought stress which affects photosynthesis (Peltzer et al. 2002; Praba et al. 2009). Disruption of photosynthesis leads to decrease in growth, which ultimately causes a reduction in biomass (Ashraf and Foolad 2007). QTLs were reported to play a role in physiological machinery for the normal smooth functioning of plants under adverse conditions to help understand the physiological traits responsible during drought tolerance for remarkable progress in crop yield (Castonguay and Markhart 1992; Malik et al. 2015). QTLs for net photosynthetic rate, cell membrane stability, and relative water contents were mapped in wheat subjected to drought. Moreover, some correlation of these traits was also worth mentioning that photosynthesis influences stomatal conductance and transpiration rate, whereas relative water content aids in cell membrane stability (Malik et al. 2015). Wheat growth is affected due to water-deficit conditions, which also cause difficulty in selection of genotypes due to genotype–environment interactions on each other (Yin et al. 1999; Teulat et al. 2002), and to overcome this problem, an alternative way is to broaden our horizon by looking into physiological changes occurring due to stress (Teulat et al. 2002; Slafer et al. 2005).

Water-soluble carbohydrate (WSC) of leaves has a pivotal role in drought stress and is a good indicator of drought tolerance (Ehdaie et al. 2006; van Herwaarden et al. 2006). Numerous works have been accomplished depicting the accumulation of WSC in wheat (Bancal and Triboi 1993; Galiba et al. 1997; Kerepesi and Galiba 2000). Considering the importance of WSC, QTLs have been dissected in wheat responsible for stem water-soluble carbohydrates also during early flowering stage and grain filling stage (Yang et al. 2007a); furthermore, grain filling of wheat is mainly dependent on stem reserves of WSC during drought (Rebetzke et al. 2008; Zhang et al. 2014).

25.3.3 QTLs Assisting in Yield Improvement Under Stress Conditions

Wheat grain yield is a complex trait which includes various components, that is, spike number, kernels per spike, and kernel weight (Reynolds et al. 2011). Grain yield can be improved with genetic improvement in its architecture by QTL mapping (Holland 2007). QTL responsible for yield variation was dissected, as it was due to either more aboveground biomass production or harvest index. It was inferred that it successfully aids greater biomass at anthesis, which leads to an increase in the number of florets per ear and ultimately increased harvest index (Quarrie et al. 2006). Chromosomal regions have a great influence on grain components contributing toward the overall net grain yield of wheat under limited moisture supply, which is only possible through QTL analysis (Bennett et al. 2012).

25.4   QTL Mapping for Stress Tolerance in Rice

Rice is the essential nutrition for the majority of the human population in the world. Among cereal group, therefore, it is of high priority for production worldwide. It needs a flooded condition for better growth throughout its life cycle (Li and Xu 2007; Toorchi et al. 2003). Water shortage is the major issue for the growth of rice, which causes serious constraint in its production and yield, specifically in the arid zone (Nguyen et al. 1997). Rice is not restricted to specific agroecosystems for its growth. It is grown on rainfed lowland to rainfed high land, deep water, and irrigated flooded lands under tropical and temperate climatic conditions. Although there is diversity of options available for rice cultivation, until now, no breakthrough has been achieved for breaking some yield barriers (Dixit et al. 2014). The lowland rice ecosystem has the potential for improvement in yield. In Asia, rice is grown on 42 million ha land area (Huke and Huke 1997); therefore, it is particularly suffering from varying intensities of drought stress every year. Drought has posed serious threats to many rice-producing parts of the globe, which has created trouble for rice researchers to come out with an appropriate solution. Therefore, rice breeders have exploited mapping studies to create drought-tolerant cultivars (Zhao et al. 2008). Currently, rapidly changing climate further exacerbates the environment for future crops (Wassmann et al. 2009), and it is predicted that

drought will be worse with the passage of time in the coming future (Bate et al. 2008). Globally, rice fields affected due to drought are approximately 23 million ha (Huke and Huke 1997; IRRI 2002). Improvements in rice genetic material are tedious (Evenson and Gollin 2003). Contrarily, drought-resistant traits are mapped in rice (Bernier et al. 2008; Kamoshita et al. 2008). Currently, QTLs for a number of drought-tolerant traits have been dissected in rice (Li and Xu 2007; Kamoshita et al. 2008).

25.4.1 Role of Roots and QTL Dissection for Drought Tolerance

Currently, breeders are more considering the role of root under stress conditions for the purpose of normal functioning and high yield of the crop (Passioura 2007). Roots are the prime source to evade drought and protect the crop from desiccation (Passioura 2012). Root traits including its structure and anatomy are responsible for searching water in limited moisture availability to cope with drought (Cruz et al. 1992; Price et al. 2000). The long thick root system of rice helps against drought conditions (Ling et al. 2002). Geneticist have discerned the root system as a powerful tool of QTLs linked for root traits (Zhang et al. 2001; Kamoshita et al. 2002). QTLs for root penetration have been reported to assist in drought tolerance (Zheng et al. 1999; Ali et al. 2000; Zhang et al. 2001; Price et al. 2000); by exploiting QTLs for root characteristics, the yield of rice is improved in drought-stricken areas (Fukai and Cooper 1995; Nguyen et al. 1997). QTLs associated with roots of rice were recognized, which are basal root thickness, number, and maximum length of the root (Li et al. 2005). Root traits assisting in drought stress were reported, which include root stele and xylem vessel diameter (Uga et al. 2010).

25.4.2 Yield Improvement by Exploiting QTL Technique against Drought Stress

Breeding rice genotypes for drought tolerance is slow (Fukai and Cooper 1995). Grain yield is mainly affected under drought stress; especially at the reproductive stage, the losses are much more to count (Venuprasad et al. 2009); however, QTLs have an enormous effect on the yield of rice (Salekdeh et al. 2002). QTL for grain yields at drought stress has been mapped (Sandhu et al. 2014). In the few recent decades, at least two or three rice cultivars have been given importance among farmers from region to region, depending on the suitability of their growing conditions; somehow, these cultivars give less grain yield under drought stress conditions. So, QTL identification for grain yield was carried out in breeding drought-tolerant cultivars (Vikram et al. 2011). Donor N22 was selected from landrace, which conferred drought tolerance and maintained high spikelet fertility (Selote and Chopra 2004; Tyagi and Chandra 2006). QTL responsible for agronomic traits in rice depicted resistance against drought (Srividhya et al. 2014).

25.4.3 QTL Mapping for Stress Tolerance in Cotton

The world's largest population is directly or indirectly linked with cotton for reasons of its value and usage. Farmers are closely associated with it to get high production; thousands of ginning industry and textile industry are dependent on cotton (Tatsiopoulos and Tolis 2003). Moreover, millions of people are associated with cotton chains for their earnings (Myers and Stolton 1999). It is also exported in the form of yarn and worthy garments, so it has been named white gold due to its value in the world (Arshad et al. 2005; Tefft 2010). Cotton (*Gossypium hirsutum* L.) is composed of 50 diverse species based on their morphology and economic characteristics. Cotton that has higher fiber quality and yield is generally tetraploids (Wendel and Cronn 2002). Cotton is a leading fiber crop globally, and it is irrigated for better growth and lint quality of cotton (Pettigrew 2004). Cotton is sensitive to drought, causing severe yield losses. However, old-era breeding techniques were successful for creating drought tolerance in cotton with modification in physiological traits. The major drawback of these was tediousness and the efforts involved. Several exertions have been done for drought tolerance, which integrates traditional breeding with contemporary genetic tools like QTL (Iqbal et al. 2013).

25.4.3.1 QTLs for Physiological Traits in Cotton

Water stress causes a change in genetic makeup of cotton (Saeed et al. 2011). A wide range of plant responses have been observed to assist tolerance against drought (Xiong and Zhu 2002). Plant's adaption under water-deficit conditions regulates physiological adjustments like osmotic adjustments for maintaining metabolic activity and growth (Ashraf and Iram 2005); therefore, QTL responsible for physiological changes was studied for better performance of cotton under water-limited environment (Saeed et al. 2011). QTLs play a role even in response to high temperatures for increased stomatal conduction to keep the plant cool under harsh climatic conditions in tropical regions (Ulloa et al. 2000).

25.4.3.2 QTL Mapping for Improving Cotton Yield and Lint Quality

Cotton yield and fiber quality are important for every farmer to earn handsome amount after the course of struggle for growing cotton; but unfortunately, poor fiber quality and low lint yield are handicaps in cotton breeding program since long ago (Meredith and Bridge 1971; Meredith 2005), but now, QTLs have provided ease in the breeding program to overcome yield-related issues (Yu et al. 2011; Fang and Yu 2012; Yu et al. 2013). QTL mapping has opened new avenues for improving crop productivity for drought tolerance (Baytar et al. 2018). Currently, 726 QTLs are reported for fiber quality of cotton (Said et al. 2013).

25.5   QTL Mapping for Stress Tolerance in Maize

Maize (*Zea mays* L.) is the principal cereal crop grown globally due to its suitability for every agroclimatic zones and its multiuses and benefits for humanity (Li et al. 2010). However, suitable growth conditions are necessary for maize crop for normal growth and yield. In some circumstances, maize suffers from adverse conditions like water deficit and its yield falls (Setter and Flannigan 2001). Water requirement of maize is 600–700 mm for optimal growth (Reddy 2006). Deficiency of water at any growth stage causes drastic yield loss (Paudyal et al. 2001). Drought stress causes the same effects to crop as any other environmental stress (Pandey et al. 2000); it causes a reduction in plant height leaf area expansion and cell division (Reymond et al. 2003). The global reduction in grain yield of maize is caused by drought stress, especially at the flowering stage. Drought also affects other growth stages of maize, such as delay in silking and increase in anthesis-silking interval (ASI), and ultimately, all these traits contribute to decrease in the overall yield of maize (Harrison et al. 2014; Vargas et al. 2006). Maize is extremely sensitive to drought during early growth stages just after the onset of flowering (Banziger et al. 2000). It is susceptible to drought due to the separation of flower parts, tassel blasting, and embryo abortion (Lu et al. 2011). Therefore, it is the need of the hour for maize breeders to develop tolerant maize varieties that can withstand drought stress conditions and provide higher yield (Messmer et al. 2009). QTL analysis for maize drought tolerance was successfully documented for the first time by Lebreton et al. (1995).

25.5.1 QTL Mapping for Physiological Characteristics under Drought in Maize

Maize stay-green is a good determinant of robust growth under any adverse conditions like drought (Xu et al. 2000a; Borras et al. 2003). Aging of plant destroys its chlorophyll machinery, which hampers growth and yield (He et al. 2005); therefore, QTL responsible for chlorophyll content was dissected, which is responsible for the greenness of maize (Messmer et al. 2011). Moreover, chlorophyll keeps the plants above threshold level necessary for photosynthesis, which is important under drought stress (Schussler and Westgate 1995). QTL analysis for stay-green characteristics of maize was documented; likewise QTLs for grain weight and ear diameter of maize (Zheng et al. 2009).

25.5.2 QTL Mapping for Yield Enhancement in Maize

Grain yield is an important factor for consideration because it is the final product that we get after harvesting the maize, so QTLs for yield-associated components and grain yield were reported (Ribaut et al. 1997; Tuberosa and Salvi 2009). Endeavors have been made to gain insight into maize architecture as tassel and ear

have a potent relationship in grain yield of maize (Upadyayula et al. 2006). In maize breeding programs, an active area of focus is short anthesis-silking interval (ASI) for tolerant maize cultivars (Li et al. 2003). Indeed, selection of small ASI is proved to be a significant trait for higher grain yield (Araus et al. 2011). QTLs for ASI were dissected on different chromosome locations under severe stress and well water regime by a cross of susceptible and tolerant maize cultivars (Ribaut et al. 1996). Consistent QTLs have been identified for grain yield under adverse conditions (Collins et al. 2008).

25.5.3 QTL Associated with Flowering and its Time

Maize flowering can be affected due to drought stress; therefore, QTLs were evaluated at the flowering stage and for yield components (ear length, kernel number per row). These traits were deeply considered for the creation of drought tolerance in maize in the future (Lu et al. 2006). Genomic regions were searched for the harboring effect of QTL on traits. It was evaluated that all chromosomes were found to have some influence on traits; furthermore, maize exhibits flowering time variation naturally (Gouesnard et al. 2002; Camus-Kulandaivelu et al. 2006); therefore, to control this variation, QTL has been observed for better understanding the flowering time and traits of maize (Chardon et al. 2004). QTLs controlling different traits are mostly on the same chromosomal region (Marino et al. 2009).

25.5.4 QTLs for Root Architecture to Alleviate Drought Stress

Root is another important trait that aids in alleviating drought stress. QTLs responsible for root functions under harsh conditions were mapped in maize (Mano et al. 2005). Root traits were exploited to address drought conditions by increased root growth in search for moisture from the soil (Lynch 2013). QTLs have been marked from maize chromosomes influencing root formation and grain yield (Landi et al. 2010) under well-watered and water stress conditions. Various fruitful reports have been documented of QTLs for maize stress breeding programs and also to enhance its growth and grain yield (Li et al. 2012; Ali et al. 2015).

25.6   QTL Mapping for Stress Tolerance in Sorghum

Sorghum is a primary nutrition for millions of people in Africa and Asia (Murty et al. 2007). The climate of these regions is prone to drought, as there is low rainfall and high precipitation due to high-temperature resulting in lower crop yield (Haussmann et al. 2002; Turner 2004). Plant under drought stress is in urgent search of water, which is normally available in lower pockets of soil (Xiong et al. 2006). The breeder's main goal for drought tolerance is on improving root and

physiological parameters (Rajendran et al. 2011). Stress causes obstruction in germination and early senescence (Khayatnezhad et al. 2010).

25.6.1 QTLs Associated with Stay-Green Characteristic of Sorghum

Stay-green trait of sorghum is an important indicator of tolerating stress, especially during the postflowering in response to drought (Rosenow and Clark 1981). Preflowering is also important for drought tolerance, as it assists plant breeders in amending the traits for stay-green in order to create drought tolerance in sorghum (Kebede et al. 2001). Stay-green indicates resistance, which confers sorghum tolerance to early senescence (Borrell et al. 2000; Borrell and Hammer 2000). It assists in grain filling under adverse drought conditions (Thomas and Howarth 2000). QTLs for stay-green trait have been located on chromosome which varies for their phenotypic variance, and this trait is also influenced by the environmental factors (Xu et al. 2000b; Harris et al. 2007).

25.6.2 QTLs for Root Morphology

Root traits also play an important role in coping with stress tolerance. Root angle was less considered for crop improvement because of the difficulty of assessing roots from a large area having various plants (Singh et al. 2011). However, sorghum is considered good for root trait under drought spells because of its seminal root system which forms the nodal root (Singh et al. 2010); therefore, QTLs responsible for root angle were mapped for validation of this trait for better yield performance under drought stress. Various QTLs were observed, but only one showed a positive additive effect for the nodal angle of sorghum root (qRA1_5), which facilitated better plant stand and added more height to plants which ultimately gives higher yield (Mace et al. 2012).

25.6.3 QTLs Assist in Contributing for Yield

Yield increment enhances their domestic production of crop; therefore, QTLs associated with yield were mapped in sorghum (Sabadin et al. 2012). The forage yield of sorghum is more if the plants produce a greater number of leaves, which is considered as an important component of yield. QTL is favorable because panicle length and the number of leaves have a robust relationship in increased transport of photosynthate (Srinivas et al. 2009; Fakrudin et al. 2013).

25.7   QTL Mapping for Stress Tolerance in Barley

Barley occupies the fourth position in terms of production in world agriculture after wheat, rice, and maize. Potential uses of barley include 75% as a feed and remaining portion of it for beverages and food (Sreenivasulu et al. 2008). Barley is adapted to adverse conditions and shows differential behavior in response to drought conditions (Nevo and Chen 2010). It is cultivated from tropical to temperate climate zones of the world (Schulte et al. 2009), exhibiting higher tolerance as compared to its tribe member, wheat (Colmer et al. 2006). Moreover, barley is an ideal crop for genetic studies having a simple background of genetics (Costa et al. 2001). Water is essential for plants to grow and produce sufficient yield. However, sometimes in some regions, plants suffer from drought, which limits their growth and ultimately affects the yield (Blum 2011; Pennisi 2008). So, to cope with such situations or make plants better survive under existing water-deficit environments, researchers have invented different molecular approaches for drought tolerance. The aim is not to make barley as a cactus plant, but to make it survive and give good yield if they face a period of drought during their growth stages. To dissect complex traits for the most appropriate approach, numerous QTL analyses have been done in barley (Teulat et al. 2001; Teulat et al. 2003; Tondelli et al. 2006).

25.7.1 QTLs for Physiological Changes Under Drought in Barley

Stress causes several physiological changes in plants. The most abundant and common one is the production of proline under drought stress. Proline is amino acid, which works as a chelating agent, plays role in antioxidative defense mechanism, and finally sends signals during stress. Therefore, it assists in stress tolerance (Hayat et al. 2012); by considering the mechanism of proline during stress, QTL associated with proline content was mapped on chromosome and observed to increase proline content due to the dominance of elite alleles over the exotic alleles (Sayed et al. 2012).

25.7.2 QTLs Associated with Vegetative Growth of Barley

QTLs for vegetative drought response in barley were observed under drought stress. QTLs reported contributing to better agronomic traits of barley, such as shoot area integral, absolute growth rate integral, dry biomass, water-use efficiency, and tiller numbers (Honsdorf et al. 2014).

25.8 Conclusion

Stress impedes normal functioning and growth response of crop, which results in devastating yield losses. For a long time, breeders are concerned with improving the yield of the crop under ideal as well as stress conditions. So, breeding for stress tolerance is of utmost importance to save crops and enhance yield. QTL mapping has provided easiness to identify different chromosomal positions controlling a specific trait; therefore, with the advent of this technique, we can thoroughly study the segment of a chromosome which makes the plant susceptible and tolerant against such stresses in the field. It has been done in almost every agronomic crop. Different studies illustrating its importance aforementioned in the chapter suggest that it is useful against stress tolerance. Table 25.4 shows QTLs reported in agronomic crops. We can improve different agronomic and physiological traits by simply exploiting QTL studies against harsh environments. These agronomic traits like root elongation aid in seeking the available moisture in soil pockets under drought stress because root is the base and an essential component of every plant for providing nutrition from soil to the top of the plants. Physiological traits have been improved by dissecting/marking chromosome positions and later developing them as a marker

Table 25.4 List of QTLs identified for various traits under abiotic stress in agronomic crops

Crops	Traits	QTL name	References
Rice	Grain yield	*qtl 12.1*	Bernier et al. (2009)
	Coleoptile length	*qCL2a, qCL2c*	Hu et al. (2007)
	Basal root thickness	*qbrt4.1*	Li-Feng et al. (2007)
	1000 – Grain weight	*qtgw6.1*	Li-Feng et al. (2007)
	Root number	*qrn1a*	Mu et al. (2003)
	Maximum root length	*qmrl2*	Mu et al. (2003)
	Flag leaf width	*qFLW3.1*	Singh et al. (2017)
	Root penetration	*qprl11.1*	Nguyen et al. (2004)
	Plant height	*qphs1.1*	Babu et al. (2003)
	Total spikelet number	*qtsn9.4*	Lanceras et al. (2004)
	Shoot length	*qsl1.1*	Srividhya et al. (2014)
	Germination rate	*qGR–1*	Mardani et al. (2013)
Wheat	Plant height	*QPH.caas–4BS.2*	Gao et al. (2015)
	Grain yield	*QYld.idw–2B*	Maccaferri et al. (2008)
	Grain yield	*Q.Yld.aww–1B*	Bennett et al. (2012)
	Stem water-soluble carbohydrates	*QSwscf.cgb–4B.1*	Yang et al. (2007b)
	Root length	*QRl.ccsu–2B.1*	Hamada et al. (2012)
	Root angle	*QRA.qgw–2A*	Christopher et al. (2013)
	Root length	*QRl.ccsu–2B.1*	Bharti et al. (2014)
	Net photosynthetic rate	*QPn2AC*	Malik et al. (2015)
	Cell membrane stability	*QCMSa2AC*	Malik et al. (2015)
	Stem reserve mobilization	*QSrm.ipk–2D*	Salem et al. (2007)
	Chlorophyll content	*Qchl.ksu–3B*	Kumar et al. (2012)

Table 25.4 (continued)

Crops	Traits	QTL name	References
Barley	Water-use efficiency	*QWue.S42IL–4H*	Honsdorf et al. (2014)
	Tiller numbers	*QTil.S42IL–3H*	Honsdorf et al. (2014)
	Chlorophyll content	*QtChl2.1*	Guo et al. (2008)
	Drought tolerance	*QDT.TxFr.2H*	Fan et al. (2015)
	Chlorophyll fluorescence	*QFv2H*	Siahsar and Narouei (2010)
	Water-soluble carbohydrate	*QWSC2H*	Siahsar and Narouei (2010)
	Proline content	*QPC.S42.3H*	Sayed et al. (2012)
	Plant height	*QPh.NaTx–1H*	Wang et al. (2014)
	Relative water contents	*qRWC6–6*	Liu et al. (2015)
	Stomatal conductance	*qGs2–10*	Liu et al. (2015)
Sorghum	Stay green	*qstg1*	Xu et al. (2000a)
	Stay green	*qstgJ*	Kebede et al. (2001)
	Lodging tolerance	*qLdg G*	Kebede et al. (2001)
	Preflowering drought tolerance	*qPrf F*	Kebede et al. (2001)
	Leaf area	*qTLA3–8*	Mace et al. (2012)
	Plant height	*qPH10*	Fakrudin et al. (2013)
	Number of leaves	*qNL10*	Fakrudin et al. (2013)
	Day to anthesis	QDan–sbi01–1	Srinivas et al. (2009)
	Total number of leaves	*QTnl–sbi01–1*	Srinivas et al. (2009)
Maize	Stay green	*qsg1*	Zheng et al. (2009)
	Grain yield	*qgy1*	Lima et al. (2006)
	Grain weight	*qgw 1.1*	Zheng et al. (2009)
	Ears per plant	*qep1*	Lima et al. (2006)
	Ear diameter	*qed 1.1*	Zheng et al. (2009)
	Plant lodging	*qpl1a*	Lima et al. (2006)
	Plant height	*qph1a*	Lima et al. (2006)
Cotton	Relative leaf water contents	*qtlRLWC1*	Amjid et al. (2015)
	Cell membrane stability	*qtlCMS*	Amjid et al. (2015)
	Stomatal size	*qtlSS*	Amjid et al. (2015)
	Stomatal frequency	*qtlSF*	Amjid et al. (2015)
	Osmotic potential	*qtlPH–1*	Saeed et al. (2011)
	Boll numbers	*qtlBN–1*	Saeed et al. (2011)
	Plant height	*qPH.SP.lg12–1*	Abdelraheem et al. (2015)
	Root weight	*qRW.SP.Ig2–2*	Abdelraheem et al. (2015)
	Plant height	*qtlPH–1*	Saeed et al. (2011)
	Boll number	*qtlBN–1*	Saeed et al. (2011)
	Osmotic potential	*qtlOP–2*	Saeed et al. (2011)
	Osmotic adjustment	*qtlOA–1*	Han et al. (2004)
	Seed cotton yield	*qtlSC–1*	Wang et al. (2006)
	Fiber strength	*QTLfs1*	Zhang et al. (2003)
	Fiber strength	*qFS–D8–1*	Shen et al. (2005)
	Fiber length	*qFL–D11–1*	Ning et al. (2014)
	Fiber length	*qFL10.1*	Tang et al. (2015)
	Fiber elongation	*qFE–c22*	Wang et al. (2015)
	Lint yield	*qLY–D8–1*	Shen et al. (2007)
	Seed cotton yield	*q–SCY–15–1*	Sankeshwar et al. (2018)
	Fiber length	*qFL–A12–2*	Keerio et al. (2018)

for further breeding programs. We can exploit them as a marker in our future breeding studies. However, one should consider that, most often, the time markers are not the gene controlling the traits. Therefore, crossover may occur any time between the QTL loci and the gene controlling the traits of interest. It is advised to breeders to check QTL marker alleles and traits of interest if they are still at linkage disequilibrium in the genetic resources in hand before the marker-assisted selection is applied.

