Mirza Hasanuzzaman · Kamrun Nahar
Md. Amzad Hossain *Editors*

Wheat Production in Changing Environments

Responses, Adaptation and Tolerance

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Preface

Food supply for the world population largely depends on the cereal production, and wheat is the most important crop among the cereals. It is the base of human civilization and has a significant role in improving food security by feeding the hungry world. Wheat is probably one of the major and most important cereals in the world providing approximately 85% calories and 82% protein to the world population (Chaves et al. 2013). It is a staple food in more than 40 countries of the world and cultivated in almost every region due to its wide adaptability. However, its production is adversely affected by various environmental adversities (Rahaie et al. 2013). The issue now has more apprehension than ever before due to the astonishing rate of recurrence and harshness of extreme climatic events and their potentially negative effects on world food economy and security, especially of developing nations. These stresses alter plant growth and development at the cellular and molecular levels (Mahalingam 2015; Pandey et al. 2015; Ramegowda and Senthil-Kumar 2015).

Abiotic stress is the main factor negatively affecting crop growth and productivity worldwide. Growth and productivity of wheat are adversely affected by various abiotic stresses such as salinity, drought, high temperature, waterlogging, atmospheric pollution, toxic metal/metalloids, etc. Wheat is a heat-sensitive plant, and elevated temperature is a global problem nowadays. Drought is also a great threat to wheat production. The high rise of sea level and frequent drought events increase the salinity of soil, which is also a major obstacle for wheat production. Rapid industrialization is adding toxic metals in soil and in irrigation water, which is also damaging the wheat plant.

Global wheat production has become more than double in the last 50 years. However, the demand for wheat is ever-increasing. Most of the increase in wheat production was due to higher yields. In spite of their high-yield potential, the modern wheat cultivars often face the problem of crop loss due to the abiotic stresses. Therefore, tolerance to these stresses is a central characteristic of yield maintenance, and its improvement has long been an objective for plant breeders. For several decades, breeders could not develop many stress-tolerant wheat varieties that could be readily adopted by farmers in hostile environments. Many criteria are required to make a tolerant variety acceptable by the farmers as they look for good grain qualities in the stress-tolerant high-yielding varieties. Dramatic climate change compels breeders to combine multiple abiotic traits into one genotype. So, multiple traits are needed to incorporate in the same cultivar of wheat. Advanced biotechnological tools, knowledge of the genetic engineering, and discovering the newer sources of tolerance are needed to be combined to develop the next generation of wheat varieties that are climate change-ready and acceptable to the farmers and wheat consumers.

In recent years, considerable progresses have been made in improving wheat for changing environments, and many reports have been published. This book provides a comprehensive collection of up-to-date knowledge on wheat responses and tolerance to various abiotic stresses. This is done through 24 chapters written by 85 experts in the field of agronomy, plant stress physiology, crop improvement, and genetic engineering, ultimately aiming to become a useful information tool for plant breeders, molecular biologists, and plant physiologists as well as a guide for students in the field of Plant Science and Agriculture. Importantly, the editors and contributing authors hope that this book will lead to new discussion and efforts toward the production of wheat under changing climate. It is a comprehensive sourcebook for wheat scientists dealing with agronomy, physiology, molecular biology, and biotechnology.

We, the editors, would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. Our profound thanks also to Mr. Abdul Awal Chowdhury Masud, Ms. Khurshida Parvin, Mr. Sayed Mohammad Mohsin, and Mr. M.H.M. Borhannuddin Bhuyan for their critical review and valuable support in formatting and incorporating all editorial changes in the manuscripts. We are highly thankful to Ms. Lee, Mei Hann, Editor (Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. We are also thankful to RaagaiPriya ChandraSekaran, Project Coordinator of this book, and all other editorial staff for their precious help in formatting and incorporating editorial changes in the manuscripts.

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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, with a scholarship from the Japanese government (MEXT). Later, he completed his postdoctoral research at the Center of Molecular Biosciences, University of the Ryukyus, Japan, as a recipient of the Japan Society for the Promotion of Science (JSPS) postdoctoral fellowship. 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. Dr. Hasanuzzaman's current work is focused on the physiological and molecular mechanisms of environmental stress tolerance. Dr. Hasanuzzaman has published over 80 articles in peer-reviewed journals. He has edited 6 books and written 30 book chapters on important aspects of plant physiology, plant stress tolerance, and crop production. According to Scopus®, Dr. Hasanuzzaman's publications have received about 3500 citations with an *h*-index of 30. 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 and 2018." He has been honored by different authorities for his outstanding performance in different fields like research and education, and he has received the World Academy of Science Young Scientist Award (2014).

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Abiotic Stresses-Induced Physiological Alteration in Wheat

Neveen B. Talaat

Contents

Abstract Wheat is one of the most important cereal crops around the world, and the greater part of the world population depends on it as their essential vital nourishment. However, in agricultural systems, wheat plants face different stress conditions, e.g., salinity, drought, heavy metals, high and low temperature, radiation, and nutritional disorders that restrict their crop productivity. These stressors produce undesired effects on plant growth and development. Exposure to different abiotic stresses during plant life cycle leads to reactive oxygen species excessive accumulation, and consequently oxidation of membrane lipids and proteins occurs. Moreover, these stresses lower the activity of cell physiology including photosynthetic efficiency and protein synthesis that could be due to the osmotic stress and nutritional imbalance. They can also increase synthesis and accumulation of different osmolytes/osmoprotectants. Accumulation of organic solutes and antioxidant molecules can protect plant cells by balancing the osmotic strength of both the plant vacuole and the external environment. Furthermore, when plants expose to adverse conditions, other physiological responses such as phytohormone signaling pathways and developmental signals are triggered to cope with the stress. Changing transcript levels of genes involved in signaling pathways or stress response was also occurred. This chapter documents the different mechanisms underlying abiotic stresses impact on wheat plants based on recent advances.

Keywords Abiotic stresses · Antioxidant defense system · Endogenous phytohormones · Osmoprotectant accumulation · Photosynthetic capacity · Stress-responsive genes

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1 Introduction

Wheat (*Triticum aestivum* L.) is considered as the most important staple cereal globally, and the greater part of the world population depends on it as its essential vital nourishment (Li et al. 2016a). It was evaluated that the worldwide yield of wheat should continually increment by 2% every year until 2020 to fulfill the prerequisites driven by increasing human population (Singh et al. 2007). However, in agricultural systems, wheat plants are confronting with a great challenge. They exposed to many stressors including salinity, drought, heat, cold, flooding, ultraviolet radiation, and metal toxicity, restricting their growth and limiting their productivity. Abiotic stress decreases productivity by 50% in most agriculturally valuable plants, including wheat (Vandenbroucke and Metzlaff 2013).

The salinity of arable land is considered as one of the most important abiotic stressors that restricted wheat production as well as its quality and security (Jusovic et al. 2018). Salinity stress remains one of the oldest environmental problems, which happens when soluble salts are lifted in soil and water. Saline soils possess 7% of the Earth's land surface, and expanded salinization of arable land will result in up to half of land misfortune by the middle of the twenty-first century (Porcel et al. 2012). Salinity stress is diminishing the region that can be utilized for agriculture by 1–2% every year ultimately, decreasing food security that outcomes in the negative ecological and financial results. In developing countries especially those located in the arid regions, more than 50% of their arable land is salt-affected. Soil salinization decreases wheat harvest's grain yield by 20–43% with 40% average loss (Singh et al. 2017). Salt stress inhibits wheat growth by disrupting ion and water homeostasis, inhibiting photosynthesis and protein synthesis, inducing hormonal imbalance, as well as inducing oxidative stress (Talaat and Shawky 2015; Shah et al. 2017; Jusovic et al. 2018). Under saline conditions, distinctive metabolic pathways are uncoupled, and electrons are transferred to molecular oxygen, prompting reactive oxygen species (ROS) formation. These ROS such as singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^{\cdot}$) are toxic molecules capable of disrupting normal metabolism through attack proteins, DNA, and membrane lipids (Mittler et al. 2004; Talaat and Shawky 2014b). Moreover, wheat plants grown under salty soils accumulate significant amounts of the osmoprotectants like proline, soluble sugars, and glycinebetaine. In fact, these solutes assume a vital role in limiting salt entry into the plant and/or regulating salt concentration in the cytoplasm (Munns and Tester 2008; Talaat and Shawky 2013a, 2014a). Salt stress also affects various signaling pathways in wheat plant that incorporate stress recognizing sensor proteins, signaling transducers, transcription factors, and stress-responsive genes (Dong et al. 2013; Sun et al. 2015; Zhao et al. 2016).

Water scarcity is a global problem that has major constrain in wheat production. It may be the most serious problem that diminishing wheat productivity by affecting various perspectives such as water relations, membrane integrity, pigment content, hormonal status, protein synthesis, and photosynthetic activity (Todorova et al. 2016; Garmendia et al. 2017; Alzahrani et al. 2018; Liu et al. 2018). It can likewise increase the generation and accumulation of ROS and consequently enhancing the oxidative stress (Talaat et al. 2015b). Moreover, wheat response to water deficiency involves activation of the expression of specific stress-related genes (Rong et al. 2014; Amalraj et al. 2016; Chang et al. 2016). Similarly, environmental change greatly affected worldwide wheat productivity. With every degree of temperature increment, wheat grain yield decrease by 6% (Gourdji et al. 2013). Wheat responses to high temperatures include several modifications at the physiological, molecular, and biochemical levels such as alternation in gene expression (Kotak et al. 2007) as well as ROS generation in cell organelles that affected the cell membranes stability by enhancing electrolyte leakage and lipid peroxidation, and also destroying photosynthetic chemical reactions in chloroplasts (Sarkar et al. 2018).

Another abiotic stress factor that has gotten enormous consideration is the metal toxicity. Substantial amounts of cadmium, lead, mercury, and arsenic can establish perilous dangers to wheat plants (Alzahrani et al. 2018). Indeed, these metals naturally exist in low concentrations; however their amounts can be expanded by anthropogenic activities. They disrupt the cellular redox status by replacing the essential metals and/or cofactors at enzyme active site. They also enhance oxidative stress and may lead to cell death that depending on the metal dose and the exposure period (Vaculík et al. 2015). Furthermore, the concentration of ozone (O_3) has increased nowadays; moreover it will continue to rise in the next few decades. Indeed, in the twenty-first century, it increased by 0.5–2% per year over the northern mid-latitudes. It is one of the most harmful country air pollutants because of its intense oxidization and phytotoxicity (Carriero et al. 2016). Wheat yield suffers seriously from O_3 pollution (Li et al. 2016b, 2018). O_3 enters the plant cell through the stomata pore in the leaves and, after that, generates different types of ROS in the apoplast causing oxidative damage (Fuhrer 2009).

The present chapter presents a comprehensive review regarding the deleterious impacts of abiotic stresses during wheat plant life cycle. Specifically, it discusses their effects on water and osmotic potential, synthesis and accumulation of osmoprotectants, ionic homeostasis, photosynthetic machinery, protein synthesis, plant hormonal status, and ROS scavenging system, as well as some key genes that are known as enhancers of wheat stress tolerance. Additionally, it highlights several transcription factor families, such as basic leucine zipper (bZIP), dehydration-responsive element binding (DREB), WRKY, myeloblastosis (MYB), and NAC that are known as positive and negative regulators of stress responses in wheat. The overall aim of this book chapter is to give an overview of different mechanisms underlying abiotic stresses impact on wheat plants. A special section dedicates to the recent progress and challenges regarding the molecular studies on stress alleviation. At the end of this chapter, future perspectives have additionally been featured.

2 Deleterious Impacts of Different Abiotic Stressors During Wheat Plant Life Cycle

Abiotic stress is characterized as environmental conditions that diminish plant development below ideal levels. Plant responses to these stressors are dynamic and complex; they are both elastic (reversible) and plastic (irreversible) (Cramer et al. 2011). Abiotic stresses cause a severe diminish in the wheat production by limiting the plant growth and development. They cause serious violations of plant metabolism (Garmendia et al. 2017; Talaat and Shawky 2017). They could disturb plant water relations, reduce water-use efficiency, disrupt photosynthetic capacity, reduce gas exchange, alter nutrients acquisition, reduce protein synthesis, as well as induce organic solutes formation and accumulation. Abiotic stressors also prompt the formation of phytohormones that can act as primary messengers in signal transduction and can regulate the metabolism inside the plant cell. Furthermore, abiotic stressors induce oxidative stress by enhancing the formation and accumulation of ROS that disturb cellular membranes, induce lipid peroxidation, as well as alter many biochemical processes leading to cell death. Consequently, activation of antioxidative pathways is detected in plants to cope with oxidative stress. Moreover, they make changes in the initiation of the molecular networks that is associated with stress discernment, signal transduction, and specific stress-related genes expression (Fig. 1).

2.1 *Limiting Plant Development and Its Production*

The primary effect of abiotic stresses like water deficiency, salt stress, heat, cold, metal toxicity, and ozone is the reduction in plant growth and development that relies upon division, enlargement, and differentiation of plant cells and also includes morphological, physiological, and hereditary activities (Fig. 1). Moreover, most of these stressors are seen first by the plant root, which keeps on developing underneath the soil and thus affecting the activation of the root meristems (Basu et al. 2016).

The saline condition is considered as the most important stressors in the last decade that induce worldwide crop production losses. It is evident from the study of Al-Whaibi et al. (2012) that adding 90 mM NaCl to the root medium had a significant negative impact on wheat plants' development (plant height, fresh and dry weight) that may be achieved by damaging effect of salinity on different metabolic activities, i.e., nitrogen assimilation, antioxidant system, and photosynthesis. Similarly, Talaat and Shawky (2012a) findings showed that increasing soil salinity level hampered plant height, shoot dry weight plant^{-1}, root dry weight plant^{-1}, number of leaves plant^{-1}, and number of tillers plant^{-1} of wheat plants at all stages of growth. These decreases were increased with advancing plant age, indicating that the effect of salinity on growth could be cumulative. Salt stress also drastically lowered the number and weight of spikes plant^{-1}, number of grains plant^{-1}, grain yield plant^{-1}, and weight of 1000 grains. Salt stress inhibited wheat

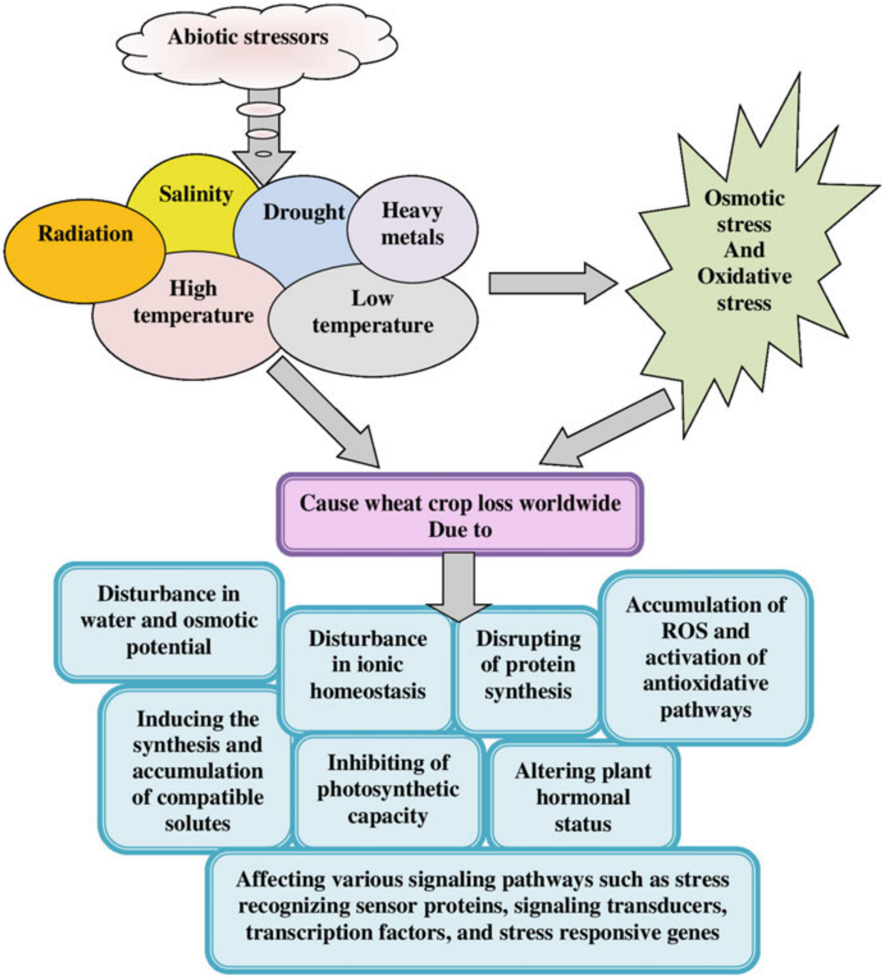

Fig. 1 Conceptual diagram on the effect of different abiotic stressors on wheat plant

growth, and productivity may result from inhibition in cell wall extension and cellular expansion, a decrease in membrane integrity, an inhibition in biochemical processes such as N and CO_2 assimilation, an imbalance in phytohormone levels, and a limitation in solute delivery to the expanding tissues. Likewise, Talaat and Shawky (2014a) demonstrated that soil salinity at 4.7 and 9.4 dS m^{-1} significantly decreased wheat productivity by reducing number of grains $plant^{-1}$ and grain yield $plant^{-1}$, which could be due to Na^+ and Cl^- toxicity, nutrient acquisition alteration, water homeostasis disruption, enzyme structure and plasma membrane damage, ROS accumulation, as well as photosynthesis, respiration, and protein synthesis inhibition. A recent study (Jusovic et al. 2018) examined the effect of 200 mM NaCl on development of wheat DELLA mutant (*Rht-B1c*) and wild-type (*Rht-B1a*) seedlings. They found that saline condition prompted a large diminish in the length of both root and leaf. This negative effect was more detected in root length than in leaf length of the wild-type plants. Moreover, wheat mutant seedlings were more salt tolerant if compared with the wild-type ones. The growth salt tolerance index of mutant seedlings was (81.6%) and (73.9%) for the length of root and leaf, respectively.

Accumulating evidence suggests that drought stress increased root/shoot ratio by inducing root growth and decreasing shoot growth. In this concern, Rauf et al. (2007) showed that under water deficiency, the root/shoot ratio of wheat plant was enhanced by 50%. The high level of abscisic acid is appeared to work as a root growth promoter and at the same time work as a shoot growth repressor. Indeed, hormonal cross talk mediated by cytokinin, auxin, gibberellic acid, and abscisic acid can play a vital role in regulating root system architecture under drought condition (Basu et al. 2016). Additionally, it is well established that enzymes such as xyloglucan endotransglucosylase that induce root development are upregulated by mild water stress, while others are downregulated (Sengupta and Reddy 2011). In lines having a QTL, qDTY12.1, more lateral root and root hair formation were detected only when grown under water deficit (Dixit et al. 2015). In contrast, Garmendia et al. (2017) found that shoot, root, and spike dry weight plant^{-1}, as well as number of spikes plant^{-1}, were decreased in wheat plants subjected to limited irrigation. Recently, Liu et al. (2018) observed that under water-deficit stress, wheat plants exhibited significantly lower biomass, heads and grains weight plant^{-1}, as well as heads, spikes, and grains number plant^{-1} when compared to their corresponding control plants.

It is well known that heat stress is a widespread problem that severely limits plant growth. It significantly reduced wheat seedling fresh weight from 25.84 to 67.79% (Sarkar et al. 2018). Furthermore, O_3 as one of the most harmful country air pollutants can also restrict plant productivity. In this context, Feng et al. (2015) reported that O_3 reduced crop yield by 6.4–14.9% and it will increase to 14.8–23.0% by 2020. According to Li et al. (2018), grain plumpness and 22.6% wheat yield were lost after 30 d of fumigation by 80 ppb O_3; however grain number ear^{-1} and ear number were not affected. Indeed, O_3 has negative impact on carbon allocation to seeds that consequently decrease the yield.

Significant decreases were recorded in shoot high, root length, fresh weight, and dry weight of wheat plants under salinity (200 mM NaCl) or temperature-stress (35 °C) conditions. Inhibition of plant growth that occurred due to soil salinity may be attributed to the accumulation of high Na^+ content and a low K^+/Na^+ ratio (Singh et al. 2017). Likewise, drought (50% field capacity), salinity (200 mM NaCl), and cadmium (2 mM Cd) stress conditions significantly decreased the shoot length, leaf area, fresh weight, and dry weight of wheat seedlings. These plant growth parameters were diminished by 42–54%, 49–57%, 54–61%, and 56–64%, respectively, in comparison to the non-stressed plants (Alzahrani et al. 2018).

2.2 Disturbance in Water Homeostasis

Measurement of relative water content (RWC) is a typical technique used to measure water balance inside water-stressed plant leaves. Likewise, it assesses a water rate inside the leaf as a small amount of the total water find in the leaf at its full turgor. Keeping up RWC in plant cells in a good manner is very important to confer the metabolic activity under stress conditions like salinity and/or drought (Talaat et al. 2015a; Talaat and Shawky 2016). However, different abiotic stressors reduced the RWC. Salt-affected plants must keep up lower internal osmotic potential to prevent water movement from roots into the soil because the salty soil solution has lower osmotic potential that diminishes the water availability to the plant.

The RWC value was diminished in wheat plants grown under salt stress that could be due to the salt's negative effect on the plasma membrane electrical potential, which decreased water absorption and consequently generating water stress (Talaat and Shawky 2012b, 2014a). Additionally, Jusovic et al. (2018) postulated that exposed wheat DELLA mutant (*Rht-B1c*) and wild-type (*Rht-B1a*) genotypes to NaCl for 9 days significantly decreased the RWC values. However, high RWC value was detected in the mutant (78.4%) compared with the wild type (71.6%). Concerning to heat stress, RWC were significantly decreased by 21.20% in heat-stressed wheat seedling (Sarkar et al. 2018). Furthermore, RWC was decreased under salinity, water stress, and Cd stress conditions by 33%, 33%, and 41%, respectively, in wheat leaves (Alzahrani et al. 2018).

2.3 Inducing the Formation and Accumulation of Osmoprotectants

Osmotic adjustment is characterized as a procedure of solutes gathering in plant cells when the water potential is diminished to maintain the turgor. Syntheses and accumulations of various osmoprotectants are a necessary defensive system in wheat plants developed under stressful environments as these organic solutes (soluble sugars, polyols, glycinebetaine, and amino acids) can accumulate to high levels to protect subcellular structures, mitigate oxidative harm caused by ROS, and maintain the enzyme activities without interfering with the normal intracellular biochemistry (Rios et al. 2017). Sugars are the fundamental solutes associated with an osmotic adjustment in glycophytic plants exposed to osmotic stress (El-Bassiouny and Sadak, 2015). Moreover, proline accumulation is an osmotic stress response since it is an essential osmolyte, involving in osmotic adjustments of plant cells (Talaat et al. 2015a). It also maintains redox potentials, scavenges the hydroxyl radical, protects macromolecules from denaturation, and reduces the cell acidity (Kavi Kishor et al. 2005). Glycinebetaine can act as organic solutes. It stabilizes the complex protein structures, protects the transcriptional machinery, maintains the membrane integrity, protects the CO_2-fixing enzymes, and/or activates the genes expression (Takahashi and Murata 2008; Yang et al. 2008).

Accumulating evidence postulates that salt-stressed wheat plants accumulate high amounts of organic solutes for intracellular osmotic homeostasis (Talaat and Shawky 2013a). It appeared from the results of Al-Whaibi et al.'s study (2012) that the presence of NaCl in root medium induced the proline accumulation in wheat tissues. Moreover, high salt amounts in root medium resulted in compatible solutes (soluble sugars, free amino acids, proline, and glycinebetaine) accumulation in wheat leaves (Talaat and Shawky 2011, 2014a). Similarly, Hassan and Bano (2016) experiment showed that wheat plants grown under saline conditions exhibited higher proline content compared with their respective control plants. In the same line, Singh et al.'s (2017) findings pointed out that proline content was increased in salt-affected plants that have strong correlation with the extent of salt exposure. Its accumulation enables wheat plants to keep up the correct osmotic balance under salt stress. However, they found that salinization decreased the content of total soluble sugars.

Upon exposure of plants to water deficiency, reduction in water content and increment in organic solutes accumulation were detected. In this context, Serraj and Sinclair (2002) indicated that drought-resistant wheat varieties accumulated more osmoprotectants than less-resistant ones. Previous studies have shown high amounts of proline in the cytosol after water stress that stabilize the cell membranes and sustain the protein conformation (Cha-um et al. 2011). Increasing its level under water-deficit conditions might be due to (a) increasing in the activities of Δ-pyroline-5-carboxylate synthetase and Δ-pyroline-5-carboxylate reductase enzymes, (b) decreasing in the activity of proline dehydrogenase enzyme, and/or (c) over expression of genes responsible for the transcription of these proteins (Sumithra and Reddy 2004). Furthermore, proline concentration is correlated with plant water stress tolerance. In this respect, Sen et al. (2017) found increasing in the proline content in wheat tolerant mutants by 29% and 48% compared to that in control plants in vegetative and flowering stages, respectively. Sugar pool also changes in relation to drought condition that is related to osmotic adjustment. When Garmendia et al. (2017) study the carbohydrate content in well-watered and water-stressed wheat leaves, they found that plants subjected to drought had higher glucose and xylose concentrations and lower sucrose and starch concentrations than plants grown under well-watered conditions. Level of proline was also increased in water-stressed plants.

Exposure to high-temperature-induced proline accumulation in wheat heat-sensitive cultivar PBW 343 when compared with the tolerant ones, C306 shows a higher basal thermotolerance level when proline content is low in plant cells (Kumar et al. 2013). Likewise, increasing the incubation time up to 12 h at 40 °C significantly enhanced the accumulation of proline and glycinebetaine in heat-affected wheat plants. Proline accumulation in heat-stressed plants is not always useful for the plant survival unlike other stressors, especially in the osmotic stress case, where proline level has a vital role in stress alleviation. Indeed, proline can enhance the deleterious effects of high temperature (Sarkar et al. 2018). Furthermore, adaptation to different kinds of abiotic stresses is the most complex process, and plants develop different mechanisms such as increasing the content of compatible solutes to cope with these harsh environments. It is evident from Alzahrani et al.'s (2018) results that the salinity, water, and Cd stresses increased soluble sugars and proline contents.

2.4 Disturbance in Ionic Homeostasis

Increasing the salt depositions in the agricultural soil produces a low-water potential zone, causing water stress and nutrient imbalance in the soil. Actually, the presence of high salt content in the growth medium induces the lethal accumulation of Na^+ ion in the plant cells that has inhibitory impacts on the uptake of the essential nutrients like N, P, K^+, Fe, Zn, and Cu and can also disturb ionic homeostasis (Moghaieb et al. 2011; Talaat and Shawky 2013b; Talaat et al. 2015a). It is well known that lethal levels of Na^+ and Cl^- ions can enter the plant cells and make their dangerous impacts on cell membranes; moreover they can also inhibit the metabolic processes activities (Rios et al. 2017). Sodium ion accumulation in salt-stressed plant tissue has negative effect on many cellular activities such as protein synthesis, photosynthesis, and nutrient transport and consequently limits the plant growth and its productivity. Plant efficiency to uptake K^+ and exclude Na^+ has been suggested as a vital way for wheat plant salt resistance. Thus, K^+/Na^+ ratio estimation is an essential method for assessing the plant salinity tolerance level (Zhu et al. 2015).

Talaat and Shawky (2011, 2013b) revealed that N, P, and K^+ levels were significantly diminished in wheat shoots and grains by high soil salinity; however an increment in shoot and grain Na^+ level was detected. Indeed, salt stress interfered with N uptake because chloride competes with nitrate on the cell membrane. It also reduced P absorption, because the ions in salty soils can precipitate phosphate. Decreased K^+ level in wheat tissues might be due to the fact that at the absorption sites, Na^+ and K^+ ions can compete each other as both of them share the same transport system on the plant root. Moreover, lower levels of Fe, Zn, and Cu were also recorded in tissues of salt-affected wheat plants. Similarly, Talaat and Shawky (2013a) found that exposed wheat plants to salt stress significantly diminished N, P, and K^+ acquisition, but it enhanced Na^+, Ca^{+2}, and Mg^{+2} uptake that could be due to ionic imbalance, nutrient lack, and specific ion lethality. Apparently, the membrane stability index (MSI) value was diminished in salt-stressed wheat plants that could be due to the salt effect on the plasma membrane electrical capability and thus influenced the ion absorption (Talaat and Shawky 2012b, 2014a). Recently, Singh et al. (2017) demonstrated that saline conditions increased Na^+ acquisition and decreased K^+ uptake in wheat tissues, leading to lower K^+/Na^+ ratio. A lower MSI was also observed in stressed plants compared with unstressed ones.

Impairment occurred on the ionic status of wheat seedlings as affected by different stress treatments. Under Cd stress condition, K^+, Ca^{2+}, and Si contents were decreased by 52%, 41%, and 50%, respectively. On the other hand, under salt stress condition, Na^+ content was significantly increased. Indeed, Na^+ levels were increased under salt stress, Cd stress, and water deficiency by 533%, 253%, and 42.5%, respectively (Alzahrani et al. 2018).

Salt stress induces the accumulation of Na^+ in plant tissues might be differential expression of ionic transporters. Furthermore, under salt excess conditions, Na^+ and K^+ ions redistribute inside plant cells which relies upon the relative expression of K^+ channels and transporters as well as the energy considerations. Some ways of Na^+ and K^+ transport across plasma membranes are selective for K^+, but most of them are not. A great variety of ion channels and transporters are expressed in plant plasma membranes, and almost little difference is found between Na^+ and K^+. These are possibly reasonable for the low-affinity Na^+ influx and the Na^+-induced K^+ efflux in salt-affected plants (Ashraf et al. 2004). Salinity-induced ionic stress is alleviated by the salt overly sensitive (SOS) pathway and also by the ionic transporters (Bharti et al. 2016).

It is well established that under saline conditions, Na^+ goes into root cell by cation channels and/or by specific or non-specific transporters, while it goes into the root xylem stream by an apoplastic pathway (Chinnusamy et al. 2005). The significant pathway for passive Na^+ goes into roots at high salty soil is the voltage-dependent nonselective cation channels (NSCCs). Several reports have postulated that NSCCs are associated with a large number of stress responses, growth and development, nutrient uptake, and calcium signaling. Nonselective cation channels can also work as external stimuli as well as signal transducers for ROS, cyclic nucleotides, membrane stretch, amino acids, and purines (Demidchik and Maathuis 2007). Because of the similarity between Na^+ and K^+, voltage-dependent K^+ inward rectifiers or outward rectifiers seem to be one way for Na^+ entry into root cells. Although the HKT gene family members are Na^+-specific transporters, they are also high-affinity K^+ transporters. Indeed, the HKT transporters of subfamily 1 have a relatively higher Na^+ to K^+ selectivity than HKT members of subfamily 2 (Yao et al. 2010).

Furthermore, Na^+ exclusion is considered one of the real systems presenting salt tolerance in grain crops. Bread wheat (*Triticum aestivum*, AABBDD) is a superior Na^+ "excluder" than durum wheat (*Triticum turgidum* ssp. *durum*, AABB), a characteristic controlled by the *Kna1* locus on chromosome 4D, which corresponds to an *HKT1;5*-like gene (Byrt et al. 2007). However, irregular durum wheat named Line 149 has a salt-tolerant phenotype like the bread wheat. That is ascribed to the presence of two genes for Na^+ exclusion, named *Nax1* and *Nax2*. The *Nax1* locus is accountable for the rejection of Na^+ from leaf blades in salt-stressed plants. Regarding the *Nax2* gene, it decreases the Na^+ transport from root to shoot (James et al. 2006). The *Nax1* and *Nax2* loci are wheat *HKT* genes of subfamily 1 with preferred Na^+ transport. *Nax2* was appeared to be homologous to Kna1 in *T. aestivum*, namely, TaHKT8 (Byrt et al. 2007).

2.5 Inhibiting of Photosynthetic Capacity

Photosynthesis is the essential physiological process that can be influenced by the different abiotic stress. The effects of these stressors on the photosynthetic machinery are either direct or secondary as a result of the oxidative damage. They affect photosynthetic pigments, reaction center complexes, electron transport system, leaf gas exchange, and the water-use efficiency (Takahashi and Murata 2008; Talaat and Shawky 2017).

Chlorophyll concentration is an important physiological index representing the degree of photosynthesis in plants (Talaat 2013), and decreasing its content under salt stress is attributed to photosynthetic machinery oxidative damage (Takahashi and Murata 2008; Talaat and Shawky 2015). Carotenoids, like chlorophylls, also play a vital role under stressful conditions. They are antioxidant compounds that protect the photosynthetic machinery from the photo-inhibitory damage by single oxygen and quench the excited triple state of chlorophyll (Triantaphylidès and Havaux 2009). They also modulate genes that are responsive to ROS (Shumbe et al. 2014). Many studies revealed that salinity stress alters the content of photosynthetic pigments, chlorophylls and carotenoids, as well as the protein composition of thylakoid membranes that brought about a diminishing in internal CO_2 concentration. Decreasing CO_2 fixation may enhance ROS formation from the excess electrons in PSI that inhibits PSII reparation by inhibiting the D1 protein synthesis at the translation step (Takahashi and Murata, 2008). It is evident from Mehta et al.'s (2010) study that salt stress caused greater damage in the PSII donor side compared to that in the acceptor side in wheat leaves; moreover salt-inducing PSII damage is reversible. Moreover, Talaat and Shawky (2012b) revealed that salty soils significantly reduced the chlorophyll content in wheat leaves that could be due to chlorophyllase activation and/or chloroplast structure destruction. Salt stress also inhibited carbonic anhydrase (CA) activity that could be associated with decreasing in internal CO_2, altering in enzyme protein, and/or rubisco inhibition. In addition, salinity caused severe inhibition in the photochemical reactions of photosynthesis, especially in PSII. Al-Whaibi et al. (2012) found a similar influence of salt stress on photosynthetic pigment content. They demonstrated that saline conditions decreased the chlorophyll content in wheat leaves; moreover chlorophyll b was found to be more affected than chlorophyll a that increased chlorophyll *a*/*b* ratio. This decrease in the content of photosynthesis pigments might be attributed to damage of protein complexes and/or chlorophyll molecules. The CA activity was also decreased under salt stress, which may be due to inactivation of rubisco that sequentially reduces the carbon metabolism, chlorophyll content, and photosynthetic capacity. Adverse effects of high salinity on wheat photosynthetic pigment content and photosynthetic efficiency were also recovered by Talaat and Shawky (2014a), who found that soil salinity drastically lowered leaf chlorophyll concentration that enhanced the Chl *a*/*b* ratio. It also made inhibition in both PSI and PSII activities. At 9.4 dS m^{-1} salinity level, PSI electron transport was inhibited by 30.6% in Giza 168 cultivar; however it was suppressed by 14.9% in Sids 1 cultivar. Regarding PSII activity, it was inhibited by 83.3% in Giza 168 and by 48.6% in Sids 1. Thus, PSI activity was less effectively suppressed than PSII under saline conditions. They also indicated that high soil salinization significantly altered the gas exchange attributes like net CO_2 assimilation rate and stomatal conductance that could be attributed to the observed decreased in leaf RWC and thus inducing stomatal closure. Close stomata decreases the CO_2 availability that reduces photosynthesis rate. Likewise, Singh et al. (2017) pointed out that wheat leaf chlorophyll *a* + *b* content was decreased under salt- or temperature-stress conditions. In the same line, Shah et al. (2017) demonstrated that increasing salinity level significantly reduced chlorophylls and carotenoid content in wheat plant. Salinity stress also lowered photosynthesis efficiency, especially due to oxidative and osmotic stresses as well as imbalance in nutrients acquisition (Rios et al. 2017).

Water deficiency reduces photosynthesis by its negative effect on leaf area and photosynthetic rate. The diminished photosynthetic rate can be due to the close of stomata and/or the disturbance in metabolic processes. Indeed, the immediate response of plants to water deficiency is stomatal closure that decreases transpiration rate, CO_2 enters, and nutrient uptake and consequently disrupts many metabolic activities like photosynthesis (Basu et al. 2016). Furthermore, under water-deficit condition, continued photosynthetic light reactions and decreased CO_2 enters may lead to the increase in the reduced photosynthetic electron transport components that diminish molecular oxygen, causing ROS accumulation and consequently destroying the photosynthetic apparatus (Lawlor and Cornic 2002). Remarkably, several parameters can be detected in wheat leaves under water shortage condition. Decreasing in stomata size and increasing in its density were detected in drought-stressed wheat flag leaves (Shahinnia et al. 2016). Suppression in stomatal conductance under water stress was also found. Recent research has shown that pre-anthesis water stress condition significantly decreased stomatal conductance. There is a positive relationship between stomatal conductance and the leaf water content (Liu et al. 2018). Moreover, under water deficiency decreased stomatal conductance is associated with reduction in both aquaporin genes expression and chloroplast surface area (Tosens et al. 2012). Notably, leaf pigment degradation is also observed under water stress. In this respect, Sen et al. (2017) showed that drought stress decreased chlorophyll concentration in wheat plants to the great extent in the flowering stage than in vegetative stage. There is also evidence that photosynthetic rates in flag leaves of plants grown under limited irrigation were significantly lower, which could be attributed to the reduction in CO_2 exchange rate and stomatal conductance (Garmendia et al. 2017).

Concerning heat stress, it is well postulated that chloroplast is the primary site of heat injury other than mitochondria and peroxisomes because PSI and PSII are the key areas of ROS generation. Photosynthetic efficacy, chloroplast ultrastructure, and total chlorophyll concentration of wheat plants were mainly influenced under heat stress condition. In this regard, Sarkar et al. (2018) found that high-temperature-distorted chloroplast ultrastructure and consequently grana and thylakoid stacking were lost. Ozone pollution also has major constrain on wheat photosynthesis. Ozone exposure significantly suppressed CO_2 assimilation rate, stomatal conductance, and transpiration rate of wheat by 36.9%, 70.8%, and 60.2% compared to non-stressed control treatment, respectively. It also decreased the intercellular CO_2 concentration/atmospheric CO_2 concentration ratio by 52.9% (Li et al. 2018). In addition, impairment occurred in the wheat photosynthetic capacity as affected by different stressful conditions. Alzahrani et al. (2018) detected negative impacts of different stress treatments on gas exchange attributes like net photosynthesis rate, transpiration rate, and stomatal conductance as well as water-use efficiency of wheat seedlings. Net photosynthesis rate was decreased under water stress, salinity, and Cd stress by 44%, 48%, and 52%, respectively. Moreover, transpiration rate was determined to be an average of 6.17 mmol $H_2O/m^2/s$ in control seedlings and 3.68, 3.36, and 3.22 mmol $H_2O/m^2/s$ in water stress, salinity, and Cd stress, respectively. For stomatal conductance and water-use efficiency, these stress treatments caused a significant decrease ranged from 17 to 54% and 1 to 11%, respectively, compared to the non-stressed plants.

Modification of DELLA proteins in wheat plant is caused by the allele *Rht-B1c* (*Rht3*), which is a mutation within the N-terminal DELLA domain at the *Rht-B1* locus. Under water deficiency wheat seedling *Rht-B1*-encoded DELLA proteins display a superior photosynthetic rate if compared with the wild type (Nenova et al. 2014). Similarly, positive influence of wheat mutant DELLA-encoding gene (*Rht-B1c*) on the photosynthetic apparatus under cadmium stress has been suggested by Dobrikova et al. (2017). Likewise, Jusovic et al. (2018) found that the negative impact of salinization on wheat plants was modulated in the *Rht-B1c* (dwarf mutant, encoding modified DELLA proteins) than that in the *Rht-B1a* (wild type, encoding DELLA proteins). In the mutant salt-stressed plants, less reduction in the content of photosynthetic pigments and in the activity of photochemical reactions of photosynthesis was detected, which was accompanied with high PSI-dependent cyclic electron flow capacity. Indeed, under stressful conditions the cyclic electron flow (CEF) around PSI can alleviate the photo-oxidative harm to the photosynthetic machinery. It achieves that by preventing the over-reduction of the electron transport chain. The CEF generates ΔpH across the thylakoid membranes, leading to ATP formation, and consequently prevents the over-reduction of PSI acceptor side. It also protects the PSII via the regulation of light-harvesting processes. Generally, the activities of photochemical reactions of photosynthesis are more in the salt-tolerant *Rht-B1c* mutant than that in the wild-type wheat. Furthermore, enhancement in the PSI-related reaction center protein (PsaB) was also observed in the mutant salt-affected plants unlike the wild type. Salinization increased the mutant PsaB amount to 116.0%. The PSI photochemistry was suppressed more strongly in the wild type than in the mutant leaves under salt stress. Hence, DELLA proteins alleviate the salt's negative impact on photosynthetic apparatus by altering the thylakoid membrane proteins and/or the pigment-protein complexes structure.

2.6 Disrupting of Protein Synthesis

Protein synthesis is among the most seriously influenced processes under environmental stresses as they retard the uptake of nitrate and reduce the activity of nitrate reductase (NR) (Talaat and Shawky 2014a). Stressed environments also enhance the ROS production, which can cause severe damage to DNA, proteins, lipids, and cellular membranes, causing disturbance in metabolic processes, ending in cell death (Mittler et al. 2004).

Salinity is considered as the most detrimental environmental limiting conditions which hamper protein synthesis in wheat plants. Salinization altered the content of nitrate and protein as well as the activity of NR. Salt excess diminished nitrate uptake in wheat plants by harming the plasma membrane function via influencing the inbuilt ATPase activity and the membrane fluidity (Talaat and Shawky 2012b). Moreover, salinity decreased nitrate uptake because of its competition with chloride at the membrane level. However, salt stress suppressed NR activity by decreasing the flux of NO_3^- from soil to plant root and/or by reducing the synthesis of NR protein (Talaat and Shawky 2012a, 2014a). In the same line, Hassan and Bano's (2016) findings showed that the protein content was significantly decreased under saline condition. Likewise, salt-affected wheat plants exhibited lower total protein content compared with their respective control plants (Singh et al. 2017). Water deficiency also has a negative impact on protein synthesis. In this context, Garmendia et al. (2017) indicated that N concentration was significantly declined in flag leaves of water-stressed wheat plants. Similarly, fumigation of O_3 significantly suppressed protein synthesis by evoking NR activity and up-regulating nitrate reductase 1 (NR1) expression level in wheat leaves (Li et al. 2018).

2.7 Altering Plant Hormonal Status

Abiotic stressors cause changes in the formation, distribution, or signal transductions of stress hormones that can induce specific protective activities (Eyidogan et al. 2012). Plants subjected to stressful environments depend on many endogenous regulators to modulate their development. One of them is the plant hormones that can regulate plant tolerance to many stress conditions such as water, cold, heat, and salt stress. A probable cross talk between auxin, ethylene, cytokinin (CK), gibberellic acid (GA), abscisic acid (ABA), and brassinosteroids (BRs) signaling in the stress response has been proposed. Recently, there are other compounds such as polyamines (PAs), nitric oxide, and strigolactone that were also added to this list. These hormones regulate plant stress tolerance by acting either close to or remote from their sites of synthesis (Nongpiur et al. 2016; Todorova et al. 2016). Remarkably, ABA and ethylene are the most important phytohormones that regulate plant stress tolerance (Zhang et al. 2007; Rong et al. 2014).

Salt stress modulates the endogenous levels of phytohormones. Abscisic acid, a plant stress hormone, acts as endogenous signal molecules enabling plants to survive under a broad spectrum of abiotic stresses (Raghavendra et al. 2010). Expositing plants to severe adverse environmental conditions increases the ABA endogenous level that may be due to inducing its biosynthetic genes expression (Zhu 2002). In this respect, saline condition rapidly activates ABA biosynthetic-related genes, such as zeaxanthin oxidase, 9-cis-epoxycarotenoid dioxygenase, ABA-aldehyde oxidase, and molybdenum cofactor sulfurase through a calcium-dependent phosphorylation pathway (Chinnusamy et al. 2006). It appeared from Saeng-ngam et al.'s (2012) findings that the stress-related genes *OsDSM2* and *OsCam1-1* were encoded an ABA biosynthetic b-carotene hydrolase and a Ca^{2+}-binding calmodulin. Moreover, Shinozaki and Yamaguchi-Shinozaki (2007) reported that ABA-related transcription factors like ABA-responsive element (ABRE) binding factors (ABFs), MYCs, and MYBs are correlated to the ABA-dependent salt stress-responsive gene expression via direct binding to ABRE (ACGTGGC), MYCRS (CAnnTG), and MYBRS (YAACR), respectively. On the other hand, NAC and DREB2 (AP2/ERF) transcription factors regulated ABA-independent pathway genes by NACRS and DRE (dehydration-responsive element binding; G/ACCGAC) binding DNA sequences on their promoter regions. Salinity stress is known to upregulate ABA and induces genes involved in salt and osmotic alleviation. Keskin et al. (2010) reported that ABA treatment induce *MAPK4*-like genes (*TIP1* and *GLP1*) in wheat plant.

In addition, there are other hormones, like CKs, indole acetic acid (IAA), and GA, that also respond to salinity in wheat plants. It is well known that CKs are produced in the root tips and then translocated to the shoot to regulate plant growth processes. Under saline environments, reduced CK biosynthesis in the plant root could modify the global gene expression network and thus elicit appropriate responses to ameliorate the stress impacts (Nishiyama et al. 2012). Decrease in CK level was detected as an early response to salinity as they have a vital impact by acting as an intermediate in the demonstration of protective role of epibrassinolide and methyl jasmonate in wheat (Shakirova et al. 2010). It has also been reported that there is the existence of cross talk among CKs, ABA, and stress-signaling pathways. CKs have an important regulatory role in ABA-mediated stress signaling. Cytokinin and ABA induce antagonistic activities during some developmental processes, such as plant stress tolerance. ABA accumulation induces stomatal closure, accelerates leaf senescence, downregulates plant growth, and induces protective substances biosynthesis that helps plants to tolerate stressful conditions. On the other hand, CKs delay stomatal closure and leaf senescence (Pospisilova et al. 2005; Nishiyama et al. 2012). Furthermore, saline condition alters IAA metabolism and distribution. Indeed, reduced plant growth under salt stress condition is achieved by altering auxin accumulation and redistribution. In this concern, Hassan and Bano (2016) postulated that the adverse effect of salinity on plant growth and productivity of wheat was greatly due to the decreases in the content of IAA and GA as well as increase in ABA content. Indeed, exposing to abiotic stresses reduced the bioactive GAs. Similar observation was also showed by Singh et al. (2017), who found considerable decrease in growth and biomass attributes of wheat plants under salinity stress. Salt-affected wheat plants also exhibited lower auxin content compared with their respective control plants.