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Abiotic Stress and Applications of Omics Approaches to Develop Stress Tolerance in Agronomic Crops

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Abstract

Abiotic stress is a multifarious factor that mainly affects the growth and yield of crop plants worldwide. Crop production is highly affected by abiotic stresses including drought, water submergence, salt, and heavy metals. The plants have developed various biochemical, physiological, and metabolic mechanisms to fight against different abiotic stresses. In order to get detailed knowledge about these complex molecular systems, we need the development of systems biology approaches, namely genomics, proteomics, transcriptomics, and metabolomics. Each one of the "omics study" has its own importance in developing the stress tolerance in agronomic crops. In order to combat changing environments, plants modify their "omics" profile for their survival. Recent developments in omics technologies provide deep insights into the molecular mechanisms and functions of particular genes and its resulting phenotypes. In recent times, these omic approaches are aimed to understand the molecular interaction and the involvement of signalling networks on abiotic stress plants. This chapter briefs about the involvement of different omics approach in understanding the effect of abiotic stress and the development of stress tolerance in agronomically important crops.

Keywords

Abiotic stress · Agronomic crops · Genomics · Transcriptomics · Proteomics · Metabolomics · Ionomics · Phenomics

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Abbreviations

2-DE	two-dimensional electrophoresis
APX	ascorbate peroxidase
CAT	catalase
CID	collision-induced dissociation
EMS	ethyl methane sulphonate
ESI	electrospray ionization
FTIR	Fourier transform-infrared spectroscopy
GC-MS	gas chromatography-mass spectrometry
GPX	guaiacol peroxidase
GSH	glutathione
ICAT	isotope-coded affinity tags
ICPMS	inductively coupled plasma mass spectrometry
ICPOES	inductively coupled plasma optical emission spectroscopy
IRT	infrared thermography
iTRAQ	isobaric tags for relative and absolute quantification
LC-MS	liquid chromatography-mass spectrometry
LEAP	late embryogenesis abundant proteins
MALDI	matrix-assisted laser desorption ionization
MAS	marker-assisted selection
MDA	malondialdehyde
MRI	magnetic resonance imaging
MS	mass spectrometry
NAA	neutron activation analysis
NGS	next-generation sequencing
NMR	nuclear magnetic resonance
PET	positron emission tomography
PiiMS	Purdue Ionomics Information Management System
QTL	quantitative trait locus
ROS	reactive oxygen species
SE	stem elongation
SILAC	stable isotope labelling by amino acids in cell culture
SOD	superoxide dismutase
TCA	tricarboxylic acid

26.1   Introduction

In the recent scenario, abiotic stresses are the major threats to the living world, especially in the plant kingdom, which have been intensified due to global warming and industrialization. They were the important reason for morphological, physiological, biochemical, and molecular changes in plants, resulting in reduced productivity of important crop plants (Hasanuzzaman et al. 2012). In the conflicting

climatic changes, crops are exposed more frequently to various abiotic stresses, such as drought, salinity, elevated temperature, water submergence, and nutrient deficiencies. Plants as a sessile organism need to hastily adapt to overcome different environmental stresses to complete their lifespan. Unlike biotic stresses, abiotic stresses are multigenic and quantitative in nature (Muthuramalingam et al. 2017a). Hence, it is necessary to understand the plant adaptation during different abiotic stresses, which is useful for the establishment of multiple responses pertaining in complex gene interactions and molecular crosstalk between several pathways (Umeszawa et al. 2006; Basu 2012). This could be addressed with the help of ultrahigh-throughput systems biology coupled with computational biology (Fig. 26.1).

Marginal efforts were made to expand our knowledge of plants in response to abiotic stresses using integrated system biology approaches. Genomics, proteomics, proteogenomics, transcriptomics, metabolomics, ionomics, and phenomics are modern system biology approaches that have been useful in studying the stress mechanism of plants (Muthuramalingam et al. 2017b). These technologies are known as "Omics Technologies." They afford new insights and open new horizons for understanding the molecular mechanism of stresses and responses with the improvement of plant responses and resistance to stress (Duque et al. 2013). These "omics" technologies are high throughput, fast data generating, and produce enormous data outputs. This chapter will provide important information for molecular
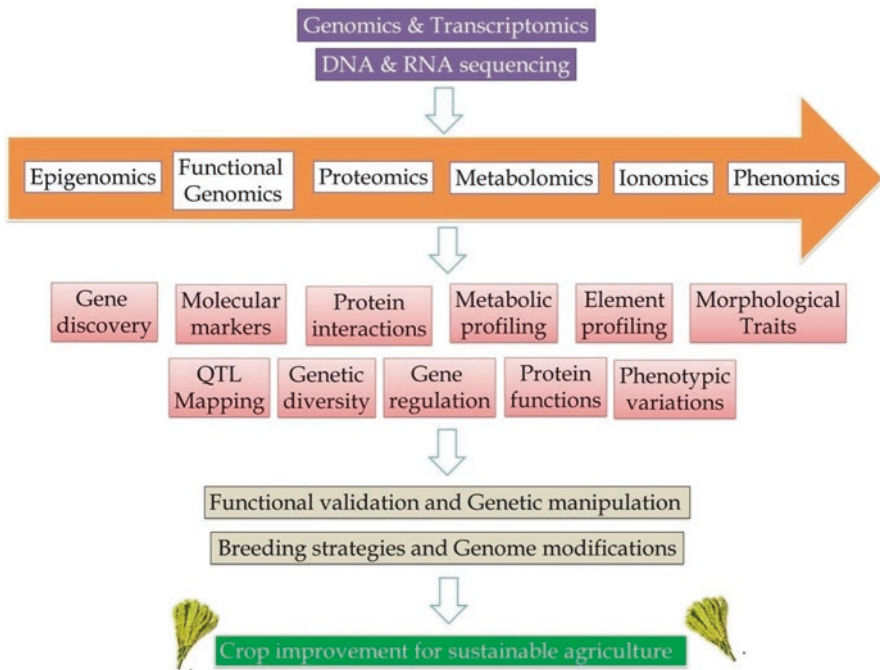
Fig. 26.1 Importance of omics technologies in crop improvement against abiotic stresses

biologist and plant physiologists to develop the large spectrum abiotic stress-tolerant crops through "omics technologies."

26.2   Agronomic Crops

Agronomic crops contribute to the greater proportion of man's food either for direct or indirect consumption through livestock products. The most important agronomic crops include cereal grains, seed legumes, and forage crops. Cereal grains, which are grown for their edible starchy seeds, are by far the most important source of concentrated carbohydrates for man and beast. They are the main items in the diet of much of the world's population, and about 70% of the harvested acreage in the world is devoted to growing them. Recent statistics showed that only three species of wheat, rice, and corn each account for essentially one quarter of the total cereal supply in the world. Seed legumes are higher in protein than the cereals and have evolved symbiotic associations with bacteria for the fixation of gaseous nitrogen. Forage crops, which include both annual and perennial kinds of grass and legumes, contribute 25–30% of the typical American's food supply through livestock products and more acreage is devoted to growing them than all other crops combined.

26.3   Abiotic Stresses

Abiotic stress will result in changes in plant growth, development, and productivity; severe stress may threaten the survival of plants. There are many environmental stresses like drought, salinity etc., cause drastic changes in plant metabolism which result in the enhanced accumulation of secondary metabolites in the plants. All plants have seasonal environmental variables; in fact, this is an inbuilt ability to adjust the circadian variables are often decisive factors of controlling in certain physiological attributes, such as the length of the vegetative phase, the onset of the reproductive cycle, flowering intensity, timing of fruit set, and induction of whole-plant senescence (Debnath et al. 2011). The primary effects of abiotic stress are ion imbalance and hyperosmotic stress. A direct result of these primary effects is the enhanced accumulation of reactive oxygen species (ROS), which is harmful to the plant cells at higher concentration. Oxidative stress occurs when there is a severe imbalance in any cell compartment among the production of ROS and antioxidant defense, leading to significant physiological challenges. Abiotic stresses such as low water availability, high salinity, high or low temperatures, heavy metals, and nutrient deficiency are among the major causes of crop failure. Plants are able to survive different environmental conditions; however, the degree of tolerance and adaptability to abiotic stresses varies among species and varieties. Crops exposed to abiotic stresses respond by activating defense mechanisms. Therefore, crops in an early stage of stress do not show visible symptoms, but their physiology can undergo significant changes (Cramer et al. 2011).

26.4   Plant Response to Environmental Stresses

The plant response is complicated as a result of reflecting off space and time and the integration of stress effects and responses at all underlying levels of organization (Blum, 1996). Under field conditions, these responses are synergistically or antagonistically altered by the superimposition of different stresses. Plants have developed several biochemical, physiological, and metabolic actions in order to combat such abiotic stresses. Often, it is complicated to predict the complex signalling pathway that is activated or deactivated in response to different abiotic stresses (Chawla et al. 2011). The plants have primary stress response mechanisms involved in the control of water transport and ion homeostasis: activation/inactivation of aquaporins and ion transport systems, acting at the plasma membrane and the tonoplast and leading to the reduction of cellular water loss or the accumulation of toxic ions in the vacuole (Boscaiu et al. 2008). Other stress responses to plants are the synthesis of protective molecules or osmolytes which includes sugars, polyalcohols, amino acids such as proline, quaternary ammonium compounds, etc. and different specific proteins such as heat shock proteins, LEA proteins, osmotin, etc. The secondary stress response involves the generation of "reactive oxygen species" (ROS), which includes H_2O_2 peroxidation and lipid peroxidation (MDA content was increased). ROS highly accumulated in the cell cytoplasm leads to antioxidant enzyme activity, which includes reduced glutathione, superoxide dismutase, catalase, ascorbate peroxidase, glutathione peroxidase, glutathione reductase, etc. (Kant et al. 2006; Turkan and Demiral 2009; Geissler et al. 2010). Specific stress activates a target gene or cluster of genes that act as signals for cascade activation events and secondary responses (Drew 1997).

26.4.1 Drought

Among different abiotic stresses, drought is one of the most devastating environmental stresses that affect the growth, development, productivity, and crop yield (Hasanuzzaman et al. 2017). Global warming and growing water crisis persistently increase drought stress in the agricultural plants (Harb et al. 2010). Plants often alter morphoanatomical traits, physiological and biochemical processes, gene expression, and metabolic regulatory networks in response to a water-stressed condition. Rice (*Oryza Sativa*) is a well-studied model crop to understand drought stress (Tripathy et al. 2000; Guo et al. 2006; Kathiresan et al. 2006; Zhou et al. 2007; Ji et al. 2012). Plants respond to changes in the environment. For example, root often grows thicker, deeper, and larger in response to drought in rice genotypes (Azhiri-Sigari et al. 2000; Asch et al. 2005; Yue et al. 2006; Ji et al. 2012; Lemoine et al. 2013). It is related to the higher proportion of dry matter and soluble sugar in the roots, which increase the leaf sucrose-phosphate synthase and root invertase activity (Wei et al. 2009). The impacts of drought include growth, yield, membrane integrity, pigment content, osmotic adjustment, water relations, and photosynthetic activity (Benjamin and Nielsen 2006; Praba et al. 2009). Plants often re-allocate

assimilates into shoot growth to root growth during drought stress condition, thereby increasing root extension of deeper soil layers (Rich and Watt 2013). Drought during reproductive and grain-filling stage causes yield reductions in wheat due to increased leaf senescence (Yang et al. 2001), oxidative damage to photo-assimilatory machinery (Farooq et al. 2009), decreased rates of carbon fixation and assimilate translocation (Asada 2006), reduced grain set and development (Ahmadi and Baker 2001; Nawaz et al. 2013), and reduced sink capacity (Liang et al. 2001). The effects of terminal drought on wheat yield are possible to extend in the near future (Araus et al. 2002; Dias de Oliveria et al. 2013). Drought stress is adversely affecting the maize crop, which accordingly blocks productivity, than other crops (Tai et al. 2011). Under drought stress, the rigidity of leaves is reduced and leaves are folded (Du Plessis 2003). Drought stress can cause a potential loss in yield and quality during kernel development (Pannar 2012). Drought stress decreased the net photosynthetic rate of barley, but it had no significant effect on the grain-filling rate under high vapor pressure deficit (Sanchez et al. 2002). The drought stress induces increased ROS accumulation; meanwhile, the antioxidant activity is also increased, and in some varieties of finger millet, it is decreased (Bhatt et al. 2011). Plants protect themselves from drought-induced oxidative damage, through a production of antioxidative enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), etc., which helps to limit the levels of reactive oxygen species. Increased enzyme activity is the direct relationship to increased tolerance to environmental stresses (Liu et al. 2011; Sayfzadeh and Rashidi 2011). The deficiency in water may cause an adverse effect on seed germination and embryo growth rate in the field, but many sorghum cultivars adapted well to semiarid areas (Patane et al. 2012). Sorghum developed two important strategies for surviving to drought stress. The primary strategy is the ability to maintain stomatal opening and photosynthesis at low water potentials and the ability for osmotic adjustment (Ludlow et al. 1990). The second mechanism is the escape from water stress due to deep and dense root formation (Mayaki et al. 1976, Jordan and Miller 1980). Drought-tolerant genotypes have a high epicuticular wax deposition on the leaf surface, which decrease the transpiration (Surwenshi et al. 2010) and reduce the cuticular conductance to water vapor and so extend water-use efficiency.

26.4.2 Water Submergence

Waterlogging is turning into a worldwide abiotic threat to several agricultural areas (Ghassemi et al. 1995). According to Sergey (2011), globally 12% of cropping areas are affected by waterlogging. Waterlogging affects the biological and chemical processes in plants and the primary effect of waterlogging is anoxia (O_2 deprivation and elevation of CO_2), and excess water itself does not react chemically with the plant. Plants required oxygen for cell division, growth, uptake, and transport of nutrients. Lack of oxygen in the root causes root damage and may weaken the plant; it will be poorly produced and may eventually die. In addition to O_2 deficiency, it produces the toxic substances such as Fe^{2+}, Mn^{2+}, and H_2S by reduction of redox potential

causes severe damage to plants (Drew and Lynch 1980; Setter et al. 2009). In early stages of plant growth, waterlogging causes severe reductions in plant height, dry matter accumulation, and yield (Mukhtar et al. 1990; Rao and Li 2003; Rosenzweig et al. 2002; Liu et al. 2001). It adversely affects the soil-water-plant relationships to create an ecological imbalance. Leaf senescence is a basic response when plants undergo waterlogging stress (Yan et al. 1996). Chlorophyll content, related photosynthetic enzymes, and photochemical efficiency were reduced due to the waterlogging stress, which resulted in the yield reduction of crops (Ren et al. 2016). In sorghum plants, long-term flooding causes a significant reduction in biomass production, leaf area, photosynthetic rate, stomatal conductance, and transpiration (Promkhambut et al. 2010). Flood leads to lack of oxygen in the roots; decreased oxygen inhibits mitochondrial respiration and ATP synthesis and also enhances a less efficient metabolism pathway – glycolysis in *Zea mays*. Among cereals, rice is well adapted to the submergence of water and can germinate in the complete absence of oxygen (Magneschi and Perata 2009), and deepwater rice cultivars have defense mechanism of oxygen escapes syndrome (Bailey-Serres and Voesenek 2008; Colmer and Voesenek 2009), which involves fast elongation of internodes to rise above the water level. Waterlogging stress reduced the concentrations of P, K, and Mg in wheat shoots, but the endogenous levels of calcium are unaffected (Stieger and Feller 1994). Flooding also reduces leaf elongation, photosynthesis, plant height (Ghobadi et al. 2007), and root and shoots growth (Sharma and Swarup 1988). It can reduce grain yield in winter wheat about 20–50% (Musgrave and Ding 1998). Waterlogging occurred during the stem elongation period (SE) is predominantly reducing the wheat yield (Marti et al. 2015).

26.4.3 Salinity

High salt is another abiotic stress closely related to drought which widely inhibits growth, development, and crop production severely. Approximately salinity affects 20% of irrigated land and reduces crop yield significantly (Qadir et al. 2014). The basic response of plants to salinity can be described in two phases. In an initial phase, ion-independent response to salinity inflicts stomatal closure, and therefore, it inhibits leaf expansion (Munns and Termaat 1986), whereas in the second phase, ion-dependent response to salinity causes premature senescence of leaves and ultimately reduces yield or perhaps death (Munns and Tester 2008). Rice is rated as a salt-sensitive crop compared to other cereal crops (Grover and Pental 2003; Joseph and Jini 2010). An excess amount of salt adversely affects the metabolic activities of rice, including cell wall damage, accumulation of electron-dense proteinaceous particles, plasmolysis, cytoplasmic lysis, and damage to ER and also accumulates citrate, malate, and inositol in leaf blades within 1 day of salt treatment (Sahi et al. 2006). Chlorophyll and carotenoid contents in rice leaves were significantly decreased after the deception of salt stress (Cha-umi et al. 2009). Sorghum is a moderate, salt-tolerant agronomic crop. Swami et al. (2011) reported that reduced leaf surface area and chlorosis were observed under salt-stress conditions. In sweet

sorghum, salinity decreased the percentage of germination (Almodares et al. 2007) and increased the duration of germination (Gill et al. 2003). Salt stress in sorghum plants causes changes in the proteome level (Swami et al. 2011). Salinity stress in finger millet shows increased caspase-like activity, H_2O_2 content, and two times more proline accumulation in shoots (Satish et al. 2016). Salinity causes a significant effect on physiological parameters of both wheat and barley (Izadi et al. 2014).

26.4.4 Heavy Metals

Heavy metal stress is one of the abiotic stresses influencing the growth and yield of crops. In higher plants, heavy metals induce oxidative stress by the generation of superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radical (OH), and singlet of oxygen ($^1O_2$), collectively termed as reactive oxygen species (ROS). The ROS can rapidly attack all types of biomolecules, such as nucleic acids, proteins, and amino acids, leading to irreparable metabolic dysfunction and cell death. In rice seedlings, cadmium stress induced superoxide anion and resulted in higher lipid peroxidation and also increased the antioxidant enzyme activity (Shah et al. 2001). It also decreased the chlorophyll content, which leads to inhibiting the photosynthetic activity and accumulates GSH and SOD in rice roots (Chen et al. 2013). Heavy metals disclosed the reduction in germination percentage, plumule length, radicle length, number of lateral roots, and biomass in *Triticum aestivum* (Athar and Ahmad 2002). Tiwari et al. (2013) reported lead cause reduction in carbohydrate and protein content in wheat. Cadmium and zinc metals reduced the lengths of the roots and leaves of the barley (Kherbani et al. 2015). The increased concentration of Cu > Zn > Pb causes an adverse effect on seed germination and early growth of rice, wheat, and barley seedlings (Mahmood et al. 2007).

26.5 Omics Approaches in Abiotic Stress of Crops

Understanding the basis of tolerance to abiotic stress responses in agronomic crops is an important and very challenging task especially in higher plants. Plants have developed several stress tolerance mechanisms, including physiological and biochemical changes which result in adaptive or morphological changes. Integrated data obtained from various omics approaches will provide a more comprehensive picture of abiotic stress responses. Omics approaches will facilitate a multitargeted assessment by allowing one to identify regulatory networks in complex hubs. Omics approaches target molecular parts transcripts, proteins, and metabolites of an organism and try to identify the functional networks or models designed to predict the activities of an organism in different environmental conditions.

26.5.1 Genomics

Genomics has generated new tools, including functional molecular markers and informatics, along with new knowledge about statistics and inheritance phenomena which will increase the efficiency of crop improvement (Varshney et al. 2005). Biological research has revolutionized by the arrival of functional genomics in several crop species and is predicted to have a high impact on plant breeding – especially in the identification of genes underlying agronomic traits (Varshney et al. 2009). Polyploidy genome complicates genomics-based breeding of agronomic crops, including wheat, potato, rice, cotton, sugarcane, and oat (Bancroft et al. 2011). The discovery of important genes and it's signal transduction pathways of plants to abiotic stress will play a major role in developing new strategies for crop improvement. The emergence of crop functional genomics greatly identifies a vast number of abiotic stress-related genes. Recent advancements in genomic technologies provide effective, high-throughput methods for genome-wide identification of stress-related genes. Especially, with the advent of next-generation sequencing (NGS) technologies, now the whole genome of several plant species was available for ease utilization of crop improvement. The genomics-based approaches also provide details on agronomically desirable genes linked with QTLs, thereby helps the improvement of abiotic stress-tolerant plants. Marker-assisted selection (MAS) is generally helping the breeders to improve drought-related traits. Cloning of important genes in target QTLs through genetic engineering was facilitated by the sequence data and the gene products. In rice, several QTL-related genes have been cloned (Xing and Zhang 2010; Miura et al. 2011; Huang et al. 2013). Genetic characterization of the cloned genes will provide a great opportunity to understand the molecular mechanisms of important agronomic traits in rice (Yu et al. 2013; Zuo and Li 2014).

26.5.2 Transcriptomics

Plants adapted to different abiotic stresses through deep changes in gene expression patterns which also resulted in changes in transcriptome, proteome, and metabolome of the particular plant species, thus, play an important role in the acclimation to the stress. Understanding the stress responses of plants is very important for successful management of abiotic stress. Sequencing and analysis of transcriptome are the simple, reliable, and cost-effective method to understand the molecular mechanisms globally in stressed plants (Shinozaki and Dennis. 2003). There are many reports available for individual stress (Tian et al. 2013; Gahlan et al. 2012) and combined stresses. Transcript-level analyses, microarray, RT-qPCR, etc. were generally used to evaluate the complex network during the abiotic stress defense. Stressors activate several genes and a large number of proteins in order to trigger the

signalling pathways associated with stress tolerance (Valliyodan and Nguyen, 2006; Tran et al. 2010). These genes are classified into two groups: the regulatory genes and the functional genes (Tran et al. 2010). Easy availability of transcriptome sequencing facility resulted in a transcriptome analysis of several crop plants, including rice, wheat, barley, and many more crops, which leads to study the exact molecular response of the plants against various stress. Availability of whole-genome sequences in rice, as well as the use of microarrays to analyze the transcriptome response, will facilitate the identification of genes involved in abiotic stress tolerance, which can be validated by RNA interference and T-DNA/transposon/EMS mutational studies.