Recently, DELLA family proteins, major GA negative regulators, are known as vital regulators that mediate the cross talk of various phytohormones and integrate plant responses to abiotic stresses (Davière and Achard 2016). Their accumulation restrains growth and enhances stress tolerance through reducing GA signaling activity and stimulating the expression of some ROS detoxification enzymes (Harberd et al. 2009). DELLA proteins can also interact with XERICO, an inducer of ABA biosynthesis, or cause inhibition in JAZ proteins to regulate salt stress response (Nongpiur et al. 2016). Moreover, Harberd et al. (2009) and Pearce et al.

(2011) postulated that the mutant DELLA proteins in wheat plants are unable to interact with the GA receptor, causing reduction in GA responsiveness. Indeed, this led to DELLA protein accumulation and, hence, plant height reduction.

Under drought condition, ABA is the real hormone that is responsible for plant adjustment to this harsh environment. ABA induces plant drought tolerance by closing stomata and increasing accumulating of various proteins and osmoprotectants that led to gas exchange disturbance and photosynthesis inhibition and consequently plant growth inhibition (Ji et al. 2011). Upon occurrence of osmotic stresses, ABA is accumulated due to increasing the expression of several ABA biosynthesis genes, such as *ZEAXANTHIN EPOXIDASE* gene (*ZEP*; also known as *LOS6* [for *LOW EXPRESSION OF OSMOTIC STRESS-RESPONSIVE* gene 6]/*ABA1*), the *ALDEHYDE OXIDASE* gene (*AAO3*), a *9-CIS-EPOXYCAROTENOID DIOXYGENASE* gene (*NCED3*), and the *MOLYBDENUM COFACTOR SULFURASE* gene (*MCSU*; also known as *LOS5/ABA3*) (Zhu 2002). In addition, drought triggers fast formation of ABA that initiates expression of wide range responsive to ABA (RAB) stress-related genes (Fujita et al. 2011). It is postulated from Shakirova et al.'s (2016) results that exposed wheat plants to water stress led to ABA accumulation and to decline in IAA and CK levels, the changes being more dramatic in the less-resistant cultivar. Ethylene is also a negative regulator of water stress response through reducing root growth, shoot/leaf expansion, and photosynthesis as well as promoting leaf senescence (Rajala and Peltonen-Sainio 2001). However, CKs can delay premature leaf senescence and death, and thus an increase in its endogenous level by expression of *isopentenyltransferase* (*IPT*), a CK biosynthetic pathway gene, induces stress adaptation (Peleg and Blumwald 2011). As regards to IAA effect under drought conditions, Xie et al. (2003) postulated that decreasing IAA content in winter wheat plants upregulated the genes encoding late embryogenesis abundant (LEA) proteins causing plant drought tolerance. GA can also regulate plant drought tolerance. Water-stressed plants exhibited lower GA content that decrease plant growth (Peleg and Blumwald 2011). Subsequently, the net result of drought stress response is regulated by a balance between hormones that promote and those that inhibit the trait, instead of individual hormones (Basu et al. 2016).

Brassinosteroids as a class of plant hormone has vital role in various physiological and biochemical processes in plants under both non-stressed and stressed conditions (Talaat et al. 2015b, Talaat and Shawky 2016; Todorova et al. 2016). 24-epibrassinolide-induced salt tolerance in wheat plants was related to higher activities of NR, CA, PSI, and PSII, as well as higher contents of relative water, chlorophyll, nitrate, carbohydrate, and protein. In addition, 24-epibrassinolide (EBL) under saline conditions enhanced glycinebetaine formation by stimulating its biosynthesis and membrane stability index as well as altered polyamine pool (Talaat and Shawky 2012b). Furthermore, Talaat and Shawky (2013a) pointed out that EBL alleviated the negative impact of salt stress on wheat plants by enhancing the acquisition of N, P, K^+, and decreasing Na^+ uptake. Such a response could be due to their contribution in many processes such as regulating the ion uptake and the expression of K^+ and Na^+ transporters and H^+ pumps. Salt-affected wheat plant treated with EBL maintained cell turgor potential by the accumulation of various osmoprotectants that generate resistance capacity by their essential roles in osmotic adjustment, protection of cellular macromolecules, maintenance of cellular pH, and scavenging of free radicals. The EBL treatment under saline conditions also changed the plants' ROS scavenging capacity by increasing antioxidant enzyme activity and antioxidant molecule content: however it decreased the H_2O_2 and MDA contents. This result could be attributed to de novo synthesis and/or activation of the enzymes. In addition, data of Shakirova et al. (2016) revealed important contribution of EBL on wheat plants exposed to drought stress. Pretreatment with EBL alleviated the negative impact of drought on the hormonal status and significantly reduced the level of stress-induced hormonal imbalance in the shoots. It significantly lowered the ABA accumulation and increased the levels of IAA and CK in water-stressed seedlings than in that untreated with EBL.

Abiotic stresses also change the composition of PAs, one of the recent classes of plant hormone. Polyamines, namely, diamine putrescine (Put), triamine spermidine (Spd), and tetraamine spermine (Spm), are involved in a variety of divergent processes (Moschou et al. 2008; Todorova et al. 2016). They can also play a vital role in stress reactions (Pang et al. 2007; Talaat et al. 2015b; Talaat and Shawky 2016). Diamine oxidase (DAO; EC 1.4.3.6) and polyamine oxidase (PAO; EC 1.4.3.4) have an important impact in production of H_2O_2, which is toxic and leads to oxidative stress (Goyal and Asthir 2010). Hence, plants can avoid the damage brought about by stressful conditions through increasing the PAs content. Furthermore, differentiation in PA values was detected in wheat cultivars grown under salt stress. High concentration of Put in wheat saline-sensitive cultivar was observed, and that attributed to K^+ starvation as Put was synthesize in leaves to replace K^+ and/or the inhibition of Spd and Spm synthesis. Moreover, high content of Spd and Spm in salt-tolerant cultivars can be due to increasing the Spd and Spm synthesis and/or inhibition in the PAO activity (El-Bassiouny and Bekheta 2005). Likewise, Talaat and Shawky (2013b) revealed that wheat cultivar Sids 1 accumulated more Spd and Spm than Giza 168; however, higher Put content was recorded in Giza 168 than in Sids 1. Thus, the individual PAs may have different roles during the response of plants to soil salinity. Saline conditions also enhanced the activities of DAO and PAO; the impact was more pronounced in Sids 1 (for DAO) and in Giza 168 (for PAO).

2.8 Inducing Oxidative Stress

Under normal cellular metabolism, ROS are created in an ordinary level. However, exposing plants during their life cycle to stressful conditions leads to excessive production of ROS like singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-). By overproduction of ROS, malondialdehyde (MDA) content and electrolytes leakage (EL) are considered to be essential biochemical markers of membrane damage. ROS generation is controlled by enzymatic and nonenzymatic antioxidant defense systems. Enzymatic antioxidant defense system includes several enzymes such as superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), peroxidase (POX, EC 1.11.1.7), ascorbate peroxidase (APX, EC 1.11.1.11), monodehydroascorbate reductase (MDHAR, EC 1.6.5.4), dehydroascorbate reductase (DHAR, EC 1.8.5.1), and glutathione reductase (GR, EC 1.6.4.2) (Alscher et al. 2002; Apel and Hirt 2004; Sairam and Tyagi 2004; Talaat 2015). Furthermore, nonenzymatic antioxidant defense system includes several molecules like AsA, GSH, carotenoids, tocopherols, anthocyanins, phenolics, etc. (Noctor and Foyer 1998; Ashraf 2009; Yildiz-Aktas et al. 2009).

Salt stress increases the production of several toxic ROS and thus induces the oxidative stress in wheat tissues. The findings of Al-Whaibi et al. (2012) clearly indicated that supplying NaCl to root medium enhanced POD, CAT, SOD, and GR activities and MDA content. Similarly, Talaat and Shawky (2013a) demonstrated that exposure of wheat plants to saline conditions increased the activities of SOD, CAT, POX, and GR; moreover it enhanced the contents of H_2O_2 and MDA. Likewise, Talaat and Shawky (2014b) showed that the activities of SOD, CAT, POX, and GR and the concentrations of GSH and AsA were increased in the leaves of wheat plants subjected to saline soils. However, these higher enzyme activities did not provide enough protection against ROS, as judged by the simultaneous increases of MDA and H_2O_2 concentrations. Salt stress also increased the EL that is consistent with the MDA level. It is also evident from Singh et al.'s (2017) experiment that the MDA, H_2O_2, and $O_2^{\bullet-}$ values were elevated by increasing salt concentration in the growing media, which indicated higher cell membrane damage and/or lower salt tolerance in salt-affected wheat plants.

It is well known that there is a close connection between drought and oxidative stress, owing to enhanced accumulation of ROS, which alters the antioxidative pathways in stressed-plants to cope with oxidative stress (Talaat et al. 2015b). Regarding Chakraborty and Pradhan's (2012) results, they found that exposed four wheat varieties to drought stress induced an initial enhancement in SOD and CAT activities; however a decline in their activities was detected during the period of stress. Moreover, Shakirova et al. (2016) postulated that exposed wheat plants to water stress enhanced MDA content. However, Sen et al. (2017) showed that the SOD, CAT, and POX activities were increased in both vegetative and flowering stages in wheat mutants under drought stress. Moreover, they found that the GR and APX activity was increased in tolerant mutants than that in cultivars with lower tolerance. In addition, Liu et al. (2018) revealed that phenolic compounds play a role in abiotic stress adaptation due to their antioxidant activities. Under drought conditions, the stress-tolerant wheat genotype accumulated high leaf total phenolic content (2880.3 mg gallic acid/100 g DW) compared to that in stress-sensitive ones (2292.6 mg gallic acid/100 g DW).

Heat stress also exacerbated the formation of ROS such as H_2O_2 and $O_2^{\bullet-}$ in wheat seedling over control and thus causing oxidative stress. Sharp increases in MDA content and EL were also detected in heat-stressed plants. The MDA and EL values were increased by 4.39-fold and 63.86%, respectively, in these plants after 12 h of exposure at 40 °C which is lethal for normal physiological and biochemical processes (Sarkar et al. 2018). SOD and POD activities were upregulated after 1 h of O_3 exposure, as a strategy to overcome O_3-induced stress. However, their activities were diminished gradually with constant O_3 exposure, which was accompanied with increasing the accumulation of H_2O_2 and MDA. ROS overproduction can aggravate membrane lipid peroxidation process, which can increase cellular membrane permeability, certified by higher MDA concentration and electronic conductivity (Li et al. 2018). Alzahrani et al. (2018) have postulated that EL was significantly increased under drought, salt, and Cd stresses when compared with non-affected plants. The increment was 192%, 142%, and 126% under Cd, salt, and drought stresses, respectively. In addition, stressful conditions caused an increase in the end product of lipid peroxidation, malondialdehyde (MDA), content by 33–49% if compared to non-affected ones. Concerning to POD, CAT, and SOD activities, they also increased under water or salt stresses: moreover further increase was observed in their activities under the condition of Cd stress.

2.9 Affecting Various Signaling Pathways

Wheat plants adapt to abiotic stress by inducing changes in gene expression, which can be considered as an important tool to understand the molecular mechanisms of stress resistance and find candidate genes to increase plant stress tolerance. Gene expression regulations are occurring at both the transcriptional and posttranscriptional levels, and it has a vital role in plant's adaptation to abiotic stresses (Lopez-Maury et al. 2008). Some drought-induced genes can induce by salinity and frost, indicating the existence of common mechanisms of the reaction of plants to oxidative stress (Gaponenko et al. 2018). Genes involved in plant response to stress conditions can be classified into three main types: (1) genes encode products that protect cells against stress-induced damage such as heat shock proteins (HSPs) or chaperones, late embryogenesis abundant proteins (LEA proteins), osmoprotectors, antifreeze proteins, antioxidants, and detoxification enzymes (Bray et al. 2000); (2) genes encode aquaporins and ion transporters that facilitate uptake and transport of water and ions (Blumwald 2000); and (3) genes encode proteins involved in signal transduction and transcription regulation, such as mitogen-activated protein kinase (MAPK), calcium-dependent protein kinase (CDPK), salt overly sensitive (SOS) kinases, phospholipases, and transcription factors (Gaponenko et al. 2018). Genes encoding transcription factors (TFs) are the main regulators of cellular processes. They are excellent candidates for modification of complex multi-gene controlled traits of crops. Under stressful conditions, TFs regulate the stress-responsive genes by binding specific *cis*-elements in their promoters and induce the activation or suppression of their transcription (Century et al. 2012). The basic leucine zipper (bZIP), dehydration-responsive element binding (DREB), WRKY, myeloblastosis (MYB), and NAC are the main TF families that participate in the response of wheat to abiotic stress (Gaponenko et al. 2018).

In regard to bZIP group of TFs, Kobayashi et al. (2008) studied the influence of bZIP-type transcription factor LIP19 in common wheat under cold stress condition. *WLIP19* was upregulated in wheat seedlings at low temperature, and its expression was increased in the frost-tolerant breeds as compared with the frost-sensitive ones.

Moreover, *WLIP19* regulated the transcription of the *Cor/Lea* genes during the formation of tolerance to abiotic stress and upregulated four *Cor/Lea* genes, *Wdhn13*, *Wrab17*, *Wrab18*, and *Wrab19*, in wheat. Zhang et al. (2009) illustrated that *TabZIP1* expression increased in wheat under high level of salt, low temperature, and treatment with ABA. Another bZIP TF, *TaABP1*, is heavily induced by ABA, high salinization, low temperature, and drought. Its expression in wheat vegetative tissues was higher than in roots. Moreover, the transgenic tobacco plants characterized by overexpression of the *TaABP1* gene showed a considerable increase in tolerance to drought (Cao et al. 2012). Overexpression of another *bZIP* gene of wheat, *TabZIP60*, provided the transgenic lines of *Arabidopsis* with improved tolerance to drought by regulating the expression of some of the key participators of the ABA-dependent signaling and cold-responsive genes (Zhang et al. 2015). Water-stressed plants showed upregulation of four cold-responsive genes, *AtRD29A*, *AtRD20*, *AtRD29B*, and *AtCOR47* that are the key regulators of the ABA-dependent signaling cascade. Wang et al. (2016) identified *AtAREB3* gene homolog of wheat, *TaAREB3*, which encodes the bZIP transcription factor of the A-group. Its overexpression provided *Arabidopsis* with high sensitivity to ABA and increased tolerance to drought and frost. TaAREB3 TF interacts with ABRE *cis*-elements of the promotors of four drought-induced genes (*AtRD29A*, *AtRD20*, *AtRD29B*, *AtCOR47*) and upregulates them under conditions of drought and frost. These genes are known to be the key regulators of the ABA signaling and provide tolerance to frost. Recently, overexpression of a wheat bZIP transcription factor gene, *TabZIP6*, decreased the freezing tolerance of transgenic *Arabidopsis* seedlings by downregulating the expression of C-repeat binding factors (*CBFs*) and some key cold-responsive (*COR*) genes, including *COR47* and *COR15B*. *TabZIP6* may function negatively in the cold stress response by binding to the promoters of *CBFs* and thus decreasing the expression of downstream *COR* genes in *TabZIP6*-overexpressing *Arabidopsis* seedlings (Cai et al. 2018).

Regarding DREB group of TFs, Morran et al. (2011) showed overexpression of *TaDREB2* and *TaDREB3* genes in water-stressed wheat plants, and *TaDREB2* was upregulated more strongly than *TaDREB3*. However, both genes were upregulated poorly at low temperature. Salt stress did not induce the expression of *TaDREB3*, and only weak upregulation of this gene was induced by ABA. Indeed, *TaDREB2* gene promotor contains both the HDZIP class I specific site (CAATTATTG), which is induced by ABA and drought, and the GATA protein binding site (AGATCCAA), the zinc finger, which is associated with activation of some of the MYB TFs in damaged tissues. In contrast to *TaDREB2*, the *TaDREB3* promotor is enriched in the drought-related elements, such as DRE/CRT, MYBR, and MYCR elements. WRKY TFs are also important in critical plant developmental and abiotic stress tolerance in wheat. Wheat WRKY genes *TaWRKY2* and *TaWRKY19* increased tolerance to drought in transgenic *Arabidopsis* plants. *TaWRKY2* binds to the *RD29B* gene promotor, and *TaWRKY19* binds to the promotors of genes *RD29A*, *RD29B*, and *COR6.6* that lead to upregulation of the genes regulated under water-deficit conditions (Niu et al. 2012). Overexpression of wheat WRKY gene *TaWRKY44* increased drought tolerance via increasing both the content of water, proline, and soluble sugars as well as the activation of the antioxidant defense system (Wang et al. 2013). Concerning MYB group of TFs, Zhang et al. (2014) showed that overexpression of wheat *TaMYB19* gene encodes R2R3-MYB protein; upregulated three genes, *RD29A*, *RD22*, and *MYB2*, in transgenic *Arabidopsis*; and increased drought, salinization, and frost tolerance. *RD29A* gene is induced in response to stress in the ABA-independent signaling cascade, while *RD22* and *MYB2* are members of the ABA-dependent signaling pathway, indicating that *TaMYB19* works in both ABA-dependent and ABA-independent signaling cascades. In regard to NAC group of TFs, Mao et al. (2014) found that transgenic *Arabidopsis* plants characterized by overexpression of three *NAC* genes of wheat (*TaNAC47*, *TaNAC67*, and *TaNAC29*) improved drought tolerance. Transgenic plants carrying *TaNAC47* gene showed an increase in the expression level of six stress-responsive genes (*RD29A*, *RD29B*, *COR47*, *RD20*, *GSTF6*, and *P5CS1*). Likewise, transgenic plants carrying *TaNAC67* gene showed an increase in the expression level of five stress-responsive genes (*DREB1A*, *RD29B*, *RD29A*, *RAB18*, and *ABI5*). In contrast, Huang et al. (2015) illustrated that transgenic plants carrying *TaNAC29* gene, the expression of some of the key regulators of ABA-dependent signaling and genes associated with fading (*RD29B*, *SAG13*, *SAG113*, *AIB1*, *ERD11*, and *ABI5*) was significantly decreased. Hence, the NAC family TFs of wheat participate in abiotic stress response both as up- and downregulators of the target genes.

Salt stress affects various signaling pathways in wheat plant that integrated to allow the triggering of appropriate cellular and physiological responses to adapt to this stress circumstance (Fig. 2). Wheat salinity tolerance can be induced by modulation of ionic homeostasis. Maintaining higher concentration of K^+ to Na^+ concentration in bread wheat leaves than that in tetraploid wheat (less salt tolerant) was governed by *Kna1* on chromosome 4D (Dubcovsky et al. 1996). High Na^+ exclusion capacity postulated that two loci, *Nax1* and *Nax2*, were associated with excluding Na^+ ions (Munns et al. 2000). Moreover, Na^+ exclusion in wheat leaves by high-affinity K^+ transporters (HKTs) has been perceived as a noteworthy system in salt stress tolerance. Accumulation of Na^+ was detected in bread wheat leaves when the expression of *TaHKT1;5-D* was decreased (Byrt et al. 2014). Additionally, a zinc finger transcription factor, *TaCHP*, facilitated salinity tolerance in wheat by improving the activity of POD that enhances ROS scavenging ability. In addition, oxophytodienoate reductase gene, *TaOPR1*, increased wheat salt resistance by enhanced ROS-associated genes (Dong et al. 2013). Phytohormone signaling pathways are triggered in salt-affected wheat plants to increase plant adaptation to this harsh condition. In this respect, wheat gene *TaAOC1* increased plant tolerance to salt stress, and at the same time, it increased the JA content (Zhao et al. 2014). *TaAOC1* and *TaOPR1* catalyzed JA synthesis and OPRI branches, respectively, which increased salt tolerance by JA- and ABA-dependent pathways (Golldack et al. 2014). The wheat *TaGBF1* gene is involved in salt tolerance and promoted blue light-mediated photomorphogenesis. Indeed, the role of *TaGBF1* in response to salt relied on *ABI5*, a key component of the ABA signaling pathway, rather than light (Sun et al. 2015). Moreover, *TaBASS2* overexpression enhanced wheat salt stress tolerance and ROS scavenging system through repression of *ABI4* expression (Zhao et al. 2016).

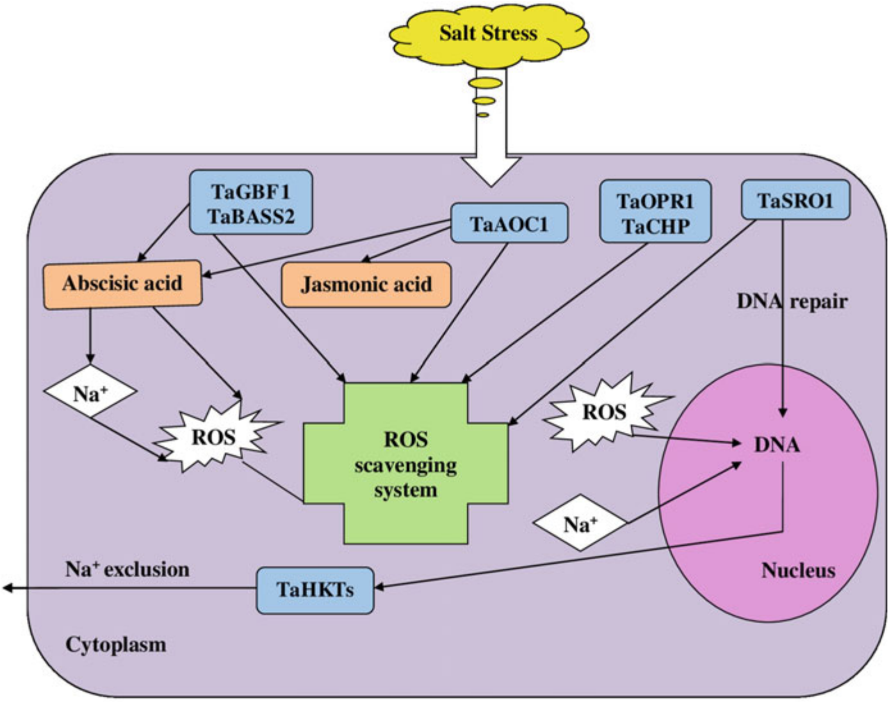

Fig. 2 Improving wheat salinity tolerance by inducing the expression of wheat genes *Ta*

Several TFs were differentially expressed under drought conditions (Ergen et al. 2009). AP2/ERF family transcription factors are classified into four sub-families in wheat; DREB, ERF, AP2, and RAV. Dehydration-responsive element binding protein (DREB) and heat shock factors (HSFs) are key regulators of complex heat-drought stress genetic networks in wheat. Stress-induced expression of DREB1A from *Arabidopsis* enhanced drought tolerance in wheat and delayed water stress symptoms (Pellegrineschi et al. 2004). Overexpression of *TaERF3* in wheat plant induced drought and salinity tolerance (Rong et al. 2014). Overexpression of *AtERF019* orthologs improves drought tolerance in wheat without any compensation of the seed set (Scarpeci et al. 2017). Furthermore, zinc finger proteins (ZFPs) are contributed to gene expression modulation under water deficiency (Chang et al. 2016). In respect to wheat WRKY TFs, four TaWRKYs (*TaWRKY16*, *24*, *59*, *61*, and *82*) were expressed under water deficiency (Okay et al. 2014). Likewise, overexpression of wheat *TaWRKY1* in tobacco enhanced drought tolerance that is achieved by inducing stomatal closure, reducing water loss, and altering osmotic adjustment (Ding et al. 2016). Remarkably, EAR (ethylene-responsive element binding factor-associated amphiphilic repression motif) facilitates recruitment of transcriptional corepressors and chromatin modifiers to abate gene expression. Amalraj et al. (2016) reported that overexpression of wheat ortholog of *RAP2.1* (*TaRAP2.1*) induced dwarfism and frost sensitivity; however overexpression of its EAR motif-inactivated variant enhanced its ability to survive drought and frost. Notably, drought condition modulated several gene expression encoding antioxidant enzymes, photosystem components, as well as enzymes representing carbohydrate metabolism and the tricarboxylic acid cycle in wheat plants (Peremarti et al. 2014; Zheng et al. 2015; Li et al. 2016a, b).

3 Conclusion and Future Perspectives

Abiotic stressors, especially, e.g., salt stress, water deficiency, metal toxicity, high and low temperatures, and radiation, are the primary causes of wheat crop loss worldwide and will soon become even more severe as desertification covers more and more of the world's terrestrial area. These stressors can affect the growth and development of wheat plant at the physiological, biochemical, and molecular levels. They can induce ionic imbalance, dehydration, hormonal imbalance, and inactivation of enzymes that influence the metabolic processes, photosynthetic efficiency, protein synthesis, and thus wheat plant yields. They can also prompt the formation of ROS and subsequent oxidative damage as well as induce the synthesis and accumulation of compatible solutes. In addition, they make changes in the activation of cascades of molecular networks involved in stress perception, signal transduction, and the expression of specific stress-related genes and metabolites. Indeed, understanding how environmental stresses affect the physiological process performance of wheat crop can be used to improve its yield potential. Improvement of yield and maintaining yield stability of wheat plants, under harsh conditions, are essential for the food security of the growing global population. Remarkably, developing high yielding wheat plants that maintain yield stability under different environmental stressors is currently needed. These wheat-resistant plants should combine a better root and shoot systems, osmotic adjustments, water relations, protein synthesis, photosynthetic capacity, and hormonal balance while avoiding the negative effects on grain yield under both normal and stressed conditions.

In nature, wheat plants face different stresses or combinations of stresses. Among the greatest challenges that remain to be addressed is conducting experiments that focused on a combination of stress responses such as those in field environments. Studying the effects of a combination of stress factors rather than an individual stress may prove advantageous because different stresses are most likely to occur simultaneously under field conditions.

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Physiological Responses of Wheat to Environmental Stresses

Sonal Mathur, Prabha Raikalal, and Anjana Jajoo

Contents

Abstract Economy of several tropical countries is regulated by productivity of wheat, which is the major staple crop. High temperature stress, salinity, osmotic stress, heavy metals, UV radiations, etc. are among major abiotic stresses that have detrimental effects on the yield of wheat. Morphological studies revealed that heavy metal, high temperature, excess light, salinity, nanoparticles, and UV stress caused a decline in plant growth, germination rate, root and shoot length, and seed filling stages in wheat plants. Biochemical and physiological studies have shown that abiotic stresses have inhibitory effect on photosynthetic active reaction centers, linear electron transport, oxygen-evolving complex, membrane integrity, and generation of reactive oxygen species (ROS). Nanoparticles, in particular, alter mineral nutrition, cause oxidative stress, and induce genotoxicity in crops and show a negative impact. However, if they are used in lower concentrations, they enhance plant productivity and crop yield. This chapter summarizes a comprehensive updated review on overall physiological responses of wheat plants to various abiotic stresses and the protective mechanisms prevailing in the plants for protection.

Keywords Abiotic stresses · High temperature · Drought · Heavy metal · Nanoparticles · Salinity · Wheat

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1 Introduction

Wheat is one of the essential food crops having worldwide production of >700 million tons that feeds around one-fifth of the human population (FAO 2011). This approximately fulfils ~ 20% of the daily protein and calories requirements for ~ 4.5 billion people all over the world (Arzani and Ashraf 2017). Wheat is called as the “King of cereals” because of its large cultivation area, economic importance, and potential for high productivity. On a global level, only 9% of the total area is contributing to crop cultivation, of which around 91% is under environmental stress conditions (FAO 2014). Various abiotic stresses, such as extreme temperature, high salt, water stress, metal toxicity, etc., drastically influence the production of wheat crop. In recent years, unpredictable weather conditions have led to increment in abiotic and biotic stresses that have affected agricultural land leading to the crop yield. Abiotic stresses exhibit major influence on plant growth, development, and productivity. Increasing attention is being given to the strategies of abiotic stress responses due to greater awareness of the threats of climate change (Wang and Xia 2018). Wheat faces a number of climatic and seasonal variations at a different stage of life cycle; however, stress if occur at reproductive phase is more harmful as compared to vegetative phase. Effect of stresses on the reproductive phase directly influences the grain setting, size, number, and dry weight (Kajlaa et al. 2015). More precisely, around 50% yield losses in crops are due to abiotic factors like high temperature (20%), low temperature (7%), salinity (10%), drought (9%), and other form of stresses (4%) (Kajlaa et al. 2015). Before introducing new varieties for various climatic conditions, it is necessary to understand the response of wheat to various environmental changes. A comprehensive understanding of the physiological responses of plants to various abiotic stresses is essential for planning future strategies for proposing plant improvement (Farooq et al. 2011).

2 Various Types of Abiotic Stresses

2.1 *Effect of High Temperature on Wheat*

Climate models envisage an increase in high temperature changes throughout the twenty-first century. This increase in temperature will have an impact on plant species, their distribution, productivity, and carbon balance. The high temperature is increasing under the drier as well as wetter conditions (Hao et al. 2013). The global mean temperature will increase 0.3 °C every 10 years and will attain around 1 and 3 °C above the current value by the years 2025 and 2100, respectively, leading to global warming (as per a report from Intergovernmental Panel on Climate Change (IPCC 2007). Plants growing in tropical, subtropical, and temperate regions are more exposed and susceptible to high temperature stress due to greater penetration of solar radiations which influence the morphological as well as the physiological behavior of plants and ultimately decline plant yield. Effects of high temperature are not only observed at the cellular level but also at the whole plant level. It may cause a shift in the transfer of assimilated carbon allocation for repair and recovery processes. There is a direct link between increase in temperature to a decrease in the photosynthetic efficiency and decreased crop yield (Mathur et al. 2011a) (Table 1). Impact of high temperature stress depends upon the intensity, duration, and change in the temperature range. Once the temperature crosses the threshold, the extent of stress increases quickly followed by complicated acclimatization effects. The magnitude and level of damage caused to a plant is dependent on the plant stage and the duration of temperature exposure (Wollenweber et al. 2003).

2.1.1 Effect on Water Relations

Relative water content, the water potential of leaf, stomatal conductance, and rate of transpiration are regulated by leaf and canopy temperature (Farooq et al. 2011). An increase in temperature in the dry or xerophytic area leads to higher vapor pressure deficit and high evapotranspiration conditions in wheat. Most species have a general phenomenon of conserving more water when the temperature exceeds above 30 °C, and thus swapping occur to balance temperature, stomatal regulations, and water exhaustion level from soil to plants (Martınez-Ballesta et al. 2009).

2.1.2 Effect on Photosynthesis

Photosynthesis is considered as one of the susceptible processes in plants to various abiotic stresses. At the whole plant level, high temperature stress influences leaf abscission, leaf area, foliar damage, growth, and reproduction (Teskey et al. 2015; Tol et al. 2017). At the leaf stage, high temperature stress inhibits photosynthesis (Mathur et al. 2011a, Mathur and Jajoo 2014a, b) and increases photorespiration and dark (mitochondrial) respiration (Wahid et al. 2007). At the biochemical level, high temperature damages photosystem II (PSII) photochemistry and electron transport (Tiwari et al. 2008), reduces fluidity of the thylakoid membrane, and reduces Rubisco activity and cell membrane stability resulting in expression of heat shock proteins and generation of reactive oxygen species (ROS) (Teskey et al. 2015).

Disruption of structure and function of chloroplasts and decrease in chlorophyll content are few characteristic features of high temperature-induced changes in photosynthesis (Mathur and Jajoo 2014b). Carboxylation during photosynthesis is synchronized by a key enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Increased photorespiration rate is often considered as a major cause for inhibition of photosynthesis due to high temperature. This can be correlated because high temperature alters the solubility of CO_2 and O_2 and the kinetics of Rubisco. For maintaining Rubisco activity, Rubisco activase (RCA) (cytosol-synthesized chloroplast protein) facilitates the removal of inhibitory sugar phosphates from Rubisco active sites (Salvucci and Ogren 1996). This step is very important because Rubisco

Table 1 Effects of various abiotic stresses on plants

Abiotic stress	Morphological changes	Physiological changes	References
High temperature	Leaf area decreases, leaf abscission, visible foliar damage, budburst, decreased crop yield and growth, floret abortion, pollen sterility, grain maturity, reduced grain yield, and grain number, reduced starch content, reduced spikelet number	Decrease in photosynthetic efficiency, damage to PSII photochemistry and electron transport reduced rubisco activity, decreased cell membrane stability, altered thylakoid fluidity, disruptions in the structure of chloroplast, reduced pigment content	Farooq et al. (2011), Mathur et al. (2011a), Mathur and Jajoo (2014a), Teskey et al. (2015) and Tol et al. (2017)
Salinity	Stomatal closure and inhibition of leaf expansion, premature senescence of leaves, reduced yield, decreased pigment content reduction in leaves number	Reduced photosynthesis and chlorophyll degradation, decreased growth and productivity, nutrient disorders and ion toxicity, the decline in carbon assimilation, inhibited electron transport rate of PSII	Negrao et al. (2017), Darko et al. (2017)
Drought	Decreased leaf area, root, decreased in the rate of seed germination, reduction in growth and yield, increased leaf senescence, reduced grain setting, reduced grain number and number of spikes	Oxidative damage to photoassimilatory machinery reduced rates of carbon fixation and assimilate translocation, pollen sterility, damage to photosynthetic pigments and photosynthetic apparatus, chlorophyll a, b and total chlorophyll content decreased	Han et al.(2016), Farooq et al. (2009), Ji et al. (2010) and Tabaeizadeh (1998)
UV	Decreased plant shoot length, and leaf protein content, reduction in plant height and leaf length/ area, leaf bronze, glazing, chlorosis and necrotic spots, the decline in net photosynthesis rate and productivity	Inhibition of chlorophyll and carotenoid content, declined Chl *a*/*b* ratio, reduced biomass, PSII electron transport activity, stomatal conductance, membrane integrity, intercellular CO_2 concentration, transpiration rate decreased	Castronuovo et al. (2014), Rahimzadeh et al. (2011), Reddy et al. (2013) and Stroch et al. (2015)
HM	Reduction in dry weight, inhibition of root and shoot growth, reduction in dry weight, reduced dry matter, reduced grain yield, reduction in biomass	The decrease in nitrogen and protein content, reduction in chlorophyll and different enzymes, reduced PSII activity, PSII electron transport, enhanced antioxidant enzyme activity	Al-Othman et al. (2016), Sazanova et al. (2012) and Mathur et al. (2016)

(continued)

Table 1 (continued)

Abiotic stress	Morphological changes	Physiological changes	References
NP	Decrease in seed germination, declined fresh and dry biomass, reduces root/shoot, reduction in growth rate of plants	Reactive oxygen species generation, proteins and DNA damage, enhanced chromatin condensation, reduced rate of transpiration, reduction in chlorophyll content, reduced nutrient uptake	Arruda et al. (2015), Hossain et al. (2016) and Ma et al. (2015)
PAH	Reduction in seed germination, decreased root and shoot growth, reduced biomass	Reduction in net photosynthesis and CO_2 assimilation, disruption of photosynthetic apparatus	Tomar and Jajoo (2015, 2017)

site gets available for carboxylation through RCA only (Salvucci and Ogren 1996). High temperature leads to deactivation of Rubisco due to a faster rate of end-product formation or due to slower reactivation of RCA, and as a result, Rubisco activase loses its capability to keep Rubisco active and efficient (Salvucci and Crafts-Brandner 2004). High temperature stress (40 °C) causes variations in availability and abundance of large and smaller subunits of Rubisco and RCA (Demirevska-Kepova et al. 2005). High temperature not only affects PSII- and photosystem I (PSI)-mediated electron transport and Calvin cycle activity but also inhibits photophosphorylation (Dias and Lidon 2009). Changes in PSII heterogeneity have been studied by Mathur et al. (2011b) in wheat plants under high temperature where they report that high temperature tends to decrease active reaction centers in PSII and reduces electron transport from Q_A to Q_B (Mathur et al. 2011b).

2.1.3 Generation of Reactive Oxygen Species (ROS) in Response to High Temperature Stress

Reactive oxygen species are known as signal molecules which not only play an important role in the cellular signal system but can also activate a complete gene (Balla et al. 2013). Under normal conditions, ROS is not accumulated in cells because the generation and scavenging of ROS are under control and balanced. In case this equilibrium is disturbed, it leads to accumulation of ROS and ultimately a reduced antioxidant enzyme activity (Luo et al. 2008). During developmental stages, if wheat is exposed to high temperature, an enhanced level of ROS is observed (Almeselmani et al. 2006). High temperature stress-induced accumulation of ROS leads to oxidative damage in plants that direct to inhibition of growth and may affect crop yield. Plants exhibit antioxidant defense mechanisms to overcome ROS-generated oxidative stress and thus protect the cell. Enzymatic and nonenzymatic antioxidant maintains the equilibrium between generation and scavenging of ROS. An increased level of superoxide dismutase (SOD) has been reported during high temperature stress (Kumar et al. 2013). Superoxide dismutases are considered as the first line of defense against ROS. In wheat during stress conditions, it is observed that the activity of most of the antioxidant enzymes is enhanced.

2.1.4 Effect on Leaf Senescence

The progressive loss of chlorophyll from leaf area, i.e., aging of leaf, due to stress or natural process, is leaf senescence. Generally, high temperature stress leads to early leaf senescence in wheat. For the reproductive development of the plant, very limited resources remain during stress conditions. Senescence-related several metabolic changes have been reported in wheat in response to high temperature stress. Chlorophyll biosynthesis is reduced during high temperature conditions which lead to leaf senescence. Due to high temperature stress, functioning of thylakoid membranes is inhibited resulting in indirect regulation of leaf senescence (Tewari and Tripathy 1998).

2.1.5 Effect on Grain Growth and Development

Grain filling and development are essential processes of the plant. This stage is very sensitive to high temperature stress. High temperature changes translocation of assimilitants during the grain filling stage which is one of the major causes of decreased crop yield. Grain filling, grain number, and grain size are temperature dependent and are readily decreased as a result of high temperature (Ferris et al. 1998). Developmental phase at which high temperature occurs is an important factor governing the effect of temperature on all these components of grain yield. The optimum temperature for wheat anthesis and grain filling ranges from 12 to 22 °C. Increased floret abortion is observed if high temperature stress is given during anthesis stage (Wardlaw and Wrigley 1994), while plants if exposed to high temperature during reproductive phase suffer from pollen sterility, tissue dehydration, lower CO_2 assimilation, and increased photorespiration. Exposure to high temperature not only affects the grain filling stage but also influences spikelet initiation, male and female sporogenesis, floral organ differentiation, pollination, and fertilization. Heat stress reduces spikelet number and number of grains per spike. If the temperature goes beyond 30 °C during floret formation, it may lead to complete sterility.

Duration of heat stress is inversely related to grain number per spike (McMaster 1997). Floral initiation is also very sensitive to high temperature and directly influences grain number. For every 1 °C (from 15 to 22 °C) increase in temperature, there is 4% decrease in grain number per spike in the 30 day preceding anthesis (Fischer 1985). If day/night temperature is increased from 25/14 °C to 31/20 °C, it not only influences grain filling but also leads to grain shrinkage via ultrastructural alterations in the aleurone layer and endosperm cells (Dias et al. 2008).

2.1.6 Starch Synthesis

Around 70% of dry weight in wheat grain is starch. Reduction in the starch deposit is considered as one of the vital causes for decreased grain weight (Bhullar and Jenner 1985). The starch synthesis process is temperature sensitive because the enzymes involved in starch biosynthesis in developing kernels are temperature sensitive (Denyer et al. 1994). As the temperature goes beyond 18–22 °C, starch biosynthesis duration and deposition in grains are reduced (Farooq et al. 2011).

2.2 Effect of Salinity Stress on Wheat Plants

Around 20% of irrigated face saline conditions which is a major problem of the world (Qadir et al. 2014) and leading to decreased crop yield. The physiological responses of plants to high salt are quite complex and varied (Table 1). Fundamentally salinity stress to plants is divided into two stages: initially within minutes to 24 hrs, shoot ion-independent response takes place which is correlated with Na^+ sensing and signaling (Gilroy et al. 2014; Roy et al. 2014). Stomatal closure and leaf expansion occur in the first phase which could be the effect of salinity on water relations (Munns and Termaat 1986). The second phase comprises of ion-dependent response of salinity which may take a long time from days to weeks. This includes buildup of ions in the shoot in toxic concentrations. It results in inhibition of photosynthesis, early senescence of leaves, and lastly reduced yield and sometimes even plant death (Negrao et al. 2017).

Salinity causes a reduction in water uptake, nutrient disorders, and ion toxicity resulting in reduced wheat growth (Esfandiari et al. 2007). The critical and sensitive stage of plant growth for salinity is germination and seedling emergence which may affect plant growth and yield (Shekoofa et al. 2013). Salinity stress is also accompanied by osmotic stress. The effect of osmotic stress includes decreased soil water potential, water uptake, cell dehydration, retarded cell elongation, stomatal closure, and decreased carbon assimilation. Ionic effect of salinity includes disturbance in integrity and selectivity of the plasma membrane and alterations in the uptake and homeostasis of essential ions. Various enzymatic and metabolic processes are disturbed due to severe salt stress. This imbalance may lead to decreased photosynthesis and enhanced chlorophyll degradation in plants. ROS generation and accumulation occur due to severe salinity which harms the plant cell and induces metabolic changes. Molecular analysis at proteomic, metabolomic, and transcriptomic levels revealed that there is a complete metabolic rearrangement in cells due to salt stress, which affects the metabolism of sugars, amino acids, and polyamines, as well as ion and redox homeostasis. These responses exhibit tissue specificity and depend largely on the species and the genotype, amount of salt, exposure time, plant developmental stage, and environmental conditions. Proline accumulation has also been observed as a result of salt stress (Darko et al. 2017).

It is reported that exposure of wheat to salinity at early seedling stage shows greater yield loss than if exposed at later stage of growth. As compared to a flowering stage, the vegetative stage is considered more sensitive to salinity stress. Decreased imbibition is also reported as one of the consequences of salinity stress. This decline in imbibition could be due to lowered osmotic potential of the medium that alters the metabolic activity. The rate of germination, the percentage of germination, and seedling growth are inhibited due to salinity stress. Accumulation of salt around rhizosphere reduces plant growth. Salinity stress is also responsible for degradation of chlorophyll content in leaves. Salt stress causes early flowering, loss in dry matter, increased root/shoot ratio, and reduced leaf size (Mass and Poss 1989). Dodd and Donovan (1999) have reported that increased transpiration rate at leaf surface could be a reason for increased salt accumulation in leaves which is indirectly related with early leaf death before maturity. Net photosynthesis decreases due to a reduced rate of photosynthesis and increased respiration per unit area of leaf. When pH of soil exceeds 8.5 or above, crop yield declines. Osmotic potential of water lowers when salts are added to water which results in the lesser availability of water to root cell. Plants also experience secondary osmotic stress due to salt stress. This suggests that various physiological responses which are invoked by water stress can also be observed under salt stress.

In salt-susceptible genotypes, a higher salt toxic level is developed in leaves which direct the senescence of older leaves, while younger leaves get damaged and become succulent resulting in decreased number of healthy leaves (Munns and James 2003). The decrease in the number of tillers and total dry matter yield is one of the major negative effects of salinity stress in wheat (Pessarakli and Huber 1991).

Various processes such as signal transduction, transpiration, membrane trafficking, and protein biosynthesis are altered under salinity stress. Feng et al. (2017) have identified 23 conserved miRNAs in wild emmer wheat which are responsive to salinity stress. On the basis of chlorophyll *a* fluorescence studies, Mehta et al. (2010) have reported retardation of PS II activity in wheat under salinity stress. According to this study, high salt stress inhibited electron transport rates at the donor side by ~75% and at the acceptor side by ~25% of PS II. As compared to the acceptor side, the donor side of PS II was more significantly affected. Increasing salt concentration led to an increase in the number of inactive PS II centers. Complete recovery of the damage caused at the acceptor side was observed, while damage to the donor side could be recovered only by ~ 80% (Mehta et al. 2010). Further, Tomar et al. (2012), in a study on wheat leaves, differentiated between osmotic and ionic effects of salinity on PSII. Osmotic stress was found to reversibly inactivate photosynthetic electron transport via shrinkage of the intracellular space. In contrast, ionic stress inactivated both photosynthetic and respiratory machinery due to leakage of Na^+ (Allakhverdiev et al. 2000; Tomar et al. 2012). They also reported that as compared to osmotic effects, the prominent decline in the reduction of PQ pool was observed due to the ionic stress of salinity.

2.3 Effect of Drought Stress on Wheat

Drought is one of the most common abiotic stresses among all the stresses that have a deleterious effect on growth and development of plant (Zalibekov 2011; Hossain et al. 2013). Out of all the losses, greatest losses to crop yield in agriculture are induced by drought in all climatic regions (Daryanto et al. 2016). Drought stress decreases leaf area in wheat seedling (Han et al. 2016). Palisade tissue cell in wheat leaf gradually became shorter, and a decrease in thickness of spongy tissue was observed under drought stress (Zhang et al. 2015; Han et al. 2016). Drought stress was found to significantly affect the rate of germination and growth of root and leaf in wheat cultivars (Duan et al. 2017). Drought stress also affected nutrient (N, P, K, Ca, and Na) uptake in the plant. Drought stress experienced by wheat crop during growth results in decline of total biomass. Drought stress enhances leaf senescence (Yang et al. 2003) and causes oxidative damage to photoassimilatory machinery (Farooq et al. 2009), reduces the rate of carbon fixation, and assimilates translocation (Asada 2006). During reproductive and grain filling stages, drought stress leads to pollen sterility (Cattivelli et al. 2008), reduced grain set and development (Nawaz et al. 2013), and reduced sink capacity (Liang et al. 2001) that ultimately leads to decreased crop yield. Reduction in the number of grains is due to the lack of fertilization of the egg, resulting in the undeveloped ovule. If drought conditions are given at young microspore stage, the pollen becomes sterile thereby reducing grain number (Saini and Westgate 2000; Ji et al. 2010). Even a brief exposure of drought during meiosis of pollen mother cells and anthesis interrupts succeeding microsporogenesis resulting in pollen sterility. This failure directly affects grain number causing a reduction in grain yield and reduces grain set by 40–50% (Cattivelli et al. 2008; Farooq et al. 2014). Spike length, number of spikelets per spike, number of grains per spike, 1000 grain weight and grain yield were considerably affected under drought stress at any growth phase (tillering, flowering, and grain filling).