26.5.3 Proteomics

Analyzing the effects of stress in plants has been studied using various tools and approaches, one of them is proteomics. Proteomics is an important omics technology used to study the functional and structural characteristics of the proteins present in an organism. Besides, major technical advances have been made easy the plant proteomics for food security (Agrawal et al. 2013). With the advent of technical developments in the proteomics, now it is easy to identify plant proteins with more reproducible manner. Complex biological mechanisms like plant response to abiotic stress tolerance were studied through proteomics approaches. Expression of stress-induced genes and proteins during the plant stress treatment leads to understanding the molecular mechanism of abiotic stress resistance in plants. In crop breeding programs, proteomics is used to detect the stress-responsive proteins through comparative proteomic analysis between control and the stressed plants. Then, the proteins responsible for particular phenotype will be assessed through expression analysis (Salekdeh and Komatsu 2007). Recent developments in methods of proteomic analysis paved ways to better explain the mechanisms of stress and stress response in plants. The conventional two-dimensional electrophoresis (2-E) coupled with mass spectrometry (MS) is used extensively in resolving proteins and to identify the stress-induced alterations in the proteome composition of plants (Isaacson et al. 2006). The alternative gel-free methods, which are based on fractionation with liquid chromatography (LC), are becoming popular (Hossain and Komatsu 2013). Breakthroughs in soft ionization methods, viz., matrix-assisted laser desorption ionization (MALDI), electrospray ionization (ESI), and peptide fragmentation by collision-induced dissociation (CID) in tandem MS have made easy to the protein identification (Ghosh and Xu 2014). Second-generation gel-free proteomic techniques, namely LC-MS-based isotope-coded affinity tags (ICAT), isobaric tags for relative and absolute quantification (iTRAQ), and stable isotope labeling by amino acids in cell culture (SILAC), were useful to assess comparatively and quantitatively, which helps to the global level effects of the plant stress (Hossain and Komatsu 2013, Ghosh and Xu 2014). Plant stress proteomics can identify possible candidate genes, which can be used for the genetic improvement of plants against various stresses (Cushman and Bohnert, 2000; Rodziewicz et al.

2014; Barkla et al. 2016). In rice, several studies have been done to identify the differentially expressed proteins during drought (Salekdeh et al. 2002), heavy metal stress (Ahsan et al. 2007), chilling stress (Huang et al. 2017), and various abiotic stresses (Kosová et al. 2011), which will provide insights into the abiotic stress mechanism and also a good starting point for further dissection of their functions using genetic and other approaches.

26.6 Role of Metabolomics in Crop Improvement

Metabolomics plays an important role in the field of plant biology, especially in the improvement of crop plants resistance to biotic and abiotic stresses. Among the various "omics" studies, metabolomics is one of the chief disciplines which opens the way for studying the dynamic biochemical composition in living systems (Dixon et al. 2006; Kusano and Saito 2012). Metabolomics has wide advantages because it has the ability to discover a huge range of metabolites from a single extract quickly and accurately. In other words, metabolomics is used to study elaborately about the cellular metabolites involved in different cellular events at a particular physiological state of a cell. Advancement in metabolomics paves the way for investigation of metabolites in mutants and transgenic lines in order to understand the metabolic networks and responsible candidate gene(s) (Hong et al. 2016; Kumar et al. 2017). In addition to that, metabolomics helps to determine the gene's function and how a particular gene involved in the metabolic pathway, regulation, and interception between linked pathways (Kumar et al. 2017). In recent days, metabolomics has been widely used in several crop species irrespective of the availability of a transgenic system. It has the ability to assist in the selection of superior traits and improvement of breeding materials (Kumar et al. 2017). In combination with the modern metabolomics, the accessibility of cost-effective genotyping assays, whole-genome sequence, and genome-wide genetic variants provides effective integration of metabolomics in crop breeding programs (Hall et al. 2002; Fernie and Schauer 2009; Kumar et al. 2017). Plants are frequently exposed to a variety of environmental stresses during their growth and development processes, which evolved series of adaptive responses at both transcriptional and posttranscriptional levels in plants, which leads to the rearrangement of functional networks to maintain homeostasis (Verslues et al. 2006; Hong et al. 2016). Commonly, environmental stresses are two types: abiotic and biotic. Once the plants are affected by stress, the receptors are activated by stress signals, which stimulates the expression of stress-responsive genes and subsequent production of specialized metabolites for the adaptation to environmental stresses (Nakabayashi and Saito 2015). The qualitative and quantitative analyses of metabolites in plants during environmental stress conditions will help not only to identify phenotypic changes but also to explore the genetic and biochemical mechanisms and also to study the plant plasticity for the production of stress-resistant/tolerant plants. There are lots of different techniques involved in metabolomics: (1) analytical techniques, such as liquid chromatography-mass spectrometry (LC-MS), gas chromatography-mass spectrometry (GC-MS), nuclear

magnetic resonance (NMR), and Fourier transform-infrared (FT-IR) spectroscopy, provide the metabolomic platform about particular sample, that is, detection and identification of metabolites. (2) Metabolite target analysis is another technique used in the preparation and analysis of samples from complex mixtures. It is widely used for the screening of phytohormones and studies the primary effect of genetic alteration directly. (3) Metabolite profiling and (4) metabolite fingerprinting – defining metabolic phenotypes. These are the four important techniques which involve the quantification of hundreds or thousands of metabolites from a complex mixture of chemicals present in cellular extracts and differentiate samples based on their genotype, phenotype, or biological relevance (Resham et al. 2014). For example, individual or combined abiotic stresses in maize have significantly changed the levels of six important metabolites, such as citrate, fumarate, phenylalanine, valine, leucine, and isoleucine, which indicate crosstalk between these metabolites, which can be used as a marker for abiotic stresses (Hong et al. 2016).

26.6.1 Ionomics

The ionome is defined as "mineral nutrient and trace element composition of an organism" and represents the inorganic component of cellular and organismal systems (Satismruti et al. 2013). Ionomics involves the quantitative and simultaneous measurement of the elemental composition of living organisms (Salt et al. 2008). The composition of ionome changes from physiological stimuli, developmental state, and genetic modifications. Ionomics helps to study the information about the genetic and developmental differences of plants under biotic and abiotic factors. Ionomics is an important factor to understand element composition and their role in biochemical, physiological functionality, and nutritional requirements of plants. Plants require many macro- and microelements for their growth within; phosphorus (P) and potassium (K) are the two key elements used as macronutrients in fertilizer for better crop yield. Plants were evolved into element uptake ability at different locations due to the various soil types (Fujita et al. 2013). This legitimizes the requirement of integrating ionomics with genomics to explore genetic variations. The ionomic analysis is a powerful approach to the functional analysis of the genes and networks of the genes that control the ionome and physiological processes which are involved in controlling ionome (Baxter 2010). Ionomics provides relatively high-throughput results in low cost and gives an easy means of analysis. Various tools used for the analysis of total ionomic profiling of plants are ICP-MS, ICP-OES, X-ray crystallography, neutron activation analysis (NAA), etc. PiiMS (Purdue Ionomics Information Management System) is the database for storing all the ionic profiles of plants (Baxter et al. 2007). The information present in this database helps in various structural and functional genetic studies of plants. For example, ionome analyzed on NaCl-treated barley shows decreased amounts of K, magnesium (Mg), P, and manganese (Mn) in roots and decreased amounts of K, calcium (Ca), Mg, and sulfur (S) in shoots, and accumulated Na and metabolites involved in glycolysis and tricarboxylic acid (TCA) cycle have been observed (Wu

et al. 2013). This study suggests the potential rearrangement of elemental profiles and metabolic processes to change the physiological mechanisms of salinity tolerance. Abiotic stress tolerance to the application of several inorganic elements has been observed. For example, silicon (Si) has shown beneficial effects on different abiotic stresses, including salinity, water stress, heavy metal stress, and UV-b (Liang et al. 2007). Ionomic profiles of plants may be useful as biomarkers for the specific physiological condition. In plants, ionomic biomarkers may be a simple way to determine if a plant has entered a particular physiological or biochemical state, for example, biotic and abiotic stress.

26.6.2 Phenomics

Phenome is defined as the complete set of phenotypic characterization of an organism that represents the sum total of its phenotypic traits and measurable physical and chemical outcomes of the interactions between genes and environments. Phenomics involves the measurement of phenomes, which includes physical and biochemical traits of an organism. Plant phenomics is the study of plant growth, performance, and composition; phenome of the plant changes from genetic mutations and environmental influences. It is further related to other "-omics" technologies like genomics, transcriptomics, and metabolomics, to analyze the plant performance in the field and further link it to the core molecular genetics. Phenomics speeds up phenotyping by using automated high-tech sensors, imaging systems, and computing power. Phenotypic data and metadata descriptions of the experimental conditions are captured for elaborated data analysis. These analyses would determine relationships between genotype and phenotype, which additionally reveal apparently unrelated phenotypes (Schauer et al. 2006; Lu et al. 2008). Stress-associated phenotype traits and their interrelationships can be analyzed with the help of advanced phenotyping techniques, such as infrared cameras to scan temperature profiles/transpiration, fluorescent microscopy/spectroscopy to assess photosynthesis/photosynthetic rates, three-dimensional camera, lidars (light detection and ranging) to measure growth rates, magnetic resonance imaging (MRI) to examine root/leaf physiology (Finkel 2009; Gupta et al. 2012), and positron emission tomography (PET) to map the functions of xylem and phloem (Hubeau and Steppe 2015). Digital imaging, considered cornerstone for measuring quantitative phenotypes, has allowed the modern researchers to monitor, measure, and track many aspects of plant development, function, and health, which was unimaginable using conventional measurement techniques. A number of software programs have been developed for extracting data from the digital images from roots, shoots, leaves, seeds, grains, etc. These tools can be used to high-throughput analysis of phenotypes in natural conditions as well as under controlled environmental conditions. Phenomics is used to screen abiotic tolerance-related traits (Vandenbroucke and Metzlaff 2013). Infrared thermal imaging (thermography) is a high-throughput technique used for screening wheat genotypes for salinity tolerance. Scanalyzer 3D imaging technique estimates the biomass of cereal plants under saline condition

(Golzarian et al. 2011). Chlorophyll fluorescence analysis has been used to investigate the photosynthesis of plants under stressful environments. Chlorophyll fluorescence has been used to access drought tolerance in winter bread wheat (Flagella et al. 1994; Roostaei et al. 2011) and arabidopsis (Woo et al. 2008). Infrared thermography (IRT) identifies the significant differences between leaf temperature, air temperature, and canopy temperature under drought and high-temperature stress in melons, tomatoes, and lettuce (Qiu et al. 2009). IRT has been used to evaluate response to salt stress in wheat and barley (Sirault et al. 2009) and water stress in grapevines and rice (Jones et al. 2002). Recently, Wedeking et al. (2017) used IRT to monitor leaf temperature and transpiration in Beta vulgaris plants exposed to continuous drought stress. Spectroscopic techniques can be used to study photosynthetic rates at leaf and biochemical activities in plants. Leaf spectrometer explores the photosynthetic electron transport feedback regulation in *Nicotiana sylvestris* (Kiirats et al. 2009). Reflectance spectroscopy monitored the photosynthetic efficiency, its activity, and biochemical pathway of pine (Busch et al. 2009) and barley (Siebke and Ball 2009). Altangerel et al. (2017) developed Raman spectroscopic technique for high-throughput stress phenotyping and in vivo early stress detection. Chlorophyll fluorescence combined with 2D digital imaging monitors *Arabidopsis thaliana* reactions under drought and chilling stress (Jansen et al. 2009). Chlorophyll fluorescence has been successfully used to monitor the photosynthetic effect of *Arabidopsis thaliana* under various abiotic stresses (Rungra et al. 2016). Recent phenomics study helps to improve crops through biotechnological approaches. For this, QTL genes controlling yield benefit under drought conditions need to be identified using genotypic and phenotypic screens and then incorporated into elite germplasm using modern breeding methods such as marker-assisted selection (Tester and Langridge 2010). The emerging tools and techniques in plant phenomics hold immense potential for the development of crop genotypes.

26.7 Concluding Remarks

Plants are primary producers on earth, and abiotic stresses caused by adverse environmental conditions alter the metabolism of plant cells, which ultimately affect the plant growth, development, and potential productivity of the plant. Under stressed condition, plants adjust themselves and adapt to existing conditions by changing the expression pattern of a gene, proteins, and metabolites so that "omics" techniques such as genomics, transcriptomics, metabolomics, ionomics, and phenomics identify those changes. These are the techniques that allow us to understand the genetic makeup of plants and their adaptability under stressed conditions. Recent "omics" studies have an excellent deal of information on transcript, protein, and metabolite levels to perceive the survival potential of plants under stress. Abiotic stress tolerance is a genetically complex process that involves many components of signaling pathways and multigenic in nature. Therefore, plant-engineering methods of abiotic tolerance depend on the expression of a gene(s) whose product(s) are concerned either in signaling and regulatory pathways or within the synthesis of functional and

structural proteins and metabolites that confer abiotic stress tolerance. Recently, several efforts are being made to improve abiotic stress tolerance capacity through genetic engineering with several achievements. However, the genetically complex mechanisms of abiotic stress tolerance and transfer of technology to field conditions make it difficult. Advances in various functional tools, resources, and "omics" have helped in the molecular characterization of the genes, metabolites, and proteins involved in abiotic stress tolerance. The integrated "omics" ultimately required to improve abiotic tolerance in economically important crop plants.

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The Possible Influence of Climate Change on Agriculture

27

Sumera Shabir and Noshin Ilyas

Abstract

The changing climate over the past few decades has been a major challenge for sustainable wheat production. Climate change includes factors such as increased carbon dioxide (CO_2) concentration, changes in precipitation, and change in growing seasons. Climate change has a lot of impact on agricultural production. Crop phenology greatly changes due to climate change, particularly in warmer climates. Anthropogenic activities result in the emission of long-lived greenhouse gases (LLGHGs) and other short-lived climate pollutants (SLCPs). Developing countries are more vulnerable to climate change due to increase in the concentration of greenhouse gases (GHGs) such as CO_2, methane (CH_4), and nitrous oxide (N_2O) produced due to anthropogenic activities. Fossil fuels are also among the main contributors of greenhouse effect due to the emission of CO_2. Elevated CO_2, high temperatures, and drought condition are affecting biomass and grain yield of crops. So, there is a need for breeding strategies to get more wheat varieties tolerant to high temperatures and drought conditions.

Keywords

Climate change · High temperatures · Drought · Greenhouse gases

Abbreviations

APSIM   Agricultural Production Systems sIMulator
BC   black carbon
CFCs   chlorofluorocarbons
CH_4 methane
HFCs   hydrofluorocarbons

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IPCC	Intergovernmental Panel on Climate Change
LLGHGs	long-lived greenhouse gases
N_2O	nitrous oxide
O_3	ozone
RCP	Representative Concentration Pathways
SLCPs	short-lived climate pollutants
TUE	transpiration use efficiency

27.1 Introduction

Climate change has a lot of impact on crop production at global as well as regional level. Climate change is largely affecting agricultural lands across the world especially due to the increase in atmospheric carbon dioxide (CO_2) levels (FAO et al. 2013; Fig. 27.1). Climate has an impact on food as it affects agriculture as a whole (Lobell and Gourdji 2012). Along with CO_2 other factors including changes in air temperature and precipitation patterns are the key drivers of crop responses to climate change, affecting crop productivity (Hatfield et al. 2011; Ludwig and Asseng 2006). Michael and MacCracken (2012) has found six clues to recognize that climate change is a real problem for any society (Table 27.1). Initial two findings are well-established facts, the second two findings are becoming increasingly focused, and the last two findings are about how to face the challenging situation (Michael and MacCracken 2012).

Fig. 27.1 Increased CO_2 trends affecting yield and plant adaptation in future 10 years. (Lobell and Gourdji 2012)
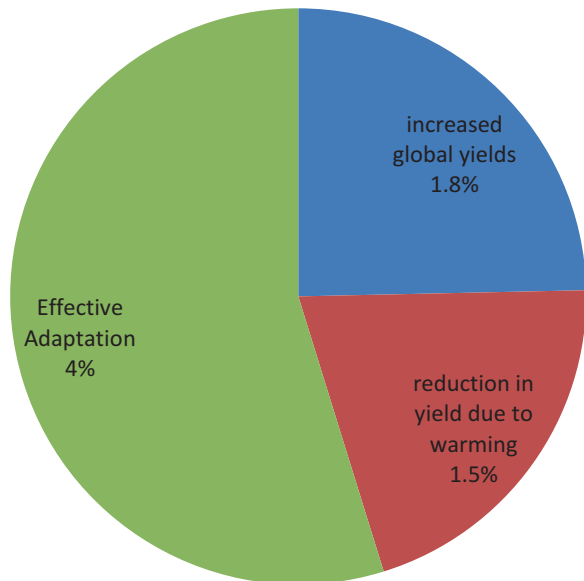
Table 27.1 Clues to recognize that climate change is a real problem for any society

1	•Anthropogenic activities including fossil fuel combustion lead to change in envirnmental composition
2	•Green house effect has a long term effect on global warming
3	•Climate change as a result of past activities and these changes are along with a human influence
4	• Future warming
5	•Environment and society both will get effected
6	•Slowing the ongoing change will require substantial reductions in greenhouse gas (GHG) emissions over coming decades to limit anthropogenic interference with the climate system.

27.2   Factors Affecting Climate Change

27.2.1 Annual Precipitation and Climate Change

There is a thumb rule that crop growth becomes more difficult after 90 °F, and most locations in the midlatitudes are rarely exposed to such temperatures. Closer to the equator this temperature is more easily attained. While the equator has the biggest impact in the coming years in food production, plants are more stressed to produce consistent yields. With average temperatures already closer to 90 °F in equatorial regions, global warming's first impacts could potentially be seen in these areas.

There is a growing demand for crop exports in midlatitudes, and higher yields are required in places such as the United States and Europe. This is why it is crucial to figure out how climate change will impact more temperate regions based on the predictions of how crop demand will only increase in the future (Godfray et al. 2010). First, climate change was observed in transpiration use efficiency (TUE) in case of wheat crop by checking the amount of grain produced per kg in per hectare as per mm transpired water from wheat crop.

27.2.2 Groundwater Contents and Climate Change

Perhaps, the most dramatic effect that climate change may bring is the amplification of droughts. Droughts are one of the most devastating phenomena on the planet. Entire ecosystems can be whipped out or severely crippled from a lack of water. Usually, in the periods of droughts, plants can restrict their water usage and transpiration by closing stomata and stopping growth all together, but over long periods, this can result in a slower development of a plant or even death (Eilmann et al. 2011). Crop yield in any dry area is totally dependent on the annual precipitation rate. Decreased precipitation severely affects crop yield in the areas where precipitation is an only water source.

27.2.3 Temperature and Climate Change

Temperature, precipitation, and CO_2 concentration have an impact on the plant yield. Increasing temperature increases the photosynthetic yield along with enhanced CO_2 (Long et al. 2005; Parrya et al. 2004; Rosenzweig and Iglesias 1998; Thomson et al. 2005) up to a temperature threshold limit. Beyond which yield is influenced negatively (Singh et al. 2014b). Increased temperature affects several physiological phenomena, including photosynthetic plant rate and respiratory activity (Chartzoulakis and Psarras 2005; Yang and Zhang 2006). IPCC (2000) declared that based on gas chromatography-mass spectrometry (GC-MS) climate change projections, in future it is expected to have a rise in global temperature from 2 °C to 4.5 °C in this century and some regions may have even more temperatures (Giorgi and Bi 2005).

27.2.4 CO_2 Concentration (ppm) and Climate Change

There are various studies in which the effect of increased CO_2 is studied especially in C_3 plant, and it is well documented that the crop yield increased as a result of CO_2 elevation if other factors are kept constant (Amthor 2001; Costa et al. 2006; Bannayan et al. 2005; Yoon et al. 2009). Fossil fuels are being used for the production of energy, and due to this reason, the concentration of CO_2 has increased from 275–280 ppm to 370 ppm since 1750 (Etheridge et al. 1996; Keeling and Whorf 2000). Cox et al. (2000) stated that by the end of this century, it might reach up to 600–1000 ppm.

Global climate change is largely due to change in concentration of CO_2 in atmosphere (Ittersum et al. 2003), and other than this, major gases are also contributing by their supportive role in climate change, including methane (CH_4), nitrous oxide (N_2O), ozone (O_3), and other halocarbons (such as chlorofluorocarbons and CFCs) (Michael and MacCracken 2012). Angulo et al. (2013) documented that CO_2 has an important impact on crop yield; other than this, climate change will have a negative effect on crop yield by 2050 and 2080 across the globe.

27.2.4.1 Impact of Past Climate and Future Climate CO_2 Trends

Biomass and grain yield get affected by CO_2 and temperature, as these are the key drivers in climate change as well as their effect on crop productivity (Mitchell et al. 1993a, b; Kimball et al. 1995; Moot et al. 1996; Manderscheid and Weigel 1997; Fangmeier et al. 1999; Manderscheid et al. 2003). Increased CO_2 trends affecting yield and plant adaptation in the future 10 years are shown in Fig. 27.1.

27.2.4.2 The Relative Role of CO_2 Trends on Wheat Productivity Trends and Grain Quality

Ewert et al. (2002) found that there is no effect on phenological development of wheat due to elevated CO_2 levels, and Pinter et al. (2000) observed that CO_2 has little effects on stomatal conductance free-air CO_2 enrichment (FACE) experiment. Mitchell et al. (1993a, b, 1996, 2001) found that elevated CO_2 (360–690 ppm) has no effects on wheat phenology. So, it can be concluded that increased temperature is mainly responsible for fastening crop maturity (Anwar et al. 2015; Cooper et al. 2009; Ludwig and Asseng 2006; Mitchell et al. 1993a, b; Sadras and Monzon 2006; Ittersum et al. 2003). Due to hasten phenological development of wheat, it results in shortening of time available for grain formation (Mitchell et al. 1993a, b). Rise in temperature since the 1980s has resulted in decreased yield by 5.5% without considering the effect of CO_2.

27.2.4.3 Impact of Greenhouse Gases and Climate Pollutants

Long-lived greenhouse gas (LLGHG) emission has led to increased temperature globally, which has pronounced negative impacts on crop yields. Other than this short-lived climate pollutants (SLCPs), non-long-lived greenhouse gases (non-LLGHG) have also negative impacts over agriculture. Temperature, precipitation, monsoon patterns, and regional radiations directly damage the plants (Ramanathan et al. 2005).

27.2.4.4 Short-Lived Climate Pollutants

Short-lived climate pollutants include greenhouse gases (methane), black carbon (BC) aerosol, tropospheric ozone, and hydrofluorocarbons (HFCs). Collectively, these chemicals have contributed in 40% of total radiative forces (Ramanathan and Xu 2010). Short-lived climate pollutants and their atmospheric lifetime are shown in Table 27.2.