Stomatal closure due to drought stress decreases CO_2 influx resulting in a decrease in carbon fixation by mesophyll cells (Chaves et al. 2003; Flexas et al. 2004). Plants subjected to drought stress during the anthesis stage face considerable damage to photosynthetic pigments. This ultimately results in the reduction of carbon assimilation process and chlorophyll content (Saeidi and Abdoli 2015). Other metabolic processes of plants like activity of Rubisco (Bota et al. 2004), regeneration of ribulose bisphosphate (RuBP), and ATP synthesis (Farooq et al. 2014) are also directly affected due to salinity. Reduction in stomatal conductance is one of the primary causes of reduced photosynthesis during the initial onset of drought (Cornic 2000). Drought at later stages of plant development may cause tissue dehydration leading to metabolic impairment (Farooq et al. 2009). Decrease in net photosynthesis rate due to drought stress in wheat is basically due to reduced RuBP content (Holaday et al. 1992). Photosynthetic apparatus including PSI may get damaged by excessive production of ROS causing a substantial decrease in carbon fixation. Photosynthesis-related proteins are significantly downregulated under drought stress (Neslihan-Ozturk et al. 2002). Drought stress decreases the photosynthetic capacity of plants by decreasing the chlorophyll *a, b* and total chlorophyll content and affects chloroplast membrane permeability and thylakoid membrane integrity (Tabaeizadeh 1998).

2.4 Effect of Ultra Violet (UV) Radiations Stress on Wheat

Life forms on earth and ecosystem are mainly sourced with energy from the sun reaching the earth surface. Different wavelengths of electromagnetic radiations largely classified as ultraviolet radiation (UVR) (20–400 nm), photosynthetically active radiation (PAR~400–700 nm), and far-red radiation (FR~700–780 nm) are part of the solar radiations. Ultraviolet radiation is considered to be most energetic although it makes only 7–9% of the total solar radiation reaching the biosphere (Frohnmeyer and Staiger 2003; Singh et al. 2012a, b). It comprises of UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (220–280 nm) components. The depletion of ozone layer thickness in the stratosphere is increasing every year. This has resulted in increased amount of harmful UV-B rays reaching the earth surface (Ashraf and Harris 2013). UV-B being most energetic has a greater potential to cause biological damage, and even a small increase in its amount could lead to significant biological damage (Zlatev et al. 2012). Increased UV-A exposure in wheat leads to an inhibition in the shoot/root length, reduced total leaf protein, inhibition of total chlorophyll, and carotenoid content. A simultaneous increase in flavonoid concentration was observed in higher plants (Rahimzadeh et al. 2011; Stroch et al. 2015). Exposure to UV-A also leads to an inhibition in PSII electron transport (Jayakumar et al. 2004).

Ultraviolet C radiation is harmful to wheat at genomic level as it causes mutations by forming pyrimidine dimers and free radicals at the cellular level, followed by impairment in metabolic and photosynthetic processes (Murali and Saxe 1984; Kovalchuk et al. 2000). Apart from this, plant photosynthetic parameters like stomatal conductance, membrane integrity, intercellular CO_2 concentration, and transpiration rate are severely inhibited by UV-C radiations. This is because UV-C induces a reduction in carbohydrate content which leads to inactivation of Rubisco activity in Calvin cycle. Teramura and Sullivan (1994) reported that as the exposure time to UV-C increases, the inhibitory effects also increase. Ultraviolet C radiation showed a decline in photosynthetic rate as well as net photoassimilation due to photoinhibition of phytohormones, retardation of essential enzymes, amino acids, aggregation of plastoglobuli in chloroplasts, decreased cell, and chloroplast size followed by disruption of the thylakoid membranes (Najeeb et al. 2011). The cell wall of mesophyll cells become contracted on treatment with UV-C radiations (Gunter et al. 2007). It is assumed that UV-C enhances the secretion of cell wall-degrading enzymes ultimately resulting in reduced thickening of the cell wall (Gunter et al. 2007). A decline in Chl content and Chl a/b ratio was observed in wheat which could be due to a reduction in chlorophyll protein complexes and modifications in the stoichiometry of these protein complexes (Cakirlar et al. 2008). Thus, all these deleterious effects caused by UV-C make these radiations extremely harmful to plants causing permanent and irreversible damage to plant's physiological as well as morphological characteristics, leading to plant death (Najeeb et al. 2011).

Several metabolic properties of higher plants, may it be morphological, physiological, or reproductive, are influenced by UV-B [e.g., biomass and yields, pigment contents, nucleic acids, PSII thylakoid membranes, and proteins] (Hectors et al. 2010). The morphological changes taking place due to UV-B include a reduction in plant height, leaf length, area (Reddy et al. 2013), leaf bronze, glazing, chlorosis and necrotic spots (Kakani et al. 2003), and decreased leaf nitrogen productivity (Zuk-Golaszewska et al. 2003). Reduction in biomass of wheat plants in response to UV-B exposure has been reported (Rahimzadeh et al. 2011). Ultraviolet B radiation alters light-harvesting complex II (LHC II) and PSII by detaching them from each other and initiating inhibitory modifications in function of quinone electrons acceptors (Q_A and Q_B) and Tyr Z and Tyr D. As reported by Kataria et al. (2014), PSI and cytochrome b_{6f} ($Cytb_{6f}$) are more robust to UV-B exposure as compared to PSII. This may be because of two binding sites of quinine of $Cytb_6$. Site one at which quinol oxidation takes place while the other where quinone reduction happens, and probably this is the reason for robustness of $Cytb_{6f}$ to UV-B exposure (Hope 1993). As reported by Brosche et al. (1999), PSI light-harvesting Chl *a*/*b* binding protein genes are also affected by exposure to UV-B radiations. Longer exposure to UV-B shows a detrimental effect at the molecular level by downregulation in the mRNA level of Rubisco subunits wherein the larger subunit of Rubisco is converted to 66 kDa protein by oxidative alteration (Wilson et al. 1995; Kataria et al. 2014). Enhanced UV-B has widespread negative role in declining the net photosynthesis rate and productivity (Teramura and Ziska 1996; Nogues et al. 1999). Ultraviolet radiation also results in transcriptional activation and repression of specific sets of genes, the disintegration of photosynthetically important proteins D1 and/or D2 (Papageorgiou and Govindjee 2004; Mathur and Jajoo 2015, 2018a). Ultraviolet B radiation directly generates ROS which are injurious to plant health and may lead to transcriptional activation.

2.5 *Effect of Heavy Metal (HM) Stress*

Heavy metals are naturally present in small traces in the environment and have been detected in soil and water. Any metallic element which is high in density and is toxic or poisonous even at a very low concentration is termed as "heavy metal." Metal and metalloids having an atomic density greater than 4 g cm^{-3}, which is five times greater than water, are grouped as HM (Hawkes 1997). For a comparison of density of HM, its chemical property is a crucial factor (Gill 2014). In soil, these heavy metals are present in the form of free metal ions, soluble metal complexes, organically bound metals, exchangeable metal ions, and precipitated or insoluble compounds, such as carbonates and oxides (Shanker et al. 2005). Heavy metals may enter and accumulate in the food chain through plants, animals, and humans. Once they are in the food chain, it is very difficult to remove them. Different biochemical responses and crop yield are triggered in plants when subjected to heavy metal stress (Mathur et al. 2016). Heavy metals interact with proteins thereby inhibiting plant growth, water regime, metabolic activities etc. In plants, under HM stress, the main cause of all the destructive functional changes is the alteration in the balance of ROS and antioxidants in plant cells. Reactive oxygen species such as superoxide anion ($O_2^{\bullet -}$), hydroxyl radical (OH•), and hydrogen peroxide (H_2O_2) are produced under HM stress (Pradedova et al. 2011). Under normal conditions, the oxidative process does take place in the cell, but antioxidant system maintains the level of ROS. Level of prooxidants and antioxidants varies according to stressful environmental factors. It is supposed that the shift of this interrelation triggers reactions of plant cell damage. Proteins and lipid peroxidation (LPO) reactions are initiated by ROS, which affects plasma membrane by increasing its permeability, breaks DNA and proteins which ultimately affects the whole metabolism, and finally leads to cell destruction.

Roots and aboveground tissues are the sites of heavy metal accumulation. Lead, Cd, Ni, As, etc. have been isolated from wheat root. As is a strong bioaccumulator found to be accumulated in a considerable amount in aerial parts of wheat plants. The most general pattern of accumulation of HM in the various parts of wheat is roots>leaves > stem> seed. Roots showed higher accumulation of metals as compared to aerial parts, and lowest levels being found in seeds and grains (Al-Othman et al. 2016). Along with inhibition of shoot and root length, HM also inhibits the growth of aboveground parts of young wheat plants. Maximum inhibition of shoot growth was observed by Ni and least with Zn (Sazanova et al. 2012). Phytotoxic effect of heavy metals was in the following order: Cd > Cu > Ni > Zn > Pb > Cr. Chromium and Pb showed the minimum effect on dry weight reduction as compared to others. Protein content decreased under changing HM concentration in wheat grains. Metal treatment also showed a decline in wheat nitrogen content. The primary target of heavy metal resulting in metal toxicity is enzymes and their functional proteins which have relatively higher affinities for heavy metals (Hampp et al. 1976). Studies have reported that Cr^{3+} if added in the sand culture of wheat under glass house conditions significantly reduces biomass, chlorophyll content, and activities of enzymes like catalase and peroxidase, while it enhanced the acid phosphatase and ribonuclease activities (Athar and Ahamad 2002).

2.6 Effect of Nanoparticles (NP)

Nanotechnology is the most promising and emerging technology of the twenty-first century. Nanoparticles indicate small-sized particles with the large surface area. This property gives them special chemical as well as biological characteristics at a nanoscale level as compared to bulk material (Fu et al. 2014; Yahyaoui et al.

2017). Because of nanosize, these are widely used in plant sciences where they are known to boost plant metabolism (Giraldo et al. 2014). It is reported that the ability to harvest light energy by chloroplast was enhanced when LHC were subjected to nanoparticles like carbon nanotubes (CNTs). Carbon nanotubes allow the plant chloroplast to harvest maximum light which are in the ultraviolet, green and near-infrared region by serving as artificial antennae (Giraldo et al. 2014). The role of CNTs in enhancing seed germination, growth, and development in wheat has also been reported (Lahiani et al. 2013; Siddiqui and Al-Whaibi 2014; Siddiqui et al. 2015). Lower concentrations of metal oxide NPs like TiO_2NPs, ZnONPS, and CNTs showed beneficial effects such as enhancement in seed germination, increased root, and shoot growth in wheat plants under water stress condition (Tripathi and Sarkar 2014; Ramesh et al. 2014). The TiO_2NPs regulate nitrogen metabolism by altering the role of enzymes involved in nitrogen metabolism such as nitrate reductase, glutamate dehydrogenase, glutamine synthase, and glutamic-pyruvic transaminase. These enzymes help in nitrate absorption from soil that increases synthesis of protein and chlorophyll which indirectly affects increasing fresh and dry weight in the plant (Mishra et al. 2014; Siddiqui et al. 2015).

Accumulation of NPs is increasing in plants due to their excessive use. Thus, it is necessary to know about the adverse effects of nanoparticles as they can be deposited and accumulated in the soil when transported through water (Hossain et al. 2015; Ma et al. 2015; Iannonea et al. 2016). Many reports focus on the phytotoxic and ecotoxic effect of NPs in wheat at varying concentrations. These concentrations affect morphological, biochemical, and physiological processes in wheat (Rico et al. 2015; Tripathi et al. 2017a). Phytotoxicity of nanoparticles is mainly because of ROS generation which causes oxidative stress in wheat. Reactive oxygen species generation due to NP is directly or indirectly responsible for genotoxicity in wheat (Yin et al. 2012). Increasing oxidative stress results in lipid peroxidation and protein and DNA damage in plants (Arruda et al. 2015). Plants take up NPs of different size which is translocated to shoot and different aerial parts of plants. Through these parts, NP gets accumulated and increases the possibility of getting cycled through various trophic levels (Monica and Cremonini 2009). This accumulation of NPs results in the degradation of crop quality by lowering the rate of seed germination, reduction in biomass, reduction of fresh and dry weight, and reduction in root/shoot length. Nanoparticles also inhibit photosynthetic apparatus, cause DNA damage, enhance lipid peroxidation and up- and downregulation of various stress-related genes, and lastly lead to apoptosis. Different growth stages, like seed germination and root elongation, have been shown to be inhibited by metal oxide nanoparticles (e.g., ZnO, TiO_2) (Dogaroglu and Koleli 2017). The AgNPs induce damaging effects on DNA by causing the formation of chromatin bridges, stickiness, disturbed metaphase, and multiple chromosomal breaks (Patlolla et al. 2012). A study by Wang et al. (2016) showed the effect of Ag_2S-NPs in the reduction of growth in wheat plants, by interfering with the process of plant defense system, ethylene signaling pathway, and upward water transport (Tripathi et al. 2017a). Maximum growth reduction was observed in wheat plants when treated with metallic nanoparticles and ionic silver. Sliver nanoparticles get accumulated in plant tissues and are a major cause of reduction in plant growth rate (Pradas del Real et al. 2017). Nanoparticles present on root surface can bring about a change in the surface chemistry of roots which eventually affects the uptake of nutrients in plant roots. The AgNPs when absorbed on root surface harm the root cells and root cell membrane, impairing cell division and leaf transpiration, and also by reducing the plant root elongation and reduction in plant biomass. Cellular organelles of root cup cells, root meristematic cells, and differentiating cells like plastids, vacuole, and endoplasmic reticulum (ER) were more sensitive. Seedling elongation was negatively affected by AgNPs (Burman et al. 2013). A concentration of 10 mg L^{-1}AgNPs resulted in light browning in root tips, which suggests that many of the AgNPs were adsorbed to the root tips. Proteomic analysis has confirmed that roots are the major targets of the toxic effects of AgNPs (Vanninia et al. 2014).

Exposure to metal oxide like ZnONPs caused enhanced ROS generation and alteration in the plant's antioxidant defense system. This damages important macromolecules such as lipids and hinders plant growth (Tripathi et al. 2017b). The ZnONPs primarily adhere to the root surface and are observed in the apoplast and protoplast spaces in root endodermis (Lin and Xing 2007) and also reduced root length (Yahyaoui et al. 2017). Higher concentration of ZnONPs in wheat plants showed decline chlorophyll *a,b* and carotenoids (Dimkpa et al. 2012).

2.7 Effect of Polycyclic Aromatic Hydrocarbons (PAH) on Wheat

Environmental pollution has an enormous effect on the complete ecosystem. Polycyclic aromatic hydrocarbons are one of the recalcitrant groups of "persistent organic pollutants" (POPs) and are known to be highly persistent in the environment (Cooke and Dennis 1983). Polycyclic aromatic hydrocarbons are present in soil, air, and sediments as well as on various consumable products. The maximum contribution for the release of PAH in the environment is through anthropogenic processes such as fossil fuel combustion and by-products of industrial processing. Forest fires and agricultural land burning (crop remnants burning) and sometimes cooking could also release PAHs. Around 90% of PAHs in the environment exist in the soil surface (Wild and Jones 1995). Furthermore, plants grown in PAH-contaminated soils absorb PAHs (near 45% of all released PAHs in the environment) and pose a problem regarding crop yield.

Hydrocarbon phytotoxicity is extremely variable and is dependent upon the type, time of exposure, concentration, and environmental conditions. Polycyclic aromatic hydrocarbons toxicity has quantitative as well as qualitative influence on various physiological and biochemical processes resulting in retardation of plant growth and development (Jajoo et al. 2014; Jajoo 2017). Entry of PAH in plants can be direct via stomata or through the root system and can hinder plant growth (Kuhn et al. 2004). Polycyclic aromatic hydrocarbons are also responsible for alteration in enzymatic activities, degradation of pigment content, damage to the membrane via lipid oxidation (Branquinho et al. 1997), inhibition of net photosynthesis, and interference with the metabolic processes in wheat. Being lipophilic, PAHs have the capability of modifying membrane permeability and integrity (Liu et al. 2009). It is assumed that because of this lipophilic nature, PAHs can build up toxicity in thylakoid membranes and are involved in negatively modifying the structure and function of photosynthetic apparatus (Kreslavski et al. 2014). A decrease in plant hormones and CO_2 assimilation has been reported as a result of PAHs phytotoxicity. This causes deformation of mitochondria, chloroplast, and other cellular structures in plants as revealed by transmission electron microscopy (Liu et al. 2009). Seed germination and germination energy have been reported to decrease in response to increasing fluoranthene exposure in wheat. Change in the endogenous level of hormones like cytokinin, ethylene, and ABA may cause change in the rate of germination of seeds in the presence of fluoranthene (Kummerova et al. 2012). Morphological alterations induced by PAHs include retarded root and shoot growth, decreased root hairs, distorted trichomes, chlorosis, late flowering, the appearance of white spots, and necrotic lesions. Molecular analysis of 21-day treated specimens detected an increase in the transcript levels of the pathogenesis-related gene PR1 and a decrease in the expression of EXP8. Tomar and Jajoo (2015) and Sharma et al. (2017) have reported that fluoranthene and anthracene decreased photosynthesis rate and plant growth in wheat plant. Tomar and Jajoo (2014) also reported declined root/shoot growth, leaf elongation, and biomass production at low concentration of fluoranthene. They also reported that PAHs have an effect on primary processes of photosynthesis, i.e., on light absorption and trapping of light in wheat plants. Dark reaction was more sensitive to fluoranthene as compared to the light reaction in wheat. Reports revealed that PAHs showed a negative relationship between carboxylation capacity and biomass production. A recent study by Tomar and Jajoo (2017) has revealed that in photosynthesis, not only linear electron transport but cyclic electron flow around PSI is also affected negatively by PAHs. Polycyclic aromatic hydrocarbons are also found to cause oxidative stress in cells during early developmental stages of wheat (Singh et al. 2012a, b).

After summarizing the effects of various abiotic stresses on the physiology of wheat plants (Fig. 1; Table 1), in the next segment of the chapter, we will discuss how wheat plants protect themselves from these harmful stresses.

3 Adaptive Mechanism in Wheat in Response to Abiotic Stresses

The damaging effects of various abiotic stresses and their implication are well known in plants. To avoid the injurious effects of these stresses, plants adopt several defense mechanisms in due course of their life cycle (Fig. 2). Being immobile, plants are forced to invest valuable resources in modifying their metabolism to prevent

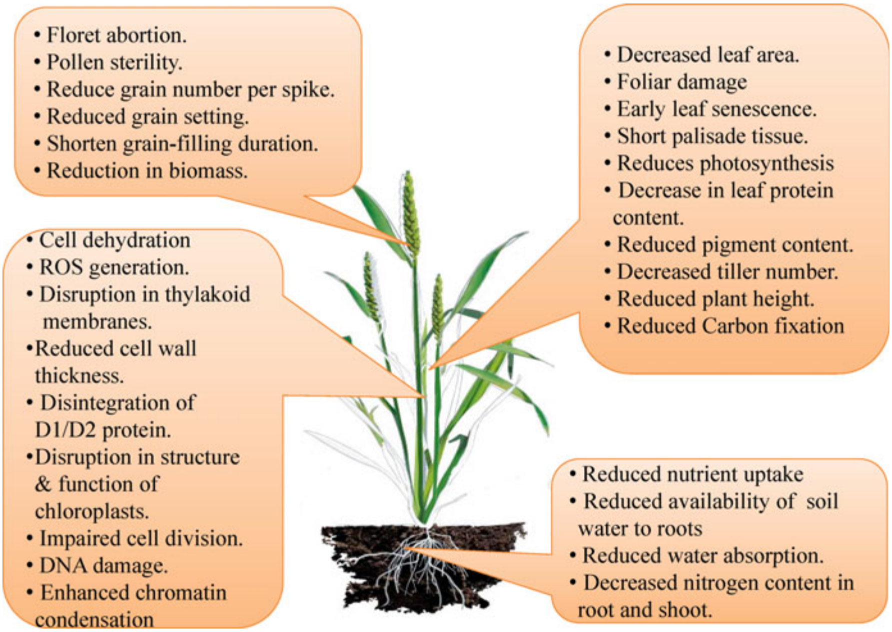

Fig. 1 Summary of various abiotic stresses on wheat physiology

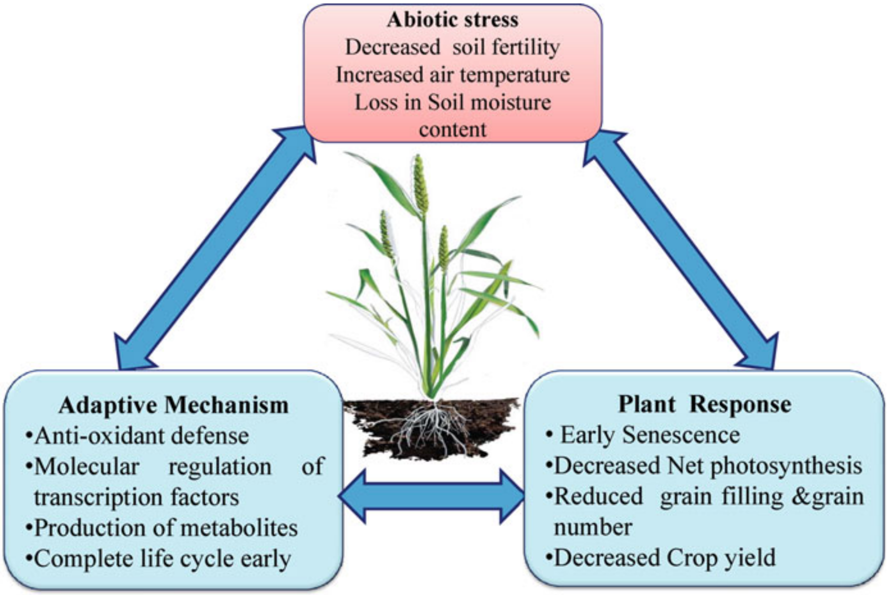

Fig. 2 Interaction of abiotic stress, its response, and adaptive mechanism in wheat

damage caused by various stresses through a process generally referred to as acclimatization. Plants have developed mechanisms for stress adaptation, defense, and repair. The biological processes in plants that are involved in adaptation to stress are complex. To handle alterations in temperatures, salinity, and drought, plants remodulate their biochemical composition to adapt and survive (Ruelland and Zachowski 2010). Plants can trigger programmed cell death in specific cells or tissues, a process that can lead to the shedding of leaves, abortion of flower or fruit formation, or even death of the entire plant. Reprogramming of transcription, proteins, metabolites, and lipids helps the plants to reset a better metabolic balance for survival and good functioning even under stress conditions.

Plants have some natural mechanisms which they adapt to overcome the hazardous impact of abiotic stress. However, research is now focused more toward protection of plants against various abiotic stresses. These strategies are beneficial for plants as well as for crop yield.

3.1 Natural Adaptive Mechanisms in Plants

Plants exhibit various physiological responses against abiotic stresses which include closure of stomata, decrease in the activity of photosynthesis, development of oxidative stress, alteration in the integrity of cell wall, signal recognition of roots, turgor loss and adjustment of osmosis, reduction in water potential of leaf, decrease in stomatal conductance to CO_2, reduction of internal CO_2 concentration, and reduction of growth rates.

Many plants complete their life cycle before the commencement of stress, especially under drought stress; this is known as “drought escape” (Chaves et al. 2003). Few important characteristics of drought escape include time of flowering, rapid phenological development, remobilization of pre-anthesis assimilates to developing grains, and developmental plasticity (variation in duration of growth period depending on the extent of water deficit) (Turner 1979). Out of all, time of flowering is considered as the most sensitive. Under stress condition, inner water potential reduces in wheat to overcome dehydration and to balance water potential. For this, osmotic adjustment processes are carried out by building up osmolytes which help the plants to maintain water balance.

The application of abscisic acid (ABA), a plant growth regulator alleviates the negative impact of many stresses. The expression and number of various salt and drought-responsive genes are modified in response to a cellular signal from ABA. Expression of MAPK4-like, TIP 1, and GLP 1 genes are induced through ABA application in wheat in response to salinity stress (Gupta and Huang 2014). Initiation and synthesis of flavonoids, phenylpropanoid pathways, and brassinosteroid pathways and initiation of antioxidant defense system (including vitamins) are few characteristic defenses and protective responses induced against UV radiations in wheat (Agati et al. 2013). Vitamin B_6 quenches singlet oxygen and superoxide and therefore shows antioxidant activity (Singh et al. 2014; Mathur et al. 2018a). Flavonoid biosynthesis is regulated by UV-A, UV-B, and visible radiations (Siipola et al. 2015) which in turn is regulated by UVR8 gene indirectly (Morales et al. 2013; Mathur et al. 2018a).

3.1.1 Antioxidant Defense System

Reactive oxygen species and certain free radicals such as hydroxyl radicals, superoxide radicals, etc. are produced in the cells under normal condition, but excess production of them may be harmful (Esfandiari et al. 2007). Heat/high temperature stress, salinity, drought, UV, PAH, and NP trigger the production and accumulation of ROS. Hence, detoxification of ROS by the efficient antioxidant systems is important for protecting plants from stress (Asada 2006; Suzuki and Mittler 2006). Enzymatic as well as nonenzymatic antioxidant systems are involved in plants. The enzymatic antioxidants include enzymes such as dehydroascorbate reductase, ascorbate peroxidase, superoxide dismutase, guaiacol peroxidase, glutathione *S*-transferase, catalase, and glutathione reductase. Nonenzymatic antioxidants include tocopherols, glutathione, ascorbate, etc. Catalase catalyzes decomposition of H_2O_2 to H_2O and O_2. Guaiacol peroxidase and ascorbate peroxidase can also detoxify hydrogen peroxide, but they need reducing agents through some reactions. Ascorbate helps in scavenging of OH•, $O_2^{\bullet -}$, and H_2O_2 for the ascorbate-peroxidase-mediated reactions, while guaiacol scavenges ROS for guaiacol peroxide-mediated reactions (Goyal and Asthir 2010).

3.1.2 Stay Green

Early leaf senescence is observed under high temperature, salinity, heavy metal, NP, UV, and drought stress. Early senescence is more prominent if these stresses are exposed during post-flowering stages of grain filling. "Stay green" refers to the maintenance of leaf chlorophyll and photosynthetic capacity. It is regarded as a stress indicator (Fokar et al. 1998). Since chlorophyll loss is associated with decreased assimilation of carbon in grains, stay-green genotypes will be capable of sustaining grain filling even under stress conditions. The stay-green trait has been evaluated in several crops (Kumari et al. 2007), but breeding for this trait has been limited in wheat (Farooq et al. 2011; Darko et al. 2017). Few stay-green sorghums and wheat genotypes have been found to contain higher specific leaf nitrogen contents, indicating that this trait is correlated with shoot nitrogen content (Borrell et al. 2001). In wheat, there is a positive correlation between the stay-green duration of the flag leaf and harvest index with water use efficiency during grain development (Gorny and Garczynski 2002).

3.1.3 Molecular Regulations

Under various abiotic stresses, regulation of gene expression involves wide spectrum of mechanisms to increase or decrease the production of the specific gene product in plants (Fig. 3). Significant regulators that control the gene expression are the transcription factors. Among them, a number of stress-responsive members are included such as bZIP, WRKY, AP2, NAC, C_2H_2 zinc finger gene, and DREB families. These transcription factor genes can control the expression of a wide range of target genes by binding the specific cis-acting element in the promoters of these genes. Expression of bZIP genes was reported to be upregulated during long-term salinity-sensitive wheat variety while downregulated in salt-tolerant wheat variety (Johnson et al. 2002). It is assumed that overexpression of NAC transcription factor mitigates salt stress in wheat and rice.

Plant defense regulated by genes in UV is very much dose dependent. For UV-B damage, UVR8 gene is the most common gene that is considered as plant savior gene. The UVR8 gene is involved in chloroplast protein repair and DNA repair, which regulate and manage many screening pigment proteins and metabolite (Singh et al. 2014). The UVR8 gene indirectly also regulates the biosynthesis of flavonoid by manipulating UV-A and UV-B radiations (Rizzini et al. 2011; Morales et al. 2013).

Expression of heat shock proteins (HSPs) is the most studied molecular response under heat stress, NP, and heavy metal stress. Heat shock proteins represent the role of molecular chaperones that maintains folding and accumulation of proteins, their localization, and degradation in plants. As chaperons, HSPs participate in refolding of proteins which prevents irreversible aggregation of other proteins during stress

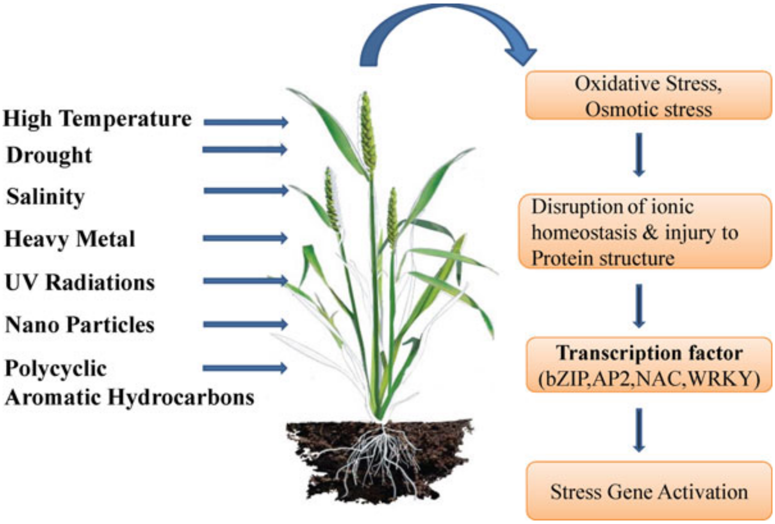

Fig. 3 Natural molecular regulation in wheat against abiotic stress

(Tripp et al. 2009). Abundance and diversity of HSPs in plant represent the extent of adaptation for particular stress in plants. In wheat under high temperature (>35 °C), NP, HM stress conditions, and HSPs are produced, but normal protein synthesis is reduced. Heat shock proteins are highly conserved in an organism. Various eukaryotes have similar gene induction mechanism for HSPs. Activation of gene expression in HSPs occurs by binding to a heat shock element (HSE) in DNA (Khurana et al. 2013; Chauhan et al. 2012). Six nuclear gene families encode all plant small HSPs (sHSPs), and each gene family characterizes the proteins found in different cellular compartments, i.e., cytosol (class I and class II), chloroplast, endoplasmic reticulum, mitochondria, and membranes (Waters et al. 1996). More than 20 sHSPs have been reported in higher plants, and 40 different sHSPs could be present in the same species (Vierling 1991). HSP16.9A, HSP16.9B, and HSP16.9C are few HSPs identified in wheat plant (Waters et al. 1996).

3.2 Man-Made Adaptive Mechanisms in Wheat

3.2.1 The Use of Biochar

One of the methods used for ameliorating the negative effect of salinity is the use of biochar. Biochar is an activated carbon soil conditioner that can alleviate the negative impacts of salinity. To investigate recovery effect for salinity stress on seed germination and growth rate of wheat, 1% and 2% concentration of biochar was used. Both levels of biochar improved the germination and growth conditions under salinity. 2% biochar level was found to be more effective when compared to 1% level. Root and shoot length increased up to 23% and 11% with 2% biochar, respectively. The maximum increase of 16% and 10% in leaf water potential and osmotic potential was noted with 2% biochar at 150 mM salt (Kanwal et al. 2018).

3.2.2 Phytoremediation

Increasing environmental pollution calls for the urgent need to develop a reliable technology for the removal and detoxification of environmental pollutant from the atmosphere. Plant-based method that utilizes plant capabilities for the removal of toxicants from environment is becoming the most promising technology known as phytoremediation. Recently, plant-based phytoremediation approaches to detoxify both organic and inorganic pollutants from the environment and to improve quality of water and soil are widely studied. Research is being focused on metal accumulator plant species used in phytoremediation (Ghosh and Singh 2005). Several plant species have been identified as hyperaccumulators and are known to accumulate metals in their tissues. Hyperaccumulator species are capable of accumulating contaminants at levels 100-fold greater than those typically measured in common non-accumulator plants. Most hyperaccumulator species bioconcentrate nickel (Ni), cobalt (Co), copper (Cu), and zinc (Zn). The Indian variety of *Brassica juncea*, *Brassica campestris*, and Pusa Jai kisan are reported for hyperaccumulating Cu and arsenic (As). *Calendula officinalis* (pot marigold), *Althaea rosea*, and *Impatiens balsamina* are also used for Cd and Pb. Understanding the mechanism of plant uptake, translocation and sequestration of the contaminants can give a better picture about the molecular mechanism of accumulation and tolerance. Similarly, traces of metals found in wetlands can be phytoremediated using aquatic plants which are also known and being successfully used to accumulate and remove metals. The suitability of aquatic macrophytes for phytoremediation has been tested with a number of metals, such as As, Cd, Cr, Cu, Hg, Ni, Sb, and Se. For example, *Azolla pinnata* and *Lemna minor* were investigated for their potential for bioaccumulating lead (Pb) and Ni and *Eleocharis acicularis* for bioaccumulating Sb, As, Cu, Cd, and Zn (Baunthiyal and Ranghar 2013).

3.2.3 The Use of Microbes (Bioremediation) Against Stress

Bioremediation is a process that makes use of microbes to induce degradation of PAHs and HM into less toxic products. Microbes offer a large surface area which facilitates their interaction with pollutants, metals, etc. in the surrounding environment. Bioremediation is considered as a safer, energy-efficient, cleaner, and economically viable remediation process than other technologies, such as surfactant flushing or incineration. This technology uses microorganisms in the soil (treatment can be *ex situ* as in bioreactors *or in situ* as in land farming) and can be carried out with minimum input, infrastructure, and care. Pollutants are converted either to carbon dioxide and water or to other compounds which are less harmful or injurious as compared to the parent compounds. These organisms possess key enzymes like ligninolytic and dioxygenases which are responsible for degradation. Microorganisms metabolize a wide range of persistent organic pollutant (POP), including PAHs, as a source of carbon and energy. White rot fungi have been extensively studied, and the ability of the fungus to degrade various types of PAHs due to their efficient enzyme systems has been reported (Valentin et al. 2007). *Polyporus* sp. *S133*, *Bacillus subtilis*, have been used for biodegradation of Anthracene (Hadibarata et al. 2012). The BMT4i (MTCC 9447) of *Bacillus subtilis* is used for degradation of benzopyrene (Lily et al. 2009), while *Pseudomonas* sp. has also been used for oil sludge (Dhote et al. 2016). Freshwater algae like chlorella and scenedesmus are also being used for biodegradation of PAHs.

There exist several mechanisms for the uptake of metal ions by a microorganism which precisely depend upon the chemical properties of metal ions, the specific and particular surface properties of the organisms, cell physiology, and other physiochemical parameters (such as pH, temperature, and concentration of the metal). In 2015, Paranthaman and Karthikeyan isolated *Pseudomonas* spp., *Pseudomonas fluorescens*, and *Pseudomonas aeruginosa* to study remediation of heavy metals. Peña-Montenegro et al. (2015) reported application of *Lysinibacillus sphaericus* CBAM5 in bioremediation of environments polluted with heavy metals.

Biomass of *L. sphaericus* was effective in the bioremediation of several heavy metals, e.g., copper, cobalt, chromium, and lead. *Microbacterium profundi* strain Shh49T was also used for multi-metal remediation. Seven isolates including *Aspergillus versicolor*, *A. fumigatus*, *Paecilomyces* sp., *Trichoderma* sp., *Microsporum* sp., *Cladosporium* sp., and *Salmonella choleraesuis* were reported for their Cadmium tolerance and bioremediation capacity (Gupta et al. 2016).

3.2.4 Inoculation with Arbuscular Mycorrhizal Fungi (AMF) to Ameliorate Stresses

Several major soil microorganisms are engaged in mutual symbiosis where arbuscular mycorrhiza fungi (AMF) are most prominent, forming a symbiotic association with more than 80% terrestrial plants (Smith and Read 2008). Arbuscular mycorrhiza fungi are one of the major microbial groups that are considered as biofertilizers and are also known to enhance tolerance to plants against biotic and abiotic stresses (Lenoir et al. 2016). Arbuscular mycorrhizae are obligate biotrophs, relying on living root tissue for carbohydrate supply and to complete their asexual life cycle. The hyphae of AMF penetrate roots and grow extensively between and within living cortical cells, forming a very large and dynamic interface between symbionts. Mycorrhizal colonization enhances plant growth and yield and lessens the effect of abiotic stresses like high temperature (Mathur et al. 2018b), UV stress (Van del Staaij et al. 2011), and drought (Al-Karaki et al. 2004). It is well established that AMF, in particular, not only increases P uptake but enhances NH_4^+, NO_3^-, Zn, Cu, and K uptake as well (Maboko 2013). Therefore, the presence of AMF in soil and its ability to form a symbiotic relationship with plants are being used by many researchers to ameliorate the effect of various abiotic stresses. Generally, AMFs are used either in mixed culture or individually. Most common used fungi are *Rhizophagus intraradices*, *Funneliformis mosseae*, and *F. geosporum*. Arbuscular mycorrhiza is not only being used for crops but also for various fruits (Huang et al. 2017) and vegetables.

4 Future Perspective

Despite our understanding of the biochemical and biophysical mechanisms involved in abiotic stresses in plants, many questions still remain to be answered. Research programs should be developed which aim to enhance the tolerance to a combination of various abiotic stresses, particularly those which are related to relevant global climatic changes (e.g., elevated carbon dioxide and ultraviolet-B radiation, drought, high temperature). An integrated approach should be adopted for the development of cultivar. It is essential to quantify the impacts of short-term and long-term effects of various abiotic stresses on growth, development, yield, and quality of crops along with several physiological functions. It will assist in improving the chances of incorporation of these effects into crop models. Improving mechanisms related to physiological and genetic nature of tolerance may eventually lead to better quality of crops along with increased grain yield. Improved understanding will help to assess the performance of the crop to future climates and also help to identify traits which can be improved to obtain higher and stable crop yields under stressful environments. Most of the future work should concentrate on recovery as well as protective mechanisms of plants against abiotic stresses under field conditions.

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Abiotic Stress and Wheat Grain Quality: A Comprehensive Review

**Rakesh Kumar, Virender Singh, Sushma Kumari Pawar,
Pankaj Kumar Singh, Amandeep Kaur, and Davinder Sharma**

Contents

Abstract Wheat is a major cereal crop and is grown in a wide range of agroecologies across the world. Abiotic stresses such as heat stress (HS), drought, waterlogging (WL), salinity, ultraviolet radiation B (UVR-B), ozone (O_3), mineral deficiency (MD), and heavy metal toxicity (HMT) are the major constraints to wheat cultivation in its present form or in the future amplified version under changing global climate. These stresses alone or in combined form can pose a serious intimidation on the grain quality and crop production. Maintaining wheat grain quality (WGQ) under stressful conditions is decisive for end-use functional properties. This review is presented with investigations and the existing understanding of

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the impact of these stresses on WGQ parameters such as starch granule (SG) size and composition, protein content (PC), glutenin (Gt)/gliadin (Gl) ratio, insoluble protein polymers, and free amino acid (AA) content. In the end, the efficacy of crop models (CM) for prediction of adverse impact of these stresses on WGQ is discussed in brief. Altogether, this review could facilitate in escalating our predictive capability to design better adaptation strategies according to climate changes.

Keywords Abiotic stress · Drought stress · Heat stress · Ozone stress · Protein · Salinity · Starch · Waterlogging · Wheat grain quality

Abbreviations

A	albumins
AA	amino acid
AGPase	glucose-1-phosphate adenylyltransferase
AL	amylose
AP	amylopectin
AX	arabinoxylans
Ca	calcium
CM	crop model
DF	dietary fiber
Fe	iron
G	globulins
GBSS	granule-bound starch synthase
GC	glucan chain
GF	grain filling
Gl	gliadins
GPC	grain protein content
Gt	glutelins
HMT	heavy metal toxicity
GS	glutenin subunit
HMW	high molecular weight
HS	heat stress
K	potassium
LC	lipid content
LMW	low molecular weight
MD	mineral deficiency
Mg	magnesium
Mn	manganese
MW	molecular weight
Na	sodium
O_3	ozone

P	prolamins
PA	phosphoric acid
PC	protein content
RER	rough endoplasmic reticulum
ROS	reactive oxygen species
SBE	starch-branching enzyme
SC	starch content
Se	selenium
SG	starch granule
SS	starch synthase
β-G	β-glucans
SSS	soluble starch synthase
TG	triglyceride
TSS	total soluble sugar
UVR-B	ultraviolet radiation B
WGC	wheat grain composition
WL	waterlogging
Zn	zinc

1 Introduction

Although wheat is a winter cereal crop, it is grown in diverse agroecologies and hence, experiences various environmental stresses like heat stress (HS), drought, waterlogging (WL), salinity, ultraviolet radiation B (UVR-B), ozone (O_3), mineral deficiency (MD), and heavy metal toxicity (HMT). Tolerance to these stresses is a central characteristic of yield maintenance, and its improvement has long been an objective for plant breeders. The issue now has more concern than ever before due to the unpredicted incidence of acute climatic events and their anticipated negative effects on global food economy.

Terminal HS is likely to severely affect wheat production and wheat grain quality (WGQ), particularly in tropical and subtropical environments (Enghiad et al. 2017). The frequency and harshness of heat waves have already been increased in most areas of Asia, Australia, and Europe (IPCC 2014). For example, in the continent of Australia, maximum daily temperature increased on average once during a two-decade period in the late twentieth century and is expected to rise to once every 3 years by the middle of the twenty-first century. Similarly, severe drought has come about on average once every 18 years in Australia since the 1860s resulted in spikes in crop commodity prices (Anderson 2014). Likewise, soils salinity is a common problem worldwide, and it has been estimated that more than 1/16 of the irrigated land suffers from salinity which covers over 800 million hectares (FAO 2012). Wheat is a moderately salt-tolerant crop, and deterioration of WGQ is due to disturbed ionic balance such as calcium (Ca), magnesium (Mg), and sodium (Na;

Guo et al. 2016). Salinity causes a decrease in the grain protein content (GPC) and starch content (SC) and an increase in phosphorous content. Approximately, 1/3 of the irrigated land suffers from WL occasionally or frequently. The WL has diverse effects on wheat growth, and its severity depends on the soil type and climatic conditions. For example, Australian soils have higher iron (Fe) profusion (ten times) than Indian soils, while Indian soils have higher manganese (Mn) availability under WL (Setter et al. 2008). The WL specifically caused salinization, roots oxygen deprivation, and mineral toxication which synergistically negatively affected production and WGQ. Wheat is a highly O_3-sensitive crop (Tai et al. 2014). Ground-level O_3 formation occurs through photochemical reactions of O_3 precursors such as nitrogen oxides (NOx), carbon monoxide (CO), and methane (CH_4). Ground-level O_3 concentrations have increased up to 40 parts per billion (ppb) in various parts of the Northern and Southern Hemisphere and are sufficiently high to cause a severe loss on crop production in wheat (Feng and Kobayashi 2009; Tai et al. 2014). On the contrary, the depletion of stratospheric O_3 caused an increase in UVR-B radiation (Madronich et al. 1998). This can seriously damage DNA, membranes, and proteins and consequently manipulate various regulatory processes directly or indirectly (Lidon 2012). Further, UV-B sensitivity is influenced by the presence of other factors particularly drought, nutrient, and visible radiation (Alexieva et al. 2001). Insufficient quantity or unavailability of an essential nutrient caused nutrient deficiency, while the excess availability causes toxicity. Both conditions led to impaired metabolism and decreased growth or quality. Many symptoms are characteristic indicators to identify a nutrient deficiency/toxicity, while other symptoms are less prominent and could indicate only one of several possible nutrient stresses (Liu et al. 2009). Heavy metals (As, Cd, Cr, Hg, and Pb) are ubiquitous in the farming soils. These metals concentrated in plant tissues and interact synergistically to be highly toxic to antioxidant enzymes, chlorophyll synthesis, and photosynthetic electron transport chain (Murzaeva 2004).

This review will focus on the abiotic stresses on WGQ such as starch granule size and composition, protein content, glutenin/gliadin ratio, insoluble protein polymers, and free amino acid content. In the end, a brief discussion on the contemporary crop models and their utility for predicting impacts of climate change on wheat production and grain quality.

2 Wheat Grain Composition (WGC)

Wheat grain mainly consists of starch (80%), proteins (10%), as well as low amount of phytochemicals and cell wall polysaccharides. In addition, lipids, minerals, phenolics, terpenoids, and vitamins are also present as minor components (Shewry 2009).

2.1 Starch

Starch is mainly composed of amylose (AL) and amylopectin (AP) in a ratio of 1:3 (w/w) (Morell et al. 2007). The AL is the linear polymer of glycopyranosyl monomers (105–106) linked by a-(1, 4) linkages (500–6000 glucose residues), whereas AP has the same backbone as AL, but it has branched glucan chain (GC) linked by a-(1, 6) linkages (Lásztity 1999). Starch synthesis in grain begins with the conversion of glucose-1-phosphate to ADP-glucose by glucose-1-phosphate adenylyltransferase (AGPase, EC 2.7.7.27). The enzyme starch synthase (SS, EC 2.4.1.21) then adds the ADP-glucose to a growing GC via 1,4-glycosidic bond to extend existing GC. Enzyme SS has two forms: a soluble SS (SSS) and a granule-bound SS (GBSS; Leterrier et al. 2008). Soluble SS has various isoforms designated as SSS-I to IV. Each isoform extends GC up to a definite length, which determines the frequency of branching in AP (Szydlowski et al. 2011). Granule-bound SS I can only synthesize AL (Sharma et al. 2018). Starch-branching enzyme (SBE; EC 2.4.1.18) creates α-(1,6)-glycosidic bonds to synthesize AP.