27.2.4.5 Effect of Ozone

Formation of ozone depends on the presence of CH_4, carbon monoxide (CO), volatile organic compounds (VOCs), and oxides of nitrogen ($NOx = NO + NO_2$). Ghude et al. (2008) and Beig and Ali (2006) suggested that in monsoon months of summer, nitrogen oxides and ozone concentration are higher than in winter months, and this might be due to higher temperatures during these months (Sillman and Samson 1995). Globally, ozone has led to crop loss over 79 million metric tons ($11 billion) during the year 2000 (Avnery et al. 2011).

Table 27.2 Atmospheric lifetime, sources, and effects of short-lived climate pollutants and greenhouse gases

Short-lived climate pollutants and greenhouse gases	Atmospheric lifetime	Sources	Effects	References
Black carbon	Few weeks	Aerosol sprays	Impact on temperature, precipitation, and crop growth; alter the solar radiations which reach in earth surface	Wallack and Ramanathan (2009) and Ramanathan and Carmichael (2008)
CO_2	NS	Anthropogenic activities, especially fossil fuel burning	Important gas in climate change, elevating temperature across the globe	IPCC (2007a, b, c)
Methane	Decades	Decomposition of organic material in oxygen-deprived conditions (fermentative digestion by livestock, stored manures, and rice grown in flooded condition) ruminants (cattle, buffalo, sheep, goats, and deer) produce extensive amounts of methane	Impact on increasing temperature	IPCC (2007a, b, c), Kanyama and González (2015) and Shindell et al. (2012)
Halocarbons	Decades	NS	Impact on temperature increase	IPCC (2007a, b, c) and Shindell et al. (2012)
Nitrous oxide	NS	Microbial transformation of nitrogen in soils and manures. Also produced during production of nitrogen fertilizers	?	IPCC (2007a, b, c)
Ozone	Month	NS	Impact on temperature and crop growth	Wallack and Ramanathan (2009) and Ainsworth et al. (2012)

NS: Not specified

27.2.4.6 Effect of Black Carbon

Black carbon has direct impacts on crop growth and radiations. It is an absorbing aerosol that absorbs direct and diffused light available to plants causing yield loss. However, its effects are not easier to isolate because it emits with other scattering aerosols or it may get mixed with them after emission. So, it causes varying radiative property (Chung et al. 2012).

27.3 Study to Access Climate Change

Most agriculture models are sensitive to emissions of CO_2 and their immediate effects on the net absorption of solar radiation, which is why accurate models for global emissions are so crucial (Cai et al. 2009). Models are applied to accurately forecasts about future crop yields by doing alteration in CO_2 availability, temperature, annual precipitation and ground water levels. This may help to depict how climate change will influence crops (Manges 2016).

27.3.1 Representative Concentration Pathways (RCP)

The use of Global Climate models helps in allocating the regions of the globe in thousands of grids, each of which calculates their own energy absorption and with the help of thermodynamic laws, we can predict the transfer of energy between grid points, and if done accurately, it depicts the cycle of energy throughout the globe. These data can be used to estimate variables such as winds, temperature, and moisture. Each model is used on historical information and then matched to historical observations. The comparison of the model run to the actual observation and its accuracy is then used to project into the future what the temperature effects will be with different net amounts of energy being retained or radiative forcing by the earth in watts per meter squared. To prevent guessing the impacts of increased carbon dioxide levels on the temperature, the use of global climate models with temperature totals is required. Representative Concentration Pathways (RCPs) are global climate change models that have been run at different CO_2 concentrations. Each RCP run represents different scenarios and what the global temperature impact will be by the year 2100.

27.3.2 Agricultural Production Systems sIMulator (APSIM)

APSIM is crop simulation model that is used across the globe for simulation of crop growth, yield, nitrogen fertilizer treatment, crop phenological development, biomass accumulation, grain yield, and soil water balance in farming systems, and it is operated daily (McCown et al. 1996; Akponikpe et al. 2010; Dixit et al. 2011; Dixit and Telleria 2015; Moeller et al. 2014; Mohanty et al. 2012; Probert et al. 1998). It is also used to study the impact assessment of climate change, optimizing planting time and management practices (Anwar et al. 2015; Araya et al. 2015; Luo et al.

2005, 2009; Ludwig et al. 2009; Yang et al. 2014; Bassu et al. 2009; Zhang et al. 2012). The APSIM is also used to access the impact of CO_2 increase over crop yield (Ludwig and Asseng 2006; Asseng et al. 2004; O'Leary et al. 2015; Reyenga et al. 1999; Yang et al. 2014).

27.4 Possible Effects of Climate Change on Agriculture

27.4.1 Cropping Systems and Crop Response to Global Change

Climate change has a negative impact over crops as a whole as temperature increases and rainfall decreases except in the regions where there are high latitudes, and the temperature is less than crop optimal ranges (Mariani et al. 2018). Elevating CO_2 levels has a pronounced effects on crops as it increases plant photosynthetic rate and increased transpiration; lessen transpiration results in increased plant production (Amthor 2001; Kimball et al. 1995; Long et al. 2004; Singh et al. 2014b; Sommer et al. 2013). So, this partially goes against the detrimental effects due to elevated CO_2 concentration especially in C_3 crops (i.e., wheat) (Singh et al. 2014a; Leakey et al. 2006).

Oliveira et al. (2013) stated that total wheat biomass and its grain yield increase regardless of increased temperature, even crop grown under drought condition. However, any big increase in temperature may result in restricting the positive effects of increased CO_2 concentration (Schütz and Fangmeier 2001; Benlloch-Gonzalez et al. 2014).

27.4.2 Effects on Different Crop Type/Global Trends in Crop Productivity

Human impact on the surrounding environment from a large-scale perspective is clear. Decreasing ice sheets in the poles and the thawing tundra may be the most visible impacts of climate change, but yet their human impacts, thus far, are small. Most population centers are at the midlatitudes and are thousands of miles from the direct impacts of melting ice. Projected sea level changes and ocean current will have a dramatic effect on the global economy in the future, but still, the small scale and current perspective are missed. Rising oceans and temperatures still have yet to dramatically impact human's wallets and most importantly our stomachs. Global warming's impact on crops is still the defining questing when predicting the severity of the impact of global climate change. Still, many uncertainties surround how precipitation around the world will be affected by temperature increases (Huntingford 2005). Midsummer temperatures in July in the United States typically cause the most water stress on the plant with temperatures exceeding 90 °F in the Corn Belt. The higher levels of rain in midsummer in most cases had the most impact in increasing yields (Changnon and Hollinger 2003). By midsummer, most crops have already flowered and have begun the processes of seeding, making this a key time for moisture absorption.

27.4.3 Future Wheat Yields Due to Climate Change

Studies have shown that there is a reduction of wheat yield in rainfed wheat by 10–40%, while irrigated wheat reduced by 20–50% (Parry et al. 1999, 2004). Asseng et al. (2015) stated that wheat production would decrease by 6% with every rise of 1 °C temperature.

27.5 GHG Emissions in Food Production

Intergovernmental Panel on Climate Change (IPCC 2007a, b, c) has declared CO_2 as a major greenhouse gas produced due to anthropogenic activities especially due to fossil fuel burning. Other than CO_2, other gases are also important climate change drivers, methane being second in this category due to its radiative forcing, while halocarbons and nitrous oxide lie in third and fourth numbers, respectively, due to their radiative forcing that varies among GHGs, for example, nitrous oxide is 300 times more efficient than carbon dioxide. Elevated levels of methane and nitrous oxide are caused primarily by agriculture. IPCC (2007a, b, c) reported that in the year 2005, 60% nitrous oxides and 50% methane from agriculture account for total global emissions. GHG emission from commonly consumed food items is shown in Fig. 27.2.

The analysis of GHG emission during food items analysis including their processing, transportation, the presence of meat, amount of N fertilizers, manure
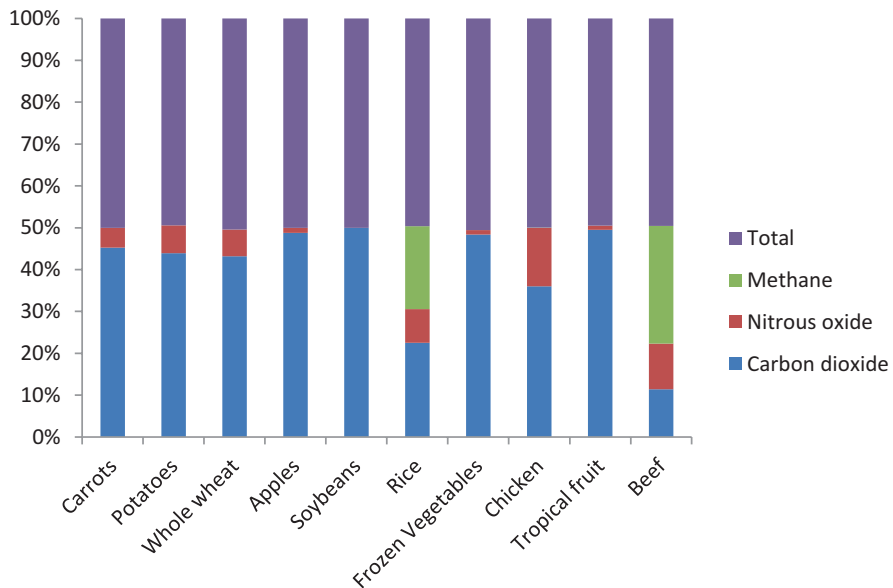
Fig. 27.2 GHS emission from commonly consumed food items. (Kanyama and Gonza'lez 2015)

application, and storage methods are considered. CO_2 emission is dominant in vegetables, and nitrogen oxide emission depends on nitrogen application. Methane and nitrogen oxide emission is considered in animal products. Calculation of GHGs for animal products and rice grown in flooded condition is more complicated (Kanyama and Gonza'lez 2015).

27.6 Conclusions and Recommendations

There is a need to study the effects of mesoscale transport of pollutants. As there are different impacts of local and transported chemical pollutants, so it is a subject for future research. A more comprehensive network could be used to investigate the surface ozone and short-lived chemical pollutants for getting to know the origin of pollutants by examining their correlations between local emissions, ozone formation, and their distribution. These data could be used to cross-check chemical transport models and to create observationally constrained emissions inventories. Several measures can be adapted to get benefit from climate change to increase crop yield and productivity.

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Effect of Agricultural Pollution on Crops

28

Fatima Bibi and Noshin Ilyas

Abstract

The basic need of humans is food and wheat is the major staple food of people in the world. Wheat is the third most-produced cereal after maize and rice and in our average diet, it is considered as an inexpensive source of calories and protein. There is a severe need of increasing wheat production as the population is increasing day by day and future demand is also rising. To get dramatic yield in less time, conventional production uses pesticides, herbicides, and chemical fertilizers. Though crop production is boosted up by application of chemical fertilizers, excessive use of these chemical fertilizers can cause many problems such as soil becoming hard, pesticides getting stronger and polluting the water as well as soil. On the other hand, the constant use of these chemicals leads to wear and tear of soil characteristics which compromises the nutritional value and edible quality of cereals and fruits due to the accumulation of heavy metals in plant tissues. As a result, the protein content of wheat crop reduces and the quality of carbohydrate of such crops also degrades. Excessive use of chemical and natural products for farming is causing contamination of related surrounding and environment, eventually resulting in agricultural pollution. Farming activities not only contribute to soil and air pollution but also to water pollution which is indirectly affecting wheat crop productivity. Agricultural productivity rise has caused considerable impact on wheat, on crop production, as well as on the environment. As nitrogen salt in chemical fertilizers is high in content and the soil absorbs nitrogen more quickly, it results in drying up and dehydrates the plant. Besides this, intake of water for the plant is lowered by using chemical fertilizers, so it can cause fertilizer burn or root burn. Agriculture and environment are interconnected to each other. As agriculture causes disturbance of the rivers and streams, agricultural pollution has been stated as one of the major sources of water reservoir pollution, which in turn is affecting the productivity of the crop.

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Pesticides cause severe threats to both human health and the environment. Overuse of nitrogen and phosphorus-based fertilizers on agricultural land has led to the high quantity of these minerals in the soil, on surface, and groundwater. Furthermore, genetically modified crops, because of their gene flow, have improved safety concerns, as well as a greater impact on biodiversity. Due to agricultural practices, health hazards are increasing while regulatory approaches have been taken in order to prevent occupational and environmental health hazards by increasing awareness and doing research regarding agricultural health and safety in the current situation. Production of food showing less impact on the environment, human and animal health is the chief aim of the organic system. The existing issues of agricultural pollution can be solved by practices like intregated pest management, waste management, and recycling of manure. Appropriate decisions and planning at the government level are mandatory to solve the current issue.

Abbreviation

AOS   Activated oxygen species
CH_4 Methane
CO_2 Carbon dioxide
CSI   Chlorophyll stability index
DNA   Deoxyribonucleic acid
GHG   Greenhouse gases
H_2O_2 Hydrogen peroxide
HMs   Heavy metals
N_2O Nitrous oxide
$O_2{}^{\cdot-}$ Superoxide anion
$OH^{\cdot}$ Hydroxyl radical
Pb   Lead
ppm   Parts per million
Se   Selenium

28.1   Introduction

Agricultural pollution may be defined as the occurrence of contamination, degradation, as well as damage to the environment and ecosystem, and health risks as a result of the byproducts of farming practices. Agriculture is not only a basis of economic progress, but also of employment, however the pollution caused by agriculture leads to many environmental and health risks. To understand agricultural pollution, there is great importance given to the nature of pollutants and the pollutant mode they behave in the environment (Abbasi et al. 2014). A major role in water pollution is governed by agriculture, which accounts for 70% of water abstractions worldwide. A greater quantity of agrochemicals, residues of drugs, saline drainage, and sediments is discharged into water bodies by farmers. As a result, there are demonstrated threats to human health and reproduction. Such threats affect every aspect of the environment and every organism from the earthworm to humans. Agricultural pollution also causes heavy economic losses. As agricultural pollution is not a solitary standing entity, its effects are carried over as air pollution and water pollution (UNEP 2016).

There are a number of reasons of agricultural pollution, and these are mainly the herbicides, pesticides, and fertilizers which are used to improve the output of arable land. These substances are used to increase yields and reduce the loss of crops but are leached into the groundwater systems through runoff mostly. One of the major hazards to the environment and human health is this agricultural runoff pollution (Ahmed et al. 2009).

28.2   Effect of Agricultural Pollution on Crops

28.2.1 Effect of Pesticides on Crops

The population of friendly microbes in the soil tends to decline due to the excessive treatment of pesticides. According to Dr. Elaine Ingham (soil scientist), "Soil degrades if we drop both bacteria and fungi. Soil organisms are affected by the excessive use of chemical fertilizers and pesticides that effect is similar to the overuse of antibiotics on a human. For a few years indiscriminate use of chemicals might work, but in the end, there aren't enough valuable soil organisms to hold onto the nutrients" (Savonen 1997).

Worldwide, the average yield of cereal crops increased by more than 98%. Alternatively, it is essential to trim down the injurious effect of pesticides on human health, on animals, and on the ecosystem (Enserink et al. 2013). Numerous researches have revealed that pesticide exposure causes severe threats to human health of both rural and urban populations because it is directly affecting cereal crop (especially farmers) (Elbaz 2009).

Presently, there is a diversity of integrated systems that include different levels of pesticide use which may lead to different levels of yield losses compared to high-input conventional systems. Pesticides are used to control pests and diseases in integrated cropping systems, and by using other cropping practices pesticide sprays can be reduced as much as possible (e.g., cultivar that is resistant, needs lower nitrogen fertilizer and minimum tillage) (Loyce 2012; Debaeke 2009). As compared to organic systems, these systems can direct to advanced yields and reduce the use of pesticides as compared to conventional high-input cropping systems. Consequently, they symbolize a fascinating compromise between high-input cropping systems and organic. They may also be more gainful for farmers than high-input systems for some crops (Kaval 2004).

28.2.2 Effect of Herbicides on Crops

Insects like aphids, lady bugs, and others can be destroyed by herbicides which are used against grasses. Pests cannot be controlled naturally if the helpful insects are missing. Rather, there may be chances of rapid increase in insect population after initial application and as a result, requirements of the further application of pesticides increase to overcome original pests. Herbicides can also kill spiders, butterflies, bees, and moths, which play another task in the environment, for instance, pollinating plants. Humans have utilized herbicides to protect their crops for several years. Crop yield is boosted up temporarily by the application of agricultural chemicals but damage by pests is restrained, which also competes for weed for nutrients and water, and a large amount of nutrients in available form are provided. However, natural processes such as the conversion of organic matter and balance of microbes in the soil environment have been disturbed, which can lead to ruthless weakening of soils in the long-term uses (Boström and Fogelfors 2002).

28.2.3 Effect of Fertilizers on Crops

Unnecessary use of fertilizers has been a big risk to wheat crops. By the excessive application of inorganic fertilizers, environmental degradation may result, consequently decreasing crop yields. Excessive use of nitrogen fertilizers for attaining optimum productivity is linked to the increased level of residual nitrate in the soil, and eventually, due to leaching and gentrification, it is contributing to atmospheric as well as groundwater pollution. The quality of crops and fruit is badly affected by the excessive application of fertilizers (Swietlik 1992).

Potassium and sodium-rich fertilizers can disturb the soil pH and structure (Good and Beatty 2011). The efficiency of field crop is declining, as the soil pH decreases due to constant use of nitrogen fertilizers (U.S. Environmental Protection Agency 2007).

28.2.4 Effect of Heavy Metals on Crops

Crops and other countless plant species can uptake higher heavy metals (HMs) from the soil. Consequently, heavy metals go into the food chain (Seregin and Kozhevnikova 2008). As anthropogenic interference is increasing, HM pollution is an extremely significant problem (Башмаков, Лукаткин 2009). Many HMs are requisite macroelements for plants since they play a part in a broad range of enzymatic redox reactions. The indispensable elements are a group of HMs that are required in trace amounts for plant growth, metabolism, and development but are also lethal at high concentrations (Ivanova et al. 2010). The metals like copper, zinc, and nickel have a high biological activity and toxicity (Seregin and Kozhevnikova 2006; Wang et al. 2009). Some other metals, particularly lead (Pb), are called nonessential elements. In cell metabolism, they are actively involved but are not necessary or toxic to plants. Heavy metals are known to act together with different cellular metabolism which inhibits plant growth (Seregi and Ivanov 2001). However, the reason for all the destructive functional changes in plants under HM stress is the amendment in the balance of antioxidants in plant cells and activated oxygen species (AOS). Heavy metals can generate and set off AOS, such as hydroxyl radical (OH$^{\cdot}$), superoxide anion (O$_2^{\cdot-}$), hydrogen peroxide (H$_2$O$_2$), etc. (Pradedova et al. 2011).

The most important inputs of heavy metals (e.g., cadmium, mercury, lead, and arsenic) into agricultural systems are an organic waste, for example, manures, fertilizers, and industrial byproduct wastes. Some farming techniques, for instance, irrigation, can bring about the gathering of selenium (Se) that occurs naturally in the soil (Ganje 1966). The germination of the wheat seed is significantly reduced when exposed to cobalt. However, it is very useful to expose the wheat crop to lower concentration of Co (up to 200 ppm, i.e., parts per million) for growth as well as for the development of morphophysiological attributes, but higher amount shows harmful effects. Results from different biochemical (CSI, i.e., chlorophyll stability index, proline, chlorophyll a/b) studies also support this. A good phytoaccumulator for Co is wheat (Sarma et al. 2014).

28.2.5 Effect of Greenhouse Gases on Crops

Radiations of sunlight, especially infrared, are absorbed by these gases and are reflected back into the atmosphere; as a result earth's temperature is sustained. This phenomenon is given the name of the greenhouse effect, but on the other hand, source and sink of these gases are not even; the concentration of these gases in the atmosphere is increasing slowly and gradually, which is a big challenge to our earth population, and now they are becoming the foremost contributors of changes in the atmosphere and climate (Preston and Leng 1989). Although agriculture is a slight emitter of carbon dioxide CO$_2$, it is the main emitter of methane CH$_4$ and nitrous

oxide N_2O (Manono 2016). Unequal uses of fertilizers not only result in nonuniform growth, emissions of gases but also a waste of fertilizer and a decline in the usage coefficient of the plant (Kasraei 1993; Malakoti 1999). Environmental degradation is mainly caused by nitrogen-containing fertilizers when they are applied to a large extent (Chen et al. 2005). One of the chief anthropogenic sources of nitrous oxide is nitrogen fertilizers, so they are also contributing to global greenhouse gas (GHG) emissions (Galloway et al. 2008; Vitousek et al. 1997).

28.2.6 Effect of Invasive Species on Crops

Worldwide, major economic and environmental problems are caused by invasive alien species. Assessing the loss of biodiversity and environmental damage due to alien species invasions worldwide is problematic due to the fact that out of 15 million species on earth, only 1.5 million species have been identified as well as described. In the latest history, the rate of changing the environment has escalated swiftly because of human population and anthropogenic activities, so the rate and threats related with alien species introductions have increased extremely (Pimentel et al. 2000). These are causing massive economic and ecological harm and control costs (Pimentel et al. 2001).

28.2.7 Effect of Agricultural Pollution on Crops

Not only the crop's quality but its production and yield are also badly affected due to agricultural pollution. Along with the number of pollutants, there are so many other conditions that adversely affect the growth and development of crops (Agrawal 2005).

28.3 Amelioration of Agricultural Pollution

28.3.1 Biological Control

Biological control is not considered as a unique initiative for agriculture system. But it is gaining attention for controlling insect pests (Hoffmann and Frodsham 1993). Manufacturing organizations and government are making rules to ensure the appropriate and secure use of biocontrol. For evaluating agent safety, deploying and measuring treatment success, biocontrol manufacturers continue to develop new protocols. Not only to humans and animals but biocontrol usually is safe to plants as well as to the environment. One of the most important benefits of biological control systems is that they drive the escalating implementation of the technology. Using chemical insecticides to a larger extent often causes environmental degradation which in consequence damages human health and the environment. Obvious reasons to promote the use of biocontrol platforms are mainly to secure biodiversity

and high benefit-to-cost ratio. It will not only require education but also understanding of the general public and especially those concerned in agriculture to permit these alternate farming practices (Leonard and Mandjiny 2016).

28.3.2 Genetically Modified Crops

Genetically modified crops are produced with the aid of genetic engineering techniques where preferred genes of the desired characteristics are inserted into crops to modify their deoxyribonucleic acid (DNA). Unlikely, mutagenesis in which mutation is created in DNA by exposing plants to radiation or other chemicals. These techniques are particularly specific and precise. Genetically modified crops result in enhanced nutrition, shelf life and increase in productivity as well as herbicide and stress resistance. However, genetically modified crops remain in debate. Encouragement is equally from two different sides, and groups have their reason either in favor of or opposed. In Europe, the probable industrial and commercial scale farming of GM crops presents vast challenges and risks for the ecosystem (Gray 2004).