2.2 Proteins

Proteins have greater variation (7–22%) in their content than endosperm starch and are a most significant determinant of WGQ. These can be simple, conjugated, or derived types (Osborne 1907). Simple proteins include albumins (A), globulins (G), prolamins (P), and glutelins (Gt) which have solubility in water, salt solutions, 70–90% ethanol, and dilute acid or alkali, respectively. Wheat grain proteins can also be divided into storage (gluten) proteins (80–85%) and a heterogeneous group of structural/metabolic (non-gluten) proteins (15–20%; Shewry et al. 2003). Gluten proteins primarily contain glutamine and nonpolar amino acids and hence are sparingly water-soluble. Gluten is present as a heterogeneous mixture of monomeric gliadins (Gl; MWs 30–80 kDa) (Ritchie et al. 1998) and polymeric Gt (MWs 80 KDa-several MDa; Kasarda 1989). The Gl is soluble, while Gt is insoluble in alcohol. These polymers are among the largest polymers in nature, consisting of different high molecular weight (HMW) and low molecular weight (LMW) subunits linked by disulfide bonds (Shewry and Halford 2002). The Gls can be structurally distinguished into α—/β-, γ-, and ω-type groups. α—/β- and γ-types are classified as "S-rich P" and closely related to the LMW-Gt (Shewry et al. 1986). In contrast, ω-type Gls are classified as "S-poor P" due to lack of cysteine residues and much fewer methionine residues. Gliadin confers gelatinous texture and viscosity to the dough whereas Gt imparts elasticity and strength. This unique combination of viscosity and elasticity in gluten make wheat dough suitable for the preparation of a great variety of eatable products (Day et al. 2006). The Gt consists of two subunits, HMW glutenin subunit (HMW-GS) (=10%) and LMW-GS (=90%). The HMW-GS forms the glucan polymers, and LMW-GS cross-linked these chains by disulfide bonds. HMW-GS contributes majorly to bread-making quality, while LMW-GS contributes majorly to dough elasticity (Shewry et al. 1992).

Amphiphilic, A and G, proteins belonged to metabolic and structural proteins and are synthesized during early grain filling (GF). These proteins are nutritionally superior due to their higher lysine and methionine content and comprise 15–20% of the grain proteins (Singh and Skerritt 2001). α-amylase/trypsin inhibitors, purothionins, and serpins are major A and G, and mainly serve amino acid during germination and act as natural insecticides and provide protection from insects (Dupont and Altenbach 2003). Non-membrane amphiphilic proteins confer grain hardness and influence dough rheology (Dubreil et al. 1998).

Two-dimensional gel electrophoresis revealed more than 15 LMW-GS and 6 HMW-GS proteins in wheat flour (Gianibelli et al. 2001; Veraverbeke and Delcour 2002). The subgroups B, C, and D of LMW-GS have molecular weights (MWs) of 42–51 kDa, 30–40 kDa, and 58 kDa, respectively. Although HMW-GS have MWs ranged from 65 to 90 kDa, their bands on SDS-PAGE appears from 80 to 130 kDa. Glu-A1, Glu-B1, and Glu-D1 loci have been mapped on the “q arm” of chromosome 1 group in hexaploid wheat (Payne et al. 1984). These loci have two alleles encoding x and y subunits for HMW and LMW-GS proteins, respectively. All hexaploid wheat cultivars essentially contain three subunits, viz., 1Bx, 1Dx, and 1Dy, in addition to the 1By and/or 1Ax and 1Ay subunits (Payne and Lawrence 1983). However, gene silencing could occur due to transposon-like insertion in the exons, and allelic variations result in altered subunits which exhibit different SDS-PAGE mobilities. At the time of original ranking of HMW-GS, the nomenclature contains the genetic locus (1A, 1B, or 1D), the type (x or y), and a number according to decreasing MWs. However, new HMW-GS intermediate was being discovered between the previously detected; numbering was continued by adding decimal numbers (2.1 vs. 2) or symbols (2.2* vs. 2.2) irrespective of MW. The HMW-GS and LMW-GS genes are located on the “q” and “s” arm of homologous chromosome 1, respectively (Payne 1987). The individual polypeptides of storage proteins are synthesized on rough endoplasmic reticulum (RER)-studded ribosomes and translocated into the RER lumen where folding and assembly of different polypeptides occur. No posttranslational glycosylation or proteolysis in wheat storage proteins have been reported (Shewry et al. 2003).

2.3 Lipids

Lipids are present in a small extent (0.5–3.0%) in wheat grain. These are mainly present in germ and bran. Essential fatty acids (linoleic, oleic, and palmitic acids), vitamins (carotenoid pigments, tocopherols, and sterols), and phytosterols are the main wheat grain lipids (Ruibal-Mendieta et al. 2004). These are present both in free and bound forms with proteins and starch inclusion complexes, and they affect dough stability and loaf volume (Ruibal-Mendieta et al. 2004). Approximately 65–75% of wheat grain lipids is comprised of non-starch lipids as triglycerides (TG; 30–36%) and other nonpolar lipids, such as glycolipid and digalactosyl diglycerides. Triglycerides have consisted of 16:0-18:2-18:2, 18:l-18:2-18:2 and 18:2-18:2-18:2 molecular species. Phosphoglycerides are majorly present as phosphatidylcholine and phosphatidylethanolamine in starch. The principal sterols are campesterol, b-sitosterol, and C-28- and C-29-saturated sterols together with a very small amount of cholesterol (Ruibal-Mendieta et al. 2004). In wheat, glycerides, phospholipids, sphingosine, waxes, as well as the isoprenoid synthesis use acetyl-CoA, while palmitic acid and stearic acid use predominately malonyl-CoA. Linoleic acid synthesis occurs by microsomal enzymes using two separate pathways. Isopentenyl pyrophosphate produced from mevalonate is utilized to form b-squalene and other steroid structures (Šramková et al. 2009).

2.4 Dietary Fiber (DF), Minerals, Phytochemicals, and Vitamins

Whole wheat grain is rich in DF, vitamins, phytochemicals, and minerals such as Ca, Fe, magnesium (Mg), phosphoric acid (PA), potassium (K), and zinc (Zn) (Nyström et al. 2008; Shewry 2009). Arabinoxylans (AX; insoluble fiber) and β-glucans (β-G; soluble fiber) are the major DFs in wheat grain. These DFs are fermented to short-chain fatty acids, butyrate in particular, in the colon. This improves bowel health and lowers the risk of colon cancer (Philippe et al. 2006). Although wheat usually has only very less β-G (0.6%) as compared to barley and oats, studies indicate its potential dietetic benefits (Brennan and Cleary 2005). β-G has manipulating effects on the cholesterol, glycemic, and insulin responses (Shimizu et al. 2008). Zn content in wheat grain ranged from 20 to 35 mg/kg and is majorly present in the embryo and the aleurone layer (Cakmak 2008). The Fe content in wheat grain has been reported to range from 28.8 to 56.5 mg/kg. Recently, new wild emmer wheat accessions have been reported to have much higher amounts of Zn (~139 mg/kg), Fe (~88 mg/kg), and protein (~380 g/kg) even under high drought stress (Peleg et al. 2008). Wheat also has a significant amount of selenium (Se; 0.02–0.60 mg/kg) and is enough to supply at least half of the daily requirement in Australia (Lyons et al. 2003). However, no significant genetic variability among commercial varieties of bread or durum wheat has been reported (Lyons et al. 2005). Phytochemicals in the wheat grain bran majorly include phenolic acids, carotenoids, tocopherols, flavonoids, and ferulic, caffeic, p-coumaric, sinapic, and vanillic acids (Verma et al. 2009).

Whole wheat is a rich source of B-complex vitamins, including thiamine (B1), riboflavin (B2), niacin (B3), pantothenic acid (B5), pyridoxine (B6), and folate (Kim et al. 2016). Although β-carotene is present in minor quantity (0.04–0.25 ppm), high consumption of wheat makes it an important carotenoid source. Lutein and zeaxanthin are the principal carotenoids (70–90%), and α-tocopherol and β-tocopherol are the major tocopherols in wheat grain. Tocopherols are mainly present in the germ and the bran fraction (Kim et al. 2016). Nonetheless, wheat grains also have a substantial amount of detrimental compounds such as phytic acid. Inorganic phosphorus (~40–80%) is present as phytate which reduces the bioavailability of other minerals (Lopez et al. 2001).

3 Heat Stress (HS)

Heat stress is a key abiotic stress affecting wheat production worldwide. According to the proposed global climate models, the average ambient temperature is expected to increase up to 6 °C by the end of the present century (De Costa 2011). Recent controlled and field-based studies have predicted that wheat production will decline by 4.1–6.4% for each global rise of 1 °C in temperature alone, and the situation can be more adverse in combination with other stresses (Bennett et al. 2012). The low-latitude zones in South Asia, the Middle East, and North Africa, where greater than 100 million hectares of wheat are grown, are primarily heat-prone areas (Braun et al. 2010). Heat stress disturbs plant water status (Hasanuzzaman et al. 2013) and reduces metabolic and photosynthetic activities (Farooq et al. 2011; Ashraf and Harris 2013), hormone production (Krasensky and Jonak 2012), reactive oxygen species (ROS) production (Wang et al. 2011), and pollen viability (Sharma et al. 2016). Heat stress reduces the duration of all growth stages in wheat. However, the reproductive phase is highly sensitive, and GF is a temperature-dependent process (Wollenweber et al. 2003; Sharma et al. 2015). Timing, frequency, and duration of HS have a significant effect on WGQ (Wardlaw 2002).

Even a short episode of supraoptimal temperature during GF can affect WGC. Temperatures between 30 and 40 °C reduced endosperm starch up to 33% (Liu et al. 2011). The starch composition has changed under HS (Hurkman et al. 2003). As temperatures rise above the optimum, starch biosynthesis ceases slowly (Yamakawa et al. 2007). The starch composition has been modified by HS and consequently alters AL/AP ratio (Dengate 1984). The AL content and the AL/AP ratio increase under the HS (Sharma et al. 2018). Small changes in AL proportion, as small as 1% variation, effectively modify starch gelatinization properties (Hurkman et al. 2003).

These alterations are assumed to be due to changes in starch biosynthetic enzyme activities. Among the enzymes, AGPase, SSS, and SBE are highly sensitive to HS (Yamakawa et al. 2007). The AGPase is the rate-limiting enzyme (Duke and Doehlert 1996). In maize, AGPase has a high turnover rate under HS (Duke and Doehlert 1996), while SSS in wheat can lose up to 97% activity at 40 °C and becomes nonfunctional. However, Rijven (1986) has reported that SSS activity does not reduce up to 30 °C and hence does not reduce SC but alters its composition. GBSS activity is not affected significantly by HS in wheat (Cheng et al. 2005;

Sharma et al. 2018). Moreover, HS can significantly alter the degree of polymerization and GC length in AP of wheat starch. It has been observed that the shorter GCs accumulate more as compared to the longer ones. These changes have been attributed to the SBE heat sensitivity (Ohdan et al. 2011). Further, HS modifies the size and shape of starch granules (SG) in wheat. Wheat starch has large A and small B granules. The size of these granules (A and B types) reduces, while their ratio increases under HS (Beckles and Thitisaksakul 2014).

Graybosch et al. (1995) showed that protein quality is highly influenced by HS. The glutens are the key determinants of end-use quality of wheat flour, while albumins and globulins are nutritionally important (Balla et al. 2011). The synthesis, accumulation, and assembly of gluten proteins are affected by HS during GF. Gluten's buildup initially gets accelerated but shortly declines due to heat inactivation of the enzymes (Altenbach et al. 2002). However, protein/starch ratio increases under HS because starch synthesis is affected more adversely than protein synthesis. Labuschagne et al. (2009) reported that the protein concentration significantly improved under HS.

Wheat bread-making quality mostly depends on the HMW Gt to Gl proportion (Laino et al. 2010). Post-anthesis HS reduces Gt/Gl ratio and negatively affects dough quality (Bencze et al. 2004). High temperature promotes the Gl synthesis, but a relative decrease in the Gts occurs (Laino et al. 2010; Balla et al. 2011). Exposure to HS during late GF adversely affects the rheological properties due to protein aggregation (Corbellini et al. 1997). Blumenthal et al. (1993) have reported that bread-making quality improves up to 30 °C, but above 35 °C, it starts deteriorating.

Blumenthal et al. (1995) have compared a set of 45 wheat heat-susceptible and heat-tolerant genotypes to investigate the effect of HS on free and bound lipid content (LC) in mature grains and have reported a massive increase in bound LC with no change in free LC. Further, amounts of stanols increased while that of AX decreased in both the germ line and endosperm under HS. In contrast, Rakszegi et al. (2014) have reported that the amount of AX increases while that of β-G decreases under HS. In addition, HS increases reducing sugars, sucrose, and sugar phosphates (Gooding et al. 2003; Halford et al. 2014).

4 Drought Stress

Drought stress primarily causes disturbance in osmotic and hormonal homoeostasis and these disturbances adversely affects nutrient and light use efficiency. These alterations enhance ROS production. Drought reduces the SC which was primarily ascribed to the decrease in AGPase activity (Ahmadi and Baker 2001). Singh et al. (2008) have reported that starch has low AL content with high final viscosity under drought stress. Differently, Lu et al. (2014) have reported that starch contains low AP under drought stress, while Zheng et al. (2009a) have observed no such changes. Likewise, drought stress significantly alters the size, composition, and distribution of SC. It has been reported that A-type SG decreases under drought stress (Lu et al.

2014). On the contrary, Singh et al. 2008 have reported that A-type SG increases, while the proportion of B-type and C-type SGs decreases under drought stress. Yu et al. (2016) have investigated the development of SGs in soft (NM13) and hard wheat (XM33) cultivars. Remarkably larger A-type SGs and a high percentage of small B-type SGs have been observed during the initial stage of GF in the two wheat cultivars. However, at a later stage of GF, NM13 contains only a small amount of B-type SGs, and XM33 has no difference in their SGs. Fábián et al. (2011) have also reported the similar results in Cappelle-Desprez wheat cultivar which contained few large A-type SGs initially under drought stress.

It is well documented that under drought stress larger protein bodies accumulated in developing grains. Rharrabti et al. (2003) and Garrido-Lestache et al. (2004) have reported an increase in grain protein content (GPC) and alveograph index (W), respectively, under severe drought stress. This indicates the improved quality of end products. Gooding et al. (2003) have observed that the impact of drought stress on quality parameters relies on the timing and intensity of stress. The grain N content has reduced only when plant experiences drought stress during the first 2 weeks of GF, whereas drought stress in the middle and end phase of GF has no such effect. On the contrary, grain S content increases under drought stress irrespective of the timing and hence results in the decrease of grain N/S ratio. In contrast to the grain N content, an increase in the Hagberg falling number and SDS volume has been observed when drought stress has been imposed during the second to the fourth week and during the end phase of GF, respectively.

The ratio of Gls to Gts increases under drought stress during GF (Fan et al. 2004; Hajheidari et al. 2007). Singh et al. (2008) have also reported a change in the ratio of dimethylformamide-soluble to dimethylformamide-insoluble proteins due to drought stress. Contrarily, Panozzo et al. (2001) have observed no such difference in the Gl/Gt ratio but have observed that accumulation of polymeric proteins initiated much earlier under drought stress conditions. Singh et al. (2008) have reported a 30–40% lower LC in wheat grains under drought stress. This reduction severely affects the hot paste viscosity, starch swelling, and AL leaching. Further, upon cooling, this reduces the retrogradation of AL due to Al-lipid complex formation which further causes a higher setback of starch (Singh and Kaur 2004). Nebesny et al. (2005) have shown a negative correlation between LC and the stability of these complexes. Lipid-deficient starches have a lower reassociation temperature, which causes the generation of less stable AL-lipid complexes (Singh et al. 2008).

Previous investigations have reported that drought stress during anthesis increases the AX content (Hong et al. 1989), while post-anthesis drought stress can have the opposite effect (Coles et al. 1997). Mild drought stress increases AX content, while severe and prolonged drought stress can decrease the AX content. Rakszegi et al. (2014) have also reported that drought stress increases the AX content in the drought-sensitive and drought-tolerant wheat genotypes except in Plainsman V, a drought-tolerant wheat genotype. Coles et al. (1991) have reported low β-G content in wheat grains developed under drought stress. Rakszegi et al. (2014) have also reported similar findings for HS and drought stress alone or in combination.

5 Waterlogging (WL)

Excess water is akin to water deficit in severity and tends to indulge wheat plant growth and development. Flooding plugs the soil pores and constrains the air exchange between soil and atmosphere. As a result, it induces anaerobic conditions which can lead to reducing the availability (hypoxia) or complete dearth of O_2 (anoxia) in the soil.

Wheat is highly sensitive to WL and experiences this disaster due to long nonseasonal rains. All growth stages of wheat are affected by WL; however, flowering and GF are the most sensitive ones (Olgun et al. 2008). Waterlogging severity depends on several factors, including timing, duration, and the presence of other stresses (Setter and Waters 2003). It induces ROS synthesis and ethylene production and inhibits root growth and nutrient and water transport and consequently can affect WGQ. However, WL-induced effects on WGQ have so far been investigated hardly only in few studies; there are not yet very sound evidence to conclude sound inference.

It has been observed that WL decreases the SC in wheat grain 25–35 days postanthesis (Jiang et al. 2009). Xie et al. (2003a) have reported that the grain starch accumulation is linked with the reduced activities of SS, SSS, and GBSS under post-anthesis WL. In a recent study, AL content has been found higher, while AP content and AP/AL ratio have been found lower under WL and acid rain conditions as compared to control (Jiang et al. 2008; Zhou et al. 2018). It is majorly due to the nonavailability of nutrients, especially N to the plant from the soil and affected metabolic pathways. Fan et al. (2005) have shown that the grain SC could be increased by supplying N from anthesis to maturity during WL. In addition, total soluble sugar (TSS) and sucrose decrease in wheat grain under WL. Grain TSS content has been found to decrease slowly from 7 to 21 days postanthesis and thereafter has decreased rapidly (Zhang et al. 2011).

It has been observed that WL causes a significant reduction in total protein content (PC) and an increase in free AA content leading to alter processing quality of wheat. Waterlogging in combination with salinity causes a significant reduction in the Gt/Gl ratio and the free AA content in wheat grain (Zheng et al. 2009b). Fan et al. (2004) have reported that WL causes a substantial reduction in PC, while starch and AL content increased markedly in wheat grain. On the contrary, Zheng et al. (2009a) have studied the effect of WL in two wheat cultivars, Yangmai 12 and Huaimai 17, and have reported that WL decreases both PC and SC. However, the effect of WL on the grain PC seems to be genotype dependent. It has been observed that WL increases A and G contents in Huaimai 17 but decreases Gl and G contents in Yangmai 12. Jiang et al. (2009) have confirmed that WL reduces the HMW-GS in wheat grains. Further, it has also been concluded that the accumulation of grain protein is associated with the reduced activities of glutamine synthetase and glutamate pyruvic aminotransferase in wheat grain under post-anthesis WL. In a different study, the pre-anthesis WL has been reported to cause markedly increases in contents of G, flour dry gluten, wet gluten, sedimentation volume, falling number, enhanced peak viscosity, holding trough viscosity, breakdown, final viscosity, setback, and peak time (Li et al. 2011). However, the pasting temperature remains unaffected. On the contrary, significant reductions have been observed in the contents of A, Gl, Gt, and total protein in the grain. In addition to the above, it has been concluded that the pre-anthesis WL treatment can essentially increase grain yield and can improve the tolerance to severe WL in wheat.

Olgun et al. (2008) have observed that WL causes a significant increase in proline content and stress-induced AA. During WL, proline content increases more in roots as compared to leaves which further alters the WGQ (Marashi and Chinchanikar 2010). In another study, it has been proposed that the level of SC and PC in grain is highly influenced by a reduction in IAA, zeatin riboside, and gibberellins and an increase in ABA level under WL (Xie et al. 2003b).

6 Ozone (O_3) and Ultraviolet Radiation B (UVR-B)

Notwithstanding the current efforts to restrict the production and use of O_3-depleting substances, shrinking of the O_3 layer and increased infiltration of UVR-B to the earth's surface will prolong to upcoming decades (Environmental Effects Assessment Panel (UNEP 2010)). Thinned O_3 layer and enhanced UVR-B will be the most important abiotic stress factors that can have significant effects on yield and WGQ.

Ozone is an atmospheric pollutant, and its concentration is being continuously increased due to the use of hydrocarbons. Currently, the global average concentration of O_3 is more than 40 parts per billion; however, it varies according to geographical location and weather conditions. Inside the plant, O_3 reacts with metabolites to generate ROS, which further lead to increase oxidative stress, accelerate leaf senescence, and reduce photosynthetic efficiency, biomass, and yield (Fiscus et al. 2005; Mikkelsena et al. 2015). Broberg et al. (2015) have observed a lower but significant negative effect of elevated O_3 on SC and volume weight. However, a significant improvement in grain PC and several nutritionally important minerals such as Ca, Cu, K, Mg, Mn, P, and Zn content has been reported on exposure to increased O_3 (Broberg et al. 2015). It has been proposed that the high O_3 dose reduces the translocation of photosynthates and reduces starch accumulation in grain (Zheng et al. 2014). In a recent study, the significant negative effect of elevated O_3 has been reported on grain starch concentration (Pleijel et al. 2018). Feng et al. (2008) have reported 6% enhancement in total grain PC despite 18% reduction in grain protein yield under elevated O_3. The baking properties such as Zeleny value and Hagberg falling number have also been positively increased by elevated O_3 (Piikki et al. 2008; Broberg et al. 2015).

Li et al. (2016) have reported that the content of various minerals such as Na, Zn, Fe, and Cu reduces in wheat grain by 72.5%, 65.5%, 33.8%, and 29.2%, respectively, by elevated O_3. Wang et al. (2017) have claimed a significant increase in Fe, Mn, and Cu contents of wheat grain by 9.37, 36.68, and 48.18%, respectively, while a reduction has been observed in Zn by 17.09% to elevated O_3. The cadmium content has reduced by elevated O_3 which could be considered as a positive effect because it is a toxic heavy metal. It has been found that Zn content in wheat grain is correlated with PC under exposure of elevated O_3 alone or in combination with elevated CO_2 (Pleijel and Danielsson 2009).

Although there are many studies available on the effect of O_3 on WGQ, very few investigations have been carried out so far to study the impact of UVR-B (Zu et al. 2004; Calderini et al. 2008; Lizana et al. 2009). Most of the investigations to study the impact of UVR-B have been carried out either at intermediate or high latitudes of the Northern and Southern Hemisphere. High-intensity UVR-B causes DNA damage and ROS production, which has a major deleterious effect on plant cell integrity, functioning, and efficiency of photosynthesis (Jenkins 2009; Li et al. 2013). Hakala et al. (2002) have conducted an experiment at Jokioinen, Southern Finland, and have reported that the development and growth rate of wheat are not affected by exposure to the increase in UVR-B. Similar results have been reported by Calderini et al. (2008) in an experiment carried out at Southern Chile and have reported that the increase of UVR-B will not affect wheat production and WGQ. Authors of this study have not found any difference in grain PC and gluten content between the increased UVR-B and control treatments. Further, another study by Lizana et al. (2009) has also confirmed the previous observations and has concluded that there is no negative effect of UVR-B on WGQ. On the contrary, Zu et al. (2004) reported that UVR-B significantly affects the grain content of free AA, protein, and total sugar in a field study on ten wheat cultivars. These radiations increase the free AAs and PC and decrease the total sugar content. However, there is no significant change observed in rough SC among the studied cultivars. In addition, nine of ten cultivars have a positive quality response index. Yao et al. (2014) have evaluated the effect of elevated UVR-B on specific development stages of winter wheat to determine which growth stage is most sensitive and what are the potential effects of elevated UVR-B on protein, starch, and nutritional element content in mature grains. Grain PC decreases when plants are exposed to elevated UVR-B during anthesis. Al/AP ratio and total SC remain unaffected by increased UVR-B. A significant improvement in grain Mn and Zn content has been observed, while Fe, N, and P contents decrease on UVR-B treatment from seedling to GF. On the contrary, a reduction in Fe content and improvement in Cu and Mn content have been observed in UVR-B treatment at tillering, heading, and flowering stages (Yao et al. 2014). Except for these studies, in recent times and to the best of our knowledge, there is no other investigation showing the adverse impact of UV-B radiation on WGQ. However, other cereal crops such as maize and rice have been shown to have a negative effect on their grain quality on exposure to UVR-B (Gao et al. 2004; Hidema et al. 2005). Hidema et al. (2005) showed that increased UV-B radiation altered GPC in rice.

7 Salinity

The salinity is a worldwide problem that affects arable irrigated land in arid and semiarid regions and reduces crop yields significantly (FAO 2012). The physiological and biochemical responses of a plant to salinity are generally complex.

Most studies regarding salinity have been carried out on the root, stem, and leaf. Very less information on salinity-induced alteration in grain quality is available in the literature. Zheng et al. (2009a) have shown a marked reduction in grain SC and PC due to salinity. Authors have also reported a perturbation in the grain Gt/Gl and AL/AP ratios due to salinity. Kahrizi and Sedghi (2013) have also reported a decrease in the PC and SC at high salinity (120 mM), whereas Houshmand et al. (2014) have reported salinity induces a significant increase in grain PC, wet and dry gluten contents, and SDS sedimentation volume. High respiration rate under salinity leads to decrease in assimilate transport to grains, and as a result, there is a decrease in the amount of stored carbohydrate and increase in the PC (Poustini 2002).

Grain composition of salt-sensitive genotypes differs much from that of salt-tolerant genotypes when grown under the same salinity condition. Zheng et al. (2009b) observed that grain PC increased significantly in salt-sensitive genotypes than in salt-tolerant genotypes. And there has been a marked salinity-induced decrease in flour yield in all the genotypes. It has also been observed that salt-tolerant genotypes resist changes in pasta quality parameters such as water absorption, wet gluten content, dough development time, and dough stability time at salinity level up to 100 mM NaCl, while pasta quality in the salt-sensitive genotype has adversely affected at all levels of salinity. A similar study showed that salt-tolerant cultivars have more gluten content and PC as compared to the salt-sensitive ones (Khan et al. 2008). In contrast, Katerji et al. (2005) observed that salinity does not change the grain quality of the sensitive cultivar but affected the grain quality of the tolerant one, mostly in a positive way by a decrease of the ash content. From the above studies, it can be concluded that salinity-induced change in grain PC and SC is genotype dependent. Shen et al. (2007) have found that protein accumulation decreases with an increase in soil salinity.

8 Mineral Nutrient Deficiency and Toxicity

A deficiency in one of the mineral nutrients may reduce utilization of the remaining components and results in poor grain quality. Galantini et al. (2000) showed that fertilization (NPK) does not add to the dry matter but considerably influences the nutrient accumulation in wheat grain. Nitrogen is the most crucial among the nutrients which influences grain quality (Ehdaie and waines 2001; Shi et al. 2010). Application of high N, no doubt, results in enhanced yields, but technological parameters of such yields still raise controversies. Besides stimulating yields, higher N rates can worsen the quality of gluten in grain by mounting the proportion of low molecular Gl (Wooding et al. 2000). Additionally, K is an essential element during the key stages of protein biosynthesis, and its deficiency causes a decrease in PC produced by a plant, and this effect occurs despite the N level and accumulation of nonprotein N (Rice 2007).

Wheat grains grown in S-deficient soils generally accumulate asparagine and arginine but have low levels of S-containing amino acids methionine and cysteine (Hesse et al. 2004). Asparagine accumulation in wheat grains under S-deficiency increases the risk of acrylamide formation when flour products are cooked (Halford et al. 2012). Interchain disulfide bonds of the Gls and Gts influence the elasticity of dough by stabilizing the polymer network formed by gluten molecules (Shewry et al. 2002). If the S supply is low relative to the N supply, the content of S-poor proteins such as ω-Gls increases while that of S-rich proteins such as γ-Gls and LMW-GS decreases (Tea et al. 2007). The gluten, methionine, and cysteine content significantly increased when S is applied along with N (Klikocka et al. 2016)

Heavy metal accumulation is one of the most severe environmental concerns of the present day, not only because many of these metals are toxic to the crops themselves but also because of their potential harm to animals and humans. Certain metals in trace amounts are vital for the plants, as they play an important role in plant metabolism and biosynthesis, by acting as cofactors for enzymes and as metabolic products (Rattan et al. 2005). Metals such as Cr, Zn, Cu, Co, and Fe are necessary to plant nutrients, but at higher concentration they become toxic. Some metals like Cd and lead (Pb) which have no known beneficial effects in plants are entirely toxic (Radojevic and Bashkin 1999; Mohamed and Ahmed 2006). Al-Othman et al. (2016) reported that seeds in comparison to other aerial plant parts have less accumulation of heavy metals.

9 Crop Models (CM)

A CM is a set of mathematical equations used to predict the future impact of various stresses on grain yield and quality by the assessment of past, present, and future agroclimatic conditions (Nuttall et al. 2017). These predictions may be very useful for policy makers and food industries to develop management strategies to deal with future climatic challenges in a better way. The concept of numerical models had started half-century back when Warren-Wilson (1967) estimated plant biomass growth as a function of intercepted solar radiation.

Wheat crop production and quality are the results of complex genetic and environmental interactions. Among various abiotic factors, heat, drought, and CO_2 are fundamental for the accurate assessment of future agroclimatic scenario. Statistical models are not usually preferred to predict grain quality characteristics due to the complex interactions and weather-governed variations depicting crop growth. Although mechanistic models describe some of the fundamental attributes of the system and can explain the "how and why" of the complex biological processes mathematically, these models cannot be used universally. On the other hand, biophysical models describe basic traits and have multiple environment applicability. But these models repeatedly require calibration when treatment-based comparisons are done comprehensively. Important wheat crop simulation models and their details are given in Table 1.

Various CMs can assess the penalty of climatic fluctuations on grain quality; however, only a few such models are available, those that deals with many quality parameters simultaneously. For example, SiriusQuality, STICS, and APSIM-N wheat CMs can predict screenings in addition to grain N and protein deposits (Brisson et al. 2003; Martre et al. 2006; Asseng et al. 2008), while other CMs such as EPIC-Wheat, WOFOST, and CropSyst cannot simulate these quality parameters (van Diepen et al. 1989; Stockle et al. 1994; Nuttall et al. 2017). Grain-N content simulation has been used in early CMs as criteria for cereal's nutritional and functional characteristics. Daily N demand and its translocation to grains have been simulated at different levels of complexity. For example, Sirius (Jamieson et al. 1998) and STICS (Brisson et al. 1998) modelled simpler harvest index approach. Likewise, Sirius modelled complex source-sink approach (Jamieson and Semenov 2000). Whilst, CERES divides the GF into different phases and simulates independent functions of starch and N accumulation (Ritchie et al. 1998). The source of starch is photosynthesis and re-translocation of reserves, while genetic variations in N accumulation are not included in this routine. Although APSIM implements a similar routine as CERES for grain protein, its estimation is not precise, especially when very low and very high N inputs combine with drought stress.

Now these days, improvement in simulation of the N dynamics and starch accumulations in grain have been proposed by incorporating genetic factors such as cultivar characteristics and environmental factors such as water availability (Pan et al. 2007). For this, individual maximum starch accumulation is used to explain variation in starch synthesis potential, while individual maximum grain N accumulation and the physiological filling duration are being used to explain differences in protein deposition across cultivars. To simulate whole-grain characteristics, an intra-spike model approach for variations in grain-size distribution based on spikelet and floret position in a single spike provides a powerful tool to envisage grain-size screening percentage, milling yield, and associated end-use parameters (Nuttall et al. 2017).

10 Conclusions and Future Prospects

Wheat is prone to various environmental stresses. These stresses specifically hinder the grain filling stage due to the poor translocation of photoassimilates to the developing grains and starch biosynthesis. These stresses have their specific as well as general effects on the principal grain components such as starch, protein, and lipids. However, from the presented knowledge, it is not yet comprehensible to what level a particular stress can alter the contents of different grain components. The previous information described in various reviews are scattered due to an

Table 1 Wheat crop simulation models

Models	Characteristics	Source
Agricultural Production Systems Simulator Model (APSIM)	Simulates growth and development of a crop in a daily time step on an area basis and weather, soil water and soil nitrogen, and management practices	http://www.apsim.info
Cropping Systems Simulation Model (CropSyst)	Simulates growth of a crop on daily time step. It is based on multi-year, multi-crop system and has been developed to study the effect of cropping systems management on productivity and the environment	http://modeling.bsyse.wsu.edu/CS_Suite/cropsyst/index.html
Decision Support System for Agrotechnology Transfer Model (DSSAT)	Simulates growth, development, and yield as a function of the soil-plant-atmosphere dynamics	http://www.icasa.net/dssat/
Environmental Policy Integrated Climate model (EPIC)	Simulates growth and development on a daily time step and predicts effects of management decisions on soil, water, nutrient, and pesticide movements and their combined impact on soil loss, water quality, and crop yields for areas with homogeneous soils and management	http://epicapex.brc.tamus.edu/
Farm ASSEssment Tool (FASSET)	The whole-farm dynamic model used to evaluate the consequences of changes in regulations, management, prices, and subsidies on a range of indicators for sustainability at the farm level, e.g., farm profitability, production, nitrogen losses, energy consumption, and greenhouse gas emissions	http://www.fasset.dk
LINTUL-4	Simulates crop growth under potential, water-limited, and N-limited conditions and climatic change	http://models.pps.wur.nl/models
Model for Nitrogen and Carbon in Agro-ecosystems (MONICA)	Simulates growth and development on a daily time step, as a function of the most important processes in soil and plant and their feedback relations	https://soil-modeling.org/resources-links/model-portal/monica
Simulateur mulTIdisciplinaire pour les Cultures Standard (STICS)	Simulates crop growth as well as soil water and nitrogen balances driven by daily climatic data. It calculates both agricultural variables (yield, input consumption) and environmental variables (water and nitrogen losses)	https://www6.paca.inra.fr/stics_eng/
SiriusQuality2 (SQ2)	Simulates the phenology and canopy development of small grain cereals and the fluxes of water, nitrogen, and carbon in the soil-plant-atmosphere continuum in response to weather and crop management	http://www1.clermont.inra.fr/siriusquality/

emphasis on particular stress, and most of these reviews specifically concentrate on the yield components, and thus, there are major lacks on the effects of various stresses on wheat grain composition and quality. Hence, it is not easy to sketch a comprehensive atlas on stress-induced alterations on wheat nutritional parameters. Thus, this area seems the center of attention for future research.

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Salt Stress Responses and Tolerance in Wheat

Neerja Srivastava

Contents

Abstract Wheat is produced in 17% of cultivated land throughout the world. It is a most widely grown cereal crop and has more calories and protein than any other crop. Approximately 35% of the world population uses it as staple food. Salt stress is one of the principal limitations in wheat production. The agricultural production in many countries is severely impaired because the world's total 6% land area, i.e., about 800 million hectares, is contaminated by salt. Many physiological as well as biochemical mechanisms have been developed in plants to survive at high salt concentration. The most effective as well as economical approach to solve the salt problem is to improve wheat adaptation under salt stress and enhance its grain yield particularly in those countries which produce wheat with less resources and facing problem of salt in soil. Various approaches like morphological and physiological testings and genetic and molecular strategies are required to understand the genetic as well as physiological mechanisms of natural differences in salt tolerance of wheat and to obtain methods to investigate the inherent genetic differences, to get new candidate genes for improving salt tolerance in wheat.

Keywords Wheat · Abiotic stress · Salt stress · Salt tolerance · Salt responses

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1 Introduction

Wheat is the principal cereal crop of the world and provides calories and protein. Approximately 85% and 82% of people of the world derive basic calories and protein, respectively, from wheat (Chaves et al. 2013). In fact, it generates various wheat products like leavened bread, flat and steamed bread, cakes, pasta, biscuits, noodles, couscous, and beer (Curtis and Halford 2014). Apart from human consumption, non-food products like fuel are also developed from it. Wheat is grown in tropical and subtropical areas in rainfed as well as irrigated cultivation due to its greater degree of adaptation. But, unfavorable environmental conditions damage crop production very badly (Rahaie et al. 2013). The major stresses are salinity, drought, water abundance, ultraviolet-B radiation, cold, heat, pathogens, insects, chemicals, ozone, and oil nutrient deficiency (Mahajan and Tuteja 2005; Cançado 2011). Under stress, plant growth and reproduction is affected at varying degree of severity in stress. The stress is highest when it happens in mixture (Caverzan et al. 2016).

Approximately, 17% of the entire cultivated area of the world is occupied by wheat which is the most commonly grown cereal crop. About 35% of the people of the world use wheat as their staple food and have more calories and protein in the diet than any other crop. One of the main limitations for wheat production is salt stress. Salt affects around 800 million hectares area of the world which is more than 6% of the total land area in the world (FAO 2008) and impairs the agricultural production in many countries. Sensitivity for salt stress is more in durum wheat than bread wheat. A number of different researchers have screened wheat for salt tolerance in seedling and maturity stages (Akram et al. 2002; Khayatnezhad and Gholamine 2011). However, a difficult challenge for plant breeders is to achieve genetic increases in yield under salt stress (Khayatnezhad et al. 2010). For improving the knowledge of tolerance mechanism and to improve salt tolerance in wheat, further screening for salt tolerance and its validation in salt-affected fields are still needed (Turki et al. 2014).

2 Salt Stress

In arid and semiarid areas of the world, crops are naturally under the influence of various abiotic stresses, because of which agricultural productivity is very low. Crop production is reduced to a great level by soil salinity (Gorham 1995; Shannon 1998; Munns 2002). There are a lot of adverse effects on plant growth in the saline growth medium because of less osmotic potential in soil solution (osmotic stress), specific ion effects (salinity stress), nutritional disparity, or a mixture of all these (Ashraf 1994; Marschner 1995). Many harmful effects on plant productivity as well as on development are observed at physiological, biochemical, and molecular level by these factors (Winicov 1998; Mansour 2000; Tester and Davenport 2003; Levitt

1980; Gorham et al. 1985; Munns 2002; Munns and James 2003). Growth or existence of the plant is estimated to assess the tolerance of plants to salinity stress, as it connects the up- or downregulation of various physiological mechanisms which occurs inside the plant (Niknam and McComb 2000; Ashraf 2004).

Various cellular functions of the plant are damaged by soil salinity, because of which the world agriculture faced a lot of problems. Agricultural land has become nonproductive because of storage of salt in fresh soil by tidal flow. About 300 million ha irrigated farmland is influenced by salt, and half of it lies in China, India, Pakistan, and the USA (FAO and ITPS 2015). High level of toxic ions particularly NaCl in soil or irrigation water poses the most severe threat to crop yield in dry areas (Moeinrad 2008). Growth and productivity of many crops are reduced in salinity stress (Schleiff 2008; Islam et al. 2011; EL Sabagh et al. 2015 a, b, c, d, e; Abd El-Wahed et al. 2015; Hasan et al. 2017; Rahman et al. 2017). The disruption of intracellular ionic concentration and osmotic gradients by salinity results in malfunctioning of photosynthesis (Islam 2012), decrease in protein synthesis and enzyme activities (Sadak and Abdelhamid 2015), low balance of nutrition (reduction of sodium, phosphorous, potassium, calcium ion, imbalanced carbon metabolism) (Abdelhamid et al. 2013; Islam et al. 2011; Islam 2012), and reduced length, width, and pith diameter of stem, blade thickness, vascular bundle length, and xylem vessels of leaf (Dawood et al. 2014; Semida and Rady 2014; Hassan et al. 2018).

3 Physiological and Biochemical Responses in Wheat Under Salinity Stress

About 20% of irrigated area is influenced by soil salinity which is a worldwide problem and drastically decreases crop yields (Qadir et al. 2014). It is very difficult to design and interpret experiments as the physiological changes in a plant to salt are mostly complicated and versatile. The development of so-called “omics-driven” research has advanced the knowledge of current plant physiology. New technologies have revolutionized physiological measurements, like high-yielding phenotyping, bioinformatics, and new analytical processes that ultimately developed fields like metabolomics. Two main phases occur in the plants’ response to salinity stress. Firstly, within minutes to days, the shoot ion-independent response occurs, which might be linked to sodium ion sensing and signaling (Gilroy et al. 2014; Roy et al. 2014). In this phase, closing of stomata and the inhibition of leaf extension take place due to the effects of salinity on water relations (Munns and Termaat 1986). In the second phase, ion-dependent changes by salt develop for a longer time (from days to weeks) and result in early aging of leaves and eventually decreased yield, or even plant dies because of the buildup of ions to toxic concentrations in the shoot and in old leaves (Munns and Tester 2008; Negrão et al. 2017).

The property of salt resistance results from those properties which are dependent on various physiological interactions and are not easy to determine. To study the effects of salinity, it is necessary to recognize not only the morphological features of the plant in response but also various physiological as well as biochemical properties such as harmful ions, osmotic potential, element deficiency, different physiological and chemical changes, and the relation between the different stresses (Munns 1993; Munns 2002; Neumann 1997; Yeo 1998; Hasegawa et al. 2000; Qados 2011).

A lot of workers have studied many anatomical, ecological, physiological, and molecular changes in plants under salinity stress (Tal 1984; Sachs and Ho 1986; Hurkman 1992; Wang et al. 1997). Complete metabolism of plant is reprogrammed from growth and development to increased induction of stress tolerance (Kosová et al. 2013a. To withstand high salt concentration, many physiological and biochemical processes are developed in plants.

Different mechanisms of salt tolerance can be present in a single plant. It is not still proved that they are selective for a single type of stress, e.g., ion exclusion restricts tolerance in the "osmotic phase" of salinity, or only one strategy is followed by a particular plant, e.g., a plant at moderate salt stress can use ion exclusion as its main tolerance mechanism, while tissue tolerance is the primary tolerance mechanism at higher salt stress. Some tolerance mechanisms may be more efficient in certain conditions like at higher salinity Na^+, exclusion is more valuable (Munns et al. 2012), while at moderate salinity, "osmotic tolerance" is more important, although their interactions in relation to other abiotic stresses, like less water availability, may also be important (Roy et al. 2014; Srivastava 2017).

3.1 Growth Responses

High salt concentration in the soil influences all stages of plants like germination to harvesting (Zheng et al. 2009). Salts can affect plants in two aspects, either by reducing the rate of water entrance into plants or through promotion of entry of toxic ions (Zhao et al. 2007). Generally, with increase in salt concentration in irrigation water, salinity problem also increases. Reduction in crop growth because of salinity is generally connected to the root-zone soil solution's osmotic potential which will give rise to some physiological changes and ultimately drastic decrease in crop yield (Siler et al. 2007). To keep the normal physiology and to tolerate the conditions of their location, plants require a right nutrition dose in salt stress condition. They need balanced amount of macro- and micronutrient elements to improve their growth and development under these circumstances. Oftenly micronutrients are ignored, and macronutrients N, P, and K are supplied extensively. However, under tough conditions the micronutrients are essential for better crop yield. Wheat crop can tolerate salinity till 7.0 dS m^{-1}, and there is reduction in its yield by 25% at 9.0 dS m^{-1} (Kramer and Amtmann 2012). This decrease in growth as well as in yield differs in between cultivars and amount of salt present in the medium (Sultana et al. 2000). The recently developed cultivars have a wider range of salts stress tolerance as they form a much diverse genetic base. Kalhoro et al. (2016) reported that the growth and yield of wheat cultivar Inqalab is affected drastically by salt stress ($MgCl_2^+$, $CaCl_2^+$,

Na_2SO_4). Its yield immediately decreased with increased salinity level because of osmotic as well as ionic toxicity.

To gain knowledge of heritable variation under salinity tolerance in the considered traits, Oyiga (2017) has evaluated the functioning of 150 genetically different wheat genotypes in varying salinity conditions in different stages of plant growth like germination, seedling, and adult. In each genotype, after giving treatment of 150 mM sodium chloride for 24 days, the amount of sodium, potassium, and potassium/sodium ratio in the various shoot parts like third leaves, stem, and remaining leaf parts were also measured. It was observed that the salt stress reduced 33%, 51%, and 82% germination vigor, seedling biomass, and grain production, respectively, and with genotypes affected all the growth stages.

Triticum aestivum L. cv. Shirodi showed sensitivity to 100 mM NaCl that had negative effects on plant growth. This observation is similar to the results of Erdal et al. (2011), according to which, diminished growth of plants under high concentrations of NaCl is due to changes in the plant metabolism of plant in relation to salinity. Plant growth is limited by salt stress as many physiological and biochemical mechanisms like photosynthesis, antioxidant capacity, and ion homeostasis are get affected by it (Ashraf and Harris 2004; Abedini 2016).

Datta et al. (2009) have studied the effect of salt stress at various salinity levels, i.e., 0, 25, 50, 75, 100, 125, and 150 mM NaCl on five wheat varieties HOW-234, HD-2689, RAJ-4101, RAJ-4123, and HD-2045. They observed that the growth attributes are affected by different levels of salinity. There is decrease in root and stem length below 125 mM salt. With subsequent treatments, fresh and dry weight of root and stem were also decreased considerably. It was observed that there is maximum germination in HD2689 at all the treatments, and greatest inhibition is in HOW234 at 150 mM salt concentration.

Sharma (2015) compared salinity tolerance of 42 wheat (*T. aestivum* L.) cultivars by growing them in half-strength Hoagland solution (control) provided with NaCl and kept at a wide range of salt resistance of 4, 8, 12, and 16 dsm^{-1}. A variety of growth responses to salinity are observed: like in some cultivars at lower salinity levels (4 and 8 EC), growth increased, while in most of the cultivars at higher levels (12 and 16 EC), growth was badly inhibited which was expressed by the stem and root lengths. Often, there is suppression of shoot growth compared to root growth. 12 EC was critical for most cultivars; only HD-2160 had good tolerance even at 16 EC. According to them, among 42 cultivars tested, IWP-72 was most sensitive to salinity stress, while HD-2160 was most salt resistant. The other 40 cultivars were between the two extremes and were categorized into different groups. Those which are having more than 60% reduction in shoot length are named as salt–sensitive, those having 40–60% reduction in shoot length are termed as moderately salt-tolerant, and those having less than 40% decrease in shoot length as salt-tolerant groups at 2 EC dsm^{-1} over control.

Chamekh et al. (2017) investigated effect of salt stress on leaf area, ion accumulation (Na^+, K^+), and component yield (grain number/spike, 1000 grain weight, number of spikes/m^2, and grain yield) in 25 durum wheat genotypes (*Triticum turgidum ssp. durum)* which were cultivated in three different regions in Tunisia center (Echbika, Barrouta, and Sidi Bouzid). These sites differ by their salinity degree in the irrigation water, respectively, 2.1 (control), 4.3, and 5.2 g/l. The flag leaf area reduced significantly for the most of genotypes with the increase of salt stress treatments except Mahmoudi, Om Rabia, N, Maali, Khiar, and Jneh Khotifa varieties. Na^+ concentrations rose with increase in salinity, but K^+ concentration decreased as salinity levels increased for all cultivars except “Mahmoudi” and “Hamira” cultivars. Salt tolerance of these cultivars was confirmed by low concentration of Na^+ accumulation and more K^+ content in these genotypes at the highest salt level. Grain number per spike, 1000 grain weight, number of spikes per m^2, and grain yield showed a reduction with an increase in root zone salinization, but the effect was varied in different durum wheat genotypes. It was concluded that resistance to salinity can be improved in wheat genotypes by breeding programs through conservation of the leaf area and a low Na^+ level in the flag leaf.

3.2 Ions Accumulation

There is ionic disturbance, special ion effects, and nutrient scarcity symptoms in those plants which are growing in salt stress due to more sodium accumulation. Plant metabolism is influenced by harmful effects of the ion storage (Agrawal et al. 1964). KRL 19 accumulated more sodium under all the stages of salinity stress, while potassium level reduced under salt stress. Earlier, in case of wheat, under salinity Moustafa et al. (1966) have also reported rise in sodium and decrease in potassium contents. It was observed that ratio of Na^+/K^+ was also low in the Kharchia 65, which indicated that the salt resistance in plant is depicted by decreased level of sodium/potassium ratio which can be exploited to gain knowledge in resistance and sensitivity of wheat varieties (Joshi et al. 1979; Sairam et al. 2002).

3.3 Water Relations

Water stress, salinity stress, and ionic imbalance stress are generally caused by salt. Due to evaporation of water being utilized by plants and storage of salt, there is decrease in water potential which causes water stress in plants. Availability of water to plants is limited by extra amount of soluble salts present in the soil solution. A common response under such situations is the decrease in plant water potential, which must instantly be balanced by a reduction in the osmotic potential, by increase in amount of solute for maintenance of turgor potential. With an increase in salinity, water potential and osmotic potential of plants lowered toward more negative values, while turgor pressure is raised. For keeping water potential gradient at steady level between leaf and soil, osmotic potential of the cell sap changes. When plant growth is connected with osmotic potential in the root medium of varying salts or mixture of salts, osmotic effects dominate. Under osmotic stress, due to the rise in osmotic pressure in developing cells to encounter the mounting osmotic pressure of the rooting medium and to retain turgor, there is decrease in growth. One of the main factors for reduced growth is the energy expenses in osmotic adjustment of abiotic stress (Greenway and Gibbs 2003; Mudgal et al. 2010).

The osmotic potential of water is lowered due to addition of salts, which results in reduced accessibility of water in root cells. Therefore, salt stress causes the plant to face another stress, i.e., osmotic stress, which means that all physiological changes which are induced in drought stress are also present in salt stress. According to Fogle and Munns (1973), the capability of wheat seedling to derive nutrients from the root medium was reduced by the osmotic restriction of root growth. Salt may injure plants through specific toxic effects with its harmful osmotic effects (Longnecker 1974). There is suppression of growth and development; decrease in photosynthesis, respiration, and protein synthesis; and disturbances in nucleic acid metabolism by salinity stress (Boyer 1965; Kaiser 1987; Lambers 1985; Levine et al. 1990). The reduction in the intake of K^+, Mg^{2+}, and Ca^{2+} decreases growth at higher level of sodium (Poonia et al. 1972; Sairam et al. 2002).

Meneguzzo et al. (2000) exposed two cvs. of *Triticum durum* Desf. Ofanto and Adamello which have different sensitivities toward drought and heavy metal stress (cv. Ofanto more resistant than cv. Adamello) in 0, 50, and 100 mmol/L sodium chloride nutrient solutions for 9 days under controlled condition. Various parameters like growth, relation of leaf water, and storage of mineral nutrient in cell saps of the seeds were measured to study the effect of sodium chloride and to observe possible variation in the reaction of the two cvs. There is decrease in stem growth, especially in cv. Adamello, and production of shoot and root biomass in the highest salt concentration. Water potential (Ψ_W) as well as osmotic potential (Ψ_π) reduced with salt stress in both cvs. With osmotic adjustment because of sodium and chloride storage and maintenance of turgor by K in the cell sap.

To investigate the plant responses in salt stress, growth rates, osmotic adjustment, ion storage, and photosynthesis were studied by Kingsbury et al. (1984) in two bread wheat, *Triticum aestivum* L., varieties with varying salt tolerance which were grown in salt solution culture. They observed that the osmotic stress in salt solution is not the main reason to endanger the survival of these plants because lines have great variation in survival ability but not much alteration in water relations under salt stress. Of course, this conclusion is limited by the experimental settings because salinity stress is being provided by airy solution culture in the greenhouse. Other factors also participate when plants grown on soils contaminated with salt in the field and may have different responses. This conclusion is based on the studies done with pressure bomb estimations of leaf water potential in the day. It showed transpiration as the cause of main water stress in the plants which would have been even more in the field. It is unlikely that only some bars of osmotic stress are principal discriminating factor affecting survival as they are small water stress during the day. The main stress influencing growth in night however would be the osmotic effect of the salt solution. Despite full osmotic adjustment after salinity treatment, the varieties differed significantly in their comparative growth rates and photosynthetic responses for many weeks. There is nominal variation in total ion absorption as well as translocation in both lines as amount of main cations and chloride ion in the plant organs were considerably same in both.

3.4 Effect on Photosynthesis

According to the study of Abedini (2016), the content of photosynthetic pigments reduced in 100 mM NaCl-treated plants. Reduction in the photosynthetic pigment content in saline conditions is reported for numerous salt-sensitive plants (Weisany et al. 2011; Askari et al. 2015). It was suggested that decrease in photosynthetic pigment content may be the result of inhibitory effects of ion accumulation in chloroplasts, such as diminished stability of pigment-protein complexes and activation of enzyme chlorophyllase (Chookhampaeng 2011).

There is decreased deposition of chlorophyll during irradiation in leaves of dark grown wheat seedlings (*Triticum aestivum*, cv. Giza 168) in salinity stress. Abdel-kader et al. (2007) have studied the influence of salinity stress on the spectral forms of Pchlide, the phototransformation of Pchlide to Chlide, the blue shift (Shibata shift), the regeneration of Pchlide, and the deposition of Pchlide from 5-aminolevulinic acid (ALA) to elucidate the process behind the salt-affected decrease in chlorophyll biosynthesis. They observed that the salinity stress not affected phototransformation of Pchlide to Chlide. After flash irradiation and in continuous light, the blue shift (Shibata shift) of recently formed Chlide was postponed. Following flash irradiation or after 3-h irradiation, the reformation of Pchlide in darkness was hindered in the salt-stressed leaves. Although Pchlide was reformed even in salt-stressed leaves following 20-h dark period, the creation of short-wavelength Pchlide was inhibited. Salt treatment decreased the quantity of Pchlide stored in leaves which floated on ALA in comparison to controls. The rise in the low-temperature fluorescence emission spectrum at 735 nm which takes place in steps during irradiation of continuous light for many hours in control leaves was totally inhibited in salt-treated leaves. It is reported that salt stress not only suppress chlorophyll deposition partly by decreasing porphyrin production rate but also by a possible decrease in the production of chlorophyll-binding proteins.

It was observed by Datta et al. (2009) that the chlorophyll synthesis in plants was considerably influenced by salinity stress ($p < 0.05$) from 75 to 100 mM. There was a continuous decrease in total chlorophyll storage in the leaves in comparison to control in entire varieties.

3.5 Metabolites Accumulation

Plants store a range of metabolites, especially amino acids which have conventionally been regarded as precursors to and components of proteins under stressful conditions and have significant part in plant metabolism as well as development.

Accumulations of sugars, inorganic ion, and organic acids are the other physiological as well as biochemical factors associated with salinity and salt stress tolerance (Morgan 1984). In many species, there are reports of the deposition of compatible solutes (Brown and Simpson 1972) that are harmless at higher level for cytoplasmic processes (Wyn-Jones and Storey 1981), and maintain turgor, and/or protect macromolecular organization against the destabilizing impact of the reduction on water activity (Stewart and Lee 1974). In barley, beet and some halophytes belonging to Chenopodiaceae quaternary ammonium compound glycine betaine are formed under salinity stress (Stewart and Lee 1974). Mannitol production capacity in transgenic tobacco improves adaptation to salinity (Tarczynski et al. 1992).

As a criteria for selecting salt stress resistance, use of deposited proline has been encouraged (Storey and Wyn-Jones 1975), but it cannot be considered as a marker for salt resistance as it is deposited under the other stresses also like temperature, drought, and starvation (Naik and Joshi 1983), while in many salt-affected plants, its concentration reduces (Siddiqui and Krishnamoorthy 1987; Sairam et al. 2002). There was a positive correlation between proline accumulation and plant stress. Under various stress conditions in plants, proline plays a highly beneficial role. During stress, it is not only an excellent osmolyte, but it also plays three other significant roles as a metal chelator, an antioxidative defense molecule, and a signaling molecule. There is extra formation of proline in plants under stressful environment which gives stress tolerance through cell turgor maintenance or osmotic balance, which stabilizes membranes to prevent electrolyte leakage, and keeping reactive oxygen species (ROS) in normal scale to prevent oxidative eruption in plants. When proline is given from outside at low level, there is increased stress tolerance. However, when supplied from outside in high quantity, proline produces toxic effects (Hayat et al. 2012).

According to Abedini (2016) proline accumulated in shoots of the studied wheat cultivar as a response to salinity. Accumulation of proline in plants organs as an adaptation mechanism to the salinity and water deficit has been previously demonstrated (Farhoudi et al. 2015). Proline contributes to the osmotic regulation of plants under saline condition. It seems that in doing osmotic adjustments during the presence of Na^+, the hydrolysis of soluble proteins provides a pool of compatible osmolytes (Ashraf and Harris 2004). The result obtained for the protein content of wheat cultivar is comparable to this view. It has been suggested that the decline in proline content may be an outcome of the dilution effect resulted from improved plants growth.

In the case of plants growing in 25–100 mM NaCl, there is enhanced level of proline accumulation (Datta et al. 2009). They have reported that in comparison to control, wheat plants also accumulated higher level of total soluble carbohydrate from 25 to 100 mM NaCl.

3.6 *Enzyme Responses*

Productivity of agricultural systems around the world is affected by salt stress which is among the major environmental stresses. There is imbalance of cellular ions due to high salt concentration which result in toxicity of ion, osmotic stress, and produces active oxygen species (Cheeseman 1988; Alscher et al. 1997, Noctor and Foyer

1998). Antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), catalase (CAT), and peroxidase (POD) and nonenzymatic scavengers like glutathione (GSH), ascorbic acid (AsA), and carotenoids are developed by plants to lessen the injurious effects of these ions (Vranova et al. 2002; Dalmia and Sawhney 2004).

In several plant species, there is a link in antioxidant capability and sodium chloride resistance (Gossett et al. 1994; Dionisio-Sese and Tobita 1998; Benavides et al. 2000). However, exact process of sodium chloride resistance is still not known. There is not much knowledge about the capability of antioxidants and improvement in resistant and sensitive cultivars of the same species of wheat seedlings under salt stress (Mandhania et al. 2006).

There is considerable rise in the activities of antioxidant enzymes SOD and POD and a slight increase in the activity of CAT at a low concentration of NaCl in the *Triticum aestivum* L. cv. Shirodi (Abedini 2016). This increase in antioxidant enzymes activity could be an indication of a protective mechanism which reduces oxidative damages induced by stress (Harinasut et al. 2003; Chawla et al. 2013). It seems that the produced H_2O_2 is effectively removed by POD and CAT at low salinity. The studied cultivar of wheat could not efficiently increase SOD, POD, and CAT enzyme activities at high salinity.

There is rise in the H_2O_2 as well as MDA amount in studied wheat cultivar under salinity. Salt stress causes water deficiency and increases ionic and osmotic effects that proceed to the production of ROS (Chawla et al. 2013). Following salt stress, O_2 is generated by plasma membrane-bound, NADPH oxidase (Aktas et al. 2006). The higher concentration of ROS in plants organs causes oxidative harm to biomolecules such as lipids and results in production of MDA as the breakdown product of polyunsaturated fatty acids in membranes. Other authors have also observed the inhibitory effect of Zn application in sufficient amount on the formation of these damaging components under salinity (Zago and Oteiza 2001; Tavallali et al. 2010; Weisany et al. 2012). Zinc have significant function in regulation of production and detoxifying free oxygen radicals as well as succeeding lipid membrane oxidation (Alloway 2008). Zn ions also prohibit membrane-bound NADPH oxidase (Kawano et al. 2002).

Mandhania et al. (2006) investigated the influence of salinity stress in two cultivars of wheat (*T. aestivum*) seedlings, namely, salt-resistant KRL-19 and salt-susceptible WH-542 on cell membrane injury, ion concentration, and antioxidant enzymes. For this, irrigation with 0, 50, and 100 mM NaCl was done in 4-day-old seedlings. The observations were made on the 3rd and 6th day following salinity treatment and 2nd day following salt exclusion. With induction of salt stress, the relative water content decreased more in WH-542 in comparison to cv. KRL-19. The ratio of potassium/sodium in KRL-19 was more in comparison to WH-542. There was more damage in WH-542 on cellular membranes because of lipid peroxidation as observed by the more storage of H_2O_2 and MDA and higher seepage of electrolytes in comparison to KRL-19. CAT, POD, APX, and GR activities were enhanced with higher concentration of salt in both cultivars, while SOD activity reduced was upon depolarization; there was recovery in these enzymes' activity in KRL-19 and very slow recovery in WH-542.

3.7 Changes in Proteins

There was an increased storage of proteins of the LEA superfamily under various stresses like drought, heat, salinity, cold, and mechanical wounding. There are at least five subclasses in late embryogenesis-abundant (LEA) superfamily, of which the major ones are LEA-II (dehydrins) and LEA-III proteins. Wheat and barley resistance to low temperatures, drought, and other stresses is correlated with transcript, protein levels, as well as phosphorylation level of these proteins (Crosatti et al. 1995; Vágújfalvi et al. 2000, 2003; Vítámvás et al. 2007; Kosová et al. 2008; 2013a; Sarhadi et al. 2010; Labhilili et al. 1995; Brini et al. 2007). Cellular transport and membrane properties are affected under these stresses. Therefore, there is an increased demand for ion transport which causes associated increase in the plasma membrane as well as tonoplast ion transporters like V-ATPase in salt stress (Peng et al. 2009; Kosová et al. 2014).

Proteins that are stored in plants in salt stress may participate in osmotic adjustment and supply a form of nitrogen which is stored and reused later (Singh et al. 1987). They may be present constitutively at low concentration or may be produced de novo in salt stress (Pareek-Singla and Grover 1997). It was observed that some cytoplasmic proteins are produced under salinity which changes cytoplasmic viscosity of the cells (Hasegawa et al. 2000; Parvaiz and Satyawati 2008). Datta et al. (2009) reported that protein concentration in leaves reduced with successive enhancement in the amount of salt in comparison to the control.

Das et al. (2016) did gel analysis of the resulting protein patterns which showed genotype-specific and salt stress-responsive protein expression. At different stages, there were more number of protein expressions in the resistant genotype in comparison to sensitive genotype. There was variation in physiological parameters with genotypes and the crop growth stages. Proteomics studies have shown that there are changes in protein levels of wheat genotypes which cause tolerance to salt stress. Information can also be obtained on how defensive mechanisms are adopted from plants through comparative proteomic studies of plants before and after specific or interactive stresses that might be helpful in the development of future strategies against salinity stress.

Yıldız and Terzi (2008) cultivated tetraploid (*Triticum durum* Desf., genome *AB*) and hexaploid (*T. aestivum L.*, genome *ABD*) wheat species as well as their diploid wild progenitors [*T. monococcum L. (A)*, *Aegilops speltoides Tausch (B)*, and *Aegilops tauschii Cosson (D)*] in 100 mmol/l sodium chloride and extracted soluble proteins from their primary leaf tissues then separated them by two-dimensional (2D) gel electrophoresis. In all species no new protein synthesized in treated plants in comparison to the controls. However, there were some differences in protein profiles of the different species. Many of these proteins were acidic in character, and their isoelectric points (pI = pH − acidity of proteins) varied from 5.1 to 6.9 and mol weight (LMW) from 20.3 to 30.6 kDa. There was increase and/or decrease in amounts of 11 low-molecular-weight (LMW) and 3 intermediate-molecular-weight (IMW, 34.8–35.4 kDa) proteins that were common between at least 2 species. Reduction or losses in protein profiles were the main changes in *Ae. speltoides*.

All the significant variations in *T. durum* were observed due to rise in proteins under salt stress. There was enhancement in some proteins of *T. aestivum*, *T. monococcum*, and *Ae. tauschii*. In wheat species of *T. monococcum L. A* and/or genome(s), this rise in the protein concentration may lead to an enhancement in the resistance mechanisms toward NaCl stress.

Sobhanian et al. (2016) studied four wheat cultivars with varying degrees of resistance grown hydroponically in salinity treatment of 0, 70, 140, and 210 mM NaCl and performed leaf sampling of five leaf stages. There were fundamental similarities among the cultivars which are shown by electrophoretogram of the soluble proteins of leaf in salinity as well as in control treatments. Not a single polypeptide band was related to the particular cultivars or to any one type of salinity treatments. The study of variations in proteins can be investigated by electrophoretic analysis in salt treatment which can be utilized for knowledge of salinity resistance of genotypes.

4 Salt Stress Tolerance in Wheat

The grain yield of wheat is considerably influenced by soil salinity of ~10 dS m^{-1} as it is moderately salt tolerant. The most effective and cheapest strategy to tackle the salinity is to improve wheat adaptation under high salinity and to enhance its grain production especially in those countries which produce wheat, have poor resources, and are susceptible to soil salinity (Oyiga 2017).

A lot of attention has been focused on identifying genetic sources that are having less transportation of sodium to leaves, are highly choosy for potassium than sodium (i.e., Na^+ exclusion), and have higher performance. In an approach to enhance salinity tolerance beyond the existing cultivated wheat gene pool, wide hybridization of some wild halophytic species of Triticeae with that of wheat has been proposed (Colmer et al. 2006). Tall wheatgrass species, e.g., *Thinopyrum bessarabicum* (Save ex Rayss) A Löve ($2n = 2x = 14$, EbEb) and *Lophopyrum elongatum* (Host) A. Löve ($2n = 2x = 14$, EE), are significant gene sources for agronomically desirable traits, particularly salt tolerance among the wild relatives (Dvorak and Ross 1986). Wheat *Thbessarabicum* amphiploids (Tritipyrums) have been produced, and one such amphiploid was shown to survive in 250 mM NaCl which is equal to half-strength seawater (Forster et al. 1988). The salt resistance potential of Tritipyrum and some of the disomic addition and substitution lines derived from across between wheat and Tritipyrum have been evaluated, and the positive contribution of 5Eb addition lines has been reported (King et al. 1997).

Cytogenetic methods and molecular markers have been used in screening addition, substitution, and recombinant lines. Recently, one of such molecular marker systems called the PCR-based landmark unique gene (PLUG) has been developed in wheat based on intron polymorphism (Ishikawa et al. 2007, 2009). Although homoeologous genes of wheat are highly similar, intron regions have more polymorphism than exon regions (Bryan et al. 1999). Therefore, it is possible to separate

PCR products derived from homoeologous genes using electrophoresis. Furthermore, the coding regions of the genes are often highly conserved between species or genera, making the EST-derived markers useful for marker development in wheat relative species such as *Th. bessarabicum*, where whole genome sequences are not yet available (Zeinali et al. 2013).

5 Mechanism of Salt Tolerance

Many abiotic stresses like cold, salinity, drought, floods, heat, oxidative stress, and heavy metal toxicity affect plants in their life cycle, of which salt stress is the major abiotic stress (Mahajan and Tuteja 2005). It negatively affects agricultural yield and ultimately plant growth which limit the utilization of land. In the world, salt stress affects around 6% of the total land and 20% irrigated areas (Unesco Water Portal 2007). Our food production is limited as population of the world is rising alarmingly and assumed to be nine billion by 2050 (Varshney et al. 2011). The main worry is for food supply to the rising world population because the green revolution has already reached its ceiling. Because of industrialization and/or habitat use, agricultural land is very fast shrinking which is a principal danger to sustainable crop production. Therefore, it is essential to raise salt-resistant plants which can efficiently utilize salt-contaminated agricultural area for sustainable crop production. Salinity is characterized by a high concentration of soluble salts. When concentration of ion(s) maintains osmotic pressure equal to that produced by 40 mM NaCl means 0.2 MPa or higher in soil, then it is considered as saline (USDA-ARS 2008). All plants have developed processes to control sodium chloride accumulation as it is the most soluble and widespread salt while other nutrients like potassium and nitrate usually present in low amount (Munns and Tester 2008). The problem of salinity is further deteriorated through irrigation and is prevalent very commonly in hot temperate regions, due to extra water loss by transpiration. An osmotic stress is the first influence of salinity stress due to the occurrence of ions in rhizosphere that limits withdrawal of water through roots and results in decreased plant growth. Ionic disequilibrium causes the second impact of salinity stress which causes inactivation of enzymes, nutrient deprivation, toxicity of ions in tissues, and oxidative stress. Oxidative stress produces ROS which harm plants by increasing lipid peroxidation, DNA damage, and prohibition of photosynthesis (Flowers et al. 1977; Greenway and Munns 1980; Turan and Tripathy 2012). If the amount of salt is higher, it causes plant death (Niu et al. 1995; Yeo 1998; Glenn et al. 1999).

Salinity tolerance in plants has interspecies and intraspecies variability (Turan and Tripathy 2012). There are various mechanisms in plants to withstand salinity stress such as removing salts or storing ions into various tissue compartments, vacuoles, or old leaves (Flowers and Yeo 1992; Munns 1993; Yeo 1998). Sodium and chloride are efficiently removed by roots, while water is drawn from the soil in most plants (Munns 2005). Plants manufacture osmolytes such as glycine betaine, trehalose, or proline in response to osmotic stress, which guard them from dehydration or protein denaturation. However, oxidative stress is caused by ionic stress and produces various enzymatic or non-enzymatic antioxidants, which defend plants from damaging effects of ROS (Shao et al. 2007). Since long, plant breeding is utilized for making salt-resistant and more productive lines, but, because of multigenic character of salt resistance and occurrence of small genetic variation in principal crops, its use is limited. Recently, for producing salt-tolerant plants, genetic engineering has played a major role. Plants can be improved for salinity tolerance through quantitative trait loci (QTLs) and molecular markers. For releasing successfully a salt-resistant crop cultivar, functional genomics and use of new techniques along with significant cognizant issues are important (Turan et al. 2012).

6 Various Strategies of Salt Tolerance

A wide range of salinity responses in plants are observed in various reports that demand a large variety of adaptations at the whole plant level (Wyn Jones and Gorham 1983; Munns 1993). Under high salinity conditions, plants have developed various mechanisms over the years that permit them to adapt, grow, and reproduce. Roy et al. (2014) have categorized these processes into three main classes: (1) osmotic stress resistance triggered before shoot Na^+ accumulation and regulated by long-distance signals which decrease stem growth; (2) sodium or chloride removal, which prohibits sodium and chloride uptake and transport mechanisms in roots to decrease the storage of these ions to a damaging level in leaves; and (3) resistance of tissue to stored sodium or chloride ions where sodium or chloride ions succeed in gaining entry into the plants and are stored in the leaf vacuole to avoid salt injury in the sensitive thylakoid membrane of the chloroplasts. All these three different mechanisms have also been described by other workers (Munns 2002; Tester and Davenport 2003; Kumari et al. 2014).

To improve the salinity tolerance of wheat, various methods have been followed like introducing genes into adapted cultivars for salt tolerance, including screens of big international collections, full field trials of selected varieties, conventional breeding procedures, and untraditional crosses with wheat relatives. The purpose was to exploit differences in salt resistance within wheat and its ancestors or close relatives to develop new wheat varieties with more resistance than modern wheat cultivars.

6.1 Osmotic Adjustment

Plants face different types of environmental stresses like salt stress, water shortage, high and low temperature, harmful metal ion concentration, and UV radiations throughout their life cycle. They restrict the growth and productivity of plants to different levels, depending upon the gravity of stress. Stimulated production of ROS like OH·, O_2·, H_2O_2, etc. is one of the stress responses in the plants. They cause considerable damage by direct interaction with various macromolecules and also by peroxidation of membrane lipid components. To keep the ROS concentration in control, cells have developed different processes. Low level of ROS participates in the signal transduction mechanism (Foyer and Noctor 2005). These ROS are removed by low-molecular-weight antioxidants like glutathione, ascorbic acid, α-tocopherol, and antioxidative enzymes such as catalase, ascorbate, peroxidase, and superoxide dismutase. The production of free radical surpasses the overall cellular antioxidative potential resulting in oxidative stress that contributes to harmful effects on plant growth under various stress conditions (Hayat et al. 2012).

Plants store large amount of various compatible solutes in response to different stresses (Serraj and Sinclair 2002). They are low-molecular-weight, highly soluble organic compounds which are usually nontoxic at elevated cellular levels. They protect plants from stress through cellular osmotic adjustment, ROS detoxification, protection of membrane integrity, and enzymes/protein stabilization (Ashraf and Foolad 2007; Yancey 1994). These are proline, sucrose, polyols, trehalose, and quaternary ammonium compounds (QACs) like glycine betaine, alanine betaine, proline betaine, and pipecolate betaine (Ashraf and Harris 2004; Rhodes and Hanson 1993).

Proline is derived from its predecessor glutamic acid in plants and under osmotic stress condition acts as an osmoprotectant (Delauney and Verma 1993). During biosynthesis of proline, two enzymes pyrroline-5-carboxylate synthase (5PCS) and pyrroline-5-carboxylate reductase (P5CR) have important role (Ashraf and Foolad 2007; Turan et al. 2012). Proline accumulation occurs under shortage of water (Hare et al. 1998), salt stress (Munns 2005; Rhodes et al. 2002), cold (Naidu et al. 1991), heavy metal exposure (Bassi and Sharma 1993; Sharma and Dietz 2006), UV radiations, etc. Proline provides stability to subcellular structures like membranes and proteins, removes free radicals, and safeguards cellular redox potential in stressed conditions (Ashraf and Foolad 2007) besides working as osmolyte for adjusting osmotic potential. They can also work as protein-compatible hydrotrope (Strizhov et al. 1997), alleviate cytoplasmic acidosis, and maintain proper $NADP^+$/NADPH ratios suited for metabolism (Hare and Cress 1997). Proline deposition under salt stress is linked with stress resistance in many plant species, and its concentration is generally more in salt-resistant plants in comparison to salt-sensitive plants (Fougère et al. 1991; Petrusa and Winicov 1997). It is normally stored in the cytoplasm for working as molecular chaperons that stabilize the proteins structure and also buffer cytosolic pH and preserve cell redox status. Its accumulation may also be component of a stress signal affecting adaptive responses.

Abebe et al. (2003) reported that mannitol enhances development of transgenic wheat in water stress as well as salinity in the callus and whole plant, which is similar with previous reports utilizing the same *mtlD* gene in tobacco (Tarczynski et al. 1992, 1993; Karakas et al. 1997; Shen et al. 1997) and *Arabidopsis* (Thomas et al. 1995). The quantity of mannitol accumulation in transgenic wheat is found to be less in tobacco and *Arabidopsis*. Mannitol accumulation in tobacco was from 1 to 7 μmol per gram fresh weight (Tarczynski et al. 1992, 1993; Shen et al. 1997), while in transgenic *Arabidopsis*, it was from 0.05 to 12 μmol per gram fresh weight (Thomas et al. 1995). It was reported that on the basis of severity of stress, wheat accumulated mannitol in the callus from 1.7 to 3.7 μmol per gram fresh weight and in the mature fifth leaf from 0.6 to 2.0 μmol per gram fresh weight. According to previous reports, the level of stored mannitol was not sufficient enough to be the cause of osmotic influences (Tarczynski et al. 1992, 1993; Thomas et al. 1995), although plant water status was not measured directly. According to Karakas et al. (1997), mannitol adds only 3×10^{-3} to 4×10^{-3} MPa for osmotic adjustment in salt-stressed transgenic tobacco.

Mannitol enhances tolerance to water deficit stress mainly by osmotic adjustment (Loester et al. 1992). Abebe et al. (2003) reported that no difference was observed in the Ψ_s values of −mtlD and + mtlD transformants either in the callus or in the mature fifth leaves and in both osmotic adjustment was similar under water and osmotic stresses. Mannitol accumulation was small in response to stress, and it has less impact on osmotic adjustment in comparison to other carbohydrates. They reported that 3.8 μmol per gram fresh weight of mannitol in PEG-stressed calli and 3.7 μmol per gram fresh weight in sodium chloride stressed calli contributed only -1.1×10^{-2} MPa to Ψ_s of fresh calli at 85% relative water content (stressed), while the input of mannitol to Ψ_s of turgid calli would be -9.9×10^{-3} (PEG stress) and -9.5×10^{-3} MPa (sodium chloride stress) at 95% relative water content (unstressed). This is just 1.2% of the Ψ_s at full turgor or 2–3% of the osmotic adjustment in stressed calli. In transgenic plants, the destiny of mannitol is not known as wheat do not produce mannitol naturally. It is not having any procedure to transfer or metabolize mannitol and most probably stored in the cytosol as a closed end product. This sugar alcohol adds -2.0×10^{-1} and -1.9×10^{-1} MPa to Ψ_s of calli in PEG and NaCl, respectively, as mannitol is stored in the cytosol which represents 5% of the whole water content in entirely turgid tissue. This corresponds to 25% of the Ψ_s at complete turgor of polyethylene glycol and salt-stressed calli, if Ψ_s and osmotic adjustment in the cytosol are the same with the values estimated on the tissue basis.

6.2 Salt Stress-Responsive Tolerant Genes

Many important genes involved in salinity and abiotic stress adaptation were recognized by Oyiga (2017) through sequences analysis of the associated SNPs. Among the categories of genes identified, 24% mainly engaged in the stress response, 18% in antiporter and transmembrane, 14% in transcription and translation, and 11% in redox homeostasis and detoxification-related activities. The transcriptome as well as RT-PCR expression analysis was done with the genes connected to the significant MTAs that show differential expressions in the different ST wheat genotypes. In fact, the amino acid sequence analysis of the putative genes exposed various sites of a nonidentical/missense mutation which may have given rise to the observed changeable salt stress responses in the dissimilar wheat genotypes. This gave new insights to understand the characters and processes related to salt stress. Therefore, to improve salt tolerance in wheat, underlying genetic and molecular response can straightaway be used by the breeders and scientists (Oyiga 2017). Zhong et al. (2009) reported an apparent modification of DNA methylation in plants because of salt stress which was dose-dependent. These modifications may suggest a procedure for plants' tolerance under salt stress.

6.3 Transcription Factors

Several signaling pathways that stimulate gene transcription and its downstream mechanism regulate plant stress responses. Plant genome consists of various transcription factors (TFs) (Wang et al. 2003).

Transcription factors (TFs) are the most important controllers that regulate genes and gene clusters (Nakashima et al. 2009). Various families of transcription factors have major role in stress responses of plants like bZIP (Uno et al. 2000), WRKY (Mare et al. 2004), AP2 (Sakuma et al. 2006), NAC (Xue et al. 2006), and C_2H_2 zinc finger (Kam et al. 2008) families (Rahaie et al. 2010). The expression of a broad range of target genes can be controlled by one TF gene by binding to the particular cis-acting element in these gene promoters known as regulon (Nakashima et al. 2009). Transcription factors (TFs) are involved in modulating developmental procedure and also give option to the plants to overcome and counter biotic and abiotic stresses (Mitsuda and Ohme-takagi 2009; Zhang et al. 2012; Rahaie et al. 2013).

It was observed by expression analysis of a set of bZIP candidate genes under long-term salt stress into different cultivars of wheat through reverse Northern blot that *bZIP1* (CN011839) was upregulated in a sensitive variety (Chinese Spring) and downregulated in a resistant cultivar (Mahouti) under salt stress. It was shown by BLASTX sequence analysis that protein of this gene is having two homologues in *Arabidopsis* (AtZIP56, E value = 1e-20] and wheat (TaABF, E value = 6e-5]. *TaABF* mRNA accumulated with *PKABA1*mRNA which is ABA-dependent protein kinase in the maturation of wheat grain and dormancy gaining, while *TaABF* transcripts rise briefly in imbibitions of dormant grains. *TaABF* transcripts are seed-specific in contrast to *PKABA1* mRNA and were not generated in vegetative tissues under ABA application or abiotic stress (Johnson et al. 2002; Rahaie et al. 2011). It was shown by analysis of gene expression through reverse Northern blot that two selected candidate wheat bHLHs (*bHLH2*: CA599618 and *bHLH3*: CJ685625) are influenced by salt stress in a resistant wheat cultivar. It was shown by the BLASTx results both contain *bHLH94* homologue in wheat (E value = 5e-85 for bHLH2 and E value = 5e-102 for bHLH3). Another homologue AtAIB for bHLH3 from *Arabidopsis* is engaged in controlling ABA signaling in *Arabidopsis* and has a role in drought resistance and ABA treatment response (Li et al. 2007; Rahaie et al. 2011). These two bHLH genes may play major role in resistance to salinity stress in wheat as shown by the high homology (Evalue = 2e-51] of these orthologues and through the outcome of reverse Northern blot hybridizations

(Rahaie et al. 2011). Through quantitative RT-PCR, a study of the expression levels in 10 MYB TF genes from wheat (*Triticum aestivum*) in two recombinant originated lines differing in their salinity tolerance with reference to salt or drought stress was done (Rahaie et al. 2010). A prospective novel MYB gene (*TaMYBsdu*1) was considerably upregulated in wheat leaves and roots under long duration drought stress. In fact, under salt stress *TaMYBsdu1* had more transcript abundance in the salt-resistant genotype in comparison to the sensitive genotype. It was suggested that TaMYBsdu1 is possibly a principal controller for wheat adaptation in both salinity and drought stresses (Rahaie et al. 2010). Two recognized MYB genes, *MYB2* (DQ353858.1) and *MYB3* (CJ920766), were upregulated in a resistant variety (Mahouti) in saline conditions but downregulated in the sensitive variety (Chinese Spring), *MYB2*. With the BLASTx sequence analysis and plant gene ontology assignment, it was observed that MYB2 is a portion of TaMYB1 (E value = 6e-155). Lee et al. (2007) reported that *TaMYB1* is engaged in abiotic stresses reactions in wheat. There is rise in this gene expression in oxygen deficiency (flooding), PEG treatment (drought), and salinity enhancements, particularly in roots. Its transcript step by step rises in the beginning of ABA and PEG treatments (Lee et al. 2007). By using wheat genome arrays, Mott and Wang 2007 compared transcriptome of salt-resistant wheat germplasm lines and observed that *TaMYB1* was among the upregulated genes with 34 times greater expression levels in stress condition in comparison to the control. It was shown by functional analysis in MYB2 homologue of *Arabidopsis*, AtMYB44 (E value = 1e-59), that it was upregulated in relation to drought, salinity, cold, and ABA treatments, particularly in stomatal guard cells and vascular tissue. Overexpression of this gene in transgenic plants provided more tolerance to these stresses as compared to wild-type plants (Jin and Martin 1999). Homology analysis of MYB3 (a member of R2R3MYB) has been done showing high homology in this gene and *AtMYB59* in *Arabidopsis* (E value = 4e-60). There was a rise in expression of *AtMYB59* in response to phytohormones like jasmonic acid, SA, gibberellic acid, and ethylene, particularly in leaf and shoot tissues (Li et al. 2006; Libault et al. 2007; Rahaie et al. 2011). The expression level of this *AtMYB59* in roots and inflorescences was less in comparison to other organs depicting its function in hormonal signal pathways in biotic stresses and plant resistance to pathogen attacks (Li et al. 2006; Libault et al. 2007; Rahaie et al. 2011). A novel R2R3-type MYB transcription factor gene, *TaMYB33*, in wheat (*T. aestivum*) was identified by Qin et al. (2012), which was produced in ABA, NaCl, and PEG stress. The promoter sequence *TaMYB33* consists of the putative ABRE, MYB, and other cis-elements in abiotic stress. There is increased resistance in drought and NaCl stress in *Arabidopsis*, but not in LiCl and KCl stresses through ectopic overexpression of this gene. The gene *AtP5CS* which is related to proline synthesis and *AtZAT12*, a C_2H_2 zinc finger transcription factor related to control of ascorbate peroxidase expression, were produced in the *TaMYB33*-expressing transgenic *Arabidopsis* lines suggesting that TaMYB33 stimulate the capacity of ROS removal and osmotic pressure management. ABA synthesis was enhanced while its signaling was restricted *as TaMYB33* overexpression lines have shown upregulation of *AtAAO3* alongside the downregulation of *AtABF3*and *AtABI1*t. Actually, TaMYB33 increases salinity and drought resistance partly through better capacity of ROS removal and osmotic balance management (Qin et al. 2012; Rahaie et al. 2013).

Another MYB gene *TaMYB3R1* is possibly connected with wheat response to drought, salinity, and cold stress. *TaMYB3R1* was cloned by Cai et al. (2011) from wheat (*T. aestivum*), and its amino acid sequence has high homology with MYB3R proteins of other plants. In epidermal cells of onion, through subcellular localization experiments, it was established that TaMYB3R1 was found in the nucleus. In yeast cells, transactivation assays confirmed that TaMYB3R1 was a transcription factor which needs the C-terminal region to stimulate the expression of the reporter gene. MSA cis-element-binding activity of TaMYB3R1 was shown by DNA-binding tests. Its expression was started after ABA treatment and slowly enhanced till 72 h after salinity or cold treatment. its expression was started after ABA treatment and slowly enhanced till 72 h after salinity or cold treatment, while, PEG treatment given an initial expression peak at 6 h of treatment, and then slowly declined (Cai et al. 2011). It was reported in the mass sequencing of full-length cDNAs in wheat (*T. aestivum*) by Zhang et al. (2009) that *TaMYB32* is a salt stress-related gene. Its sequences were cloned from various varieties of hexaploid wheat as well as its diploid progenitors. It was seen through analysis of sequence that two kinds of sequences are found in the diploid progenitors and four in the hexaploid wheat. It was observed that one of them was similar in both diploid and hexaploid wheat which means that TaMYB32 was preserved in the wheat evolution. Its genomic sequences confirmed it as non-intron genes following comparing their cDNA sequences and were mapped to homologous group 6 of wheat utilizing the electronic mapping approach, while in each genome of hexaploid wheat, two copies of the gene were present. It was shown by the homologous analysis that TaMYB32 share 72.4% homology with some R2R3-MYB proteins from rice (*Oryza sativa* L.) and 73.7% with maize (*Zea mays* L.). Salt stress also induces the expression of *TaMYB32* in roots, shoots, leaves, pistils, and anthers of wheat (Zhang et al. 2009).

The full-length cDNA sequence of new wheat (*T. aestivum*) NAC transcription factor, *TaNAC8*, was described by Xia et al. (2010a, b) through in silico cloning, RT-PCR, and 3′ rapid amplification of cDNA ends PCR procedures. It has close homology to rice OsNAC8 with N-terminal NAC domain as well as transmembrane helices motif of the C-terminus. It was confirmed by yeast one hybrid analysis that C-terminal area of TaNAC8 worked like transcriptional activator. There was rise of *TaNAC8* synthesis in leaves after 24 h of inoculation/treatment with an unsuitable isolate of the stripe rust pathogen *Puccinia striiformis* f. sp. *tritici* or action with MeJA or ethylene in wheat. However, there was no noteworthy influence on expression of SA and ABA genes. Abiotic stress treatments such as high salt, PEG, and cold activated *TaNAC8* expression, which suggests that it may work as a transcriptional activator related to wheat defense reactions to both abiotic and biotic stresses (Xia et al. 2010a, b). Mao et al. (2012) obtained a portion of *TaNAC2* from suppression subtractive cDNA libraries of PEG-treated wheat, while its full-length cDNA was derived through screening a full-length cDNA library of wheat. It was shown by profiling of gene expression that TaNAC2 was linked to the response of drought, salinity, low temperature, and ABA stress. There was increased resistance to drought, salinity, and cold stresses due to overexpression of *TaNAC2* in *Arabidopsis* which overlapped with increased expression of abiotic stress-responsive genes and various physiological indices (Mao et al. 2012). Abiotic stresses like high salinity, wounding, and cold also expressed *TaNAC4*, which is similar to *TaNAC8*, suggesting its role as a transcriptional activator under biotic and abiotic stresses in wheat (Xia et al. 2010a, b). Rahaie et al. (2011) have observed that *NAC67* (BU672229), a possible family member of NAC family, was expressed more in salt stress. Its protein has a strong homology in wheat (TaNAC69, E value = 2e-151) (Rahaie et al. 2011; Xue et al. 2006). AtNAC2 is also a NAC67 homologue in Arabidopsis in relation to salt stress, ABA,ACC, and NAA treatments, but its production in salt stress needs ethylene as well as auxin signaling pathways. The expression level of *AtNAC2* in roots and flowers has been higher than in other tested tissues (He et al. 2005; Rahaie et al. 2011, 2013). Zhang et al. (2016) have studied the functions of a novel wheat *TaNAC47* gene whose overexpression in *Arabidopsis* increased the resistance of transgenic plants to drought, cold, and salinity stresses and rose ABA sensitivity. An interaction in protein encoded by *TaNAC47* and ABRE *cis*-element has shown that *TaNAC47* controls plant resistance toward several abiotic stresses and is a possible candidate gene to enhance stress resistance in crops. Two chosen candidate genes of wheat, bHLHs (bHLH2: CA599618 and bHLH3: CJ685625), are influenced by salinity stress in a resistant wheat cultivar as shown through gene expression analysis via reverse Northern blot. It was observed through BLASTx results that both of them have a homologue bHLH94 (E value = 5e-85 for bHLH2 and E value = 5e-102 for bHLH3) in wheat. Another homologue AtAIB for bHLH3 in *Arabidopsis* has a role in the control of ABA signaling, in drought tolerance, and in ABA treatment response (Li et al. 2007; Rahaie et al. 2011). There is strong homology (E value = 2e-51) in these orthologues which together with the reverse Northern blot hybridizations result showed that these two bHLH genes have major role in salinity resistance of wheat (Rahaie et al. 2011).

6.4 Signaling Molecules

Until recently, salt and drought stress signaling was not known, but now molecular characters of some of these signaling molecules have been recognized, though there is no clear picture formed yet. The most difficult part in solving the matter is the inadequate information. Therefore, many signaling elements have to be identified in the future. Signaling particularity and interference can be properly understood, once more components are known. Whether a component is portion of salinity or drought signaling pathways cannot be established only by the alterations in gene expression or concentration of protein or activity under water stress. When possible, every signaling portion has to be recognized through functional requirement and functional adequacy. That means all plant phenotypes either molecular, biochemical, or physiological are needed to determine that a specific element participates in water stress signaling. Few genes which are thought to be linked to salinity or drought signaling meet this condition.

Pathways for ionic and osmotic homeostasis signaling, detoxification response, and for growth regulation are present in salt and water stress signal transduction. A calcium-dependent SOS3-SOS2 protein kinase complex regulates the expression as well as activity of ion transporters like SOS1 in the ionic aspect of salinity stress which is signaled through the SOS pathway. Various protein kinases together with mitogen-activated kinases are activated by osmotic stress which may intervene osmotic homeostasis as well as detoxification reaction. Osmotic stress activates variety of phospholipid systems which produces a varied range of messenger molecules, of which few may work upstream of the osmotic stress-induced protein kinases. Biosynthesis of abscisic acid is controlled by osmotic stress at numerous steps. Constitutively expressed transcription factors are modified by ABA-dependent as well as independent osmotic stress signaling which give rise to the expression of initial response transcriptional activators that stimulate downstream stress resistance effector genes (Zhu 2002).

In salinity, drought, ABA, or low-temperature signaling, the major missing elements are the sensors or receptors. There is a candidate osmosensor in *Arabidopsis* named histidine kinase, AtHK1, which can complement a yeast osmosensing mutant (Urao et al. 1999). AtHK1 level is upregulated via osmotic stress as in a number of other potential regulatory genes. There is also induction of a receptor-like kinase gene in abscisic acid, dehydration, high salinity, and low-temperature treatments in *Arabidopsis* (Hong et al. 1997). The functional importance of these transcripts induction during osmotic stress is not much.

Progress in knowledge of water stress signaling will surely increase by the more extensive use of forward as well as reverse genetic analysis in model plants and with the development of genomics and proteomics techniques which can help in improving salinity or drought hardiness in plants more effectively. The primary stage of genetic engineering in stress hardiness is to merely express single or many resistance effector genes by continuously expressed or stress-inducible promoters. The second stage to enhance stress resistance through engineering is more efficient signaling. This can be achieved partly by overexpressing initial-response transcription activators that can switch on several downstream effector genes (Jaglo-Ottosen et al. 1998; Liu et al. 1998). For improving stress tolerance, portions upstream of transcription factors may be exploited (Kovtun et al. 2000). In the future more clearer image of salinity and water stress signal transduction pathways can emerge, and many other examples of genetic improvement of drought stress tolerance through improving plant sensing and signaling systems can be seen (Zhu 2002).

Nitric oxide (NO) is recently being viewed as a significant signaling molecule as well as antioxidant which is a very reactive and membrane-permeable free radical. To establish plant stress tolerance, it triggers directly or indirectly various types of redox-controlled (defense-related) gene expressions (Polverari et al. 2003; Sung and Hong 2010). Use of sodium nitroprusside (SNP), a NO donor, provides resistance to many abiotic stresses in plants by increasing their antioxidant guard system (Neill et al. 2002; Tian and Lei 2006; Sheokand et al. 2008; Zheng et al. 2009; Singh et al.