28.4 Conclusion

Agricultural pollution not only affects soil, water, and air but also causes issues associated with diverseness and health, particularly due to the utilization of organic matter, pesticides, chemical and gas emissions. There is increased public awareness regarding the impact of agricultural pollution on the environment in general. There is a demand to create foremost agricultural production for meeting up the increasing need for food. It is essential to increase wheat yield to fill the gap between consumption and production. Throughout human history, farmers misused the practices to lift the crop quality and productivity. Though there are rules and laws, they are not implemented in agriculture as they are in alternative industries. Thus to stop agricultural pollution and its severe effects on the surroundings should be a primary focus. There is a need to reduce its effects on our environment and ecosystem and to enhance the yield, improve quality, the agricultural practices, and the wellbeing of human being and biodiversity. For this purpose, correct policies ought to be created on native to world level. There is a severe need for producing crops in such a way that they do not require traditional fertilizers, pesticides, and herbicide. On the other hand, to fulfill the demand for crops and food, there is need of such techniques that can protect the crops from insects and pests without causing harm. It is becoming more difficult to supply fresh water, so alternatively we have to find and adopt sustainable techniques for producing food. Adverse effects of agricultural pollution on wheat are the biggest challenge caused by anthropogenic activities that we should defeat to see a tomorrow and guarantee our generation a safe and healthy food. We should always remember that agricultural pollution not only affects the environment but all organisms. It is our obligation to do our best to protect this beautiful place called earth.

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Toxicity of Soil Hydrocarbon Pollution in Field Crops and Its Remediation

29

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Abstract

Soil hydrocarbon contamination is an emerging constraint across the globe. The presence of hydrocarbon alters the physical, chemical, and biological properties of soil and makes it unfit for plant growth. The intensity of effects varies according to types of contaminants, the extent of contaminants, type of soil, and its properties. Mainly, hydrocarbon in soil decreases the germination of seed, growth, and yield of wheat. As different physical and chemical methods are used to treat polluted soil, such methods are not environmentally friendly and have certain disadvantages. Bioremediation is one of the environmental friendly and cost-effective techniques used for treating the contaminated site. Microorganisms, plants, or both plants and microbes can be used for remediation. The effectiveness of technique depends on the amount and type of contaminants. Microbial degradation is not effective for a large area. Similarly, phytoremediation also has certain limitations. But the combination of both methods has shown a better result. So, there is a need to utilize such a method for remediation purpose and make soil favorable for the growth of crops.

29.1 Introduction

The more urbanization and improvement in mechanized agriculture has led to an increase in the utilization of petroleum and its compounds (Ekpo and Nya 2012). Unintentional and unhurried crude oil spills have been and continue to be a

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considerable source of environmental pollution, and start of serious environmental problem, due to the possibility of air, water, and soil contamination. Hydrocarbon-polluted soils are well known across the globe because of more need of petroleum as an energy source. Petroleum (crude oil) and its product enter the soil via oil tank ruptures, crude oil pipe leakages, and uncritical dumping of refinery products, resulting in changes in soil properties. Soils polluted with petroleum hydrocarbon (PHC) have less fertility and hence, do not sustain adequate crop growth and development (Abii and Nwosu 2009).

Hydrocarbons are carbon and hydrogen containing organic substances. By structure, they are divided into two categories: one is straight chain hydrocarbons, which are again divided into single bond hydrocarbons and double or triple bond hydrocarbons. Another group of hydrocarbons contains a ring structure such as benzene (Palmroth 2006).

The main constituents of crude oil are hydrocarbons. Their percentage varies according to the isolation procedure and type of oil. In addition to hydrocarbon, crude oil also contains sulfur, nitrogen, oxygen, and heavy metals like lead, nickel, and cadmium (FGS 2009). The high content of hydrocarbons is due to the breakdown of dead remains of animals and plants. The effect of hydrocarbons on the environment varies according to their chemical structure and type of environment in which they move (Taylor 2007). The entry of hydrocarbon in to soil is determined by the density of hydrocarbon, water content, temperature, and texture of soil (Chaineau et al. 2003). During low temperature, flat movement of polyaromatic hydrocarbons in soil occurs, while under high temperature PHCs have a tendency to enter perpendicularly into soil (McGill et al. 1981).

Hydrocarbon content in the soil can be absorbed on the surface of soil forming an external layer or it may move down and block the pores of soil (Trofimov and Rozanova 2003). Amount of hydrocarbons in soil relay on amount and types of solutes in nearby areas, kind of clay minerals, amount of organic matter, pH, and temperature of soil (Semple et al. 2003). Suleimanov et al. (2005) documented that in forest soils, more content of PHC is present in the eluvial horizons that has the larger pores, on the other hand, less content of PHC is present in the illuvial horizon that has small-sized pores.

29.2 Effect of Hydrocarbons on Soil Properties

Hydrocarbon-contaminated soil has variations in physical, chemical, and biological characteristics "as compared to" uncontaminated soil (Robertson et al. 2007). The first response of soil contaminated is a decline in microbes. On the other hand, there is an improved population of oil remediating microbes (Seghers et al. 2003). Hofman et al. (2004) documented that with the passage of time, more population of microbes tends to decline. Hydrocarbon inhibits the movement of auxin, that is why preventing the association of a fungus with plants (Kirk et al. 2005). There is a decrease in soil oxygen in contaminated soil. Nevertheless, soil rich with humus has shown less poisonous effect of hydrocarbons. The water content of the soil is also

decreased with hydrocarbons (Nwaoguikpe 2011). But, the structure of the soil is improved with hydrocarbon pollution (Certini 2005).

The pH and carbon content of soil have also been increased with the contamination of crude oil (Marinescu et al. 2011). Iron and sodium ions have also improved in such soil (Trofimov and Rozanova 2003). Contamination with crude oil has no remarkable effect on the properties of soil. For illustration, although Marinescu et al. (2011) recorded an improvement in the nitrogen content of contaminated soil, Obire and Nwaubete (2002) documented a decline in nitrogen of soil. In the same way, while Akpoveta et al. (2011) observed a decrease of phosphorus in contaminated soil, Marinescu et al. (2011) documented an improvement in phosphorus in the same soil. These divergences might be justified by the nature and preliminary characteristics of soil respectively (Semple et al. 2003).

29.3   Effect of Hydrocarbon-Polluted Soils on Crop Growth

Crop growth needs an accurate content of minerals, oxygen, water, and microbes. Hydrocarbons change the nutrient content of the soil and therefore decrease the capacity of holding the plants (Abii and Nwosu 2009). The acidity of soil results in damage of leaves, turning it into yellow and reducing plant growth.

Acidic soils resulting from this pollution may cause yellowing of leaves and stunting of crops. The concentration of magnesium and calcium ions also declines in such soil. Moreover, plants growing in such soil are more susceptible to disease. The decline in pH of soil due to hydrocarbons increases the content of heavy metals in the soil which can be harmful to plants by their absorption. Likewise, plant growth is affected as hydrocarbon causes reduction in necessary nutrients such as nitrogen and phosphorus (Obire and Nwaubete 2002; Akpoveta et al. 2011).

Microbes grow rapidly due to the high carbon content of hydrocarbon-contaminated soil. Although such microbes are not harmful to plant development, the opposite matter of their presence in large number offers struggle to get nutrients, in comparison to plants, thus resulting in a decrease in plant development (Trofimov and Rozanova 2003).

As water is necessary for good plant growth, hydrocarbon-contaminated soil makes water unavailable to plants and causes a reduction in germination of seeds. Crude oil blocks the pores of soil and causes unavailability of oxygen (Adam and Duncan 2002). Likewise, Rahbar et al. (2012) documented a decline in the root and leaf area in *Helianthus* annuus growing on a hydrocarbon-contaminated soil. It is quite justified that more the penetration of plant roots, more is their resistance to crude oil contamination, importantly in case of the surface of the soil. However, these hydrocarbons are beneficial to plants in fewer amounts. Moreover, Nicolotti and Eghi (1998) observed that such contaminants are harmful to plants as indirect interaction with plant tissue.

Zhu et al. (2012) reported that hydrocarbon contamination does not have a significant effect on germination of wheat crop as compared to soybean and sunflower. However, plant height, fresh and dry biomass of wheat have shown drastic reduction

due to hydrocarbon in contrast to its respective control. However, the plant height of sunflower has shown no considerable reduction due to hydrocarbon contamination. Sunflower and soybean have stronger potential to grow in oil-contaminated soil because they are less sensitive as compared to wheat.

29.4 Bioremediation of PHC-Polluted Soils

Bioremediation is the utilization of living organisms for remediating contaminated soils. The living organisms can be microbes or plants that reduce, transfer, or remove the harmful compounds using biological systems. Bioremediation could take place naturally or it can be performed to reduce contaminants of soil. The end products of this process, such as water, carbon dioxide, and biomass, are not dangerous for crops. It is quite a cost-effective method, as it does not need any complex method for its effectiveness. It can occur at a contaminated site reducing the need for transferring the contaminated soil. In addition to such positive aspects, it also has some disadvantages, as it requires a longer period as compared to traditional methods. Some studies have shown that it is not effective for ringed hydrocarbons and heavy metals (Kumar et al. 2010). Nevertheless, this mostly focus on the use of microbes, as plants can be effectively used for reducing such contaminants (Ghosh and Singh 2005).

Bioremediation can be classified into two classes based on the presence and types of contaminants. These categories are in situ and ex situ bioremediation. The first category focuses on the remediation of contaminants at a contaminated place without transportation of soil. There is a limitation of remediation, as its effectiveness reduced with more depth of soil (Pal et al. 2010). The basic types of in situ bioremediation include:

29.4.1 Bioventing

It is the most famous method of remediation based on enhancing the activity of naturally occurring microbes by providing nutrients by wells to contaminated area, and it is more effective when contaminants are present in subsoil (FRTR 2005; USEPA 2005).

29.4.2 Biosparing

This method focuses on the oxidizing ability of indigenous microbes by supplying oxygen. Degradation potential and penetration of contaminated area are the main limitations in this process (USEPA 1994).

Ex situ bioremediation is based on the movement of contaminated soil to various areas for particular treatment. There is a high potential of contact of contaminants during the transport. Examples of ex situ treatments include:

29.4.3 Land Farming

It is a cost-effective treatment that involves spreading and mixing of soil to enhance the transformation of contaminants in less toxic form by microorganisms.

29.4.4 Composting

This method is based on the use of organic waste like animal and plant waste material to enhance the decomposition of contaminants by native microbes. The addition of waste increases the temperature of soil, which stimulates the decomposition process.

29.4.5 Biopiles

This method is a mixture of composting and land farming. It is focused on the loss of contaminants by making piles. It is mostly used for topsoil.

29.4.6 Bioreactors

It is based on the use of tubes for degrading contaminants. Soil solution is prepared and shaken inside the tube (Robles-Gonzalez et al. 2008). The interaction of contaminants and microbes is enhanced by shaking and increasing the decomposition of contaminants. Abiotic factors like pH and temperature can be maintained in a vessel to enhance degradation, although it is quite expensive in contrast to other remediating methods.

29.5   Use of Microorganisms for Soil Remediation

Different microbes have the ability to degrade pollutants. They utilize contaminants as a source of energy and carbon. Many of such microbes are oxygen-dependent bacteria like *Pseudomonas*, *Mycobacterium*, *Rhodococcus*, *Arthrobacter*, *Acinetobacter*, *Nocardia*, and *Bacillus* (Chaillan et al. 2004).

Few fungi also have the potential of bioremediation. For example, white rot fungus (*Phanerochaete chrysosporium*) has the ability to degrade lignin and also degrade polyaromatic hydrocarbons and other dangerous contaminants (Pal et al. 2010). For efficient bioremediation, association between microbes and contaminants is necessary and subsequently different kinds of contaminants are present in soil, a broad variety of microbes is needed for good degradation.

It is deliberately effective only when the action is done in a rational time period in contrast to other methods. Bioremediation could be done by the method of biostimulation that is focused on the degradation of contaminants by microbes

previously present in soil. Consequently, circumstances which enhance their actions are ready to increase degradation. This can be done by adding nutrients in the state of biological biomass as changing pH of the soil, water content, and presence of oxygen. The number of microbes in contaminated area governs the range of efficiency of biostimulation as a method of bioremediation. Biostimulation is a rapid and efficient technique for the already contaminated area as compared to the area of without contamination. The reason behind that is the number of oil-degrading microbes present in the contaminated site. An additional feature of biostimulation is that additions of nutrients enhance the microbes' decomposing potential, as these nutrients are utilized by all microbes, regardless of the types of microbes. That is why, there is no surety that nutrients will be utilized particularly by decomposing microbes (Naidu et al. 2010). Still, research has proved that biostimulation can be an efficient method for the treatment of contaminated area (Sarkar et al. 2005).

Bioaugmentation is another technique of bioremediation. In this method, a consortium of hydrocarbons decomposing microbes is added in the contaminated site. Now, genetically modified organisms (GMOs) are also utilized, but there is a certain restriction in the use of genetically modified organisms because of their disputed behavior (Urgun-Demirtas et al. 2006). Research has proved that growth and establishment of plants improved in hydrocarbon-polluted soil. Adedokun and Ataga (2007) documented a considerable increase in cowpea (*Vigna unguiculata*) growth in a hydrocarbon-contaminated area with the addition of cotton biomass and sawdust. They documented that the treatment of contaminated area increases the germination of seeds, plant height, biomass, and leaf area. The related research by Kyung-Hwa et al. (2004) confirmed the increase in the length of red beans and corn in hydrocarbon-contaminated soil in addition to *Nocardia* spp. as compared to respective control. While in uninoculated soil, the length of red beans and corns was 16% and 49%, respectively. Similarly, researchers documented that the damaging effect of experimental plants decreased by microbe remediation. Njoku et al. (2008) documented an improvement in chlorophyll amount, fresh and dry weight of soybean grown in hydrocarbon-contaminated site treated with cow dung. Remarkable improvement in the germination, growth, and yield of soybean was observed in contaminated soil inoculated with *Bacillus*, *Pseudomonas*, and waste material of poultry (Nwadinigwe and Onyeidu 2012). The results proved that bioaugmentation is more effective as compared to biostimulation concerning growth and establishment of plants.

29.6   Use of Plants for Soil Remediation (Phytoremediation)

Phytoremediation is a kind of in situ bioremediation focused on the utilization of green plants to maintain, remove, or decompose contaminants from the contaminated site. It is important for remediating heavy metals in cultivated site. Still, it could be utilized to degrade hydrocarbons. The procedure and effectiveness of this technique is based on kind, amount of the contaminants, plant type, and characteristics of soil (USEPA 2012). It is more effective as contaminants are present in the

plant rhizosphere. Plants promote the treatment of contaminated soil by various methods specifically:

1. Phytostabilization/phytoimmobilization: In such a technique, plants decrease the movement and bioaccessibility of contaminants in the area due to the absorption of contaminants. Penetrating substances are attached to plant surface and never returned to the surroundings. It is effective for less amount of contaminants. Contaminants remediating by this technique are heavy metals and cyclic organic compounds.
2. Phytoextraction/phytoaccumulation: This technique is based on the storage of contaminants in root and stem of plants that absorb from the soil, afterwards plants can be uprooted and burned. It is mainly utilized for treating heavy metals.
3. Phytodegradation/phytotransformation: Contaminants are decomposed by substances released by plants. It is effective for the degradation of water-loving compounds like atrazine and equally important for treating nonwater-loving compounds.
4. Phytovolatilization: This method is based on the absorption and discharge of contaminants or their by-products into the atmosphere (Palmroth 2006; Pal et al. 2010). Site contaminated with organic and inorganic contaminants like trichloroethylene can be treated by such technique.
5. Rhizodegradation/phytostimulation: Such method focuses on the degradation of contaminants in less harmful substances by rhizospheric microbes. It is a beneficial association as plants make the availability of nutrients for microbes.

Mostly, cereals and pulses are utilized for the treatment of hydrocarbon contaminated site due to increase in rhizospheric area made by root area (Merkl et al. 2005). Certain illustrations of cereals have shown that their effectiveness in degradation in hydrocarbons comprises signal grass, guinea grass, rye grass, and prairie grasses (McCutcheon and Schnoor 2003). Such plants are capable of decomposing hydrocarbons that exist in the soil. Ogbo et al. (2009) documented that weeds like *Sida rhombifolia* and *Mariscus alternifolius* decrease almost 60% of straight chain hydrocarbons as used for phytoremediation of the area contaminated with oil.

Plants with phytoremediating potential have particular restrictions. Rahbar et al. (2012) documented that sunflower can survive in 18,000 mg/kg hydrocarbon-containing soil. The best technique based on the determination of plants for phytoremediation ability is to noted the species indigenous to the contaminated area. The main features of plants include deep root system, the storage capacity of hydrocarbons in plant parts, high water-holding capacity, and rapid growth (ISAAA 2006).

Remediating soil with plants is a long time-dependent method and also causes the contamination of plants and food chain, if not done properly. Still, phytoremediation is preferable in soil with large amount of contaminants due to its less cost. It is also effective at low amount of contaminants. At last, it could be used in combination with other techniques as plants are its last site remediator (Pal et al. 2010).

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Drought and Heat Stress in Cotton (*Gossypium hirsutum* L.): Consequences and Their Possible Mitigation Strategies

30

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Abstract

Drought and heat are the most important abiotic stresses that adversely affect phenology, growth, fiber yield, as well as the quality of cotton across the world. The problem will become more severe in future climate change scenarios because of the frequent occurrence of high temperatures and water shortage. Development of high yielding cotton genotypes, resistant to drought and heat stress, is one of the most important priorities of cotton breeders. Therefore, it is important to evaluate the genotypic performance for heat and drought stress and also important to understand the physiological, biochemical responses to stresses as well as

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the agronomic performance of the genotypes under stress conditions. The correlation between yield and physiological as well as biochemical (nonenzymatic antioxidants and enzymatic antioxidants) responses of cotton under heat and drought stress conditions is also the most important factor to develop the efficient genotypes that are possible to grow. Whereas, screening of cotton genotypes under heat and drought stress is one of the essential protocols that can be used to select a large number of population within the shortest period. This approach can be used to differentiate the agronomical, physiological, and biochemical attributes of cotton genotypes contrasting for drought and heat stress tolerance. The present review tried to highlight the management strategies that could be useful to mitigate the drought and heat stress by using antioxidant, phytohormone, nutrient management, and other appropriate management strategies for maximizing cotton yield. While, among the compatible antioxidants, exogenous application of proline or glycine betaine is a good option to improve drought and heat tolerance in cotton. Therefore, foliar application of antioxidants in combination with soil-applied organic fertilizers is very effective for reducing the negative effect of drought and heat stress and to increase productivity.

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Abbreviations

PAR	Photosynthetically active radiation
AA	Ascorbic acid
ABA	Abscisic acid
APX	Ascorbate peroxidase
APX1	Cytosolic ascorbate peroxidase 1
CAT	Catalase
Chl	Chlorophyll
CMT	Cellular membrane thermostability
CSI	Chlorophyll stability index
CTD	Canopy temperature depression
DSI	Drought stress index
GA3	Gibberellic acid
GB	Glycine betaine
GMP	Geometric mean productivity
GR	Glutathione reductase
HSI	Heat susceptibility index
JA	Jasmonic acid
LEL	Leaf electrolyte leakage
MDA	Malondialdehyde
MeJA	Methyljasmonic acid
MP	Mean productivity
POD	Peroxidase
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicylic acid
SOD	Superoxide dismutase
SSI	Stress susceptibility index
STE	Stress tolerance efficiency
STI	Stress tolerance index
VPD	Vapor pressure deficit
YSI	Yield stability index

30.1   Introduction

Cotton (*Gossypium hirsutum* L.) is the most important fiber crop of the world that provides raw fiber to the textile industry (Zahid et al. 2016). The major cotton producing countries include India (26%), China (24%), USA (13%), Pakistan (9%), Brazil (6%), Turkey (3%), and Uzbekistan (4%), which together produce about 80% of global cotton production (Gillson et al. 2004; ICAC 2009). These kinds of

Cotton production statistics of major growing countries
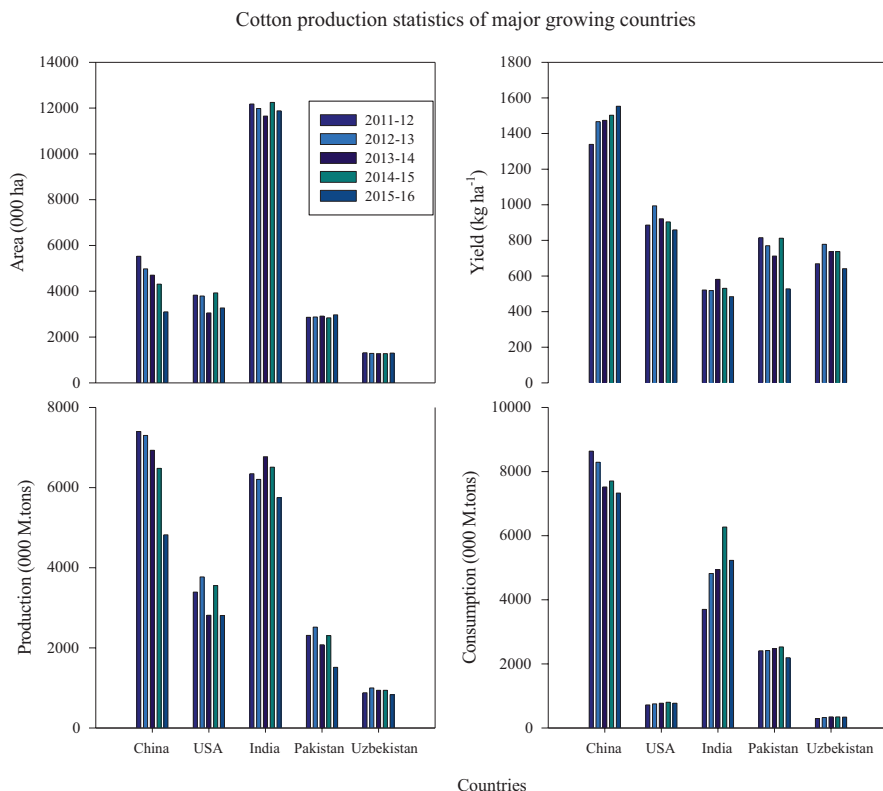
Fig. 30.1 Area, yield, production, and consumption of cotton plant–producing countries. (Source: Statistics 2016)

countries produced 60% of the total worldwide production of cotton fiber in 2004–2005, compared to 47% of 30 years ago. The area, yield, production, and consumption of major cotton producing countries of the world are shown in Fig. 30.1. Despite the strong competition with synthetic fiber, the demand for cotton fiber is continuously growing. About 21 million tons of cotton fiber was produced across more than 75 countries during crop season 2015–2016, and the major share comes from developing countries, which depicts the social and economic significance of cotton worldwide (ICAC 2017).

Improving the productivity and maintaining the stability of cotton yield under favorable as well as stressful conditions are necessary to cater to the demand of growing worldwide population (Basu et al. 2016). The current study on climate change predicts that plants will be subjected to the combined effects of drought and heat more often in forthcoming years, than in the present. The heat and drought stress are two major issues because of increasing temperature trends and water shortage in climate change scenario. The combined effects of both stressful

conditions are very dangerous because drought stress further increases the negative impacts on plant growth.

These limit crop productivities worldwide and combined with these kinds of stresses lead to several physiological changes that influence crop production and quality (Rizhsky et al. 2004). Similarly, Oosterhuis (2002) and Barnabas et al. (2008) reported that temperature and drought stress are the main abiotic factors that harmfully affect cotton productivity, and *also in arid and semiarid climates cotton yield has strongly depended on irrigation* (Khalik et al. 2012). Therefore, it necessitates that cotton yield should be improved to fulfill the growing demand for fiber and to sustain the income of growers. The recent research also examined the effects of heat and drought stress and indicated that genetic tolerance to the stress combination differs from the genetic tolerance to individual stress (Cairns et al. 2013). It is apparent that high temperature and drought often occur together.

In this context, the present review aims to clarify drought and heat stress effects on agronomical, physiological, and biochemical profile for characterizing responses of cotton genotypes to different stress conditions. Moreover, we attempt to provide a better understanding of antioxidant enzyme activities and physiological mechanisms of stress tolerance and consequently to contribute to understanding the agronomic performance for genetic nature of tolerance potential of cotton genotypes for future breeding.

30.2   Cotton Responses to Heat and Drought Stress

30.2.1 Heat Stress

Among the abiotic factors, heat stress is one of the most significant limiting factors that affect cotton productivity (Snider et al. 2009, 2011), through negatively influencing the growth and reproductive performances of plant by reducing the nutrient use efficiency, leading to higher abortion rates of bolls as well as lint yield (Oosterhuis and Snider 2011; Snider and Oosterhuis 2012). Snider et al. (2009), Loka and Oosterhuis (2010), and Snider et al. (2010) also reported that heat stress causes a decrease in the production of carbohydrate, while, increase in carbohydrate starvation throughout the period of high respiration. Bibi et al. (2004) noticed that photosynthesis and leaf extension growth of cotton plants were decreased at temperatures >35 °C that ultimately lead to decrease in the bolls as well as lint yield. In addition to this, heat stress also resulted in a significant reduction in the growth and net assimilation (Wahid 2007). Similarly, Ekinci et al. (2017) reported that the development attribute of cotton was affected significantly by heat stress, hence it is depending on genotypes, stress duration, and intensity. The shedding of fruiting parts is accelerated during heat stress, and very few squares and flowers mature into bolls (Tariq et al. 2017). Akhtar et al. (2013) reported that boll retention at the first position was decreased, due to high-temperature stress both in the field and controlled environmental conditions. Heat stress also reduces the rate of boll formation

and boll seed rate in the first position (Reddy et al. 2004) fruiting rate and a number of seeds (Brown et al. 1995; Brown and Zeiher 1998), and the number of nodes in the first position. The leaf temperature plays an important role in stomatal closure and it closes during heat stress to save water in the plant body, resulting in decreased photosynthesis rate and concomitant yield reduction (Carmo-Silva et al. 2012). Bibi et al. (2008) stated that the prime temperature for the photosynthetic carbon fixation was substantially 33 °C and photosynthesis reduces when temperatures reach at 36 °C or higher. The higher temperature accelerates the advent of various phenological stages of cotton (Ahmad et al. 2017) like maize, sunflower, and sugarcane (Ahmad et al. 2016; Abbas et al. 2017; Tariq et al. 2018). It means global warming would have shortened the crop growing season and ultimately poor yield will be achieved. However, it may prolong the cotton season by increasing number of summer days in areas where cotton growth cycle is reduced by early occurrence of the fall season. Heat stress promotes the production of reactive oxygen species (ROS) in chloroplasts and mitochondria by disturbing membrane stability and biochemical reactions, resulting in photorespiration (Sharkey 2005; Jaspers and Kangasjarvi 2010). Under high-temperature stress, the destructive impacts on cells and ROS might be due to different signaling molecules that are controlled by several biological operations such as stomatal closure, growth, development, and stress signaling (Demiral et al. 2011). The negative impacts of heat stress can be minimized by modifying certain management practices that would aid in plant stress tolerance. These may include shifting planting time, optimizing fertilizer, and irrigation management.

30.2.2 Drought Stress

The various physiological and metabolic processes that are taking place within the plant body are managed by the water contents of the plant (Mubeen et al. 2012), while its deficiency adversely affects the growth of crop plants including cotton from seedling growth up to crop maturity (Farooq et al. 2009). Whereas, supplementary irrigation at all the phases, normally six irrigations, is very important for achieving optimum seed cotton yield (Mubeen et al. 2012). While under drought stress, cotton leaf temperature increases between 3.5 and 4.5 °C due to deficit water stress (Carmo-Silva et al. 2012), through the reduction of transpiration (Shahenshah and Isoda 2010). Under drought stress, plant growth is affected by a number of morphophysiological disorders that cause a reduction in nutrient uptake and impaired active transport of photosynthates (Jaleel et al. 2009). Majumdar et al. (1991) found that under water deficit condition, chlorophyll (Chl) contents in plants were varied due to stress injury.

Drought stress also affects the relative water content (RWC), osmotic potential, and leaf temperature (Fanaei et al. 2012). Whereas, high cell electrolyte concentration disturbed the normal metabolic functioning of cell organelles, as reported by Mahajan and Tuteja (2005). Similarly, cell turgidity, the growth of cells and plant tissues are directly affected by drought stress (Reddi and Reddy 1995), which results in impaired cell elongation (Nonami 1998). While, Yuncai and Schmidhalter

(2005) reported that under drought condition, restricted nutrient uptake and their transport from root to shoot ceased the growth and development of plants, because of the restriction of transpiration rates, impaired active transport, and membrane permeability. Singh et al. (2007) suggested some biophysiological techniques select efficient genotypes that are tolerant to abiotic stresses; such as cellular membrane thermostability (CMT) and canopy temperature depression (CTD), chlorophyll fluorescence, as well as biochemical traits such as chlorophyll contents and these techniques are getting popularity nowadays. Meanwhile, antioxidant activities decreased in drought-susceptible genotypes but increased in drought-tolerant genotypes (Ahmadizadeh et al. 2011).

Therefore, it can be concluded that drought is one of the limiting abiotic stresses that adversely affect the growth and development of plants which finally adversely affects the yield of crops. However, development of drought-tolerant genotypes is the best way to mitigate the stress under changing climate. Without this, different biophysiological approaches such as cellular membrane thermostability and canopy temperature depression, chlorophyll fluorescence as well as biochemical traits, that is, chlorophyll contents and management approaches, such as the exogenous application of different antioxidants and soil application of organic amendments, could be used as alternative ways to mitigate the drought under changing the environment.

30.2.3 Combined Heat and Drought Stress

The extreme temperature and drought or their combination are inauspicious for growth and development of plants (Mittler and Blumwald 2010). However, the stress effect on crops is not always additive to the outcome of specific crops/plants (Choudhary et al. 2016; Ramu et al. 2016). Hossain et al. (2012a, b) found that the adverse effect of high temperature in combination with drought was more perilous, compared with their individual effect on all crops in the south-eastern arid region of Russia.

Therefore, the selection of cotton is an important issue for plant breeders to identify the cotton genotypes with tolerance to high temperature and drought and would be useful in both present and future climatic conditions (Kakani et al. 2005). Among the selection criteria, cellular membrane thermostability, canopy temperature depression, chlorophyll fluorescence as well as biochemical traits such as chlorophyll contents as well as stomatal conductance might be an identification criterion with higher productivity under extreme and normal temperatures (Rahman et al. 2000). Similarly, chlorophyll fluorescence and membrane leakage may be used as a sensitive and practical approach to quantifying high-temperature resistance genotypes under controlled and field conditions (Oosterhuis et al. 2009).

Selection of cotton genotypes, which survive and give better yields in stressful conditions, has greater scope in breeding programs. However, a need for an efficient protocol to determine the stress tolerance of cotton germplasm is of prime importance. So, it is very important for the development of drought and heat tolerance genotypes through conventional breeding approaches, availability of a technique,

which could help to identify a huge number of varieties/lines quickly (Wahid et al. 2007; Fita et al. 2015).

However, antioxidant mechanisms play a vital role in response to a combined effect of drought and heat stress. Among the antioxidants, proline was found to be accumulated in plants only under drought condition, but does not accumulate under the drought and heat stress combination (Rizhsky et al. 2004). From the discussion, it is confirmed that the combined effect of high temperature and drought is more hazardous as compared with their individual effect. Therefore, the selection of cotton genotypes and their management techniques are important issues for plant breeders to identify the cotton genotypes with tolerance to high temperature and drought and would be useful in both present and future climatic conditions.

30.3 Physiology and Metabolism of Cotton Plants Under Heat and Drought Stress

Physiological responses of plants, such as photosynthesis, hormonal profile, lipid accumulation, and transcript expression, are affected by drought and heat stress and their combination (Rizhsky et al. 2004). While, under stressful conditions plants carry out various physiological mechanisms to survive. Under stress conditions, photosynthetic capacity of susceptible crops is reduced by stomatal closure and also reduces metabolic impairments of proteins that are associated with photosystem and chlorophyll (Pirzad et al. 2011), resulting in lower CO_2 intake and finally photosynthates (Lawlor and Tezara 2009), which make plants susceptible to photodamage (Lawlor and Cornic 2002). Therefore, chlorophyll fluorescence should be considered as the most promising and stable heat tolerance identification technique as compared with the determination of membrane leakage (Bibi et al. 2003). Moreover, several of these plant responses to drought and heat stress are fine-tuned by a network of hormonal signaling pathways, including phytohormones (Peleg and Blumwald 2011; Kazan 2015; Llanes et al. 2016). In addition, phytohormones and hormonal crosstalk play an important role in the molecular mechanisms that optimize plant responses to stresses when they occur simultaneously in the environment. Abscisic acid (ABA) is considered as the main hormone involved in several developmental processes, such as shoot growth inhibition, stomatal movement, leaf senescence, and primary root growth and as a modulator of responses to abiotic stresses. Moreover, different signal molecules, such as calcium ion, reactive oxygen species, and several protein kinases, play essential important roles in ABA signal transduction for plant response to stressful conditions such as drought and heat stress (Ding et al. 2013). Indeed, the transcriptional modulation of hormonal signals could be an important way for plants responding and adapting to stress conditions. Thus, a large number of genes are induced or repressed in plants under abiotic stresses (Lindemose et al. 2013). Several types of researches have shown that transcription factors, such as bZIP, HD-ZIP, NAC, MYB, MYC, and AP2/ERF, are involved in plant responses to abiotic stresses. For example, Quin et al. (2016) isolated and analyzed two cotton Di19 (drought-induced 19) proteins. They suggest that Di19 proteins may be potential downstream targets of ABA signaling pathway in plants exposed to abiotic stresses. Thus,

activated Di19 proteins transduce the signals to downstream ABA and stress-responsive genes promoting plant responses to abiotic stresses.

On the other hand, other phytohormones such as gibberellins, ethylene, and auxins, among others, could also contribute, in part, to the development of stress-tolerant cotton plants. Thereby, Lu et al. 2016 found that long noncoding RNAs (lncRNAs) of cotton plants under drought stress showed enriched expression in several pathways of plant hormone signal transduction. In these plants, the content of gibberellins and ethylene increased. This response could be related to an increase in the biosynthesis of proteins and nucleic acid to encourage the use of water in stressful conditions. The content of cytokinins and auxins decreased in some degree because the plants could reduce their energy and growth regulating substances demanded in the mechanism to stress tolerance (Pandey et al. 2003; Lu et al. 2016). However, a deep understanding of phytohormones regulating the drought and heat stress responses would be an important step toward improving cotton plant growth under these stressful conditions.

Accordingly, plants growing under different stress conditions (such as drought and heat, and their combined effect) modify their photosynthesis, fluorescence, chlorophyll content, cell membrane thermostability, and hormonal profile, which could be used as identification criteria for seed cotton production (Azhar et al. 2009); specifically, the relative cell injury rate in cotton could be used to determine heat tolerance criteria (Zhang et al. 2014).

Under high temperatures, plant growth is reduced by affecting the shoot net assimilation rates, finally decreasing the total dry weight of the plant (Wahid et al. 2007). Whereas, different injuries such as scorching of leaves and stems, leaf abscission and senescence, shoot and root growth inhibition, or fruit damage occur when the crop is exposed to high-temperature stress, resulting in decreased crop yield (Vollenweider and Günthardt-Goerg 2005).

Whereas, under heat stress condition, the membrane structure is altered for improving permeability and electrolyte leakage increases eventually, as a result, causing the cell death (Azhar et al. 2009; Saifullah et al. 2015). Heat stress also directly influences the leakage of fluids from the cells, which showed higher value in the leaf of heat-sensitive crop cultivars (Singh et al. 2007; Cottee et al. 2010). However, the drought stress leads to an increase in electrolyte leakage in plant leaves (Sibet and Birol 2007). The cell membrane stability index was found to be higher in tolerant genotypes than susceptible genotypes under drought stress conditions (Collado et al. 2010).

Relative water content (RWC) is an indicator for the amount of water present in the leaf tissue, and it is highly correlated with water deficit tolerance of a genotype (Silva et al. 2007; Colom and Vazzana 2003). The high RWC under drought stress conditions would be preferable to maintain the water balance. Therefore, the higher RWC in leaf might be a selection criterion to breed plants tolerant to drought stress (Rahman et al. 2000).

Although, photosynthesis is a very sensitive process for growth and development of plant under stress conditions, it is not practical for identification of a great number of genotypes for heat stress tolerance (Burke 2007; Bibi et al. 2008; Karademir et al. 2012). Generally, plants try to change their architecture and hypocotyls and petioles

elongate resembling the morphological responses of shade avoidance to survive under heat stress condition (Hua 2009; Tian et al. 2009); change in cellular structures, organelles, and the cytoskeleton, and membrane functions (Weis and Berry 1988) and also a decrease in the synthesis of normal proteins and translation of heat shock proteins (Bray et al. 2000). Similarly, the modification of hormonal levels or hormonal signaling pathways and the production of antioxidants and other protective molecules also took place under heat stress condition (Maestri et al. 2002).

Further, chlorophyll '*a*' and chlorophyll '*b*' play a significant role in photosynthetic activity which ultimately improves crop growth and productivity (Taiz and Zieger 2006). Drought stress is a significant factor that affects chlorophyll '*a*', '*b*' total chlorophyll, and *a*/*b* ratio (Hamayun et al. 2010).

30.4   Antioxidant Metabolism of Cotton to Heat and Drought Stress

Plants' resistance to stress resulted in increasing antioxidant activities that face increased levels of ROS (Shao et al. 2008). Meanwhile, antioxidant activities decrease in drought susceptible genotypes and vice versa (Ahmadizadeh et al. 2011). The stress-tolerant genotype has higher phenolic contents than the drought-sensitive genotype (Yildiz-Aktas et al. 2009). Malondialdehyde (MDA) content is estimated as a marker for a degree of lipid peroxidation where the MDA is produced by peroxidation of unsaturated fatty acid on plant cell membrane. Lower MDA level displays higher antioxidative ability, improving the plant tolerance to drought stress (Shao et al. 2008).

Hydrogen peroxide (H_2O_2) is a nonradical reactive oxygen species (ROS), produced by normal aerobic metabolism in plants. At low concentrations, H_2O_2 acts as a signal molecule involved in the regulation of specific biological/physiological processes such as photosynthetic functions, cell cycle, growth and development, plant responses to biotic and abiotic stresses. While, excess H_2O_2 accumulation causes the eventual cell death in plants through oxidative stress (Sofo et al. 2015).

While, an increase in proline content in drought, heat, and salinity stresses is an adaptive mechanism for a plant to survive under stress condition (Mattioni et al. 1997). Proline accumulation in plant cells exposed to stress is often considered to be involved in stress resistance mechanisms (Chen and Gallie 2004). They reported similar results for drought-tolerant genotypes. The proline accumulation in tolerant genotypes could be explained by increasing biosynthesis or inhibition of proline degradation under stress conditions.

Ahmadizadeh et al. (2011) reported that the tolerance of plants to stress such as drought and heat stress resulted in increasing antioxidant activities, which face increased levels of free radicals. Whereas Saneoka et al. (2004) noticed that increased levels of free radicals during the stress condition damage the membrane polar lipids. Plants that are susceptible to drought face oxidative stress that produces an increased level of lipid peroxidation in the plants.

Plant enzymatic defenses are found to minimize cellular damage caused by reactive oxygen species during environmental stresses (Racchi 2013; You and Chan 2015). Enzymatic activities are essential to restrict oxidative injury and destroying active oxygen species (Shao et al. 2008; Jaleel et al. 2009). Therefore, identification of nonenzymatic and enzymatic systems may be correlated with stress conditions and could be used as indicators of stress tolerance. The nonenzymatic antioxidants (proline) and enzymatic antioxidants are synthesized to minimize cellular damage caused by reactive oxygen species (ROS), such as superoxide, perhydroxy radicals, hydrogen peroxide, and hydroxyl radicals (Khatun et al. 2008). Water deficit conditions generate reactive oxygen species, consequently, H_2O_2 is produced in the chloroplasts and mitochondria of stressed cells causing cell damage (Foyer and Harbinson 1994).

However, it is essential to understand the biochemical mechanisms for the selection of crops that are tolerant to heat and drought stress (Ullah et al. 2017). Similarly, identification of nonenzymatic and enzymatic systems may also be associated with stress and could be used as indicators for identification of stress tolerance in plant. On the other hand, understanding the correlation between antioxidant activities and yield attributes could also be helpful to develop an efficient screening method to select large amounts of plant materials within the shortest time (Bita and Gerats 2013). Therefore, the integration of conventional breeding with the antioxidants as screening criteria offers new opportunities for improving stress tolerance in cotton.

30.5 The Agronomical Response of Cotton to Heat and Drought Stress

Environmental stresses cause a wide range of physiological and biochemical modifications that harmfully affect the growth and productivity of cotton. Heat stress is the major factor of abiotic stress, affecting cotton productivity. High temperature adversely affects the agronomic traits through shortening the crop growth period (Khan et al. 2008). Similarly, it also affects the shoot development and flowering (Saifullah et al. 2015). Consequently, identifying cotton genotypes with high degree temperature tolerance would be favorable in both present and future climates (Kakani et al. 2005; Soomro et al. 2001).

The reduction in seed cotton yield occurs due to the decrease in a number of bolls and boll weight under drought stress (Basal et al. 2009). Drought stress influences the lint quality of cotton in various ways, especially during the fiber elongation period, which results in a reduction in fiber length and produces immature fiber (Mert 2005).

For the development of drought and heat tolerance in adapted genotypes through conventional breeding approach, availability of an efficient and reliable technique could be helpful to identify a huge number of varieties/lines. Selection of cotton genotypes, which survive and produce better yield in stress, has greater scope in breeding programs. Thus, there is a need for a protocol to determine the stress tolerance of cotton germplasm.

30.6   Correlations Between Growth Traits and Yield Attributes

It is important to establish a protocol to produce new opportunities to improve heat and drought tolerance in cotton. By understanding the correlation between yield and physiological traits as well as nonenzymatic and enzymatic antioxidant activities, we can develop an efficient screening method that could be able to screen a large number of plant materials in the shortest time. Physiological operations affecting cotton performance and their correlation with high-temperature stress were previously observed. For example, there was a strong positive relation between photosynthesis and high temperature (Schrader et al. 2004).

Under drought treatment, correlation analyses revealed that yield was positively and significantly correlated with all studied antioxidants (except lipid peroxidation, which was negatively and significantly correlated). Maximum correlation values were recorded by superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and phenolic content. This is in agreement with those of Ali et al. (2007). A significant association between seed cotton yield and fluorescence was observed on cotton genotypes, and chlorophyll fluorescence was assumed to be one of the practical implements to develop seed cotton yield in huge breeding experiments (Karademir et al. 2012).

30.7   Genotype Selection by the Resistance/Tolerance Indices

Stress tolerance selection is the main interest of cotton specialists. Khalili et al. (2012) revealed that geometric mean productivity (GMP), mean productivity (MP), and stress tolerance index (STI) were positively associated with stress yield. STI and GMP indices, which produced the maximum association with yield under both control and stress conditions, might be used as the superior indices for the programs of breeding to produce drought resistance genotypes (Jafari et al. 2009).

Heat susceptibility index (HSI) is one of the important selections that estimate stress tolerance in genotype on the basis of yield reduction under stress condition in comparison with a favorable environment (Abro et al. 2015). The HSI values <0.5, >0.5 <l.0, and >1.0 represent the highly tolerant, moderately tolerant, and susceptible, respectively (Fischer and Maurer 1978). While, the higher-ranking genotypes for heat tolerance achieved the least values of heat susceptibility index (HSI<1) and high production under stress condition (Saifullah et al. 2015). But for cotton, Ekinci et al. (2017) reported that cotton genotypes of high HSI value were high seed cotton yielding and their attributes under normal conditions, thus these traits were much more sensitive to high temperature.

Other selection indicators, like chlorophyll stability index (CSI), are the ratio between total chlorophyll under drought to total chlorophyll under normal irrigation. While high CSI is an indicator of drought tolerance. Patil et al. (2011) revealed that CSI was greater in drought resistance genotypes compared to susceptible genotypes. Effective identification technique must assess plant performance at critical developmental stages (Johnson 1980).

## 30.8   Strategies to Induce Heat and Drought Tolerance in Cotton

Oxidative damage normally occurs in plants facing abiotic stresses by the formation of ROS. These ROS pose a serious threat to cell functioning by damaging lipids and proteins (Fahad et al. 2017). Osmoprotectants could be used to enhance crop tolerance against environmental stresses. Osmoprotectants elevated osmotic adjustment to improve turgor pressure and developed an accumulation of antioxidants to detoxify ROS, thus sustaining the enzymes and other macromolecules under environmental stresses (Anjum et al. 2011; Ullah et al. 2017). Osmoregulatory compounds are protecting plants by osmotic adjustment, maintaining membrane integrity, protecting macromolecular structure and acceleration of reactive oxygen species scavenging systems (Rontein et al. 2002; Hayat et al. 2012). In addition, genes involved in osmoprotectant biosynthesis are upregulated under osmotic stress, and the concentration of accumulated osmoprotectants correlates with osmotic stress tolerance (Rontein et al. 2002).

Application of proline causes improvement in its endogenous rates in plant tissues treated with water stress conditions and promotes plant tolerance (Ashraf and Foolad 2007). Proline at optimum level has different roles such as osmoprotectant, in turgor generation, in carbon and nitrogen storage, in maintenance of protein structure, in maintenance of cytosolic pH, in the balance of redox status, by acting as a part of stress signal, an inhibitor of lipid membrane peroxidation, and antioxidant as significant quencher of ROS formed in plants under stress conditions (Ashraf and Foolad 2007; Hayat et al. 2012).