2009; Xu et al. 2010). Many studies have displayed the defensive impact of NO to abiotic stress which is strongly connected to the NO-mediated decrease of ROS in plants (Beligni and Lamattina 1999; Wang and Yang 2005; Hasanuzzaman et al. 2010). It was reported by Shi et al. (2007) that salinity-induced damages are reduced by the application of NO donor, while its influences were removed by applying NO scavenger. NO also safeguard plant cells against oxidative procedures by inducing GSH synthesis besides direct reactive oxygen species removal activity and the alteration of lipid peroxidation by lipoxygenase prohibition. The GSH synthesis is enhanced by NO in plant as well as in animal cells (Moellering et al. 1998; Kim et al. 2004; Innocenti et al. 2007). The control of GSH synthesis through NO questions the physiological function that may be continued by such a change. It has been shown by recent work that GSH has main function in controlling the MG concentration and increases the oxidative stress resistance of plants (Yadav et al. 2005a, b; Hossain et al. 2010; El-Shabrawi et al. 2010; Hasanuzzaman and Fujita 2011). The induction of GSH synthesis through NO may offer a regulatory function in MG detoxification through affecting glyoxalase pathway enzymes because the first enzyme (Gly I) in this pathway utilizes GSH as a cofactor in MG detoxification (Yadav et al. 2005a). Regulatory function of exogenous NO in the antioxidant defense as well as MG detoxification system of wheat seedlings was investigated by Hasanuzzaman et al. (2011) under salt stress.

7 Salinity-Resistant Varieties Developed by Conventional Breeding

Very less research has been made in the area of wheat breeding for salinity tolerance. Several plant breeders reported requirements for salinity tolerance, but the major limitation is drought besides various other limitations; therefore salinity resistance is especially not targeted. Targeted breeding is mostly done in India and Pakistan. The most successful Indian varieties are KRL1-4 and KRL 19 released by the Central Soil Salinity Research Institute (CSSRI) at Karnal while in the Pakistani varieties are LU26S and SARC-1 developed by the Saline Agriculture Research Cell (SARC) at Faisalabad and in the Egyptian is Sakha 8 developed by the Agricultural Research Centre at Giza.

Almost every salt-resistant wheat germplasm in India is developed from Kharchia 65, which is a line derived through collections from farmers' fields in the sodic-saline area of the Kharchi-Pali region of Rajasthan (Rana 1986). KRL1-4 which is a cross between Kharchia 65 and WL711 performed well in the saline soils of Northern India although done badly in Pakistan because of the more heavy soils and higher problems of waterlogging (Hollington 2000). KTDH 19, a line characterized by extraordinary sodium exclusion, is another by-product of Kharchia 65 derived by crossing Kharchia 65 with that of TW161. It worked well in Spain

(Hollington et al. 1994), but in India as well as in Pakistan, its grain yield was very low due to its maturation around 2 weeks after the local genotypes, although it was more resistant in the case of total dry matter (Hollington 2000). Mutation breeding has reduced its maturation time by 3 weeks without influencing productivity at 150 mM NaCl (Mahar et al. 2003). The Pakistani variety LU26S showed enhanced yields in saline soils of Pakistan (Qureshi et al. 1980), but it is sensitive to rust and not suited for heavily saline-sodic soils because of possible waterlogging. LU26S was crossed with Kharchia and salt-tolerant genotypes, S24 and S36, which were chosen from F3 seed at 24 and 36 dS m^{-1} salinity, respectively (Ashraf and O'Leary 1996). Because of its less leaf Na^+ storage, S24 had salinity resistance comparable to Kharchia and SARC-1 (Ashraf 2002). To improve salt tolerance in wheat, other methods are utilizing physiological characters to choose germplasm which are dependent on process of salinity resistance. In wheat, salinity resistance is linked with less movement of sodium to shoots and more selectivity toward potassium than sodium (Gorham et al. 1987, 1990). There is a less storage of sodium and increased K^+/Na^+ bias in bread wheat (hexaploid, ABD genomes) which is regulated by a locus (Kna1) at chromosome 4D (Dubcovsky et al. 1996). The gene or genes linked to this locus are not recognized. There is more storage of Na^+ and reduced K^+/Na^+ bias in durum wheat (tetraploid, AB genomes) (Gorham et al. 1987; Munns et al. 2000) which has low salt resistance than bread wheat. Locus (Nax1) is present in an odd durum genotype on chromosome 2A regulating Na^+ storage (Lindsay et al. 2004), and in breeding programs to introduce the character of less Na^+ storage in the durum, a tightly linked molecular marker is being used. There is a relation in grain yield and Na^+ removal from leaves with the linked increased bias for K^+/Na^+ in wheat (Chhipa and Lal 1995; Ashraf and O'Leary 1996; Ashraf and Khanum 1997). Although this relation does not hold true for every genotypes (Ashraf and McNeilly 1988; El-Hendawy et al. 2005) which indicates that Na^+ removal is not the single mechanism of salinity resistance.

8 Mutation Breeding

To develop genetic variability between genotypes for salt resistance, mutation breeding techniques have been used, which have important role in plant breeding as well as in genetics. It has been exploited to develop various new crop species which are provided to farmers for growing. It is a fast, less costly, robust, nonhazardous, and environmentally friendly technique. In this, selfing of mutants is done until the expressed trait is stable in the future mutant generations. Four salinity-resistant mutant wheat varieties are released publically for commercial purpose and are included in the mutant varieties database (https://mvd.iaea.org/). They are Jiaxuan 1 (released in 1974), Changwei 19 (released in 1978), Emai 9 (released in 1980), and H6765 (released in 2004, Chijioke 2015).

9 Marker-Assisted Selection and Breeding

Among the most important progress in the area of molecular biology and biotechnology is the improvements in the molecular markers for the manipulation of DNA polymorphisms in plants (Soto-Cerda and Cloutier 2012). DNA marker is the fragment of DNA which is present on a chromosome and closely associated with an identified gene-regulating variation of the trait in a given population. Conventional breeding is difficult in salt tolerance as it is polygenic and influenced by environment and genotype. The application of DNA marker systems has become more popular in plant breeding, due to the absence of interaction between the genotype and environment, epistatic influences, and also easy selection of homozygous plants which are highly differentiated from the others in initial generation (Kumar et al. 2015). If a marker is associated with gene/QTL providing the trait variation like salinity resistance in the crop species, they can be utilized like "surrogate" to introduce the gene into the commercial crop species through either marker-assisted selection (MAS) or transgenic strategy. To introduce the Na^+ removal gene HKT1;5 into the sensitive commercial durum wheat, MAS has been successfully used (Munns et al. 2012; James et al. 2012). These DNA markers are utilized to tag/map various genes or QTL providing salinity resistance in cereals. An established strategy for improvement of the crop with difficult and complex characters like salinity stress resistance is the linking and using of the indirect selection markers genetically associated with the character of interest (Im et al. 2014). To reveal the genetic basis of salinity tolerance in many crops, this approach has contributed immensely (Chijioke 2015).

For crop improvement, the current plant breeding strategies highlight the significance of the genes/QTL position regulating concerned trait. To recognize QTL as well as genes providing variability (Takeda and Matsuoka 2008) in a studied population, molecular genetics which need either or both forward and reverses genetic strategies are used. The association mapping (AM), at the start, achieved great success in human and animal genetics and till recently was used to investigate genetic architecture regulating significant plant phenotypes. But, now the biparental linkage mapping strategy has been widely utilized for mapping quantitative traits. The QTL mapping populations are generally categorized into two groups: (1) family-dependent linkage populations and (2) natural populations which utilize linkage disequilibrium mapping strategies (Semagn et al. 2010; Mackay and Powell 2007). Opposite to the biparental mapping methods, AM populations cautiously sampled different lines which show the variety of natural or breeding crop populations (Zhao et al. 2007a, b; Zhu et al. 2008). Highly developed mapping populations also called as next-generation populations (NGPs) are recently used in several crops in order to counter the restrictions imposed through both the biparental linkage and association mapping strategies. To improve the genetic resolution of mapping, the NGP strategy requires crossing of multiple parents and/or higher-generation intercrosses with additional improvement of generations (Morrell et al. 2011). Nested association mapping (NAM) populations, multi-parent advanced generation intercross (MAGIC) population, and advanced intercross recombinant inbred lines (AIRILs) are included in the NGP which is used for QTL mapping in crop improvement. The researcher must decide on the type of population, DNA marker systems, and QTL analysis procedures to be used for successful identification of QTL/genes underlying complex traits (salt tolerance). There are various types of cloned genes which were earlier recognized by QTL analysis which shows the strength of QTL analysis for searching genes regulating significant agronomic traits (Chijioke 2015).

Soil salinization and degradation are the outcome of climatic change. Wheat breeding for this trait can be accelerated by recognition of main salt resistance genes and marker-assisted selection (MAS). 154 wheat F_2 lines resulting from a cross of salt-resistant and salt-sensitive varieties utilizing the Axiom Wheat Breeders Genotyping Array were genotyped by Hussain et al. (2017). For salinity resistance traits and mineral level in salt, a high-density linkage map of 988 SNPs was created and used for QTL mapping. Six QTLs were for sodium ion exclusion (NAX), and two QTLs (qSNAX.2 A.1, qSNAX.2 A.2) at chromosome 2 A matched with a reported main NAX QTL (Nax1 or HKT1;4) in the 49 mapped QTLs. Two additional major NAX QTLs were present on 7 A, which provided 11.23 and 18.79% salinity resistance, respectively. Twenty-seven QTLs for phosphorus, zinc, iron, manganese, copper, sulfur, and boron level in tissues under salinity were also present with Ca^{+2} and Mg^{+2} QTLs. Under salinity, 1293 segregating SNPs were found annotated/located within genes for several ion channels, signaling pathways, transcription factors (TFs), and metabolic pathways, while 258 of them illustrated differential expression in silico. These results will provide novel opportunities for salinity resistance breeding procedures.

To recognize quantitative trait loci (QTL) of yield and yield components in normal (2 ds m^{-1}) as well as in saline (10–12 ds m^{-1}) situations, a population of 186 recombinant inbred lines of bread wheat (Superhead#2/Roshan) was examined by Azadi et al. (2015). A genetic map was created with 451 markers plus 23 simple sequences repeats (SSRs) and 428 diversity arrays technology markers (DArTs). Through use of QTL Network v2.1, the main-effect QTL were recognized by composite interval mapping (CIM) analysis utilizing QTL Cartographer v2.5 and Qgene v4.3.2 and a combined model-based composite interval mapping (MCIM) method. On two examination positions on 20 chromosomes, a total of 98 significant QTLs were found. Just 40 QTLs were discovered through no less than two of these software procedures. On 10 chromosomes, a total of 24 QTLs were identified for grain yield, most of which had a minor effect, which gives less than 10% of the total phenotypic variation. Two grain-yield QTL intervals were detected on 1A1 and 3B, which contributed 11.02% and 10.3% to the total phenotypic variation, respectively. Roshan alleles were found to be associated with enhancement of grain yield in stress conditions on 1A1, 2B3, 3B, 6B1, 1D, and 2D1. Chromosome 3B in addition to 27 QTL as well as two unique cluster regions were the most significant among the 20 chromosomes. SSR markers gwm282, gwm247, gwm566, and gwm33 were strongly associated with QTL for the similar or diverse traits and responsible for about 17, 43, 43, and 20% of the whole phenotypic variation, respectively, in normal, stressed, or both conditions. These markers are appropriate for marker-assisted selection to enhance grain yield in normal as well as saline conditions.

To genetically evaluate the wheat response to salinity stress, a population of 114 recombinant inbred lines (RILs) were developed by crossing Opata85 with W7984, which recognized 47 QTL mapping entire wheat chromosomes except 1B, 1D, 4B, 5D, and 7D. Ten of these QTLs were effectual in the germination stage while 37 at the seedling stage. Various traits linked to salinity resistance are mapped at common chromosome intervals like *Xglk683-Xcdo460* on chromosome 3A, *Xfbb168-Xbcd147* on chromosome 3B, *Xcdo1081-Xfbb226* on chromosome 4DL, and *Xpsr106-Xfbb283* on chromosome 6DL. During the germination stage, QTLs situated in the interval *Xcdo1081-Xfbb226* (chromosome 4DL) were efficient, while those in the interval *Xfbb231.1-Xmwg916* (chromosome 6DL) were related to the seedling stage. The QTL in the intervals *Xglk683-Xcdo460* (chromosome 3AS) and *Xfbb168-Xbcd147* (chromosome 3BL) were useful at both the germination and seedling stages (Colmer et al. 2006).

Use of molecular markers is a fast method to breed for desired traits. In using them, it is necessary to determine the linkage between quantitative trait loci (QTL) and such markers. The study of Amin and Diab (2013) was conducted to investigate the genetic dependence of salt responses in Egyptian bread wheat (*Triticum aestivum* L.). In this context, a doubled haploid (DH) population (SGDH) of 139 was produced from the cross between two Egyptian breeding cultivars (Sakha 93, salt tolerant) and (Gemmeza 7, salt susceptible). The DH population was tested under saline hydroponics culture, and various plant responses were measured. A molecular genetic map of the SGDH population is covering 3645.3 cM, was constructed using restriction fragment length polymorphism (RFLP), microsatellite or simple sequence repeats (SSR), and amplified fragment length polymorphism (AFLP) markers. In total, 325 loci along the 21 wheat chromosomes were mapped. The B genome showed the maximum number of mapped markers followed by the A and the D genomes, respectively. Interval and composite interval mapping (using QTL cartographer) were utilized to recognize the genomic regions regulating the traits linked to salt tolerance with a threshold of LOD 3. Analysis of QTLs has revealed the approximate location of the significant markers associated with 12 traits related to salt tolerance traits across the A, B, and D genomes. Fifty-five significant QTLs were detected on 15 of the 21 chromosomes mapped in this study, for some of these more than one QTL was identified. In many cases QTL were mapped very close to each other, indicating possible gene clustering or pleiotropy. For some traits, the total percentage of phenotypic variation explained by all QTL exceeded 50–60%, but on average it was in the region of 15%. Chromosomes of homologues groups 2 and 5 exerted the biggest effect on most phenotypic traits, especially chromosomes 2B and 5B. The results indicated that there is significant possibility for enhancing salt resistance of hexaploid wheat by utilizing marker-assisted selection (Amin and Diab 2013).

Multiple QTLs were found for almost all traits at different regions in this work. The number of QTL recognized for each character varied from 3 to 6, which shows that the genome contains multiple genes affecting each trait. Either there are tightly associated genes or the identical gene is influencing various traits as shown by the overlapping of these QTL. The correlated traits may be components of a more complex variable, or multiple traits can be correlated due to linkage, pleiotropy. It is important for breeding and scientific reasons to distinguish between linkage and pleiotropy. However, at best one can draw conclusions based on morphological and/or physiological relationships in the considered traits as such distinction would be difficult to make without the fine resolution mapping or molecular cloning of QTLs. The main practical use of the recognized QTL is to carry out marker-assisted selection intended to competent pyramiding of favorable QTL alleles to enhance wheat yield and agronomic traits under salt stress. Additional QTL studies are useful for identifying the chromosomal regions that are more consistently associated with salt tolerance. Further studies involving fine mapping of genomic regions associated with salt tolerance across genetic backgrounds or species will be required for cloning of genes controlling resistance to salinity in plants.

10 Conclusion

Among the most serious abiotic stresses faced by plants is salinity which is constantly enhancing because of climatic changes and inadequate irrigation management practices. It affects about 800 million hectares area in the world consisting of over 20% irrigated cultivated land. There is considerable decrease in growth and crop because of this stress. Enhancing the salt resistance of crops is major challenge and aim of plant breeders along with expected geometric enhancement in the world population. To ameliorate the impact of salinity on crop plants, various strategies have been extensively used, but due to the difficult nature of salt resistance in a crop, these strategies have not produced the desired results. Salt tolerance is tough to breed because of its relation with various physiological processes which are regulated by several genes and plant growth stage and also affected through environmental factors. The grain yield is considerably influenced in wheat in the soil at ~10 dS m^{-1} salinity, so it is moderately salt tolerant. Enhancing wheat adaptation to high salt is the most useful and cost-effective approach to solve the salt stress problem and improve its grain yield particularly in the underprivileged wheat-producing countries which are sensitive to soil salinity. There is need of various morphological and physiological assessments and genetic and molecular strategies to understand the genetic and physiological processes causing natural variation for salt tolerance in wheat and to provide means to discover the inherent genetic variation, with the ultimate purpose to find novel candidate genes which can be utilized to enhance salt tolerance.

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Wheat Responses and Tolerance to Drought Stress

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Contents

Abstract Drought is an environmental worldwide problem affecting crop productivity earnestly, and recent climate change has made this status more critical. The projections point out an increase in water request used in agriculture leading to more drought stress. In the future by 2025, about 60% of world peoples may suffer from water scarcity. Adaptation to drought is mainly identified through three mechanisms, i.e., drought tolerance, drought escape, and drought avoidance. Wheat plants are responses to water deficit relative to its growth stage, metabolic activity, and yield potential. Germination, flowering, and grain filling are considered as critical periods for water stress. Exposing wheat plants to drought are adversely affecting phenological development, physiological and biochemical processes, and yield. Increasing water stress degree causes a decrease in shoot elongation of seedlings. Stomatal conductance and photosynthetic rates were reduced when plants exposed to water deficit, which include some signals like ABA accumulation. The photosynthetic system may be damaged under extreme drought condition. In response to water deficit, wheat plants can minimize the deleterious effects by increasing osmotic adjustment through the accumulation of solutes within the plant. The stress plants recorded lowest values of total carbohydrates (TC) and total free amino acids (TAA), while well-irrigated plants obtained the highest values of total soluble sugars (TSS) and total phenols (TP). Proline appears to assist plants in drought tolerance. A gradual increase in proline content is exposing wheat plants to drought degrees compared to its content in well-watered plants. The reduction in photosynthesis under drought stress resulted in reducing the efficiency of biochemical processes,

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which lead to reduce plant growth and yield. It is supposed that new wheat varieties that have higher water-use efficiency (WUE) and strong grain sink under water deficit condition had more drought tolerance and produced more yielding than other varieties.

Keywords Wheat · Drought mechanisms · Phenological development · WUE · Yield

Abbreviations

ABA	abscisic acid
CAT	catalase
CO_2	carbon dioxide
EC	electrical conductivity
ET	evapotranspiration
GA	gibberellic acid
IAA	indole-3-acetic acid
K	potassium
MI	membrane integrity
N	nitrogen
NR	nitrate reductase
OP	osmotic pressure
P	phosphorus
pH	acidity
POD	peroxidase
POX	phenoloxidase
RNA	ribonucleic acid
RWC	relative water content
TAA	total free amino acids
TC	total carbohydrates
TP	total phenols
TSS	total soluble sugars
WUE	water use efficiency
Ψw	water potential

1 Introduction

Drought is an environmental worldwide problem, especially in arid regions, affecting crop productivity earnestly, and recent climate change has made this status more critical (Anjum et al. 2011). Across the world, the projections point out an increase in water request used in agriculture leading to more drought stress (Turral et al. 2011). Also, Qadir et al. (2007) stated that 60% of the people in the world may suffer from water scarcity by 2025. High temperature combined with absence each of rainfall or water applied, for a period long, cause soil moisture depletion, which in turn causes disturbance of physiological processes in plants (Wang et al. 2011; Ahmed et al. 2017). Wheat (*Triticum* spp.) is a sensitive crop to drought stress specifically during germination, heading stage, and grain filling period. Exposing wheat plants to drought adversely affects phenological development, physiological and biochemical processes, and yield (Waraich and Ahmad 2010; Akram et al. 2014; Hammad and Ali 2014). Water often limits crop growth and development. Plant roots grow into moist soil and absorb water until a critical water potential (Ψw). Soil moisture availability is affected by some soil properties (texture, electrical conductivity, pH, etc.). A clay soil concludes more available water ranged 18–20% of its weight, whereas the sandy soil holds about 6–7%.

Stomatal closure during water stress period reduces CO_2 uptake and consequently carbohydrates accumulation. Wheat responses to water deficit are relative to their genotypes performance, growth stage, metabolic activity, the timing of stress, and degree of stress (Blum 2011; Nakhforoosh 2014).

This chapter focuses on wheat responses to drought through understanding the drought mechanisms and the changes in phenological development and physiological process in plants grown under water deficit levels.

2 Drought Mechanisms

Adaptation to water stress is mainly identified through three mechanisms, i.e., drought tolerance, drought escape, and drought avoidance. Enhancement of wheat growth and yield by agricultural practices and/or breeding for drought adaptation strongly depends on drought duration and occurrence time (Blum 2011). It could affirm that the three ways of drought adaptation are not separated because the same plant can possess more than one mechanism of water deficit adaptation. This occurs through physiological management and genetic modifications. Wheat faces water stress by drought escape via reducing transpiration rate and vegetative growth, early flowering, and maturity, which enable the plant to evade water deficit stress (Shavrukov et al. 2017). Drought avoidance by water saving via increasing root distribution and reducing stomata numbers and leaf area/canopy ratio. Improving topsoil root length density, root volume, and deep rooting caused an increase in soil water absorption (Nakhforoosh 2014). Water-use efficiency is referring to yield production in relation to water used during growing season to produce this yield. High water-use efficiency (WUE) reduces water loss and allows the plants to ready up for changing environmental condition and be adaptive with drought (Shavrukov et al. 2017) especially during the grain filling period. A modification of genetics by plant breeding programs through conventional and molecular methods can be an effective way for wheat breeding to drought tolerance via improving osmotic adjustment ability and increasing cell wall elasticity (Araus et al. 2008; Xu et al. 2010). New wheat varieties that had superior WUE and photosynthesis rate via high leaf chlorophyll content produce more yield (Nakhforoosh 2014).

3 Wheat Responses to Drought

Wheat plants response to water deficit condition by complex mechanisms via molecular genetic expression, biochemical metabolism, and physiological processes (Fig. 1). Wheat plants are a response to water deficit relative to its growth stage, metabolic activity, and yield potential, as well as the timing of water stress and its degree (Blum 2011).

3.1 Germination and Seedling Vigor

Germination is considered as a critical stage for water stress. Germination is an important stage affecting seedling vigor and plant population in the unit area. Increasing RNA and protein in wheat grain are the first indicators that indicate germination beginning (Zhang et al. 2009). After grain absorbs water directly, these processes are established. Increasing water stress degree causes a decrease in shoot elongation of seedlings (Esfandiari et al. 2008).

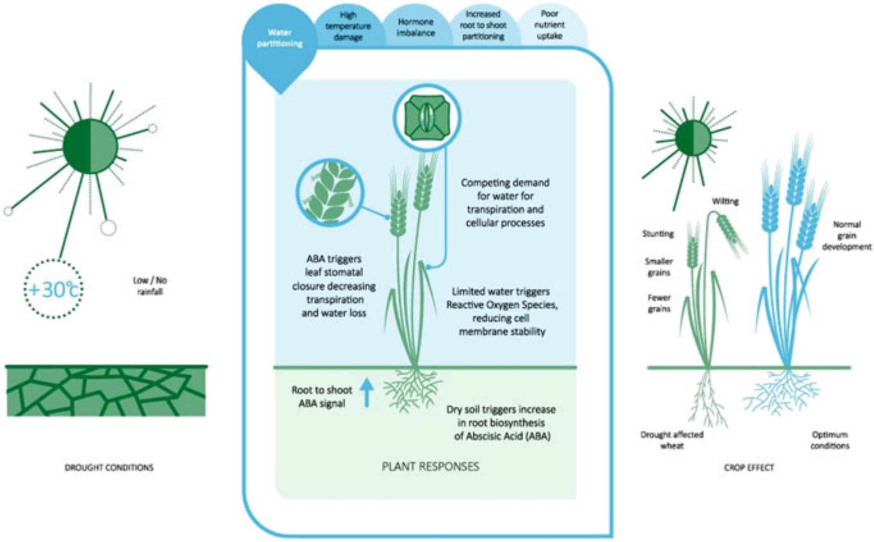

Fig. 1 Wheat plant responses to drought. (Adapted from http://www.plantimpact.com)

3.2 Phenological Development

Differences among drought stress regimes found to be significant for growth traits, i.e., plant height, numbers of tillers and leaves per individual plant, root and shoots dry weights plant^{-1}, flag leaf area, and leaf area plant^{-1}. All characters were negatively affected by lower water supplies during the growth stage. Root elongation and its dry weight are not affected as much as leaf area, stem elongation, and shoot dry weight. Roots were expanding into an area where available water is not depleted. High root densities occur in upper soil zone where water is extracted rapidly, but as water becomes limiting in this zone, roots expand into lower soil profile where water is more abundant (Anjum et al. 2011). The inhibition in stem elongation, leaf area, and shoots dry weight of wheat plants grown under moderate drought were amounted to 17.35, 14.50, and 18.54% while reached 29.53, 32.34, and 43.90% under severe water stress, respectively, compared with well-watered plants (Hammad and Ali 2014). The most dramatic effect of the early vegetative water deficit was a reduction in leaf area and shoots dry weight. Restricted internode elongation and leaf expansion can occur under water deficit through inhibiting cell expansion (Waraich and Ahmad 2010). Drought causes losses in tissue water contents that reduce turgor pressure in the cell, thereby inhibiting enlargement and division of cell causing reduction of plant growth and dry mass production.

3.3 Stomatal Conductance and Photosynthesis

The stomatal response can be different in wheat genotypes and stage of development. The stomatal closure had to be the factor reducing the photosynthesis. Stomatal closure during water stress period reduces CO_2 uptake. A continuation of water deficit causes a more reduction in photosynthesis rate. Stomatal conductance and photosynthetic rates were reduced when plants exposed to water deficit, which include some signals like ABA accumulation. The photosynthetic system may be damaged under severe drought condition (Le et al. 2017). The stronger association could be detected between chlorophyll content and photosynthetic rate. Carotenoids are as signaling molecules and have been engaged to have a role in the interactions of plants with their environment (Esteban et al. 2015). Statistical analysis shows significant decreases in chlorophylls and carotenoids content by increasing water deficit as compared with normal water applied (Hammad and Ali 2014). The decrease in photochemical activities of chloroplast occurred by water deficit can be correlated with the decrease in the accumulation of chlorophyll. A decrease in net photosynthetic rate under water stress is also related to disturbances in biochemical processes of a non-stomatal nature, caused by oxidation of chloroplast lipids and changes in the structure of pigments and proteins (Marcinska et al. 2013). A significant decrease in CO_2 assimilation rate with increasing water deficit levels

(Waraich and Ahmad 2010). Many investigators have proposed the response of wheat photosynthetic rate to water deficit (Ali et al. 2007; Maria et al. 2008).

3.4 Plant Water Relations

Relative water content, osmotic pressure (OP), and membrane integrity (MI) are important indicators that affected plant-water relations. Wheat plants grown under severe drought condition followed by moderate drought condition produced the highest significant values of OP and MI compared to well-watered plants. However, there was a gradual reduction in RWC by increasing drought stress degree, which reached about 15.15% under severe drought (Hammad and Ali 2014) compared to normal water applied (irrigation at depletion 50% of available water). Relative water content has been an important indicator of water stress in leaves, which is directly related to soil water content (Rampino et al. 2006; Waraich and Ahmad 2010). This indicates greater resistance to water flow at the soil-root interface or decreased hydraulic conductivity of soil at low soil moisture. In response to water deficit, wheat plants can minimize the deleterious effects by increasing osmotic adjustment through the accumulation of solutes within the plant. Under stress condition, cell membranes are subject to changes often associated with the increase in the cell permeability (Iqbal 2009). Wheat drought-tolerant genotypes maximize WUE by lowering the water loss. Improved crop management and plant breeding have led to substantial acquire in WUE. The authors usually conclude that plants need strong and deep root systems during water deficit condition, and increases in rooting depth increase the total quantity of water available for extraction during the growing season (Evans and Sadler 2008).

3.5 Biochemical Responses

Under water deficit, the expression of many genes is enhanced, influencing the metabolism of several biochemicals, e.g., enzymes, hormones, amino acids, and carbohydrates (Yang et al. 2010). Water stress significantly affected TSS, TC, TAA, and TP. The stress plants recorded lowest values of TC and TAA, while well-irrigated plants obtained the highest values of TSS and TP (Iqbal 2009; Hammad and Ali 2014). The reduction in severe plants could be ascribed to that water-induced loss of solutes from guard cells, leading to stomatal closure. Soluble carbohydrate in well-watered wheat plants exhibited higher content than those obtained from stressed plants (Zhang et al. 2009).

A gradual increase in proline content when exposing wheat plants to drought stress compared to its content in well-watered plants. Proline appears to assist plants in drought tolerance (Ahmed et al. 2017). It does not only act as an osmolyte, but it also contributes in stabilizing subcellular structures (e.g., membranes and proteins) under water deficit (Iqbal 2009; Alaei et al. 2012). Proline is believed to stabilize membrane phospholipids which helps the plants to overcome periods of drought stress (Rampino et al. 2006).

Water stress negatively affected N, P, and K percentages and their uptakes in leaves' tissues compared to plants grown under normal condition. The maximum reductions were recorded under severe stress, which reached about 22.11, 29.73, and 15.98% for N, P, and K, respectively (Hammad and Ali 2014). Uptake of NPK also took the same trend with increasing water stress degree in comparison with well-watered plants (Baque et al. 2006 and Maria et al. 2008).

POD, POX, CAT, and NR enzymes in wheat leaves were negatively affected under drought conditions. Enzyme activities were decreased in response to water stress, and maximum decreases were recorded in severe stress (Caravaca et al. 2005; Iqbal 2009; Hammad and Ali 2014) with increasing duration of water stress at both booting and grain filling stages.

Plant responses to water deficit are known to be generally determined by endogenous phytohormones (Pandey et al. 2015). Water deficit causes change in the balance of endogenous phytohormones by increases in the growth inhibitory hormones with a decline in growth-promoting hormones. Water stress caused a significant increase in ABA while decreases in IAA and GA contents of wheat leaves (Barnawal et al. 2017). Stressed plants growing in a soil water level near permanent wilting point showed a significant increase in endogenous ABA content in leaf and root compared with well-watered plants. Under water deficit, the inhibition of plant elongation is as likely to be due to elasticity loss as to ABA accumulation. It is well known that the changes in endogenous hormones levels after heading period might indirectly influence starch and protein accumulation in wheat grains by affecting the regulatory enzymes (Xie et al. 2003).

3.6 Yield

The timing of water applied and the quantity of irrigation water applied were important factors controlling biomass yield. Grain yield is the final product of many of the developmental processes revolving throughout growth, influenced by environmental conditions (Mwadzingeni et al. 2016). Wheat grain yield is mainly based on three components, i.e., number of spikes per unit area, number of grains per spike, and 1000 grain weight. These components are determined according to the plant responses to resource availability at different development stages (Akram et al. 2014). Delays in first irrigation, crown root initiation stage, have reduced yield by 27%. In addition, the flowering stage and grain filling periods are considered as critical stages, which need water supplements (Hunsigi and Krishna 1998). At anthesis, soluble sugars can represent 5–7% of the total dry matter. It seems likely that this stem reserve of carbohydrate buffers grain filling and grain yield against reductions in post anthesis photosynthesis caused by water deficit. After 3 weeks after pollination, water deficit no longer affected grain number per spike but did decrease grain weight, indicating that the moisture stress reduced photosynthetic and translocation to spikes. The translocation rate to formed spikes under water deficit was not enough to develop their grains normally. Grain yield of modern wheat varieties has increased considerably over the last periods. This yield has been achieved without much increase in seasonal evapotranspiration (ET) because the WUE has increased along with increases in the yields. It is supposed that new wheat varieties that have higher WUE and strong grain sink under water deficit condition had more drought tolerance and produced more yielding than other varieties (Khakwani et al. 2012; Nakhforoosh 2014). Numerous studies showed that wheat varieties differed extensively in their physiological processes which determine yield (Ali et al. 2015; Ahmed et al. 2017). Water stress-affected wheat plants might lie not only in the variations in physiological processes like an accumulation of osmolytes, antioxidant capacity, and stomatal conductance but also in changes in the phytohormonal balance (Iqbal 2009). During water-limiting conditions, photosynthesis reduction happens, resulting from reducing the efficiency of biochemical processes, which led to suppressing vegetative growth and dry matter production. Decreasing grain, straw, and biomass yields could have occurred due to inhibition of physiological and biochemical processes. Increasing drought stress decreases the grain yield by about 14.63% and 41.37% under moderate and severe drought, respectively, compared with normal irrigation condition (Hammad and Ali 2014).

3.7 Nutritive Value of Grains

Significant depression in total protein and carbohydrates content, while a gradual increase in total fibers of wheat grains were occurred when exposing plants to severe drought. Irrigation until soil water reached 50 up to 65% depletion had the effect of increasing grain protein and carbohydrates content (Kilic and Yağbasanlar 2010; Hammad and Ali 2014). This could have occurred due to more NPK uptake from the soil compared to severe drought condition (Dromantiene et al. 2009; Bakry et al. 2012).

4 Conclusion

Exposing wheat plants to drought is adversely affecting phonological development, physiological and biochemical processes, and yield. New wheat varieties that have higher WUE and strong grain sink under water deficit condition had more drought tolerance and produced more yields than other varieties. Therefore, there will have to be concerted efforts to integrate genetic response with good agronomic practices of wheat crop in order to assure that there is maximum grain supply for all the world's populations.

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Wheat Responses and Tolerance to High Temperature

Mingming Xin, Huiru Peng, Zhongfu Ni, Yingyin Yao, Zhaorong Hu, and Qixin Sun

Contents

Abstract Hexaploid wheat (*Triticum aestivum*) is a globally important crop. Heat stress dramatically reduces wheat yield and quality, and model predictions indicate that global wheat production will fall by 6% per 1 °C increase in temperature. Correspondingly, wheat has developed a series of molecular mechanisms to cope with climate variations and to protect themselves from injury and damage. Therefore, investigation of how wheat responds to elevated temperatures will provide important strategies to help develop new varieties adapted to temperature variations, but the underlying molecular mechanisms are still largely unknown. In this review, we focused on the recent studies of heat responses in wheat from omics perspective and shed light on understanding heat-responsive mechanisms that gene expression, protein synthesis, and epigenetic modification are significantly altered when subjected to heat stress. With the development of wheat transformation technique, it would be applicable to modify heat responses by manipulating expression patterns of related genes, and the omics findings paved the way to identify candidate genes improving heat tolerance in wheat.

Keywords Wheat · Heat stress · Transcriptome · Proteome · Epigenome

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1 Introduction

Hexaploid wheat (*Triticum aestivum* L. AABBDD), as one of the main food crops, nurtures more than one third of the world population by providing nearly 55% of the carbohydrates (Breiman and Graur 1995; Gill et al. 2004), which serves as the staple food source for more than 30% of the human population (IWGSC 2014). Environmental constraints, such as extreme high temperature (or heat stress), severely perturbed physiological, biological, and biochemical processes during wheat development (Asseng et al. 2015). Therefore, heat stress can cause dramatic wheat yield reduction and quality loss, and model predictions indicate that global wheat production will fall by 6% per 1 °C increase in temperature (Asseng et al. 2015), which significantly intensifies the growing demand of food supply.

The previous study indicated that pre-flowering and anthesis stages are the most sensitive stages to high temperature during wheat development (Cossani and Reynolds 2012). Specifically, short periods of high temperature at the pre-flowering and flowering stages can reduce grain number per spike and yield. This can be attributed to the lower ability of pollen germination and pollen tube growth rate (Feng et al. 2014). For example, wheat plants exposed to 30 °C during a 3-day period around anthesis stage generated abnormal anthers, both structurally and functionally, in 80% of florets (Cossani and Reynolds 2012). In addition, starch accumulation is also sensitive to heat stress due to the susceptibility of the soluble starch synthase I in developing wheat kernels, which is the limiting enzyme controlling starch deposition in seeds (Keeling et al. 1993; Jenner 1994). Besides, it is reported that the expression levels of starch biosynthesis-related genes, e.g., ADP-glucose pyrophosphorylase; starch synthases I, II, and III; granule-bound starch synthase; and starch branching enzymes I and II, are also significantly suppressed by heat stress (Hurkman et al. 2003).

To cope with climate variations and to protect themselves from injury and damage, wheat has evolved complex systems to achieve enhanced tolerance. Therefore, understanding the complicated responses of wheat to heat stress will provide important strategies to help develop new varieties adapted to temperature variations (Ni et al. 2018).

2 Physiological Response to Heat Stress

Many physiological processes are severely impaired under heat stress in wheat, including but not limited to the maximal efficiency of photosystem II, cell membrane stability, and lipid peroxidation. These physiological responses to heat stress effectively determine genotype resistance or susceptibility.

Photosynthesis is the most sensitive process to high temperature. Thylakoid membranes and PS II are the most heat-sensitive cell components (Ristic et al.

2007), which showed significant phenotypic variation under heat stress condition. Heat stress can result in physical separation of the chlorophyll light-harvesting complex II from the PS II core complex and disruption of PS II-mediated electron transfer (Ristic et al. 2008). Besides, heat stress can lead to chlorophyll loss and subsequently reduce wheat photosynthetic capacity (Ristic et al. 2007, 2008), which then accelerates plant senescence. The previous study showed that the expression level of chloroplast protein synthesis elongation factor, *EF-Tu*, is associated with heat tolerance in wheat, and wheat cultivars' overaccumulation of EF-Tu protein displays better tolerance to heat stress (Ristic et al. 2008; Bukovnik et al. 2009). Dhyani et al. (2013) compared chlorophyll content and leaf area index (LAI) changes between heat-tolerant and heat-sensitive wheat genotypes under timely and late sown conditions and revealed that these two indexes were dramatically reduced by heat stress in sensitive genotypes, whereas proline content, which could have a protective function against environmental stress, was promoted in tolerant genotypes compared with sensitive genotypes under late sown conditions (Dhyani et al. 2013). In addition, Feng et al. (2014) found that the photosynthesis rate decreased significantly in flag leaves of both heat-sensitive cultivar XM26 and heat-tolerant cultivar JM22 after heat stress, but with different variation degree, that is, 69.9% and 59.3%, respectively. Further investigation indicated that the rapid decrease of photosynthesis rate was attributed to the decline in rubisco and photosystem II (PSII) activity. Besides, heat stress also resulted in alteration of mesophyll cell ultrastructure (Feng et al. 2014).

Heat stress also disturbs the balance of reactive oxygen species (ROS, including superoxides [O_2^-], hydrogen peroxide [H_2O_2], and hydroxyl radicals [OH^-]) production and scavenging, either by increasing the production of active oxygen or by decreasing the free radical scavenging ability in the cell. The rate of ROS production abruptly increases in wheat and acts as a signaling molecule to regulate gene expression in response to heat stress (Kumar et al. 2012). Meanwhile, a high concentration of ROS is associated with oxidative damage and tends to cause cell death in the plant; thus ROS scavenging system-related enzymes such as superoxide dismutase (SOD) and catalase (CAT) are also activated after heat stress (Kumar et al. 2012). In addition, the overaccumulation of ROS promotes lipid peroxidation and adversely affects membrane stability. Correspondingly, malondialdehyde content, the product of lipid peroxidation, was increased in heat-sensitive genotypes of wheat (Sairam et al. 2000). Furthermore, heat stress can enhance protein denaturation and increase unsaturated fatty acids, which then disrupt water, ion, and organic solute movement across membranes, leading to increased cell membrane permeability and, in turn, inhibition of cellular function (Cossani and Reynolds 2012). Increased electrolyte leakage disrupts the signaling process and leads to cellular dehydration and death in response to heat stress, which has been considered as an index of membrane stability to identify heat-tolerant genotypes in wheat (Blum and Ebercon 1981). Therefore, the detoxification by antioxidant systems is important for protecting plant cell against damage caused by heat stress.

3 Transcriptome Response to Heat Stress

Wheat transcriptome profiling is greatly altered in response to heat stress, although the underlying mechanisms are not fully understood. A genome-wide analysis of gene expression patterns was performed using microarray in a pioneering study to compare transcriptome profiling of wheat leaf between heat-susceptible cv. Chinese Spring (CS) and heat-tolerant cv. TAM107. The results revealed that thousands of genes involving multiple biological pathways were changed following short and prolonged heat treatments. The author proposed that the differences in heat tolerance between two cultivars may be associated with multiple processes and mechanisms involving HSPs, transcription factors, and other stress-related genes. Heat acclimation has little effects on wheat gene expression under prolonged heat treatments, however, which altered gene expression under short-term heat stress. Besides, Szucs et al. (2010) analyzed the effects of heat stress on wheat seed development and storage product accumulation using microarray methods and found heat and drought stress together can enhance gene expression changes in wheat seed and accelerate nutrient uptake. Kumar et al. (2015b) identified 1525 differentially expressed transcripts under heat stress using RNA-seq analysis and found that metabolic processes, protein phosphorylation, and oxidation-reduction processes were significantly influenced. Moreover, Liu et al. (2015) further analyzed the leaf transcriptome changes under normal conditions and drought stress, heat stress, and their combination using deep RNA-seq methods and found that 1328 TFs distributed in 50 families were differentially regulated in response to at least one stress, among which, HSFs and DREBs regulate complicated and partially overlapped gene networks in response to DS, HS, and HD. Gene Ontology (GO) enrichment analysis of HS-responsive genes revealed a complexity of functional pathways, including "response to heat," "heat acclimation," and "response to water deprivation."

As an allohexaploid, bread wheat contains three subgenomes, namely, A, B, and D, and showed improved tolerance to abiotic stress compared to their progenitors (Dubcovsky and Dvorak 2007). With the support of the high-throughput sequencing and released wheat genome by IWGSC, Liu et al. (2015) reported that the expression patterns of approximately 68.4% wheat homeologs were diverged in response to heat stress, suggesting expression partitioning of homeologous genes may facilitate abiotic acclimation of wheat. However, the potential causes resulting in these biased expression patterns are still ambiguous.

Other than expression variation, alternative splicing (AS) also likely contributes to heat tolerance in wheat. Liu et al. performed genome-wide analyses of AS responses to heat stress in wheat seedlings and found 3576 genes exhibiting significant AS pattern changes under heat stress condition. In addition, wheat homeologous genes exhibited differential AS responses under stress conditions that more AS events occurred on B subgenome than on A and D genomes. Comparison of genes regulated at AS and transcriptional levels showed that ~40% of HS-induced AS genes were subjected to transcriptional regulation, indicating both expression variation and AS changes play an important role in response to heat stress in wheat (Liu et al. 2018).

4 Proteome Response to Heat Stress

Wheat responses to heat stress are not only at transcriptional level but also at the translational level. Wheat cultivars were grown in warm areas and generally share related characteristics, such as reduced grain weight and higher dough extensibility, than those grown in cooler areas. Two-dimensional electrophoresis (2-DE) and matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF-MS) have been widely used to discover proteins involved in heat stress response (Majoul et al. 2003, 2004; Laino et al. 2010; Yang et al. 2011). For example, 37 protein spots were identified as significantly changed in response to heat stress during grain filling stage of bread wheat, of which, 26 spots were characterized by MALDI-TOF-MS coupled with database searching, including 25 upregulated spots and 1 downregulated protein spot after heat stress (Majoul et al. 2003). The authors continued to analyze the effects of heat stress on water-soluble albumins and globulins in the wheat endosperm and identified 24 upregulated and 19 downregulated protein spots in response to heat stress. Of these, enzymes involved in starch synthesis pathway and carbohydrate metabolism were revealed including granule-bound starch synthase and glucose-1-phosphate adenyltransferase. In addition, heat shock proteins, and some defense-related proteins, were also found differentially expressed under heat stress (Majoul et al. 2004). Recently, proteome analysis of wheat leaves at grain filling stage revealed that proteins related to photosynthesis, glycolysis, stress defense, heat shock, and ATP production were differently expressed in leaves after heat stress. Further analysis showed that the abundance of proteins related to signaling transduction, heat shock protein, photosynthesis, antioxidant enzymes, ATP synthase, and GAPDH was upregulated in the heat-tolerant cv. 810 compared with heat-sensitive cv. 1039, whereas proteins related to nitrogen metabolism were downregulated. An interesting finding was that glucose-1-phosphate adenyltransferase, a starch synthesis enzyme, was significantly decreased after heat treatment, providing further evidence that starch synthesis is highly sensitive to heat stress (Wang et al. 2015).

Recently, Zhang et al. (2017) exploited isobaric tags for relative and absolute quantitation (iTRAQ) method to investigate grain protein expression profile changes in wheat cultivar Jing411 under heat stress. In total, 256 proteins were differentially expressed in wheat cultivar Jing411 after heat stress, among which, 126 were upregulated and 130 were downregulated. GO enrichment analysis indicated that these differentially expressed proteins were mainly involved in stimulus response, abiotic stress response and stress response, kinase activity, and transferase activity. Noticeably, the authors found that eight differentially expressed proteins were likely to form an interaction network in response to heat stress in wheat grain (Zhang et al. 2017).

5 Epigenome Response to Heat Stress

Adapting to the surrounding climate change, wheat needs constant and frequent changes at the molecular level. Epigenetic modification contributes to the efficient and effective controls in gene expression and ultimately improves the stress tolerance. Thus, epigenetic modification plays an important role in regulating heat response in wheat, including DNA methylation, miRNA and long noncoding RNA, etc.

Gardiner et al. (2015) assayed 293,076 cytosine residues across wheat genome in 12 °C and 27 °C seedling samples and found 0.1% sites showing differential DNA methylation between two temperatures. Further investigation revealed that 27 sites exhibited subgenome-specific methylation status, and 67.5% sites might be associated with either temperature sensitivity or methyltransferase activity. In addition, by comparing gene expression profiling and DNA methylation patterns, 20 genes were found both differentially expressed and differentially methylated between the two samples, indicating differential methylation could be linked to expression changes. These genes are associated with GTP/ATPases, envelope proteins, and stress response. Although there are only minor differences in methylation patterns between wheat in 12 °C and 27 °C conditions, the authors confirmed DNA methylation was associated with small changes in gene expression which have a temperature-dependent expression profile, including heat shock and stress-related gene (Gardiner et al. 2015). These results suggested DNA methylation might be involved in heat response in wheat.

miRNAs are a class of 20–24 nt small RNAs, which regulate gene expressions by splicing targeted transcript and might play a role in regulating heat response in wheat (Xin et al. 2010; Kumar et al. 2015a; Ragupathy et al. 2016). The expression of miR156 was upregulated after heat treatment in both heat-tolerant genotype TAM107 and heat-sensitive genotype CS, whereas miR159 was downregulated only in CS genotype after 2 h heat treatment. Further study found that wheat miR159 can directly bind to its targets *TaGAMYB1* and *TaGAMYB2* and directed their cleavage. Rice transgenic lines with overexpressing wheat *miR159* exhibited heat-sensitive phenotype compared with the wild type, indicating wheat *miR159* might participate in a heat stress-related signaling pathway in wheat and contribute to heat stress tolerance (Wang et al. 2012).