Application of different osmoregulators such as glycine betaine (GB) or proline had a significant role in plant growth promotion and seed yield under normal or stress conditions as observed in canola (EL Sabagh et al. 2019a) and soybean (EL Sabagh et al. 2019b). GB is the most well-known quaternary ammonium compound in higher plants that induced and endogenously synthesized in the chloroplasts in response to various abiotic stresses such as drought (Silva et al. 2011) and oxidative stresses (Liu et al. 2011) in many crops and its concentration correlated with the level of tolerance. Raza et al. (2014) stated that interaction between GB at 100 mM and potassium (K) at 1.5% is the best strategy to ameliorate the drought impact on wheat grain yield.

Salicylic acid (SA) is a phytohormone, and it may be a potential growth regulator for improving plant growth under limited water availability (Kobeasy et al. 2011). In addition, it is reported that SA significantly induced the thermotolerance in plants (Hayat et al. 2009). SA sprayed on cotton plants exposed to high temperatures decreased the membrane oxidative damage and increased antioxidative systems (Wang and Li 2006). Therefore, SA can improve plant adaptation to stressful conditions by mechanisms such as increasing antioxidative protection (Xu and Tian 2008), lessening photosynthetic damage (Arfan et al. 2007), and accumulating specific tolerance compounds (Poór et al. 2013).

Ascorbic acid (AA) has useful effects on crops under stress conditions. It has an antioxidative function in plant scavenging the ROS and enhancing crop productivity (Kamal et al. 2017). The performance of ascorbic acid as a vital molecule antioxidant included to ameliorate stress has been well documented in the literature, the latter
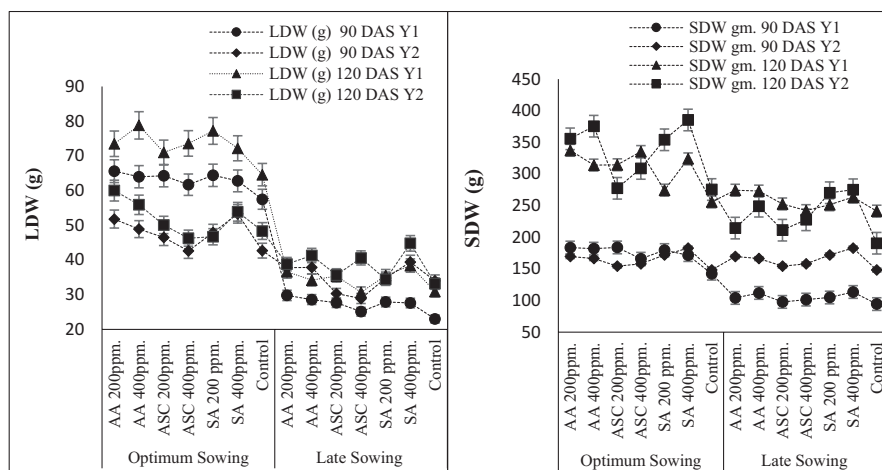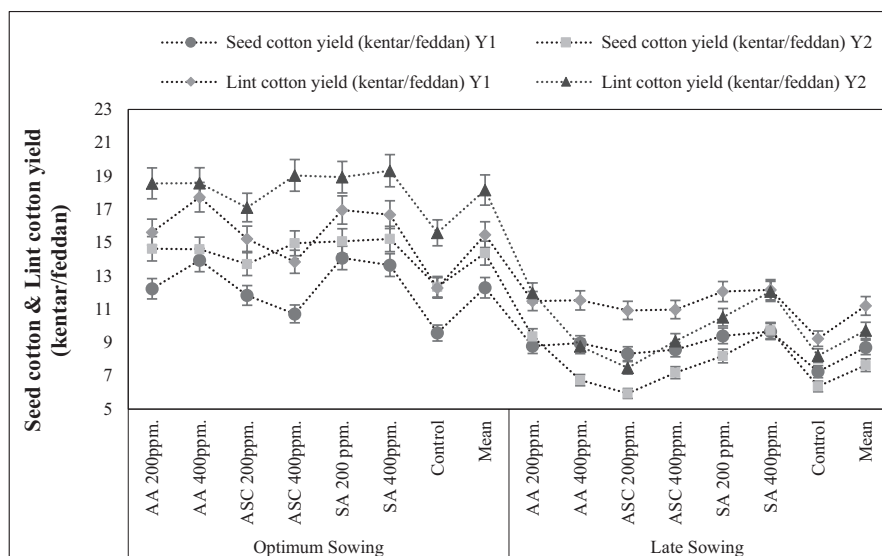
Fig. 30.2 Leaves (LDW) and stem dry weight (SDW; g) of cotton variety "Giza 94" influenced by the foliar application of ascorbic, ascobine, and salicylic acids through alleviating negative effect of late sown heat stress (*AA* Ascorbic Acid, *ASC* Ascobine and *SA* Salicylic Acid)

research revealed that it also participated in the detoxification of produced reactive oxygen species due to environmental stresses (Dolatabadian et al. 2009).

Silicon is an important trace element and its presence is necessary to induce resistance to distinct stresses, diseases, and pathogens of plants. The addition of silicon dioxide (SiO_2) to plant medium reduces the penetrability of the plasma wall of the leaf cells resulting in the loss of lipid peroxidation and also, SiO_2 protects the cell wall against heat and drought stress (Zhu et al. 2004). Application of nano-Si caused a significant increase in the activities of catalase and peroxidase (POD) in plant leaves, but caused a decrease in the activities of superoxide dismutase and glutathione reductase (GR) (Kalteh et al. 2014).

Two-year results of El-Okkiah (2017) showed that the optimum sowing date gave the largest area of a single leaf area (SLA) as well as the tallest plant (plant height (PH)) at 90 and 120 DAS (days after sowing) (Fig. 30.2). The optimum sowing date also induced an increase in stem and its organs' dry weight (g) at 120 DAS. While the late sowing significantly reduced the leaves and stem dry weight recorded at 90 and 120 DAS in both the years (Fig. 30.2) (El-Okkiah 2017).

Both the seed cotton (SCY) and lint yield (LCY) were significantly increased in optimum sowing condition and sharply declined as sowing date was delayed (Fig. 30.3). However, there is no constanting effect on fiber properties by sowing dates. Also, sowing dates had no significant effect on both oil and protein seed content. Accordingly, organic compounds, viz., ascorbic acid and salicylic acid, exhibited an improvement in growth and productivity of cotton crop in late sowing, compensated the reduction that occurred in any character, and overcame the adverse effect by mitigating the harmful effect of the late sowing (heat stress) cotton.

Fig. 30.3 Seed cotton and lint cotton yield (kentar/feddan) of cotton "Giza94" influenced by the foliar application of ascorbic, ascobine, and salicylic acids through alleviating negative effect of late sown heat stress (*AA* Ascorbic Acid, *ASC* Ascobine and *SA* Salicylic Acid). (Adapted from El-Okkiah 2017)

30.9   Summary and Conclusion

Drought and heat are the major environmental stresses that affect the growth, productivity, and quality of cotton plants. The better knowledge of antioxidant mechanism and physiological responses of plant stress tolerance will contribute to understanding the agronomic performances for genetic nature of tolerance of potential cotton genotypes. The present review highlighted the several management strategies that could be useful to mitigate the drought and heat stress by using antioxidant, phytohormone, and nutrient management as well as other appropriate management strategies for sustainable cotton production under changing climate. While, among the compatible antioxidants, exogenous application of proline or glycine betaine is a good option to improve drought and heat tolerance in cotton. The study revealed that the foliar application of antioxidants in combination with soil-applied organic fertilizers is very effective for reducing the adverse effect of drought and heat stress on growth and yield of cotton.

Conflict of Interest The authors declare that there is no conflict of interest regarding the publication of this work.

Disclaimer We hereby declare that the review contains no materials which have been accepted for the award of any degree or diploma in any university/institute. To the best of our knowledge and belief, the manuscript contains no copy of any material previously published or written by another person except where due reference is made in the text.

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Adverse Effect of Drought on Quality of Major Cereal Crops: Implications and Their Possible Mitigation Strategies

31

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Abstract

Cereal crops are the major contributors to the global dietary intake of nutrients, and therefore, grain quality is an important trait for crop improvement. Grain quality in cereals is strongly influenced by genotype and environmental factors. Drought stress alone significantly reduces grain yield and quality of cereal crops worldwide. The present paper discusses the impact of drought on qualitative traits of cereal

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crops and suggests strategies to enhance grain quality. Drought significantly affects the nutritional properties and quality traits of crops by modifying morphological, physiological, and biochemical traits in plants. This understanding may help plant breeders in developing drought-tolerant varieties while maintaining the desired quality characteristics. Various management techniques have been suggested to enhance grain quality of crops under harsh environments. Among those, exogenous application of potential osmoprotectants (OSP) alone or in combination with soil organic amendments is a promising approach to alleviate drought stress and could be helpful in ameliorating the harmful effects of drought stresses on crop quality.

Abbreviations

ABA   Abscisic acid
AC   Ash content
AsA   Ascorbic acid
AY   Ash yield

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chl *a*   Chlorophyll *a*
chl *b*   Chlorophyll *b*
CI   Conventional irrigation
DSI   Drought stress index
DW   Dry weight
Fe   Iron
FW   Fresh weight
FYM   Farm yard manure
GB   Glycinebetaine
GW   Grain weight
GY   Grain yield
MDA   Malondialdehyde
OSP   Osmoprotectants
OY   Oil yield
PAL   Phenylalanine ammonia lyase
PC   Protein content
POD   Peroxidase
Pro   Proline
RLWC   Relative leaf water content
ROS   Reactive oxygen species
RWC   Relative water content
SA   Salicylic acid
SC   Starch content
Se   Selenium
SI   Supplemental irrigation
SOD   Superoxide dismutase
SY   Starch yield
Tre   Trehalose
TW   Test weight
UV   Ultraviolet radiation
Zn   Zinc

31.1   Introduction

Food security may become a more vulnerable issue as compared to the past due to global climate change and increased uncertainties in weather patterns (FAO 2016). Change in climate is mainly attributed to the unrestricted increase in greenhouse gases that bring changes in rainfall pattern, temperature, and drought (Ali et al. 2017). Li et al. (2011) reported that approximately 25% of the global agricultural land is affected by drought that enforces to limit more than 50% average yield and quality of most major crops in many countries (Wang et al. 2007; Dabiry et al. 2015), especially in arid and semiarid regions (Rajala et al. 2009; Shiri et al. 2010).

The occurrence, severity, and duration of drought distressing the crop productivity which are associated with global climate changes, consequently, the question arises how best to address the ever-increasing demand for quality grain and ensuring food security (Ashraf 2010). It is challenging not only for farmers and governments to meet these demands but also for researchers and plant breeders to address the issue (Gous and Fox 2017). Numerous studies have discussed the impact of abiotic stresses on grain yield (GY), starch (SC), and protein content (PC) (Hakim et al. 2012; EL Sabagh et al. 2018a, b).

Drought is one of the serious abiotic stresses that inhibit nutrient uptake by arresting root development and consequently influences grain yield (Bagci et al. 2007). It causes a major loss in cereal yield and quality in most of the cereal-growing areas throughout the world (Akanda 2010; Bagci et al. 2007; Passioura 2007). Depending on the species and geographical location, drought occurring at vegetative and reproductive phase has a negative effect on crop life. Drought at vegetative phase affects shoot apical and may render stunted growth, at reproductive phase, it may deteriorate crop quality and yield. Drought during floral initiation and development of inflorescence delays flowering (Winkel et al. 1997; Wopereis et al. 1996). Final grain yield and quality are the results of interaction between genotypic potential and the environmental conditions, which are modified by different agronomic management (Mariani and Ferrante 2017). Protein and starch are arguably the most important components of the grain quality and contribute considerably to its nutritional and commercial value (Gous et al. 2015).

Crop quality is considered as one of the most essential dietary components in human as well as animal feed, which strongly varies with crop cultivars as well as growing conditions. Therefore, maintenance of nutritional quality in crops may offer good opportunity to provide quality human food as well as animal feeding under stressed environments. Adverse environmental conditions during critical growth phases, such as anthesis and grain-filling period, have been identified as a major constraint to crop productivity and grain quality (Jiang et al. 2009).

Recently, attention has been drawn to examine the various effects of drought stress on grain quality of cereal crops, as well as stress mitigating strategies as the possible role of exogenous application of osmoprotectants (OSP) (i.e., proline (Pro), glycinebetaine (GB), trehalose (Tre)) with organic fertilizer in the provision of drought tolerance in plants against drought stress conditions (Ali and Ashraf 2011). However, limited information is available on the relative importance of their interaction with genotype and environment on grain quality (Rharrabti et al. 2003). Therefore, evaluation of grain quality of crops under drought and further understanding of the current status of crop quality and to clarify their interaction on major quality traits is of prime importance. It is also essential to assess the degree of Exo-application of osmoprotectants that could alter seed/grain quality of crops under environmental stress conditions.

31.2   Adverse Effect of Drought on the Quality of Crops

Drought stress is a major factor that affects yield and grain quality of wheat during grain developmental stage (Ahmed and Fayyaz-ul-Hassan 2015). Grain yield and quality of a crop depend on the frequency and severity of extreme climatic events (Thornton et al. 2014). Among the crop growth stages, the reproductive stage is considered most sensitive to drought (Alqudah et al. 2010). Negative effects of drought on seed quality have been well documented in wheat (Balla et al. 2011) and many other crops. Drought shortens the time of anthesis or grain filling in cereal crops such as maize, wheat, barley, and rice leading to reduced seed size and poor grain quality (Estrada-Campuzano et al. 2008; Fahad et al. 2017).

31.2.1 Adverse Effect of Drought on Grain Yield and Quality of Major Cereals

31.2.1.1   Maize (*Zea mays* L.)

Maize is an important cereal crop that requires ample water supply and is sensitive to drought and hence growth is negatively affected by the scarcity of water (Byrne et al. 1995; EL Sabagh et al. 2018a, b). Storage components of the mature kernel of maize (starch, protein, and oil content) are the major determinants of the final grain weight (GW) (Boyer and Hannah 2001). Drought has been reported to reduce grain starch, granule size and increase relative protein content in maize (Balla et al. 2011). According to Zhao et al. (2009), maize protein is very sensitive to drought stress during grain-filling stage. While Rehman et al. (2011) reported that grain protein, oil, and starch content of maize are generally stable in different environments. Similarly, EL Sabagh et al. (2017, 2018a, b) opined that water deficit stress remarkably influenced maize productivity.

Barutcular et al. (2016a) reported that drought significantly reduced soil, starch, protein, and ash contents in maize (Table 31.1). Gooding et al. (2003) pointed out that variations in flour quality were related to the changes in protein structure from drought stress throughout grain-filling stage. Similarly, Ghassemi-Golezani and Dalil (2011) also reported that seed protein and oil yields of maize were decreased significantly under drought condition, due to a sharp decline in the grain-filling period (Ghassemi-Golezani and Lotfi 2013).

Drought has also been shown to cause a small reduction in total protein content in maize cultivars (Ali et al. 2011; Barutcular et al. 2016a, b). It seems that initial increase in total soluble proteins during drought stress is associated with the expression of new stress proteins, but the decrease was due to a severe reduction of photosynthesis (Mohammadkhani and Heidari 2008). Drought decreases carbon assimilation (Havaux et al. 1987) and protein synthesis. The dwindling of total soluble proteins under drought stress was consistent with the findings of Riccardi et al. (1998) and Ti-da et al. (2006) in maize.

Table 31.1 Irrigation regimes effect on grain quality parameters of maize hybrids in the growing seasons of 2014 and 2015

Treatments	GW (mg)	TW (kg hl⁻¹)	SC (%)	PC (%)	OC (%)	AC (%)	SY (kg ha⁻¹)	PY (kg ha⁻¹)	OY (kgha⁻¹)	AY (kg ha⁻¹)
Irrigated (control)	292	72.2	64.0	8.05	2.63	1.07	9159	1150	376	152
Deficit irrigated	275	72.0	64.1	8.09	2.60	1.05	8069	1020	328	133
Reduction	−0.06	0.00	0.00	0.01	−0.01	−0.01	−0.12	−0.11	−0.13	−0.13
Probability level	*	Ns	Ns	Ns	Ns	Ns	**	**	*	*

Adapted from Barutcular et al. (2016a)

ns Indicates nonsignificant. *GW* grain weight, *TW* test weight, *SC* starch content (%), *PC* protein content (%), *OC* oil content (%), *AC* ash content (%), *SY* starch yield (kg/ha), *PY* protein yield (kg/ha), *OY* oil yield (kg/ha), and *AY* ash yield (kg/ha)

*, **, and ***, significant $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$ probability, respectively

31.2.1.2 Wheat (*Triticum aestivum* L.)

Wheat is a major cereal crop that contributes more calories and protein to the world diet than any other cereal crop (Abd-El Haleem et al. 2009). Water deficit (drought) at grain filling shortens grain-filling duration in wheat and ultimately reduces grain number and size (Gooding et al. 2003; Barutcular et al. 2017). Flour quality is comprised of attributes such as gluten, glutenin, gliadin, and protein. Drought has been reported to significantly reduce this grain quality train (Eivazi et al. 2006). Protein composition of grain plays a key role in determining the quality of wheat for bread-making, which has been deteriorating due to increasing drought (Mikhaylenko et al. 2000). The protein contents and baking quality of wheat grain mainly depend on the genetic as well as environmental factors, and drought stress during grain filling greatly affects grain quality (Luo et al. 2000; Rharrabti et al. 2001). Gooding et al. (2003) noted that if wheat plants face drought during grain filling, flour quality diminishes due to deteriorated protein composition of grain. Similarly, drought also reduces the test weight (TW) of wheat through decreasing carbohydrate (starch), protein, and other mineral content of wheat (Pierre et al. 2008). Barutcular et al. (2016c) found that grain weight, protein, starch, test weight, Zeleny test, dry gluten, gluten index, and grain flour content of 16 bread wheat genotypes were significantly decreased under water deficit conditions (Table 31.2).

Starch accumulation has a direct relationship with sucrose content in wheat grains (Yan et al. 2008). Reduction in grain starch leads to low sucrose content and enzyme activity associated with starch synthesis. Environmental factors, especially drought, play a significant role in starch accumulation (Bhullar and Jenner 2005). Water stress has a significant effect on B-starch granules per endosperm and decreases its contents and reduces the size of the largest A-starch granules, while the number of A-starch granules remained unaffected by drought (Brooks et al. 1982).

Guttieri et al. (2001) found that drought at grain filling increased protein and sedimentation volume of wheat but reduced grain yield, 1000-grain weight (Aslani et al. 2013). Similarly, Noorka and Teixeira da Silva (2012) noticed that under water stress, the ranges of protein content varied from 12.47% to 13.92%, while under

Table 31.2 Performance of studied traits for 16 bread wheat genotypes under two irrigation regimes

Water regime	GW (mg)	GPC (%)	GSC (%)	TW (kg/hl)	ZT (ml)	DG (%)	GI (%)	GFC (%)
Rainfed (drought)	24.3	18.1	60.7	76.3	32.3	14.2	86.3	44.9
Irrigated	35.3	15.2	63.8	83.4	31.7	12.9	85.5	49.5
Drought effect (%)	−45.3	16	−5.1	−9.3	1.9	9.2	0.9	−10.2
Probability levels	**	**	**	**	NS	**	NS	**

Adapted from Barutcular et al. (2016c)

ns nonsignificant. *GW* grain weight, *GPC* grain protein content, *GSC* grain starch content, *TW* test weight, *ZT* Zeleny test, *DG* dry gluten, *GI* gluten index, *GFC* grain flour content

** is significant at 0.01 probability level

well-irrigated condition these values varied from 11.20% to 13.78%. Both the studies indicated that drought increased the grain protein quality, where 1000-grain weight decreased.

Hammad and Ali (2014) observed a significant reduction in total protein and carbohydrates and a gradual increment in total fibers in wheat grains under severe drought conditions. On the other hand, moderate drought during grain filling was found to increase grain protein content, although a slight decrease in grain yield was also observed in wheat (Rezaei et al. 2010). Balla et al. (2011) showed that drought causes a disproportionate reduction in the glutenin fraction compared with gliad in fraction in wheat grain. Ali et al. (2010) showed that drought stress conditions not only cause a reduction in grain oil content by 40% but also cause oleic acid to increase to >25% of the total at the expense of linoleic acid.

Drought significantly reduces the grain nutrients such as nitrogen (N), potassium (K), calcium (Ca^{2+}), manganese (Mn), and zinc (Zn) contents of wheat as compared to the well-watered condition (Naeem et al. 2018). In drought treatment, grain macro- (N, K, Ca) and micronutrient (Zn, Mn) contents decreased considerably as compared to well-watered conditions, indicating that nutrient uptake was restricted under drought conditions that might be due to declined transpiration rate, reduced active transport, and lowered membrane permeability (Naeem et al. 2017).

31.2.1.3 Barley (*Hordeum vulgare* L.)

Drought is a major factor that contributes to grain quality as well as feed quality, such as dry matter digestibility, protein, starch, different minerals, and fiber content, etc., in barley (Gous et al. 2012). Similarly, 1000-grain weight, which is also a determining character for grain yield and product quality of barley, is affected by drought stress (Prokesova et al. 2016). El-Shawy et al. (2017) recorded the adverse effect of drought on grain weight of different barley genotypes (Fig. 31.1). A significant reduction in the grain yield of barley under drought conditions occurs mainly due to fewer fertile tillers which resulted in poor grain formation and reduced 1000-grain weight (Samarah 2005).
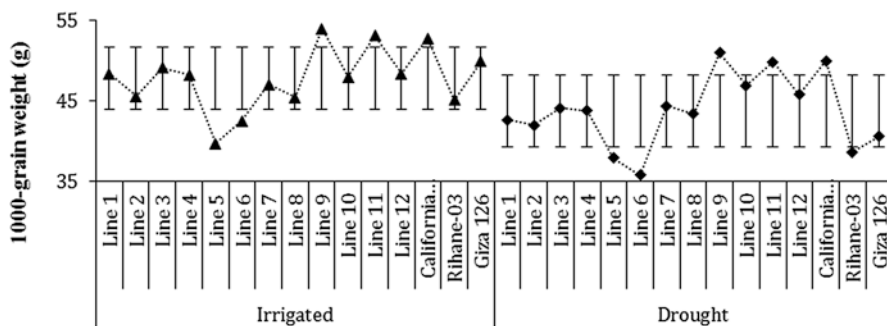
Fig. 31.1 Thousand-grain weight of 15 barley genotypes grown under two water regimes. (Adapted from El-Shawy et al. 2017)

Barley quality parameters such as grain size, weight, starch content, extraction potential, and malt quality have industrial values (Newman and Newman 2008). Drought increases the protein content but reduces the starch content (SC) in barley grain (Ahmed et al. 2012). These parameters varied with genotypes, but the effect of the growing environment has a great impact on these quality parameters (Psota and Kosar 2002).

Abiotic stress like drought can negatively impact grain content and quality by affecting starch biosynthesis, resulting in structural changes in starch (Hollmann et al. 2014). These structural changes may affect starch properties, which may make the grainless suitable for downstream quality-driven industries such as malting and brewing (Hollmann et al. 2014).

When barley crop is subjected to water stress after anthesis, a reduction in grain weight is observed though the protein content increases (Wu et al. 2017). On the other hand, total protein content in barley grains is generally increased under drought or heat stress (Qi et al. 2006).

31.2.1.4 Rice (*Oryza sativa* L.)

It is generally recognized that rice quality is determined both genetically and environmentally (Krishnan and Rao 2005). A proportion of 50% of head rice is generally usable, since its other 50% is wasted as husk and bran after milling (Bleoussi et al. 2016). About 13% (156 million ha) rice is cultivated as rainfed under upland conditions in the globe where moisture stress affects its growth, yield, and quality (Carlos et al. 2008).

Drought might be a major factor for the gap in producing enough quantity of rice as well as grain quality (Tomlins et al. 2005). It reduces the production of rice, through changing morphological, physiological, biochemical, and molecular characteristics (Al-Ashkar et al. 2016). Carlos et al. (2008) also reported that soil moisture stress caused a reduction in grain weight and quality. The influence of water deficit on rice quality could be variable for upland and lowland rice cultivars (Cheng et al. 2003), depending on genetic makeup and their growing environmental conditions (Krishnan and Rao 2005; Pandey et al. 2014). The occurrence of soil moisture stress at the grain-filling stage affects several physiological, biochemical, and enzymatic activities, resulting in poor quality of rice (Samonte et al. 2001). Similarly, Bleoussi et al. (2016) also found that water deficit during the reproductive stage of rice reduced the market quality of rice due to less swelling as well as stickiness. Anis et al. (2016) revealed highly significant differences existed among the tested rice genotypes (Fig. 31.2). The hulling percentage of rice could be attributed due to the genetic makeup of the specific rice genotype (Anis et al. 2016). Pandey et al. (2014) reported that protein content in rice grain was associated with head rice ratio, milled grain dimensions, milled grain appearance, and viscosity parameters. Although hamylose content of rice grain was decreased under drought, there was a passive link between amylose and protein content of rice grain under water stress.

Drought increases the total protein content in rice grain (Fofana et al. 2010). The dramatic influence of soil water status on grain quality of rice was observed during the grain-filling period (Dingkuhn and Gal 1996). The milled rice recovery and the
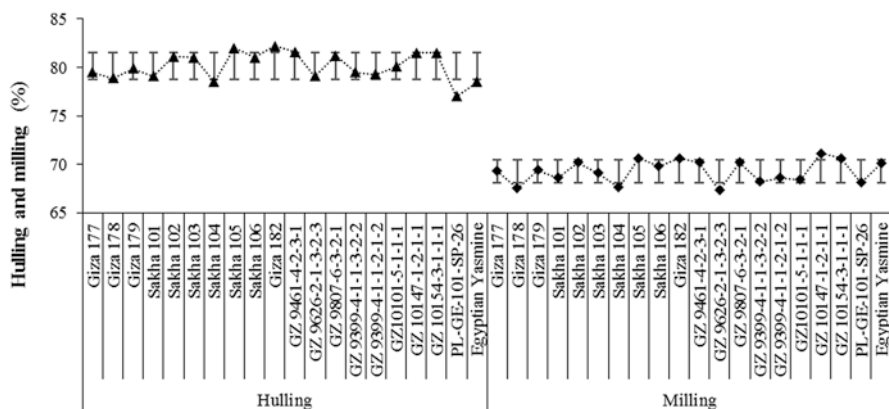
Fig. 31.2 Mean performance of hulling and milling values of rice genotypes during 2014 and 2015 (combined data). Bars indicate standard errors. (Adapted from Anis et al. 2016)

brown rice protein content significantly increased due to reduced soil moisture content, but the percentage of unripened grains was decreased, meanwhile, the amylose content in milled rice was decreased under water deficit conditions (Renmin and Yuanshu 1989).

Drought affects plant growth and reduces grain yield and quality of rice (Carlos et al. 2008). The occurrence of soil moisture stress affects many of the physiological processes such as photosynthesis and transpiration resulting in reduced growth and poor grain filling in rice (Samonte et al. 2001). Therefore, soil moisture stress appears to be a major factor for the gap in producing enough quantity as well as grain quality of rice (Tomlins et al. 2005). Drought-induced reduction in crop yield might be the possible reason for several factors including reduced photosynthesis (Flexas et al. 2004), less partitioning of assimilates (Farooq et al. 2009) as well poor flag leaf development (Rucker et al. 1995). Drought treatment affected the photosynthesis process, which altered carbohydrate formation and its translocation to seeds. In the end, the lack of carbohydrate caused more seeds not to be fully formed or to become unfilled grains (Jaleel et al. 2009). The occurrence of water deficit during grain ripening stage can be considered as a factor that increases grain quality as preferred by the local consumer because of a lower rate of broken grains (Sakurai et al. 2006). Late drought that occurs during ripening appears to increase the main characteristics defining rice grain quality including total milling rate, head rice ratio, and protein content of rice (Fofana et al. 2010).

31.3 Management Strategies

Abiotic stresses such as salinity, heavy metals, cold, heat, light, drought, flood, UV, hypoxia, etc. are the major threat to a plant through adversely affecting growth and development, finally the end product of target crops by altering physiological and biochemical processes of the plant. Abiotic change can not only hamper plants' growth and development but also reduce crop yield which can in a broad sense

promote famine and other calamities. Therefore, it is a global concern to manage abiotic stresses as their severity is increasing due to global changing climate. As a part of evolution, plants build a complex and integrated self-defense mechanism against stressful condition by changing morphological, physiological, biochemical, and molecular level to adapt as well as to survive. The extreme climate change over the world sometimes constructs its extreme challenges to grow tolerance against abiotic stress conditions.

31.3.1 Management of Drought to Improve the Yield and Quality of Major Cereal Crops

Under extreme environmental stresses (i.e., drought, salinity, heat stress, ultraviolet (UV) radiation, and heavy metals), exogenous application of growth regulators and osmolytes at various crop growth stages plays a significant role in inducing resistance against abiotic stresses including drought (Fahad et al. 2017). The glycinebetaine (GB) and proline (Pro) are two major organic compatible osmotic solutes that gather in a variety of plant species (Ashraf and Foolad 2007; Farooq et al. 2013; Hossain et al. 2013). These solutes are applied through various approaches such as seed priming (Farooq et al. 2006) and foliar application. Although, many researchers already noted that both GB and Pro have positive roles in mediating the osmotic adjustment to help plants survive under drought stress through influencing the physiological and biochemical activity such as enzymatic and membrane integrity, while their actual roles in plant osmotolerance still remain debatable (Ashraf and Foolad 2007).

31.3.1.1 Maize

Ali et al. (2013) reported that exogenous Pro significantly improved the oil saponification and iodine values, but the oil unsaponifiable matter reduced due to exogenous applied Pro both under normal and drought stress conditions. Similarly, Ali and Ashraf (2011) noticed improved grain yield and oil quality of maize under normal and water deficit conditions by applying Pro and GB.

However, there is a significant association between the total phenolics, carotenoids and antioxidant activity has been recorded in cereals (Dykes and Rooney 2007). While, foliar application of osmolytes, such as GB and Pro, alters chemical composition in seeds such as fatty acids, tocopherols, carotenoids, phenolics, and flavonoids, particularly in the seed oil of maize (Ali et al. 2013). In their other studies, a significant relationship was observed in seed oil antioxidant activity and different lipophilic antioxidant compounds in maize under water deficit condition, due to exogenous application of different compatible osmolytes (Ali et al. 2010; Ali and Ashraf 2011).

Similar to other organic osmoprotectants (OSP), application of abscisic acid (ABA) and yeast significantly improved protein and oil of maize under water deficit conditions (Abdelaal et al. 2017; Figs. 31.3 and 31.4). The valuable effects of ABA and yeast on protein, oil, and moisture percentages were associated with the enhancement of chlorophyll concentrations, relative water content, antioxidant, enzymes activity, and reduce lipid peroxidation (Dolatabadian et al. 2009).
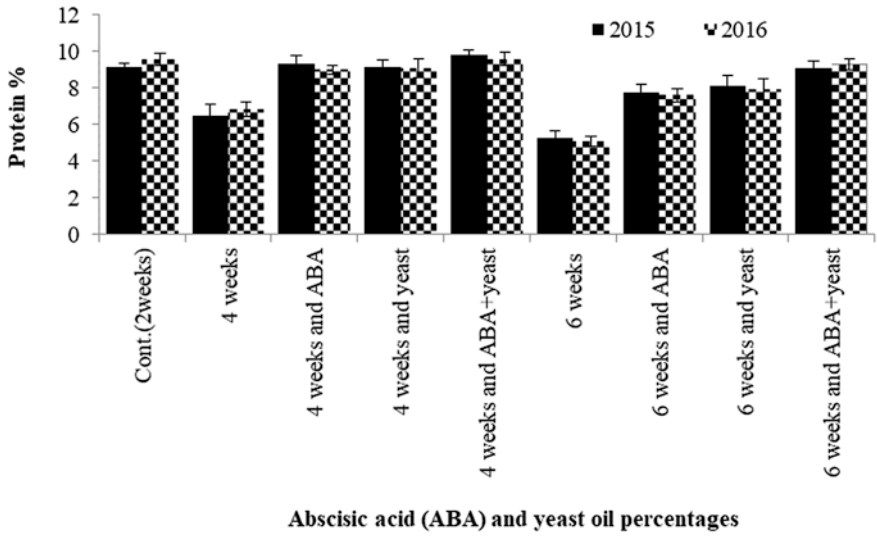
Fig. 31.3 Effect of abscisic acid (ABA) and yeast on protein percentages of maize plants under water deficit conditions during 2015 and 2016 seasons. (Adapted from Abdelaal et al. 2017)
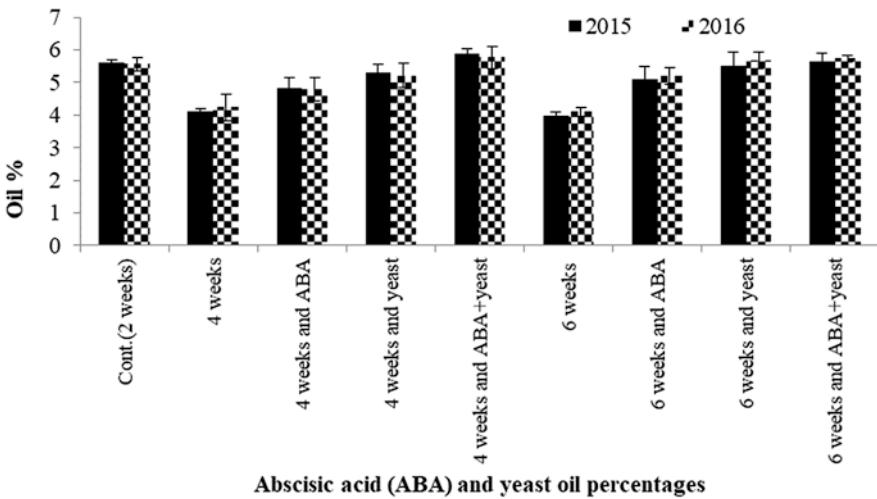
Fig. 31.4 Effect of abscisic acid (ABA) and yeast oil percentages of maize plants under water deficit conditions during 2015 and 2016 seasons. (Adapted from Abdelaal et al. 2017)

The use of proline and gibberellic acid is an innovative and promising way to reduce the impact of drought on maize yield and grain quality (Al-shaheen and Soh 2016). ABA, under drought-regulated protein content in maize plants, may help to elucidate the underlying mechanisms of ABA-enhanced tolerance to drought stress in maize (Zhao et al. 2016).

Exogenous application of salicylic acid (SA) treatment of drought-stressed plants with different levels (0.5 and 1.0 mM) not only caused a decline in the adverse effect of drought in yellow Maize (*Z. mays* L.) plants, but also stimulated physiological traits, productivity by enhancing plant resistance to drought stress (Elgamaal and Maswada 2013). The SA can enhance some physiological processes and can inhibit others depending on its concentration, plant species, developmental stage, and environmental conditions (EI-Mergawi and Abdel-Wahed 2004).

Exogenous treatment of calcium-containing fertilizers (Ca^{2+}) improved tolerance to drought stress (Naeem et al. 2017). Calcium is relatively immobile in plants, and their uptake reduces in above-ground portions of plants (shoots and leaves) as well as in roots under drought conditions due to decline in transpiration rate (Brown et al. 2006).

Under limited irrigation water in the arid regions, application of farm yard manure (FYM) has improved crop water productivity and helps to reduce irrigation water up to 15%. Therefore, application of FYM can be used as a strategy to improve water productivity and grain yield of maize under dry conditions where water is limited (Abd el-wahed et al. 2015). Majid et al. (2017) found that full irrigation is the best treatment to achieve the optimum growth and yield of maize under arid and semiarid regions. They also opined that increasing soil moisture within the root zone during crop growing period through irrigation has a great concern to enhance water use efficiency as well as crop productivity.

31.3.1.2 Wheat

Among the abiotic stresses, drought stress is considered as a major threat that hinders plant growth, grain yield, and quality of crops including wheat (Ashraf and Foolad 2007; Farooq et al. 2013; Hossain et al. 2013). Water stress reduced 30.0% and 13.8% grain yield of wheat as reported by (Barutçular et al. 2017). While, development to tolerant genotypes in relation to different improved management practices such as the foliar application of GB, Pro, and soil applied of organic amendments could ameliorate the adverse effect of drought on yield and grain quality parameters of crops including wheat (Dabiry et al. 2015). This ameliorating effect of exogenous application of Pro altered the seed chemical parameters through maintaining the turgor in plants both under well-watered and water stress conditions, by this means of preserving more photosynthates (Ali et al. 2007), resulting in the dissemination of more assimilates to developing seeds of wheat (Mäkelä et al. 1998).

Nawaz et al. (2015) reported that selenium (Se) seed priming, fertigation, and foliar spray influenced the yield and nutritional quality of wheat under both normal and water deficit conditions through enhancing the production of OSP and improved the antioxidant enzymes activity of wheat. They also found that grain Se, Fe, phosphorus (P), Zn, and magnesium (Mg) contents were significantly decreased when drought stress occurred. Noori et al. (2017) found that NPK

(nitrogen-phosphorus-potassium) fertilizers enhanced the productivity and grain quality such as minerals, crude proteins, and water-soluble pentosane of wheat grain under drought stress through ameliorating the adverse effects of drought.

Under arid and semiarid regions of Mediterranean environment (dry land agricultural system) conventional irrigation (CI), supplemental irrigation (SI) with different sprinkler line-source systems increased the yield and grain quality such as protein content, wet gluten content, and sedimentation volume of wheat variety "Adana 99" during flowering and grain-filling stages of wheat. Among the irrigation systems, CI with full irrigation system achieved the highest grain yield, quality parameters, and maximum net return. They also found that CI with full irrigation system helped to improve the grain quality when higher drought stress occurred in the dry year, indicating that CI full irrigation with different sprinkler line-source systems could be helpful to obtain higher grain yield and good quality under Mediterranean environmental conditions (Alghory and Yazar 2018).

Whereas, Farooq et al. (2006) reported that seed priming (presowing hydration) is an important and short-term approach that helps to initiate the germination metabolism but the emergence of radicle is escaped under drought condition. Ajouri et al. (2004) recorded a 44% increase in the germination of wheat seeds through seed priming under drought conditions. Seed priming with ascorbic acid (AsA) resulted in improved drought resistance of wheat cultivars due to the better accumulation of the Pro through maintaining the tissue water content and membrane stability (Farooq et al. 2013). Whereas, seed priming with potassium chloride improved the performance of some wheat cultivars under drought conditions as reported by Fahad et al. (2017).

Application of yeast extract and amino acids improved wheat grain quality, and yeast extract is superior to amino acids on grain quality (Abbas 2013). Mohamed (2005) found that active dry yeast as the foliar application had a beneficial effect on growth, yield, and chemical constituents of plants.

The cultivation of high-quality winter wheat varieties needs an adequate supply of micronutrients, which act as stimulants for macronutrients, in particular, nitrogen (Potarzycki 2004). The high nitrogen dose can also increase the amount of gluten in wheat grains (Woźniak and Gontarz 2011). Gharib et al. (2016) found that application of N in combination with the foliar application of ascobein increased N use efficiencies and also increased the productivity of wheat under stress condition.

Amino acids for the production of biostimulants are obtained by chemical synthesis, from plant proteins (e.g., algae, corn, and soybean), as well as from animal proteins by chemical or enzymatic hydrolysis (Calvo et al. 2014; Kucińska et al. 2014). Laboratory tests showed that biostimulants led to an increase of technological characteristics of grain-like ash content (AC), zeleny sedimentation index, and content of protein (Popko et al. 2018).

Calcium-applied alleviation of drought-induced damage has been elucidated in numerous plants, for example, *T. aestivum* (Nayyar and Kaushal 2002). Therefore, the foliar fertilization can be an effective approach to improve the nutritive status of plants (Shabbir et al. 2015).

Silicon application lowered down the oxidative damage under water stress through improved membrane stability (Pei et al. 2010) and enhanced production of antioxidants such as glutathione reductase, catalase, peroxidase (POD), and superoxide dismutase (SOD) under water stress conditions in wheat (Gong et al. 2005).

31.3.1.3 Barley

Crop losses due to abiotic stresses may be reduced through applying OSP and soil application of different organic manures and chemical fertilizers (Annicchiarico et al. 2011; Hamail et al. 2015). Among the OSP, GB is accumulated by some plants to survive under stress conditions by altering the physico-biochemical process of plants. Mäkelä et al. (1996) found that application of GB under drought condition increased the above-ground biomass, leaf area index, leaf chlorophyll, yield and quality of barley, oat (*Avena sativa* L.), spring wheat, and summer turnip rape (*Brassica rapa* ssp. *oleifera* DC.) under a greenhouse research. Similarly, Ashraf and Foolad (2007); Farooq et al. (2013); Hossain et al. (2013) reported that exogenous OSP improved the drought resistance in plants through altering the physiological, biochemical, and enzymatic activities of the drought-affected plants. Hussain et al. (2008) also found that the application of GB can help plants to survive under stress condition through improving their physiological process under drought conditions.

Similar to OSP, other studies (Gong et al. 2005; Hattori et al. 2005) also reported that exogenous application of silicon in drought-affected plants, that is, wheat, rice, maize, and sorghum, increased the drought tolerance of plants through improving root growth, stomatal conductance, photosynthetic rate, and antioxidant defense. Barley seeds treated with GB improved the drought tolerance ability by improving cell membrane stability, the rate of photosynthesis, balancing the leaf water status, as well as osmotic adjustment (Wahid and Shabbir 2005).

Fahad et al. (2017) demonstrated that the spraying of growth regulators and OSP at various growth phases played a significant role in inducing the tolerance against drought. While, under drought condition seed Pro is an important technique that influences the germination metabolism of seed through short-term presowing hydration of seeds both under normal and drought but the emergence of radicle is interrupted (Farooq et al. 2006, 2007; Bajwa and Farooq 2016). Similarly, the application of spermidine has also been found beneficial in minimizing the harmful effects of drought in barley (Kubis 2003). Silicon under chromium stress resulted in the stimulation of antioxidants (SOD, POD, and CAT), enzyme activities, improved barley germination and growth (Ali et al. 2013).

Nitrogen fertilizer is applied in order to increase the agronomic yield and improve grain quality (Nowotna et al. 2007). High rates of nitrogen application increase the protein content, especially the hordein component, which is of poor nutritive value when compared with other proteins (Duffus and Cochrane 1993).

31.3.1.4 Rice

Applications of nutrients in rice underwater-stressed conditions improved most of the yield contributing characters. Silicon (Si) is not directly involved in quality enhancement (Wang et al. 2015), but it manages diseases and different environmental stresses

to improve the quality of crops (Shashidhar et al. 2008). Silicon application improved grain diameter in rice plant (Ahmad et al. 2013). Seed priming has proved beneficial in improving early stand establishment of crops under stress conditions (Farooq et al. 2007; Bajwa and Farooq 2016).

Application of compost along with the foliar application of ascobein can be saved from 50 to 110 kg N ha^{-1} without reducing grain quality (Gharieb et al. 2016). Application of GA3 remarkably improved the seed quality of rice by increasing the rate of germination percentage, germination index, and early seedling growth (Abo-Gendy et al. 2016), however, in seed treated with SA, no improvement was recorded in seed quality for germination rate, germination index, and initial growth and establishment (Tavares et al. 2014). Proline plays a positive role in plants exposed to drought stress through improving their tolerance ability against drought stress conditions (Verbruggen and Hermans 2008). Whereas, Pandey and Shukla (2015) found that exogenous application of proline in plants under stress condition increases the accumulation of Pro that helps the plant for repairing the damage under stress by improving antioxidant activity in plants. Exogenous application of GB improves crop growth and yield (Hussain et al. 2008) by improving stomatal conductance, photosynthetic rate, and proline accumulation in plants against drought conditions (Ma et al. 2007).

Silicon application under water stress improved plant height, leaf area, dry matter, and yield of rice crop (Singh et al. 2006). A number of research findings have demonstrated the positive effect of foliar application of Si in suppressing a foliar plant disease in different crops, such as rice (Cacique et al. 2013). Application of Si improves the crop quality as reported by Shashidhar et al. (2008) and Si (0.50% silicon solution) produced maximum grain diameter and grain protein (Ahmad et al. 2012). Si treatment increased the insoluble protein accumulation and decreased total soluble protein in different rice cultivars in drought stress conditions (Emam et al. 2014). Using Si solubilizers, one would expect to raise the nutrition demand, yield quality many folds of rice and fulfill the demand of overgrowing population in the upcoming years under severe climate change conditions (Sarma and Shankhdhar 2017). Different studies also showed that silicon application helps in improving the drought resistance in major crops including rice through improved root growth, stomatal conductance, photosynthetic rate, and antioxidant defense (Gong et al. 2005; Hattori et al. 2005). While genetically improved genotypes tolerant to stress with high grain quality is the most important approach of rice under changing the climate (Fazaa et al. 2016).

31.4   Conclusions

The present review demonstrated that drought is the most detrimental stress that significantly influenced the yield and quality traits of major cereal crops. The negative effect of drought stress has been observed in almost all crops depending on crop species and their stages. In addition, the review discussed strategies that can improve the grain quality and adopted to cope with the effects of drought stress on crops,

producing several ideas to overcome the negative effect of drought stress conditions. However, in recent decades, exogenous application of antioxidants has been observed to improve crop quality under drought stress conditions. Exogenous application of OSP and nutrients ameliorates the adverse effects of drought stress on the seed quality of different crops.

Conflict of Interest Authors declared no conflict of interest.

Disclaimer We hereby declare that this review contains no material which has been accepted for the award of any degree or diploma in any university, and that, to the best of our knowledge and belief, the review contains no copy of any material previously published or written by another person except where due reference is made in the text.

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The book was inadvertently published with an incorrect spelling of the author's name in Chapter 7 as M. Riwan whereas it should be M. Rizwan.

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