Moreover, Xin et al. (2011) found long noncoding RNAs were also involved in heat response in wheat. The authors identified 77 wheat long noncoding RNAs in response to heat stress; these long noncoding RNAs might function as a long transcript or by generating siRNAs or miRNAs, e.g., TahlnRNA27 was probably the precursor of Ta-miR2010, which was upregulated at 1 h after heat treatment in heat-tolerant cultivar TAM107, whereas TalnRNA21 comprising siRNA sequences was upregulated after heat stress in both CS and TAM107. Interestingly, H3K9 acetylation is likely to regulate the expression of long noncoding RNAs in response to heat stress in wheat (Xin et al. 2011).

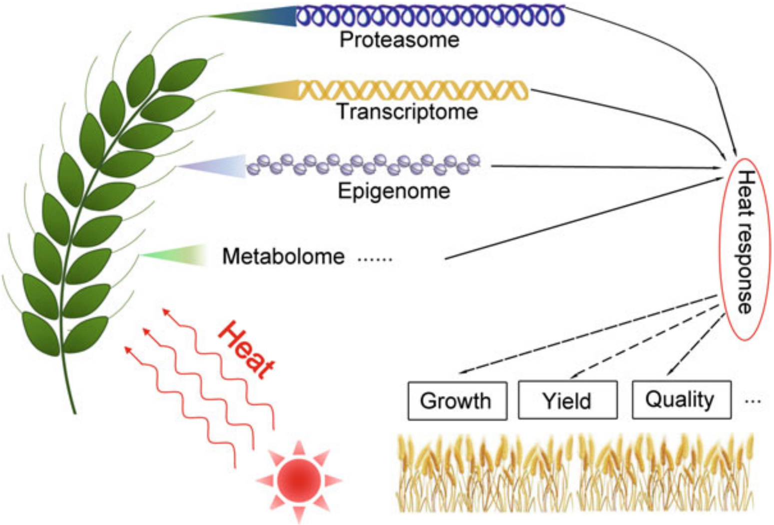

Fig. 1 Schematic diagram of wheat responses and tolerance to high temperature

6 Conclusion

Heat stress severely limits crop growth and causes dramatic yield losses worldwide, particularly for chimonophilous wheat, which prefers cool weather. However, unfortunately, it often suffers heat stress during the development and results in severe damages in many aspects including photosynthesis, respiration, transpiration, etc., especially at flowering and filling stages. In this review, we focused on the recent studies of heat responses in wheat from omics perspective (Fig. 1). Although the regulatory network of heat tolerance is still ambiguous in wheat, transcriptome, proteome, and epigenome responses shed light on understanding heat-responsive mechanisms from genomic levels, indicating heat response is a systematic biology question, which merits further investigation in the future.

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Wheat Responses and Tolerance to Terminal Heat Stress: A Review

Davinder Sharma, Rajender Singh, Ratan Tiwari, Rakesh Kumar, and Vijay Kumar Gupta

Contents

Abstract Supraoptimal temperatures and unpredictable fluctuations in global climate adversely affect plant growth and development resulting in a severe threat to wheat production. Although all the growth stages of wheat are sensitive to supraoptimal temperatures, the reproductive phase is the most sensitive one as it affects both grain setting and grain filling (GF). High temperature can alter biochemical, physiological, and morpho-anatomical behavior in wheat, which in turn affects its growth and development causing a reduction in pollen viability, duration of GF, and starch synthesis in the endosperm. At flowering, temperature above optimum results in seed sterility, while post-anthesis heat stress (HS) causes a reduction in starch biosynthesis and alters its composition. Wheat crop has evolved appropriate mechanisms such as escape, avoidance, and/or stay green to cope with HS. In addition, plants hasten the production of HS-related proteins such as heat shock proteins (HSPs) as their defense approach. An overview of wheat responses and tolerance to HS at biochemical, physiological, and morpho-anatomical behavior may help in formulating appropriate breeding strategies for wheat crop improvement.

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Keywords Heat stress · Heat shock proteins · Starch composition · Quantitative trait loci · Wheat

Abbreviations

AGPase	Glucose-1-phosphate adenylyltransferase
CT	Canopy temperature
EC	Electrical conductivity
GBSS	Granule-bound starch synthase
GF	Grain filling
GFD	Grain filling duration
GN	Grain number
GW	Grain weight
GY	Grain yield
HMW	High molecular weight
HS	Heat stress
HSF	Heat shock factor
HSP	Heat shock protein
LMW	Low molecular weight
PT	Productive tillers
QTLs	Quantitative trait loci
ROS	Reactive oxygen species
RWC	Relative water content
SBE	Starch branching enzyme
SS	Starch synthase
SSS	Soluble starch synthase
TGW	Thousand grain weight
THS	Terminal heat stress

1 Introduction

Wheat (*Triticum* spp.) is a staple food in more than 40 countries of the world with an estimated production of 754 million tonnes in 2016/2017, making it the second most produced cereal after maize (1073 million tonnes; www.igc.int updated 24 Aug 2017). It is grown in a wide range of agroecologies across the world and experiences various abiotic stresses. Tolerance to these stresses is a central characteristic of yield maintenance, and its improvement has long been an objective for plant breeders. The issue now has more apprehension than ever before due to the astonishing rate of recurrence and harshness of extreme climatic events and their potentially negative effects on world food economy and security, especially of developing nations. Tropical and subtropical environments, where maturing wheat crops coincide with terminal heat stress (THS), are likely to put the grain yield (GY) and quality at alarming threat (Enghiad et al. 2017). Episodes of HS have already been augmented in most regions of Asia, Australia, and Europe (IPCC 2014). According to the proposed global climate models, the average ambient temperature is expected to increase up to 6 °C by the end of the twenty-first century (De Costa 2011). Recent controlled and field-based studies have predicted that wheat production will decline by 4.1–6.4% for each global rise of 1 °C in average temperature alone in the perspective of climate change and can have a more adverse effect in combination with other stresses (Kuchel et al. 2007; Bennett et al. 2012; Liu et al. 2016). Although all the growth stages of wheat are sensitive to supraoptimal temperatures, the reproductive phase is the most sensitive one as it affects both grain setting and grain filling (GF; Wollenweber et al. 2003).

2 Terminal Heat Tolerance: A Major Abiotic Stress

Wheat growth characteristics are usually influenced by genotype and genotype × environment interactions. The most favorable temperature during flowering and GF ranges from 12 to 22 °C. Heat stress can alter biochemical, physiological, and morpho-anatomical behavior in wheat leading to declining in pollen viability, duration of GF, and starch synthesis in the endosperm. A supraoptimal temperature at the flowering stage results in seed sterility due to the sensitivity of microspore and megaspore development (Tashiro and Wardlaw 1990). Reduction in starch biosynthesis and alteration in its composition has been reported in response to post-anthesis HS (Sharma et al. 2018). During the reproductive phase and early GF, HS has been found to reduce grain number (GN) and GY by 63% and 78%, respectively (Gibson and Paulsen 1999). It is predicted that further increase of each 1 °C in temperature will result in 6% loss in wheat production (Asseng et al. 2014). Lobell et al. (2008) have estimated GY loss up to 17% for each °C rise in northwest India and Pakistan. In other studies, a GY reduction up to 23% has been reported in response to HS during GF for short-term HS (Hays et al. 2007; Mason et al. 2010). In addition, genotypes assessed in the field under late season or controlled houses to create HS during GF have been found to have a lower GY (Rane et al. 2007; Garg et al. 2012; Paliwal et al. 2012; Sharma et al. 2015). Others have also reported a significant reduction in GN post-anthesis, resulting from short-term high-intensity heat shock shortly after pollination (Plaut et al. 2004; Hays et al. 2007). Heat stress alters the composition of starch in grain (Labuschagne et al. 2009; Sharma et al. 2018). Heat-tolerant varieties that maintain yield components under both long-term and short-term heat shock have been identified, and the emphasis is now being placed on incorporating these heat-tolerant sources into current breeding programs.

2.1 Effect of Terminal Heat Stress on Physiology

Heat stress, either individually or in combination with other stresses, adversely affects plant phenology growth and development. Heat stress manipulates various physiological processes like to assimilate partitioning, excess heat dissipation, electrolyte conductance, photosynthesis, plant water status, and senescence (Wahid et al. 2007; Hasanuzzaman et al. 2013). Heat stress causes loss of cell water content leading into a reduction in the cell size and ultimately the growth (Rodríguez et al. 2005). A high evaporative demand under HS lowers relative water content (RWC; Hall 2001) and accelerates senescence-related metabolic changes which result in poorer assimilate partitioning leading to severe reductions in harvest index (Wahid et al. 2007) and thousand grain weight (TGW; Ahmad et al. 2010a). During anthesis, an ambient temperature of 31 °C is normally suggested as an uppermost limit of sustaining the water status of a plant (Akter and Islam 2017). Heat stress-related dehydration is accompanied by decreased osmotic potential (Ahmad et al. 2010b) and increased water conductivity of plasma membrane due to augmented aquaporin activity (Martinez-Ballesta et al. 2009). Relative water content is the measure of membrane stability, and decreased membrane stability under HS reduces the rate of assimilate transport from source to sink (Taiz and Zeiger 2006; Wahid et al. 2007; Farooq et al. 2011). Membrane malfunctioning and disruption due to HS cause an increase in EC (Hemantaranjan et al. 2014). Heat stress provokes oxidative stress which significantly reduces the membrane thermostability by 54% leading to enhanced electrolyte leakage and reduced cell viability in wheat (Savicka and Škute 2010). Leaf RWC, stomatal conductance, and rate of transpiration are influenced by canopy temperature (CT; Farooq et al. 2009). Studies have shown that CT lowers the plant water status (Pask et al. 2012) and stay green ability (Pinto et al. 2010; Lopes and Reynolds 2012).

Photosynthesis is the most sensitive physiological process. Chloroplast stroma and thylakoid lamellae are primarily affected sites in wheat (Ristic et al. 2008; Mathur et al. 2014). The inactivation of stromal enzymes, photorespiratory electron transport chain, and reduced activity of rubisco reduces the leaf photosynthesis rate (Ainsworth and Ort 2010; Hasanuzzaman et al. 2013). Wheat leaf exposed to an HS (~40 °C) causes irreversible changes in rubisco, rubisco activase, and photosystem II (Mathur et al. 2011). Raines (2011) has reported that rubisco activase gets dissociated under HS causing a significant reduction in the photosynthetic efficiency in wheat. Heat sensitivity of photosystem II is due to disordering the fluidity of thylakoid membranes and dissociation of the light-harvesting complex II from the photosystem II (Dias et al. 2009; Iwaia et al. 2010). These consequences are attributed to increased production of reactive oxygen species (ROS). The respiration rate and mitochondrial activities get changed by heat stress showing an initial increase with the rise in temperature, reach a critical level, and then decline due to photorespiratory damage (Prasad et al. 2008). The increased carbon loss due to photorespiration reduces the production of ATP and boosts the generation of ROS in the rhizosphere (Huang et al. 2012). Photorespiration in flag leaf of wheat has been found to be significantly higher under HS because of change in solubility of O_2 and CO_2 and the affinity of rubisco for these gases (Almeselmani et al. 2012; Cossani and Reynolds 2012).

Leaf senescence is one of the outcomes of heat damage and is characterized by chloroplast destruction, vacuolar collapse, and finally a break of plasma membrane integrity and cellular homeostasis (Akter and Islam 2017). At high HS, plants can die in the very short period due to denaturation or aggregation of proteins, while prolonged and moderate HS leads to gradual senescence; both types can reduce growth or even death (Rodríguez et al. 2005; Hasanuzzaman et al. 2010, 2013).

2.2 Effect of Terminal Heat Stress on Yield Components

Morphologically, THS causes considerable reduction in relative growth and dry weight, reduced size of internodes, unproductive tillers, accelerated senescence, and reduced biomass in plants. It may lead to cell size reduction, reducing water loss by the stomatal closure. In wheat, survival of productive tillers (PT) at higher temperatures is severely affected which is one of the major causes of yield loss in wheat crop. Several reports suggest that the ability to produce PT in wheat plant and their survival depends on genotype, agronomic management practices, and temperature (Longnecker et al. 1993). Hasanuzzaman et al. (2013) have also reported that HS inhibits the initiation and survival of PT in wheat. Late sown spring wheat crop in subtropical countries encounters low soil temperature, which reduces germination, and also causes decreased production of PT and poor early stand establishment (Hakim et al. 2012; Hossain et al. 2013).

Grain size and number are sensitive to HS, and severity depends on the developmental stage (Ferris et al. 1998). Heat stress affects spikelet initiation, male and female, pollination, and fertilization. Porter and Gawith (1999) observed spikelet initiation and sporogenesis get accelerated under HS which causes sterile spikelet production. Semenov (2009) has reported that HS (>20 °C) during heading and anthesis accelerates the enlargement of the spike but diminishes the number of spikelets, while HS during floral initiation negatively affects microspore and pollen cell development which in turn causes complete sterility (Anjum et al. 2008; Kaur and Behl 2010). In wheat, 3-day HS during flowering results in structurally abnormal and/or nonfunctional florets (Hedhly et al. 2009). Further, HS of 31/20 °C (day/night) leads to grain size shrinking due to change in structures of the endosperm cells and aleurone layer (Dias et al. 2008). Inadequate availability of assimilates due to reduced photosynthesis at HS during floret development has been reported to limit GN (Demotes-Mainard and Jeuffroy 2004). Abnormal anther development and reduced pollen viability under HS result in poor fertilization and grain formation (Ferris et al. 1998).

Postfertilization GF is the final phase of growth in cereals. Its duration and rate determine the final grain weight, the most significant determinant of the total yield (Barnabás et al. 2008; Mitra and Bhatia 2008). Photo-assimilate accumulated in the stems and sheaths utilized to synthesize up to 40% of the grain dry matter, and hence GF occurs synchronously with the whole-plant senescence (Yang and Zhang 2006). Heat shock during GF has detrimental effects on GY by hastening maturity, triggering premature senescence, shortening grain filling duration (GFD), and a decline in grain weight (GW; Plaut et al. 2004; Hays et al. 2007; Modhe et al. 2008; Bala et al. 2014). The reduction in GW due to HS during the early periods of GF results in the lower number of endosperm cells, while in the later stages, HS halts starch synthesis either because of insufficient photo-assimilates or the inactivation of starch biosynthetic enzymes in the grain (Yang et al. 2004). Under HS, wheat crop completes its life cycle much quicker than under normal temperature conditions (Nahar et al. 2010; Alam et al. 2013, 2014) due to shortened duration. The continuous supraoptimal temperature during GF is known to cause a significant reduction in the duration in grain fill and only a marginal increase in its rate (Wardlaw 2002; Dupont and Altenbach 2003). Ambient temperature regime (37/28 °C) reduces GFD by 3 weeks (Hurkman et al. 2003). Temperatures above the optimum (>20 °C) have been found to shorten GFD but accelerate the rate of GF (Dias and Lidon 2009). HS during GF tends to stop grain growth prematurely and to hasten physiological maturity. Hanchinal et al. (1994) reported a reduction in the grain growth phases under HS. It has been estimated that for every 1 °C above the optimal growing temperature of 15–20 °C, GFD is reduced by 2.8 days (Streck 2005). Yin et al. (2009) have reported that 5 °C increase in temperature above optimum reduces the GFD by 12 days in wheat. Bala et al. (2014) reported that HS shortens the GFD by 0.4 day for each 1 °C increase in mean temperature from optimum temperature. A 3–12-day reduction in GFD by HS can reduce average GW up to 36% (Vignjevic et al. 2015). Although HS supports a high GF rate, reduced GFD cannot be compensated by the enhanced growth rate (Zahedi and Jenner 2003). Wardlaw and Moncur (1995) have investigated the rate and duration of GF in heat-tolerant and heat-sensitive wheat cultivars and found that tolerant cultivars have a very high rate of GF under HS indicating that increased rate compensates for reduced GFD. Accelerated GF with reduced GFD appear to be a desirable trait for conferring tolerance to severe HS.

Grain weight has been recorded to decline by 85% when the temperature rises from 20/16 °C (day/night) to 36/31 °C from 7 DPA till maturity (Tashiro and Wardlaw 1989). In winter wheat, GY, GN, and GW have been found to be reduced by 78%, 63%, and 29%, respectively, under HS during its GF, while HS imposed from 20 days after anthesis led to a decrease in GW by 18% (Gibson and Paulsen 1999). Delayed planting shortens the overall phenology which ultimately causes a reduction in yield and yield components (Din and Singh 2005). Abdullah et al. (2007) have recorded a decline in GW progressively with delayed sowing and have shown a 33% reduction due to HS. Dias et al. (2008) observed grain shrinkage due to THS.

2.3 Effect of Terminal Heat Stress on Starch Biosynthesis and Composition

Starch is the main component which constitutes one-third of the wheat and is mainly composed of amylose and amylopectin that occur in a ratio of 30:70 (w/w) (Tester et al. 2004; Morell et al. 2007). Amylose is the linear polymer of glycopyranosyl monomers linked to each other by α-(1, 4) linkages, whereas amylopectin is akin to amylose but branched by α-(1, 6) linkages (Sharma et al. 2018). Plants produce starch by first converting glucose-1-phosphate to ADP-glucose in an ATP-dependent reaction catalyzed by glucose-1-phosphate adenylyltransferase (AGPase, EC 2.7.7.27). Starch synthase (SS, EC 2.4.1.21) transfers glucosyl residues from ADP-glucose to a nonreducing end of the existed glucan chain via α-(1, 4)-glycosidic bond to produce linear amylose. Starch synthase has two forms: soluble starch synthase (SSS) and granule-bound starch synthase (GBSS). Based on sequence phylogeny, these were further divided into few groups, viz., SSI-SSIV and GBSSI (Leterrier et al. 2008). Most isoforms share functional overlapping to introduce variation in glucan chain length and rate of recurrence of branch points in amylopectin (Szydlowski et al. 2011). Granule-bound starch synthase I can synthesize only amylose (Denyer et al. 1996; Sharma et al. 2018). Starch branching enzyme (SBE; EC 2.4.1.18) introduces α-(1, 6)-glycosidic bonds in these chains after 20–25 glucose residues, creating the branched amylopectin.

Grain development is a temperature-dependent process, and reduction in grain dry weight by HS is well documented (Denyer et al. 1994; Hurkman et al. 2003; Jiang et al. 2003; Yamakawa et al. 2007; Barnabás et al. 2008; Singh et al. 2008; Yan et al. 2008; Zhao et al. 2008). A reduction up to one-third of total endosperm starch can occur under high temperature (30–40 °C) because of reduced efficiency of starch biosynthetic enzymes (Zhao et al. 2008; Liu et al. 2011). Among the enzymes involved in the pathway of starch biosynthesis in wheat endosperms, AGPase and SSS are the most sensitive to HS (Hurkman et al. 2003; Spiertz et al. 2006; Yamakawa et al. 2007). AGPase catalyzes the rate-limiting step (Ito et al. 2009).

Soluble starch synthase in wheat loses up to 97% activity at 40 °C and becomes nonfunctional (Keeling et al. 1993). Further, gene expression analysis in wheat has revealed that HS causes a greater reduction in the transcript number for SSS than for other enzymes involved in starch biosynthesis (Hurkman et al. 2003). However, Sharma et al. (2018) have reported that the loss of SSS activity up to 30 °C is not large enough to reduce starch deposition but can alter its composition. Granule-bound starch synthase activity is not affected significantly by HS in wheat (Sharma et al. 2018).

Starch branching enzyme II (SBEII) enzyme is sensitive to HS and alters the glucan chain length in maize and rice endosperm starch (Ohdan et al. 2011). In addition, transcriptional profiling of starch biosynthetic genes has been investigated in rice (Yamakawa et al. 2007), barley (Mangelsen et al. 2011), and wheat endosperm (Hurkman et al. 2003) under HS and has revealed a similar directional alteration in gene expression of AGPase, SSS, GBSSI, and SBEs as in their enzyme activities (Cheng et al. 2005; Ohdan et al. 2011).

Starch biosynthesis occurs synchronously with grain development. Heat stress during GF reduces the content and, usually, modifies the composition of starch in the endosperm (Hurkman et al. 2003). The functional properties of starch, particularly the dough characteristics in the presence of heat, are affected by variations in the ratio of amylose to amylopectin and the size of starch granules (Dengate 1984; Hurkman et al. 2003). Variations in the starch composition in wheat endosperm by HS are assumed to be due mainly to heat inactivation of SSS, a key enzyme in the starch biosynthetic pathway.

Amylose content is the most important quality parameter to characterize starch properties. Small changes in amylose may affect starch characteristics as suggested by the report that 1% variation in amylose effectively alters starch gelatinization and pasting properties (Hurkman et al. 2003). The chain length distribution of amylopectin glucan chains may be modified under HS. In wheat, the accumulation of shorter glucan chains increases (Matsuki et al. 2003; Diane and Thitisaksakul 2013), while in rice, the long glucan chain fraction increases (Suzuki et al. 2004; Yamakawa et al. 2007). Amylose content and the amylose: amylopectin ratio increase under HS (Labuschagne et al. 2009; Sharma et al. 2015). Sharma et al. (2018) have observed that there is no reduction in starch content, but its composition in the mature grain gets altered. Amylose content increases in grains of WH730, a heat-tolerant genotype, under HS. Authors have explained this interesting observation by concluding that WH 730 stays green for too long and, in the later phase of GF under late sown conditions, SSS activity is reduced due to HS, while GBSS, a thermostable enzyme responsible for amylose formation, might have remained active. The wheat starch granule size and proportions got altered due to HS. The size of both A- and B-granules decreases, with the proportion of the large A-granules increasing at the expense of the small B-granules (Hurkman et al. 2003; Diane and Thitisaksakul 2013). Large A-type granules cause more reduction in maximum viscosity in comparison to small (B-type) granules, and this specificity is utilized to introduce variation in the final texture of processed foods and nonfood products (Soh et al. 2006).

2.4 *Effect of Terminal Heat Stress on Protein Content and Composition*

Protein content and composition are significant determinants of wheat grain quality and exhibit a greater variation (7–22%) than starch. These can be simple, conjugated, or derived types (Osborne 1907). Simple proteins include albumins (water soluble), globulins (soluble in salt solutions), prolamins (soluble in 70–90% ethanol), and glutelins (soluble in dilute acid or alkali). Wheat seed proteins can also be divided into storage (gluten) proteins (80–85%) and a heterogeneous group of structural/metabolic (non-gluten) proteins (15–20%) (Shewry et al. 2003). In wheat, HS hardly affects the grain protein concentration (Lizana and Calderini 2013) but diminishes the flour quality by plummeting gluten strength-related parameters, lactic acid retention capacity, and mixograph peak time (Li et al. 2013). In contrast, HS during the early GF phase results in higher grain protein content (Castro et al. 2007). Iqbal et al. (2017) have also observed an elevation in grain protein content with an increase in leaf nitrogen content and the increase in essential amino acids fraction and sedimentation index. Under HS, sedimentation index decreases due to a reduction in essential amino acid content (Dias et al. 2008).

2.5 Tolerance Mechanisms of Terminal Heat Stress

The capability of plants to survive and maintain their normal growth under HS is generally regarded as heat tolerance (Wahid et al. 2007). Wheat has evolved appropriate mechanisms such as escape, avoidance, and/or stay green to cope with HS (Fig. 1; Wahid et al. 2007; Farooq et al. 2011). Plants can escape THS by shortening its GFD with accelerated GF rate using stem reserves to maintain yield. Avoidance is the maintenance of an optimum plant water status by reducing water loss (by stomatal closure, trichomes, wax on leaves, leaf rolling, change in leaf angle, senescence of older leaves, etc.) or exploits water availability (by better root architecture and growth). Stay green behavior involves tolerance to low water potential, cooler canopies, active photosynthetic state to sustain the supply of current assimilate, better radiation use efficiency, and long GFD to maintain GF in elevated temperatures. Terminal heat stress-induced biochemical, cellular, morphological, and physiological changes described above are mediated through several transcription factors and signaling molecules which are eventually governed by transcriptome and proteome of the cell. Several chromosomal regions have also been identified to be related with various traits through quantitative trait loci (QTLs) mapping and can be used in breeding programs using map-based cloning approach (Devos et al. 2009).

2.6 Temperature Sensing and Signaling

When plant perceives HS, cascades of non-specific and specific stress signals occur for turning on adaptive response mechanisms (Chinnusamy et al. 2003). Non-specific responses originated from the membrane due to change in its fluidity by stress involve chemical signals such as Ca^{2+} which activate genomic reprograming via signal cascades (Joyce et al. 2003; Suzuki and Mittler 2006). The sharp increase in cytosolic Ca^{2+} evokes MAPK cascades to adjust the expression of HSPs (Larkindale and Knight 2002; Sangwan and Dhindsa 2002; Liu et al. 2003; Kaur and Gupta 2005). However, Gong et al. (1997) have observed that Ca^{2+} is not necessary for the production of HSPs, despite the fact that HS accelerates the uptake of Ca^{2+}. However, this may provoke the activity of antioxidants to maintain

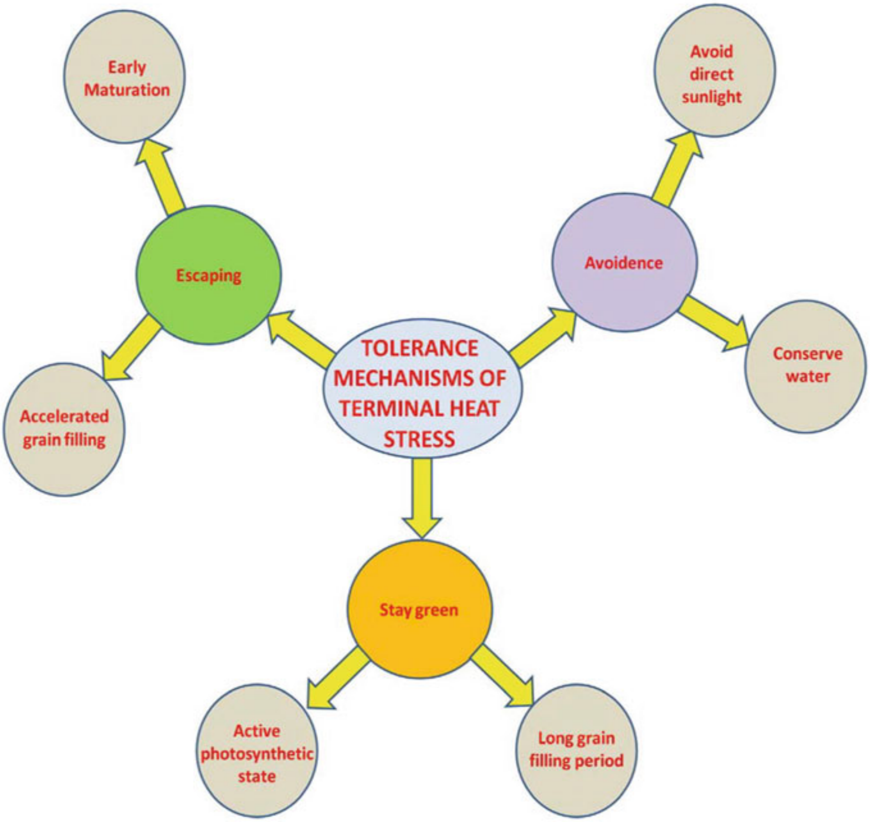

Fig. 1 Different adaptive mechanisms to terminal heat stress in wheat

turgor in the guard cells (Webb et al. 1996; Gong et al. 1997). Specific signaling molecules like salicylic acid, abscisic acid, calcium chloride, hydrogen peroxide, and 1-aminocyclopropane-1-carboxylic acid may induce thermotolerance by reducing oxidative damage by activation of different antioxidant enzymes (Dat et al. 2000; Larkindale and Huang 2004; Vinocur and Altman 2005; Almeselmani et al. 2006; Chakraborty and Pradhan 2011). These help in the reestablishment of homeostasis and membrane structures.

2.7 Heat Shock Proteins

Synthesis and correct folding of proteins get disturbed under HS. To deal with this survival-threatening situation, plants hasten the synthesis of HS stress-related proteins popularly known as HSPs as the defense strategy (Gupta et al. 2010). These

Table 1 An outline of basic functions of heat shock proteins (HSPs) in plant system for heat stress tolerance

Heat shock protein	Functions
HSP110/104	Protein folding
HSP100	ATP-dependent dissociation and degradation of aggregate protein
HSP90	Co-regulator of heat stress linked signal transduction complexes and manages protein folding. It requires ATP for its function
HSP70	Primary stabilization of newly formed proteins and necessary for translocation and folding
HSP60	Refold and prevent aggregation of denatured proteins in posttranslational modification in mitochondria and chloroplast
HSP40	Co-factor of Hsp70
HSP27	Microfilament stabilization, antiapoptotic
Small HSP (sHSP)	sHSPs lack the folding and refolding capacities of the major chaperones and, however, bind to denatured proteins as holding chaperones prevent aggregation. Forms high molecular weight oligomeric complexes which serve as a cellular matrix for stabilization of unfolded proteins
	HSP100, HSP70, and HSP40 are needed for its release

proteins function as chaperones for facilitating correct protein refolding, stabilization, and compartmentalization to improve membrane stability, water, and nutrient use efficiency and assimilate partitioning under HS (Diamant et al. 2001; Panchuk et al. 2002; Wang et al. 2004; Wahid et al. 2007; Hasanuzzaman et al. 2013; Hemantaranjan et al. 2014). Heat shock proteins can be broadly grouped as low molecular weight (LMW) and high molecular weight (HMW) (Table 1; Wahid et al. 2007). Low molecular weight HSPs constitute complexes with the newly synthesized or unfolded proteins and create a platform for HMW-HSP action to ensure correct refolding of nonnative proteins (Wang et al. 2004). Aggregation of LMW-HSPs in the chloroplast membrane facilitates photosynthetic electron transport under HS. Various chaperones function in complementary and sometimes in overlapping mode (Wang et al. 2004; Scarpeci et al. 2008). For example, HSP100, HSP70, and HSP40 are essentially required for the release of HMW and small HSP complex from fully refolded protein (Hasanuzzaman et al. 2013).

HSP100 degraded aggregated proteins in ATP-dependent process. HSP90 acts as a co-regulator of HS linked signal transduction complexes and manages protein folding. Taipale et al. (2010) have observed an increase in expression of HSP90 in response to HS. HSP70 is the best characterized of the HSPs, with specific family members showing tissue-specific expression in response to HS (Sung et al. 2001). HSP70 and HSP40 mainly stabilize the newly formed proteins by ATP-dependent binding and release mechanism. Hsp23.5 is highly expressed during heat shock in *Arabidopsis thaliana* (Waters 2013). Nguyen et al. (1994) detected mRNA accumulation of HSP16.9 at HS in wheat genotypes which shows its role in heat tolerance. PCR-based SNP marker of HSP16.9 explains 29.89% and 24.14% phenotypic variation for GW per spike and TGW, respectively, across 28 spring wheat genotypes (Garg et al. 2013).

2.8 Reactive Oxygen Species

Reactive oxygen species are extremely powerful oxidants produced as normal metabolites during cellular metabolism. Their production and removal are highly regulated; however, the equilibrium gets disturbed during various stresses, including HS stress (Savicka and Škute 2010). Mittler et al. (2011) have proposed that continual HS in plants may cause accumulation of ROS in cell plasma membrane with depolarization of cell membrane, activation of ROS producing the enzyme respiratory burst oxidase homolog D (RBOHD), and trigger of programmed cell death. Miller et al. (2009) have found that HS increases O_2^- production in roots by 68% and malondialdehyde content in leaf by 27% at early stages and 58% at a later stage of seedling development. Several studies have shown that antioxidative enzymes such as ascorbate peroxidase, catalase, dehydroascorbate reductase, glutathione reductase, glutathione peroxidase, and glutathione *S*-transferase, monodehydroascorbate reductase, and superoxide dismutase can alleviate the HS by scavenging excess of ROS (Suzuki et al. 2011; Caverzan et al. 2016).

2.9 Transcriptomics and Proteomics

To cope with abiotic stresses such as HS, plants execute a number of physiological and metabolic responses which are regulated mostly at the gene level (Boghireddy et al. 2014). Now these days, transcriptomics and proteomics approaches are being used to identify stress-responsive genes and proteins in several crops including wheat (Table 2). Microarray analysis of heat susceptible (Chinese Spring) and tolerant wheat (TAM107) genotypes has revealed 313 differentially expressed transcripts related with heat tolerance (Qin et al. 2008). The putative heat-responsive genes encode HSPs, heat shock factors (HSF), phytohormones, ribosomal proteins, secondary metabolites, signaling molecules, and transcription factors. Chauhan et al. (2011) have generated 3516 heat-responsive ESTs by using PCR-select subtraction technology. The proteome analyses have revealed an increase in the abundance of proteins related to HSP, HSFs, signal transduction, and photosynthesis but a decrease in the abundance of proteins related to nitrogen metabolism under HS (Wang et al. 2015). Majoul et al. (2004) have reported an increase in the level of small HSPs belonging to the family of 20 kDa. In addition, three heat-upregulated proteins show similarities to elongation factors (EF) or eukaryotic translation initiation factors (eIF) indicating that the translational activity is involved in response to HS. A heat shock transcription factor, TaHsfA6f, is over expressed to alleviate the impact of HS (Xue et al. 2015). Interaction networks between proteins have revealed eight critical regulatory differentially expressed proteins under HS, including calcineurin B-like 3, C-5 sterol desaturase, brassinosteroid receptor 1, DPBF4, protein disulfide isomerase, a chaperone protein, starch phosphorylase L-1, and peroxiredoxin B in the grain of wheat cultivar Jing411 (Zhang et al. 2017a).

Table 2 Heat stress-induced transcriptomics/proteomics studies in wheat using various approaches/tools

Category (genes/proteins/miRNAs/siRNAs)	Approach	Differentially expressed genes/proteins/miRNAs/siRNAs	References
Gene	Microarray	*Hsfs*, *HSPs*, *DREB2B*, *DREB6A*, *ERETC*, and member of *MBF1*	Qin et al. (2008)
Gene	Microarray	b-ZIP transcription factors and TaCAM3–1 (zinc finger with calmodulin)	Chauhan et al. (2011)
Gene	Microarray	HSPs, transporters, protein modifiers, and signaling molecules	Khurana et al. (2011)
miRNA	Solexa sequencing	miR156, miR159, miR160, miR166, miR168, miR169, miR172, miR827, and miR2005	Xin et al. (2010)
siRNA		siRNA007927_0100_2975.1, siRNA002061_0636_3054.1, siRNA05047_0654_1904.1, and siRNA080621_1340_0098.1	Yao et al. (2010)
Protein	LC-MS/MS analysis	Calcineurin B-like 3, C-5 sterol desaturase, brassinosteroid receptor 1, DPBF4, protein disulfide isomerase, chaperone protein CLPB1, starch phosphorylase L-1, and peroxiredoxin B	Zhang et al. (2017a, b)
Protein	LC-MS/MS analysis	Hsp70, BRI1-KD interacting protein 114, rubisco activase, sedoheptulose-bisphosphatase and fructose-bisphosphate aldolase involved in RuBP generation, peptidyl-prolyl-cis-trans isomerase, 2-Cys peroxiredoxin BAS1, glutamine synthetase	Wang et al. (2015)
Protein	LC-MS/MS analysis	TaHsfA6f	Xue et al. (2015)

MicroRNAs (miRNAs) and small RNAs (siRNA) are a class of small noncoding regulatory RNAs, which are the key players in stress response in plants. Solexa siRNAs high-throughput sequencing has revealed a downregulation in the expression of miR172 and an upregulation in the expression of miR156, 159, 160, 166, 168, 169, 393, 827, and 2005 under HS (Xin et al. 2010). Similarly, Yao et al. (2010) have reported that siRNA007927_0100_2975.1 gets upregulated, while the siRNA002061_0636_3054.1, siRNA005047_0654_1904.1, and siRNA080621_1340_0098.1 get downregulated during HS conditions.

2.10 Chromosomal Regions Associated with THS Tolerance

In the last two decades, DNA-based molecular markers have become the dominant marker system for genetic analysis. These molecular markers are especially useful to breeders for selecting QTLs and genetic linkage map construction. A genetic linkage map shows the relative position genetic markers in terms of recombination frequency along a chromosome (Collard et al. 2005). Significant genetic variations for traits associated with heat tolerance exist in wheat germplasm. Therefore, several QTL studies related to HS tolerance have been done in wheat (Pinto et al. 2010; Vijayalakshmi et al. 2010; Paliwal et al. 2012; Tiwari et al. 2013; Mason et al. 2010, 2011, 2013; Acuña et al. 2014; Talukder et al. 2014; Sharma et al. 2016). A total of 736 QTLs have been identified associated with heat and drought tolerance in wheat (Acuña et al. 2014). Yang et al. (2002) have found two marker loci (Xgwm11-1B and Xgwm293-5A) for grain filling duration under HS, which contributed to 23% of the phenotypic variation. Kuchel et al. (2007) have also established the association of gwm11 on chromosome 1B with yield under HS stress. Mason et al. (2010) have investigated the effect of HS during early grain filling and reported five stable QTLs for HSI of single grain weight (1A and 2A), grain weight (3B), and GN(2B and 3B) explaining up to 22% of phenotypic variation under short-term HS in controlled conditions. Few QTLs have been identified for the stay green trait in wheat (Vijayalakshmi et al. 2010). Pinto et al. (2010) have identified a QTL for CT on chromosome 4A. Seven loci are found to co-localize for both HSI of main spike yield components and temperature depression of the main spike indicating a strong genetic link between the cooler canopy and HS tolerance (Mason et al. 2011). Paliwal et al. (2012) have reported a significant association of genomic regions on 2B, 7B, and 7D with HSI of grain weight and GFD and with the expression of canopy temperature depression under a late sown condition in field experiment explaining more than 15% phenotypic variation for these traits. Seven stable QTLs have been identified related to HSI of GFD, TGW, GY, and CT on chromosomes 1D, 6B, 2D, and 7A, respectively (Tiwari et al. 2013). Five QTLs have also been identified in a greenhouse experiment associated with plasma and thylakoid membrane damage and chlorophyll content on chromosomes 1B, 1D, 2B, 6A, and 7A. These QTLs have explained up to 33.5% of the phenotypic variation (Talukder et al. 2014). Sharma et al. (2016) have identified stable QTLs associated with GFD, GN, and PT on chromosomes 1B, 2B, 3B, 5A, and 6B in field experiment explaining up to 22% phenotypic variation (Table 3).

2.11 Transgenic Approach for Heat Stress Tolerance

Genetic editing approaches are being used to improve HS tolerance in plants (Chapman et al. 2012; Zheng et al. 2012). Recently, several transcription factors involved in different abiotic stresses tolerance in cereal crops have been engineered (Wang et al. 2016). The functions of few wheat genes involved in HS signaling and tolerance have been characterized by overexpression in model plants such as *Arabidopsis*, rice, or wheat. The constitutive expression of elongation factor (EF-Tu) in transgenic wheat has been reported to improve HS tolerance (Ristic et al. 2008; Fu et al. 2012). Overexpression of TaHSFA6f gene has shown an

Table 3 A summary of major and stable QTLs for heat stress tolerance

Chromosome	Closest marker	R^2	Traits	Germplasm	Treatment	References
1A	cfa2129	27.4, 22.6	HSIGN, HSISGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
1B	gwm190	13.1	SSIGW	144 RILs Kauz/MTRWA116	Controlled, 35 °C for 3 days	Mohammadi et al. (2008)
1B	2249474|F|0	15	HSIGFD	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
1B	agg/cat-4	24.2	NDVI	167 RILs, SeriM82/Babax	Field, late sown	Pinto et al. (2010)
1D	wmc216	16.84	HSIYD	DH 138, Berkut/cv. Krichauff	Field, late sown	Tiwari et al. (2013)
1D	wPt9664	12.43	HSICT	DH 138, Berkut/cv. Krichauff	Field, late sown	Tiwari et al. (2013)
2A	gwm294	17.8	HSISGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
2A	gwm356	21	HSISGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
2A	wmc407	15	HSIGFD	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
2A	cgt.tgcg-349	26	SEN	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
2A	gwm356	17	SEN	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
2B	barc200	21.6, 25.9	HSIGN, FLW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
2B	gwm111	24.8	HSIGW, HSIGN	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
2B	gwm1273	20.2, 17.8	HSIGFD, HSITGW	148 RILS, NW1014 / HUW468	Field, late sown	Paliwal et al. (2012)
2B	1161184|F|0	15	HSIGN	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
2D	cfd56	23.5	DH	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)
2D	gwm261	19.3	HSISGW	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)

(continued)

Table 3 (continued)

Chromosome	Closest marker	R^2	Traits	Germplasm	Treatment	References
2D	gwm484	15.2, 32.8	DM,FLL	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)
2D	cfd233	20.53	HSIGFD	DH 138, Berkut/cv. Krichauff	Field, late sown	Tiwari et al. (2013)
3B	wmc326	21.2	HSIGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
3B	wmc527	19	HSIGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
3B	gtg.agct-205	18	SEN	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
3B	1145590|F|0	18	PT	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
4A	wmc89	13.5	HSISGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
4A	barc170	15.5	HSIGN	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
4B	gwm368	17	LA	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
5A	barc197	13.8	HSIGN	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5A	gwm126	32.1	HSIGN	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5A	gwm291	21.9	HSIGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5A	wmc150	16.4	FLW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5A	gwm126	14.6	CTD	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)
5A	gwm156	30	LA	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
5A	1079678|F|0	22	HSIGFD	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
5B	gwm213	24.6	HSIGN	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5B	wmc160	13	FLL, DH	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
5B	gwm408	13.4	HSIGN	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)

5B	gwm133	29.5	HSIGW	144 RILs Kauz/ MTRWA116	Controlled, 35 °C for 3 days	Mohammadi et al. (2008)
6A	CAG.AGC-101	26	SEN	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
6A	CGT.GTG-343	30	SEN	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
6B	1109194|F|0	20	PT	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
6B	2280984|F|0	12	HSIYD	92 RILs, K 7903/RAJ 4014	Field, very late sown	Sharma et al. (2016)
6D	gwm325	38.6, 13.1	HSIGW,HSIGFD	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
6D	cfd42	32.1	CTD	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)
6D	cfd49	14.7	HSISGW	121 RILs, Halberd/Karl92	Controlled, 38 °C for 3 days	Mason et al. (2011)
7A	gwm282	31.6	HSISGW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
7A	gwm60	19	FLW	64 RILS, Halberd/Cutter	Controlled, 38 °C for 3 days	Mason et al. (2010)
7B	gwm577	21	LA	101 RILs Ventnor/Karl 92	Terminal heat at 30 °C at 10 DAP	Vijayalakshmi et al. (2010)
7B	gwm1025	20.3, 13.2	HSITGW, LSYLD,	148 RILS, NW1014 / HUW468	Field, late sown	Paliwal et al. (2012)
7D	Gwm3062	9.8, 7.4	HSITGW, LSDM	148 RILS, NW1014 / HUW468	Field, late sown	Paliwal et al. (2012)

CT canopy temperature, *CTD* canopy temperature depression, *DH* days to heading, *DM* days to maturity, *FLL* flag leaf length, *FLW* flag leaf width, *HSICT* heat susceptibility index canopy temperature, *HSIGFD* heat susceptibility index grain filling duration, *HSIGN* heat susceptibility index grain number, *HSIGW* heat susceptibility index grain weight, *HSISGW* heat susceptibility index single grain weight, *HSITGW* heat susceptibility index thousand grain weight, *HSIYD* heat susceptibility index yield, *LA* leaf area, *LSDM* days to maturity under late sown, *LSYLD* yield under late sown, *NDVI* normalized difference vegetation index, *PT* productive tillers, *SEN* senescence enhancement in HS tolerance in wheat (Xue et al. 2015). Likewise, ectopic expression of wheat *TaB2*, *TaFER-5B*, *TaGASR1*, *TaMBF1c*, and *TaOEP16–2-5B* in *Arabidopsis* has revealed improvement in HS tolerance (Qin et al. 2015; Singh and Khurana 2016; Zhang et al. 2017b). Recent improvements in transformation technology and the availability of gene libraries and huge sequencing repositories are likely to pave the way for engineering wheat genome for improved HS tolerance.

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Wheat Responses and Tolerance to UV-B Radiation: An Overview

Sunita Kataria, Meeta Jain, Mansi Kanungo, and Sonika Sharma

Contents

Abstract The elevated ultraviolet-B (UV-B, 290–315 nm) has sensitive alarm because it causes drastic effects on growth, photosynthesis, and crop yield. Globally, increased UV-B has a great challenge for production of wheat. Therefore, in this chapter, a brief attempt has been made to summarize the wheat responses and tolerance to UV-B radiation. Over the last two decades, most of the studies were on the mechanisms of UV-B tolerance along with the physiological, biochemical, and morphological responses of wheat plants to UV-B stress. The experimental results showed that ambient UV-B (aUV-B) and supplemental UV-B (sUV-B) radiations have adverse effects on growth of wheat crops such as shortening plant height, reducing leaf area, slowing physiological activity, and decreasing biomass and photosynthetic performance and yield. The perusal of literature recommended the enhanced UV-B irradiation lessens the production of crop yield via disturbing the number and weight of grains. The levels of superoxide radical ($O_2^{\cdot -}$) and hydrogen peroxide (H_2O_2) were enhanced by UV-B (ambient and supplemental) along with enhanced peroxidation of lipids (LPO) and electrolyte leakage. Wheat plants possess many protective and tolerance mechanisms to reduce the effect of oxidative stress

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caused by UV-B stress. In response to aUV-B and sUV-B, defense mechanisms get activated in the form of the increased superoxide dismutase, catalase, ascorbic acid, and guaiacol peroxidase activities, and all nonenzymatic antioxidants are found to increase in wheat. Enhanced and ambient UV-B radiation had harmful effects on photosynthetic parameters like photosystem II (Hill reaction, chlorophyll, chlorophyll *a* fluorescence, electron transport rate (ETR), and yield), thylakoid, and enzymes of the dark reaction like carbonic anhydrase (CA), ribulose bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEPC), malic dehydrogenase (MDH), and chlorophyllase in wheat. Inter- and intraspecific variations were observed in the susceptibility of wheat to UV-B which imply the potential efforts in breeding programs for improved tolerance to UV-B radiation. On the other hand, exclusion of solar UV-B from solar spectrum enhanced the growth, biomass, photosynthetic performance, and yield of wheat plants as compared to the ambient and enhanced UV-B.

Keywords Growth · Biomass · Defense · Photosynthesis · Rubisco · Sensitivity · Wheat · UV-B · Yield

Abbreviations

ABA	Abscisic acid
APX	Ascorbic acid peroxidase
AsA	Ascorbic acid
CA	Carbonic anhydrase
CAT	Catalase
CFCs	Chlorofluorocarbons
ETC	Electron transport chain
GR	Glutathione reductase
GSH	Glutathione reduced
IAA	Indole-3-acetic acid
MDA	Malondialdehyde
MDH	Malic dehydrogenase
NR	Nitrate reductase
PAR	Photosynthetically active radiation
PEPC	Phosphoenolpyruvate carboxylase
POD	Peroxidase
PPF	Photosynthetic photon flux
RI	Response index
ROS	Reactive oxygen species
Rubisco	Ribulose bisphosphate carboxylase/oxygenase
Si	Silicon
SiNp	Silicon nanoparticles
SNP	Sodium nitroprusside

1 Introduction

Abiotic stresses deteriorate the environment and result into loss of crop yield worldwide (Wang et al. 2003a). The stratospheric ozone (O_3) lessening is one of the tremendous universal anxieties of environmental changes, mostly owing to the discharge of chlorofluorocarbons (CFCs). Due to anthropogenic activity, amount of UV-B radiation increases at the surface of earth. In the upper atmosphere, as CFCs can remain with a half-life ranging from 50 to 150 years, it will take until 2065 to return to the pre-1980 levels providing no further release occurs (UNEP 2008). According to the Montreal Protocol, revival of the O_3 layer is not supposed to prior than 2070 (Caldwell et al. 2007; McKenzie et al. 2011). Until that time UV-B is assumed to continue to exist at an elevated level (Weatherhead et al. 2005). Ultraviolet (UV) represents approximately 7% of the electromagnetic radiations radiated from the sun which is Earth's primary energy source. However, stratospheric ozone layer absorbed 90% of UV-B radiation, and the remaining is being transmitted to Earth surface (Kataria et al. 2014; Sharma et al. 2017). Solar UV-B radiation range is narrow even though it is an important band of solar spectrum reaching the biosphere. Hence plants being sessile are inevitably exposed to ultraviolet radiations while using sunlight for photosynthesis (Kataria et al. 2014).

In addition to environmental harsh conditions, the world's cultivation tolerates severe challenges to convene demand, together with increased expenditure, allowance of land for other uses and the use of chemical goods with inference for health security (Curtis and Halford 2014). Presently, food safety measures mainly depend on the improved production of three cereals: wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.). Wheat is one of the initially cultivated crops broadly distributed in the world; worldwide it supplies the essential foodstuff to the community (Lantican et al. 2005). Globally, wheat is one of the major cereals, and it is the major reserve of calories and protein (Chaves et al. 2013). Curtis and Halford (2014) reported that the wheat is a cereal which is used in the invention of a range of wheat foodstuffs, like flat and steamed breads, leavened bread, pasta, biscuits, cakes, couscous, noodles, and beer. Wheat is also used for the improvement of non-foodstuffs like fuel. Due to its high level of adaptation, wheat is cultivated in tropical and subtropical provinces and in both rainfed and irrigated cultivation. Wheat is known to grow in heterogeneous types of weather ranging from latitudes of 30°N to 60°N and 27°S to 40°S, temperature from 3° and 32° C, and precipitation from 250 to 1750 mm (Enghiad et al. 2017). Among all crops, the wheat crop has significant contribution with worldwide production being 759.6 million tons in 2016–2017 (FAO 2018). Though crop production is rigorously exaggerated by unfavorable environmental stresses like salinity, drought, high temperature, UV-B, etc., these stresses cause a wide range of morphological, physiological, and biochemical responses in plants during adaptation to these adverse conditions (Kataria and Guruprasad 2012, 2015; Rahaie et al. 2013).

The UV-B (280–315 nm) radiation has enough energy to cause large photobiological effects on higher plants, some plants are predominantly susceptible to UV-B

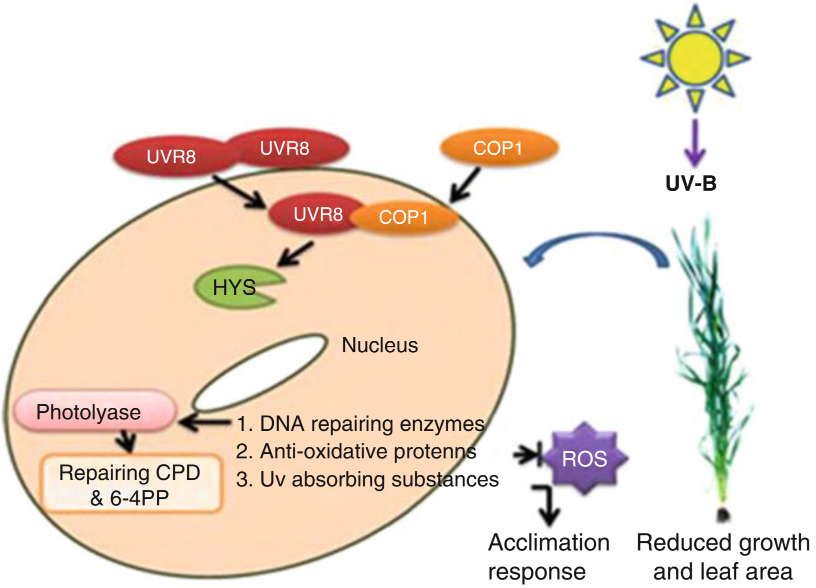

Fig. 1 Morphological, physiological and biomolecular changes in response to UV-B in wheat

which showed damage to the nucleic acids, lipids, and proteins, and some responds to the perception of UV-B as induced acclimation (Kataria et al. 2014; Robson et al. 2015). The effect of UV-B on various morphological, biochemical, and molecular characteristic of plants has been examined; however the majority of the responses observed were extremely variable and depend on the species, cultivars, experimental conditions, levels of UV-B, and the correlation among UV-B and photosynthetically active radiation (PAR) (Frohnmeyer and Staiger 2003; Brown et al. 2005). Figure 1 illustrates the morphological, physiological and biomolecular changes in response to UV-B radiations in the wheat plants. Rizzini et al. (2011) found inhibition of hypocotyl elongation is controlled by the UV RESISTANT LOCUS (UVR8) and UV-B-specific photoreceptor which modulates photomorphogenic responses by regulating the appearance of genes involved DNA repair, antioxidative defense, and synthesis of phenolic compounds. In support to the damaging effect of increased UV-B, Liu et al. (2015) reported reduction in the cell mitosis and the chromosome aberration in wheat.

Ambient UV-B (aUV-B) and supplemental UV-B (sUV-B) cause reduction in growth, biomass accumulation, and photosynthetic performance in wheat seedlings (Kataria and Guruprasad 2012, 2015; Liu et al. 2015). Additionally, some observable signs such as plants dwarfism, changes in shoots, and marked reduction in length and width of leaf in wheat seedlings (Liu et al. 2015) were noticed after UV-B exposure, which is associated with alteration in cell elongation or cell division (Singh et al. 2014). Further, Tripathi et al. (2016) suggested the decrease in growth of wheat seedlings under UV-B stress might be associated with elevated levels of

ROS that cause a harmful impact on lipid molecule present on the membrane. Moreover, the oxidative stress generated by UV-B radiation affected the growth of wheat seedlings resulted in decreased rate of photosynthesis (Agrawal and Rathore 2007; Kanungo et al. 2013).

The intensity of ambient UV-B radiation in sunlight varies regarding to latitude and is comparatively high in tropical regions than in temperate regions. The effect of the ambient UV radiation is particularly higher in tropical environment, where plants are exposed to longer time of sunlight (Sahoo et al. 2005). Therefore, alternatively studies were performed on the removal of solar UV radiation from the solar spectrum to find out the effects of aUV-B on crop plants in the tropical countries. These studies suggested that the aUV-B radiation has significant deleterious effects on growth and development of wheat (Kataria et al. 2013; Kataria and Guruprasad 2012, 2015; Zhu and Yang 2015). Wheat is one of the major world food crops and potentially susceptible to sUV-B and aUV-B, and the tropics and subtropical regions are the major regions of wheat production (Teramura 1983; Zu et al. 2004; Kataria and Guruprasad 2012). Thus increase in UV radiation may influence major wheat production and in turn affect wheat exporters, wheat prices, and food security.

In the present chapter, we discuss wheat responses and tolerance to UV-B radiation and the basic mechanism responsible to these responses.

2 UV-B and Growth of Wheat

Due to depletion of stratospheric ozone layer, increased UV-B caused damaging effect on growth and production of wheat. Decrease in growth is one of the most frequent responses to sUV-B and aUV-B in wheat and other crop plants (Kakani et al. 2003; Kataria et al. 2013, 2014). Reduction in growth by UV-B is may be due to its effect on both the cell division and cell elongation (Hopkins et al. 2002).

Most of the studies of sUV-B radiations on wheat showed the decreased vegetative growth (plant height, leaf area, tiller number), leaf photosynthesis, and enhanced the synthesis of UV-B absorbing substances like flavonoids and phenolic substances (Li et al. 2000a, b, 2010; Ou et al. 2018). These major consequences leads to several of secondary and tertiary effects resultant in distorted growth and development of crop, which ultimately affected the light interception that decreased the photosynthesis, biomass, and yield of wheat (Kakani et al. 2003; Pal et al. 2006; Agrawal and Rathore 2007; Kataria and Guruprasad 2012, 2015). Figure 2 illustrates the effect and responses of enhanced and ambient UV-B on wheat growth, biomass, and yield. Wang et al. (2003b) studied the effect of both aUV-B and sub-aUV-B irradiation (15.3% UV-B irradiance reduced from ambient level) responses in winter wheat and found that sub-aUV-B irradiance improved wheat growth and production and confirmed that aUV-B irradiance also has an adverse effect on wheat. Further, Li et al. (1998) reported that at the early tillering stage of wheat plants, UV-B treatment caused delay in developmental stages and reduction in plant height. However, at the ripening stage, UV-B radiation altered the crop formation of wheat by diminishing the total number of tillers produced and raising the number of dead shoots, which consequently

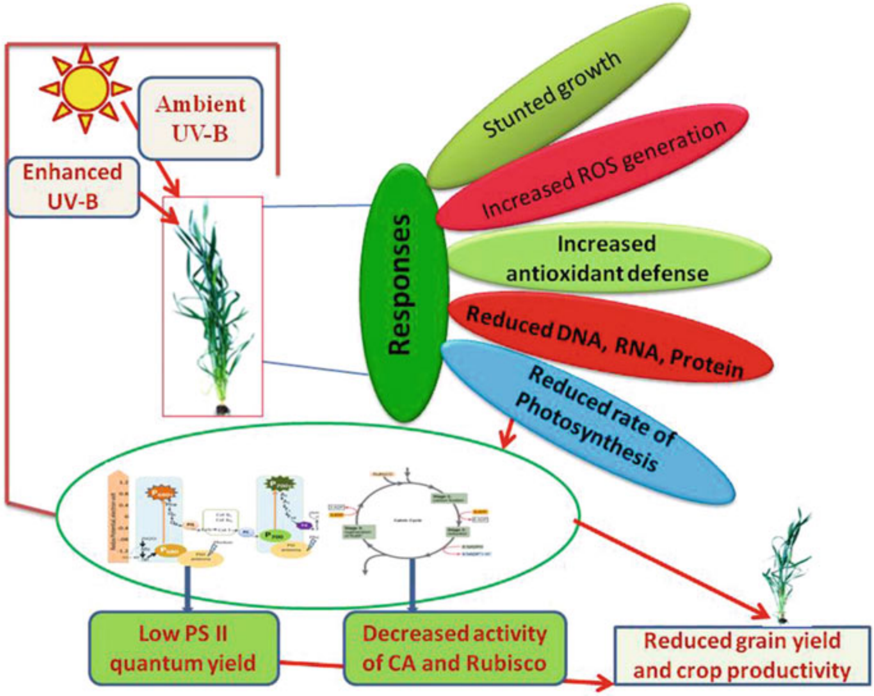

Fig. 2 Effect of enhanced and ambient UV-B on the growth, photosynthesis and yield of wheat plant

reduced the number of head-bearing shoots, and decreased the production of dry mass and yield. UV-B radiation reduced leaf area and leaf area index as well; however, it improved the specific leaf weight (Yuan et al. 1998; Carolina et al. 2009). The UV-B radiation altered the patterns of biomass partitioning by diverting carbon allocation, which might be correlated with the wheat crop yield (Li et al. 1998). In addition, sUV-B radiation significantly decreased the plant nutrients and decomposition and dry matter yield of spring wheat but had no considerable effect on harvest index of spring wheat (*Triticum aestivum*) (Ming et al. 1998). The accumulation of N, P, K, Mg, Fe, and Zn in several plant parts and whole wheat plant was usually reduced apart from leaf N mass which was increased *via* sUV-B. sUV-B reduced the soluble carbohydrates concentration in the leaves and augmented that of holocellulose and soluble proteins in wheat (Ming et al. 1998).

Shoot biomass is prime indicator of UV-B radiation effect on growth (Teramura 1983). The decrease in shoot biomass of wheat plants under sUV-B and with aUV-B were observed in the greenhouse and in fields as well (Teramura 1980; Barnes et al. 1990; Li et al. 1998, 2000a; Kataria and Guruprasad 2012). Further, greenhouse experiments demonstrated that sUV-B radiation increase or not cause any alteration in biomass of wheat plants (Teramura 1983). Tian and Lei (2007) observed decrease in the fresh weight of wheat seedlings significantly due to oxidative damage caused by UV-B radiation. Further, Li et al. (2000a) and Kataria and Guruprasad (2012) demonstrated that UV-B caused clear inhibitory effects on plant height of different wheat varieties. Moreover, the decreased in plant height was due to the reduction in length of internodes; however, node number in wheat remains unaffected (Li et al. 1998), and the same observation was found in soybean (Li et al. 2002). It may be owing to photooxidative damage to the phytohormones like indole acetic acid (IAA) followed by decreased extensibility of cell wall as confirmed in sunflower seedlings (Ros and Tevini 1995; Correia et al. 2000).

Under UV-B stress the alterations in the phytohormones like ABA and IAA were observed in wheat (Li et al. 2010) and rice (Huang et al. 1998). The growth, morphology, and biomass of wheat plants were drastically affected by UV-B because UV-B decreased the IAA content in cultivars of wheat (Li et al. 2000a, 2010). UV-B radiation either directly decompose IAA or through stimulation of peroxidase (Borman 1989; Jansen et al. 2001). Agrawal et al. (2004) found that sUV-B caused reduction in length of shoot and root, biomass, yield, and harvest index of wheat cultivars (HD 2329 and HUW 234). The wheat plants showed more inhibitory response when they were grown without fertilizers, while under additional nutrient supply, they were less affected by enhanced UV-B (Agrawal et al. 2004).

Wheat seedlings exposed through various amount of increased UV-B radiation exhibited inhibition in plant height and root length and dose-dependent (Chen and Han 2014). Liu et al. (2015) found that the growth and development of root and root tip meristematic area of wheat were stimulated by low dosage of UV-B; however high dosage has inhibitory effects. Ran et al. (2018) also found significant alterations by UV-B in the number of adventitious roots, average root length, root biomass, and root vigor of wheat. These authors reported that at the early stages of the irradiation treatment, the protein content in the UV-B radiation treatment group was higher than that of the control group, while protein content of UV-B treated group was lower than that of the control group with an increased time of irradiation in wheat.

In triticale (*Tritico secale* Wittm.) crop, enhanced UV-B induced reductions in plant height, leaf area, total biomass, grain yield, number, and weight of grains (Bacelara et al. 2015). The exclusion of solar UV-B studies suggested that ambient UV-B significantly reduced the ratio of leaf mass per area, leaf area, and specific leaf weight of flag leaves in wheat varieties (Pal et al. 2006; Kataria et al. 2015). Ambient UV-B and sUV-B caused the harsh effects on growth and development of wheat (*Triticum aestivum*) seedlings, along with distortion in fundamental leaf structures and reduce photosynthetic efficiency (Tripathi et al. 2016).

3 UV-B and Photosynthesis of Wheat

Photosynthesis is an important phenomenon of plant physiology. It is a necessary process for primary carbohydrate biosynthesis and other aspects of metabolism such as the assimilation of nitrogen into organic compounds within the chloroplast

(Blankenship 2002; Forde and Lea 2007). The reductions in the biomass of crop plants are responsible key factors associated with inhibition of photosynthesis caused via UV-B (Agrawal et al. 2004; Kataria et al. 2014). The harmful effects of UV-B were extensively reviewed on plants, which suggested that UV-B specifically damage DNA, proteins, and lipids and impair the chloroplast function, reduced biomass accumulation, photosynthesis, and protein synthesis (Kakani et al. 2003; Kataria et al. 2014). Both sUV-B and aUV-B have detrimental effects on the performance of photosynthesis in plants mainly due to the reductions in the chlorophyll and carotenoids levels (Gaberscik et al. 2002; Kataria et al. 2013), alterations in ion permeability of thylakoid membranes (Doughty and Hope 1973), decrease in Rubisco activity (Vu et al. 1982; Kataria et al. 2013; Kataria and Guruprasad 2015), and diminution in the expression of important photosynthetic genes (Mackerness et al. 1997; Casati and Walbot 2003). In wheat plant, sUV-B and aUV-B reduced the biomass accumulation, effectiveness of PSII activity, photosynthesis, and yield of grains (Ambasht and Agrawal 2003; Agrawal et al. 2004; Zheng et al. 2003; Pal et al. 2006; Carolina et al. 2009; Li et al. 2010; Kataria and Guruprasad 2012, 2015; Kataria et al. 2013). The results of these studies indicated that the presence of aUV-B and sUV-B decreased the photosynthetic pigments like chlorophyll *a* and *b*. Li et al. (2000b) reported that 13 cultivars out of 20 wheat cultivars (from South China, North China, and Mexico) exhibit significant alterations in content of total chlorophyll and the most of these species are sensitive; it has been found that chlorophyll a/b ratio decreased due to strongly reduction in content of chlorophyll *a*, while chlorophyll *b* content reduced to a smaller extent. On the other hand, an increase in chlorophyll a/b ratio was observed under sUV-B in some species. However, UV-B radiation significantly decreased the photosynthetic rate in wheat cultivars due to reduction in the chlorophyll contents (Dai et al. 1995; Feng et al. 2003; He et al. 2006; Li et al. 2010; Kataria et al. 2015), decreased stomatal density as well as alterations in stomatal conductance, intercellular CO_2 concentrations, and transpiration rate. Reduction in the photosynthesis by UV-B also caused by injury to molecular machinery of the photosynthetic procedure (Mackerness et al. 1997; Jansen et al. 1998; Casati and Walbot 2003).

Through a decrease in chlorophyll content and increase in antioxidant defense mechanism, the supplementation of mineral nutrients in wheat (*T. aestivum* L. cultivars HD 2329 and HUW 234) mitigates the harmful impact of sUV-B (Agrawal and Rathor 2007). Further, numerous studies have confirmed that the UV-B exposure reduces the net rate of photosynthesis in crop plants (Teramura 1983; Strid et al. 1990; Correia et al. 1999). This decline may be possibly strongly associated with ultrastructural changes in chloroplasts, decrease in the enzymes activities related to photosynthesis, and increases in stomatal and mesophyll resistance (Jordan et al. 1992; He et al. 1994; Greenberg et al. 1997). Zheng et al. (2002) investigated the sUV-B effects on the dry matter accumulation, allocation, and photosynthetic activity of winter wheat. Zu et al. (2004) found changes in the level of the content of amino acid, protein, and total sugar of wheat grain by UV-B radiation. These authors found a significant increase in proteins in some of the tested wheat cultivars like Dali 905, Mianyang 20, Wenmai 3, Chuxiong 8807, Yunmai 39 and Huining 18 whereas there was a significant reduction in total sugar in Dali 905 and Chuxiong 8807.

Several mechanisms may potentially inhibit photosynthesis under UV-B stress; several reports proposed that the primary target of UV-B damage is PS II (Melis et al. 1992), whereas other studies suggested that the decrease in CO_2 assimilation by UV-B can occur earlier than the alteration in PS II, or it may involve the destruction in Calvin cycle probably mediated by Rubisco (Allen et al. 1999). The perusal of relevant literature suggested the deleterious effects of enhanced and ambient UV-B radiation on photosynthesis in wheat like efficiency of PS II (chlorophyll, Hill reaction, parameters related to chlorophyll fluorescence yield, and transport rate of electron), the thylakoid (optical absorption ability, cyclic photophosphorylation, Ca^{2+}-ATPase, and Mg^{2+}-ATPase), and Rubisco, PEPC, CA, MDH, and chlorophyllase enzymes of the dark reaction of photosynthesis (Kataria et al. 2013; Chen and Han 2014; Kataria and Guruprasad 2012, 2015).

UV exclusion studies demonstrated that ambient solar UV-B significantly reduced the rate of photosynthesis in flag leaves of wheat varieties due to reduced quantum yield of PS II and performance index and reduced activities of CA, Rubisco, and nitrate reductase (NR) (Kataria and Guruprasad 2015). Supplemental UV-B radiation also reduced the activities of Rubisco and PEPC in maize (Correia et al. 2005). However, Tripathi et al. (2016) found that supplementation of both silicon (Si) and silicon nanoparticles (SiNp) defend wheat plants from the adverse effect of UV-B stress through defending photosynthesis and activating the antioxidant defense system. SiNp protect the wheat seedlings from harmful effect of UV-B stress through NO-mediated activation of antioxidant defense system, which consequently compensate the ROS-stimulated damage to photosynthesis (Tripathi et al. 2016). Chen and Han (2014) investigate the application of He-Ne laser treatment to alleviate the effects of enhanced UV-B radiation on photosynthesis of wheat plants. They found that He-Ne laser treatment stimulated the activities of key enzymes and altered various parameters involved in photosynthesis of wheat seedlings.

An induction in NR activity was observed by the exclusion of solar UV in leaves of wheat varieties as compared to plants grown under aUV-B (Kataria et al. 2015). Similarly, the activity of NR was enhanced in common bean, barley, and wheat plants grown under exclusion of solar UV-B (Pal et al. 2006; Moussa and Khodary 2008). The solar UV exclusion study of Kataria and Guruprasad (2015) reported that increase in NR activity in wheat varieties was because of the enhanced ATP supply *via* increase in the activity of PS II, hence it confirmed that ambient UV causes a reduction in NR activity in crop plants. Dohler et al. (1987) have also revealed that UV-B hindered activity of NR and also another key enzyme of nitrogen metabolism i.e. Nitrogenease. UV-B radiation altered the nitrogen content of leaves (He et al. 1993; Alexieva et al. 2001) and grain protein; it might also affect the crop yield as leaves are an important sources of nitrogen for growing wheat grains. Supplemental UV-B at the time of flowering and during various growth stages significantly decrease the N concentration in wheat grains (Yao et al. 2014). Thus, sUV-B affected the N nutrition assimilation capability of plants all through the flowering stage due to the reduction of NR activity (Yao and Liu 2007).

4 Antioxidant Defense System Against UV-B Stress in Wheat

Plants have enzymatic and nonenzymatic antioxidative defense systems in cellular compartments to keep minimum injury caused by UV-B radiation (Bowler et al. 1992). UV-B exposure is identified to cause the generation of reactive oxygen species (ROS) and ultimately cause oxidative stress in plants (Hideg et al. 2003; Kalbina and Strid 2006; Kataria et al. 2014). These ROS perform as signaling molecules during UV-B exposure besides function as destructive radicals (Mackerness et al. 1997, 2001; Mackerness and Jordan 1999). Wheat plants possess enhanced antioxidant defense mechanisms towards the alleviation of an oxidative stress caused by abiotic stresses, for example, drought, cold, heat, salinity, and UV-B radiation (Caverzan et al. 2016). Response of wheat plants also depends on the type of tissue, length and strength of the stress in addition to the detoxification of ROS, and its effect on the antioxidant system (Caverzan et al. 2016). UV irradiation provokes the production of ROS and oxidative stress, which have detrimental effects on macromolecules, and it can eventually cause cell death (Zu et al. 2010; Czégény et al. 2016). The nonenzymatic antioxidants like increase of phenolic substances in the vacuoles of epidermal cells decrease the penetration of UV wavelengths deep into leaves (Berli and Bottini 2013).

UV-B can stimulate the formation of lipid oxidation products, demolish the natural lipid-soluble antioxidants (Salmon et al. 1990; Jain et al. 2004), and stimulate the appearance of the genes which encode for antioxidants (Strid et al. 1994). Previously, it has been established that plant cells and tissues defend themselves against oxidative damage caused by UV-B exposure via upregulation of antioxidants like ascorbic acid (AsA) and α-tocopherol and antioxidant enzymes (Jain et al. 2004; Kataria et al. 2007).

In wheat, the main enzymatic antioxidant defense system against UV-B (ambient or enhanced) includes enzymes such as SOD (EC 1.15.1.1), catalase (CAT; EC 1.11.1.6), APX (EC1.11.1.11), guaiacol peroxidase (POD; EC 1.11.1.7), glutathione reductase (GR; EC1.6.4.2), and dehydroascorbate reductase (DHAR; EC1.8.5.1) (Tripathi et al. 2016). Under diverse abiotic stresses, changes in the ROS content and the activities of SOD, APX, CAT, GR, and POD were observed in the wheat plants under field and laboratory conditions (Wang et al. 2008; Varga et al. 2012; Mishra et al. 2013; Rao et al. 2013; Kong et al. 2014). These studies confirmed the positively activated mechanisms of ROS detoxification are present in wheat plants. In wheat plants, it is well known that aUV-B or sUV-B caused oxidative stress by the production ROS (superoxide radical, $O_2^{\bullet -}$ and hydrogen peroxide, H_2O_2) and as a defense plants have higher antioxidant enzymes activities like SOD, APX, CAT, GR, and POD (Fig. 3).

Superoxide dismutase rapidly converts $O_2^{\bullet -}$ to H_2O_2, which can then change into water and oxygen by CAT (Noctor and Foyer 1998). No uniform responses have been reported for SOD activity in response to UV-B exposure. For example, in pea

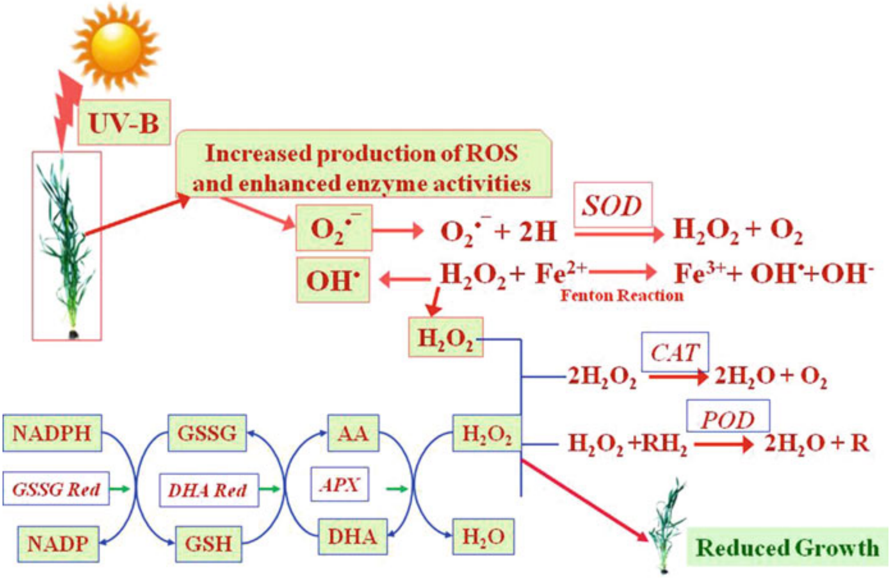

Fig. 3 Proposed scheme showing oxidative stress caused by ambient and enhanced UV-B in wheat and increased production of ROS decreased the growth of wheat plants, and as a defense, the activities of antioxidant enzymes are upregulated by UV-B

and wheat SOD activity was increased by UV-B radiation (Alexieva et al. 2001). The increment of CAT and peroxidase (POD) activities in pea plants after UV-B exposure while the increase of CAT and decrease of POD activity was observed in wheat plants also reported by Alexieva et al. (2001). Agrawal and Rathore (2007) have been reported that sUV-B increased the activity of POD and SOD, while CAT activity decreased in sUV-B exposed cultivars of wheat under field conditions. Besides SOD, APX activity was also increased simultaneously by UV-B in the six cultivars of wheat, and it was recommended that APX played an essential function in the control of endogenous H_2O_2 content (Singh et al. 2012). Zu et al. (2004) found that the contents protein and total amino acid in five cultivars of wheat were increased in response to sUV-B radiation. Li et al. (2000b) found great intraspecific variations in activity of SOD and MDA content in wheat seedlings. It was observed that seed pretreatment with H_2O_2 enhances drought and salt tolerance in wheat seedlings (He et al. 2009; Li et al. 2011). Yao et al. (2010) reported the increased activities of antioxidant enzymes (POD, SOD, and CAT) and enhanced the rate of $O_2^{\bullet -}$ production in wheat seedlings in response to sUV-B radiation. H_2O_2 signaling is the main aspect which contributes to the stress tolerance in cereals. Ibrahim et al. (2013) found that heat and UV-B irradiation alone caused a significant reduction in the photosynthetic pigments, radical scavenging activity, and superoxide radical scavenging activity in the *T. aestivum* and *T. durum* plants, but the SOD and glutathione peroxidase (GPX) were increased. According to their findings, joint effect of heat and UV-B provides cross-tolerance; or else, single stress was found to intensify the responses. The activities of SOD, POD, and APX improved under drought, UV-B, and the combination of these stresses, whereas CAT activity reduced under the combined stress as compared to the controls (Tian and Lei 2007). As a result, the combined application of drought and UV-B had drastic effects on the wheat seedlings.

Whereas on the other hand the addition of 0.2 mM sodium nitroprusside (SNP) enhanced wheat seedling growth under drought, UV-B, and combined stress, probably due to declining the accumulation of H_2O_2 and LPO as well as stimulation of the antioxidant enzymes (Tian and Lei 2007), ROS content and oxidative stress in above- and belowground parts of wheat seedlings were also reduced by selenium (Se) treatments when these seedlings were subjected to UV-B irradiation. Se contribute in alleviation of the damage of enhanced UV-B on wheat seedlings to some extent due to a significant reduction in malondialdehyde (MDA) content and the production of $O_2^{\bullet -}$ (Yao et al. 2010, 2011). He et al. (2011) studied the enhancement in H_2O_2 in the treated (drought or UV-B) wheat plants as compared to the controls, and the induction was more evident in the UV-B-treated plants as compared to drought-stressed plants; consequently UV-B caused severe damage on wheat seedlings than the drought stress. Activity of the two important antioxidant enzymes like SOD and CAT increased following all the treatments compared to the control plants which was also observed in the study of He et al. (2011); however their patterns of expression were found to be different in various genotypes of wheat and the distinct stress conditions. According to He et al. (2011), the combined application of drought and UV-B together brought out detrimental effects on vulnerable variety of wheat seedlings; however more positive effects were observed in the resistant wheat genotypes.

Tripathi et al. (2016) found that aUV-B and sUV-B radiation produce harmful effect on growth of wheat (*T. aestivum*) seedlings, along with reduced photosynthetic performance and enhanced levels of $O_2^{\bullet -}$ and H_2O_2. Activities of SOD and APX were decreased by UV-B, whereas CAT and POD and antioxidants were enhanced by UV-B (Tripathi et al. 2016). The activity of SOD, APX, POD, and GR were higher in wheat plants grown under ambient UV as compared to the plants grown under UV excluded conditions (Kanungo et al. 2013). Hence, the production of ROS was observed under UV-B stress in wheat seedlings consequently an increase in antioxidant defensive mechanisms mitigates the UV-B induced damage by quenching of toxic radicals. Ou et al. (2018) established that when the intensity of UV-B was enhanced, content of flavonoids in wheat mesophyll cells increased, and with the prolonging of the treatment time of wheat, the content of flavonoids in wheat leaves at the jointing-booting stage was significantly higher than that in seedling stage and panicle stage. Similarly, UV-B-absorbing substances under aUV-B were also higher when compared to UV-B excluded conditions in wheat seedlings (Kataria and Guruprasad 2015).

5 UV-B and Wheat Yield

For overall development and production of wheat crop along with UV-B, the other factor like environmental conditions, growing conditions, stage of growth, length, and the proportion of amount photosynthetic photon flux (PPF) to UV-B also accounts (Teramura et al. 1991). Further, it has been reported that the exposure to enhanced and ambient UV-B radiation affects physiological and biochemical processes in vegetables and crop plants. The decrease in photosynthetic rate and nitrogen uptake in the presence of UV-B affects plant biomass, average grain size, and grain-N content (Kataria and Guruprasad 2012, 2015; Kataria et al. 2013; Sharma et al. 2018). Contradictory results were reported in the relevant literature of effect of enhanced UV-B on the yield of wheat grains. Most of the studies showed significant reductions in grain yield (Li et al. 1998, 2000a; Zheng et al. 2003), while others observed very slight effect on the grain yield (Teramura et al. 1990; Hakala et al. 2002). Similar to wheat, divergent results have been reported in other small grain cereals like rice, barley, and oat (Mazza et al. 1999; Hakala et al. 2002; Kakani et al. 2003; Hidema and Kumagai 2006).

Li et al. (1998, 2000a) found that when supplemental UV-B was given at wheat crop growth phase of three-leaf stage to ripening stage, then a 50% decrease was observed in number of grains and 30% decrease was found in weight of 1000 grains. In some studies, biomass was unaffected by UV-B exposure because of adaptive biochemical responses concerned with UV-B acclimation of plants to defend them from this damaging radiation. These adaptive biochemical responses involve an increases in antioxidant substances like anthocyanins and phenolic sunscreens (Becwar et al. 1982; Tosserams et al. 1996; Day et al. 1999) and increase of free and bound phenolic substances like flavonoids and hydroxycinnamic acid in leaf epidermis (Sullivan et al. 1992; Visser et al. 1997).

Al-Oudat et al. (1998) found decreased weight of the spikes and grains of wheat plants which revealed an alteration in allocation of photosynthates by UV-B irradiation. Li et al. (1998, 2000a) observed that biomass and yield of wheat grains were decreased by 18 and 57% when UV-B radiation was enhanced by 2.5 and 5.3 kJ/m^2 higher than the ambient level of UV-B. Yue et al. (1998) reported the reduced assimilate allocation to grains due to enhanced UV-B in spring wheat. Calderini et al. (2008) reported sensitivity of wheat to UV-B at various phonological phases. They found that the penetration of UV-B may be more effectual in decreasing grain yield in wheat plants when plants were exposed to UV-B irradiation between anthesis and the end of grain filling stages. Lizana et al. (2009) found that increased UV-B radiation at the three-leaf stage to booting stage of wheat plants and then the aboveground biomass and grain yield were decreased by 11–19 and 12–20%, respectively. Yao et al. (2014) found that enhanced UV-B significantly reduced yield of winter wheat throughout the growth phases, i.e., since seedling to grain filling stage was owing to the severe effects of UV-B during the heading and flowering stages. In contrast, UV-B exclusion studies also showed that aUV-B reduced the yield of wheat in terms of number and weight of ears/grains, (Kataria and Guruprasad 2012; Kataria et al. 2013).

6 Sensitivity and Tolerance to UV-B in Wheat Varieties

Wheat crop is prone to oxidative stress as the UV radiation has ionization potential to ROS; however, the extent of damage depends on the genotypes with varied level of sensitivity and tolerance (Kataria and Guruprasad 2012, 2015). Although the varied level of response toward UV-B radiation may exist in plant species and genotypes, the regulation of intraspecific responses and the factors involved in it is remaining fully unexplained. However, UV-B causes disturbance in plant hormones, such as photooxidative damage to the IAA which affects the cell wall extensibility (Jansen et al. 2001) moreover, UV-B activates H_2O_2 enzymes, thus causing decreased in IAA contents (Lin et al. 2002) further increase in level of ethylene, a promoting factor of radial growth and ABA hormone modulates the plant growth (Predieri et al. 1993; Caldwell et al. 1995; Yang et al. 2004). Moreover, in Chinese wheat cultivars, UV-B altered the endogenous hormones like it decrease the IAA content, which in turn reduces the growth and biomass accumulation of wheat (Li et al. 2010) and it also increases the ABA content in some cultivars of wheat, which subsequently decrease the growth and gas exchange ability of the stomata (Yang et al. 2000; Li et al. 2010). Effect on wheat varieties to increased UV-B radiation and the intraspecific variation among 20 wheat (*T. aestivum*) cultivars were observed (Li et al. 2000a), and the sensitivity was evaluated by parameters like wheat growth and grain yield. Generally it is assumed that crop cultivars developed near the equator are more resistant to UV-B radiation; since aUV-B radiation is high at lower latitude as compared to higher latitudes. Response or sensitive indexes were ascertained as main markers for the sensitivity of plants to enhance and aUV-B radiation (Dai et al. 1994; Kataria and Guruprasad 2012). Li et al. (2000a) found that out of seven tolerant cultivars, five cultivars originated from South China (low latitude). The most sensitive cultivars, i.e., Huining 18 (RI 231.91) and Longchun 16 (RI 224.23), belongs to North China (high latitude). In addition, Li et al. (1998) found that exposure to UV-B radiation resulted in shortened internode length resulting in a short height of spring wheat (Lanzhou 80101). Further, interspecific and intraspecific variations in sensitivity toward sUV-B in wheat (*Triticum aestivum* L.cv. HD 2329 and HUW 234) and mung bean (*Vigna radiata* L. cv. Malviya Jyoti and Malviya Janpriya) was studied in detail (Agrawal and Rathore 2007). The order of sensitivity among cultivars to sUV-B was Malviya Janpriya < Malviya Jyoti < HD2329 < HUW 234 (Agrawal and Rathore 2007).

The intraspecific variations in wheat responses to UV-B radiations have been studied extensively; however the majority of studies were on the effect of enhanced UV-B radiation with supplementation of UV-B specifically on the morphological, physiological, and biochemical aspects of wheat (Li et al. 1998, 2000a, b, 2010) and very few studies on the aUV-B (Kataria and Guruprasad 2012, 2015). Intraspecific variations were also observed in sensitivity toward UV-B in wheat, which were known to be related to the differences in the growth, biomass, photosynthesis, yield, antioxidant defense, and UV-B-absorbing substances in the leaves (Li et al. 2000a, b, 2010; Agrawal and Rathore 2007; Kataria and Guruprasad 2012, 2015). However, it is important to perform a more realistic assessment for studying the UV radiations on wheat growth and production. Ambient UV exclusion in field conditions helps in determining interspecific and intraspecific variations in the more practical way. In exclusion studies, the UV-B (280–315 nm) and UV-B + A (280–400 nm) were removed by specific UV cutoff filters to evaluate the ambient UV-B effects in field conditions (Kataria and Guruprasad 2012, 2013; Sharma et al. 2018).

Intraspecific variation studies with UV exclusion have been carried out on different crops. The detailed study on four Indian wheat varieties (Vidisha, Purna, Swarna, and Naveen Chandausi) was conducted to study the intraspecific variations and sensitivity to aUV-B in wheat varieties of central India (Kataria and Guruprasad 2012, 2015). Exclusion of UV resulted in considerable increase in plant height, number of tillers, area of flag leaf, biomass accumulation, and also the yield attributes such as grain number and yield of grain in different Central Indian varieties of wheat. Among the four tested varieties, Purna was found to be the most susceptible and Naveen Chandausi the least susceptible variety of wheat to aUV-B (Kataria and Guruprasad 2012). Apart from the morphological parameters, the photosynthetic performance was also evaluated in these varieties, an enhancement in the activities of enzymes like CA; Rubisco and NR were observed in all the varieties after UV exclusion, which contributes in the enhancement in grain yield production in different varieties of wheat (Kataria et al. 2013; Kataria and Guruprasad 2015).

7 Conclusions

Global change will certainly bring the alteration in agricultural ecosystems that will change the productivity of the plants. The depletion of the stratospheric ozone layer by man-made pollution has drastically enhanced the UV-B invade on the surface of earth. As UV-B radiation has harmful effects on growth of plants, it causes various damages such as DNA and membrane injuries and disorders in photosynthetic and hormone systems in the wheat crop plants. aUV-B and sUV-B reduced the growth of root, shoot, and leaf and decreased the photosynthetic efficiency which ultimately reduced the grain yield and quality of wheat (Fig. 2). It was found that sensitivity of wheat showed great intraspecific variations in response to UV-B radiation. Supplemental UV-B exposures drastically reduced the yield of grains and productivity of wheat crop when it was given at the time of heading, flowering, and complete stages of wheat growth. Thus, to better protect wheat crop from the drastic effects of UV-B, some methods must be explored for the duration of the heading and flowering stages. Several methods for adaptation in wheat plants to UV-B radiation have been explored; research studies revealed that plants possess numerous repair and defense strategies to defend themselves from the damaging effects of UV-B. The most important mechanisms are an enhancement of UV-B-absorbing pigments such as flavonoids and phenolics, by which wheat plants lessen the detrimental effects of UV-B. However, the prediction of increased UV-B radiation may perhaps have a major impact on the productivity of wheat crop worldwide. The perception that UV-B radiations generate the production of new substances, the enhancement in antioxidants (AsA,GSH) and activity of antioxidant enzymes (SOD, POD, APX, GR) or the increase in flavonoids and phenolic compounds in response to UV-B (Fig. 3) and it can be used for improvement of food quality.

In spite of a large number of studies in the laboratory and glasshouse conditions and the variety of responses of wheat crop when exposed to UV-B radiation, the understanding of the intricate connections among UV-B and wheat will always be inadequate by failure to mimic the natural environmental conditions. However, UV exclusion field studies have unlocked a new possibility of research to increase the crop production by protecting the plants from harmful effects of solar UV-B even in the present level. In the absence of solar UV-B components, the wheat plants also have the potential of increased fixation of atmospheric carbon dioxide that can decrease the global warming. UV exclusion studies on wheat showed the better assessment of the adaptability of the varieties to aUV-B received at a particular latitude, and it also helps in the assortment of the best-suited variety for the given latitude. Crops are growing near to the equator region or lower latitude considered as more tolerant than the crops that at higher latitude. In the present scenarios of global environmental changes, UV-B-tolerant species identified by the response index can be further selected as a potential donor for genetic breeding programs. The resistant breed will be having higher grain yield potential and ability to withstand under enhanced UV-B radiation and will help in better agronomic management practices. Importance of genetic breeding is emphasized, as a multidisciplinary activity, which has an important role in obtaining varieties more suitable to the constraints associated with the environment, as well as any changes due to climate change. Thus genetic breeding is the way to improve wheat production in the new scenarios of consequences of global environmental changes.

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Tropospheric Ozone and Its Impact on Wheat Productivity

Richa Rai

Contents

Abstract Tropospheric O_3 is considered as the most widespread secondary pollutant and one of the components of global climate change. Agriculture plays a very important role in human welfare. O_3 has been recognized as a prime threat to agricultural production. The projected levels to which O_3 will increase are critically alarming and have become a major cause of concern for global food production. Impact of tropospheric O_3 on wheat production has been widely studied. Wheat is identified as sensitive to O_3. It enters into the plant through the stomata, affecting directly cell membranes, generating O_3-induced ROS, and up- or downregulating ROS signaling molecule-associated genes, genes, proteins, and metabolites which ultimately affects growth and yield of wheat. The objectives of the chapter are to present an overview picture on the effect of O_3 on wheat productivity and to summarize the vast number of available reports on the impact of O_3 on wheat physiology and morphology, its defense and variation in allocation pattern of photosynthates, and its yield and quality.

Keywords Tropospheric O_3 · Abiotic stress · Wheat · ROS · Physiology · Growth and yield

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1 Introduction

The environment within which crops and agronomic practices developed over the past 10,000 years is rapidly changing due to human-induced climate change (IPCC 2014). Increasing food demand for a growing world population combined with changing environmental patterns causes concern about the future availability of food which include climate change and air pollution.

The tremendous increase in pollutant concentrations is one of the major environmental problems. The major anthropogenic activities responsible for intensifying air pollution problem are industrialization and urbanization. Earlier attention on air pollution was more focused on fossil fuel burning and its associated gas, sulfur dioxide (SO_2), emitted from both domestic and industrial sources. Subsequently, the concern shifted away from these pollutant sources to vehicular emission, which is tremendously rising. The main pollutants emitted from vehicular exhaust are oxides of nitrogen (NOx). During the past few decades, the issue of tropospheric ozone (O_3) as an air pollutant has been intensified several folds and assumed to be a global concern (Mauzerall and Wang 2001). Ozone is a secondary pollutant which is not emitted directly by any specific source but formed due to atmospheric photochemical reactions which involves oxides of nitrogen and reactive hydrocarbons emitted from automobiles (Krupa and Manning 1988). These reactions are principally controlled by sunlight and temperature. Even increased emissions of reactive hydrocarbons and nitrogen oxides in urban areas have significantly increased the ground-level O_3 concentrations in rural areas (Rai et al. 2007).

Among air pollutants, ozone is the most important because of the widespread occurrence of this secondary pollutant and its known risk for effects on vegetation and human health. Current levels in surface air are often sufficiently high to reduce yields of major staple crops such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), corn (*Zea mays*), and potato (*Solanum tuberosum*), which is a priority issue for food-insecure regions (Ashmore 2005; Ashmore et al. 2006). Wheat is the third largest crop in the world with over 760 million tonnes produced globally per year (FAO 2015). Unfavorable climatic conditions reduced wheat yield in Europe by 4.4% in 2016 compared to 2015 (Eurostat 2017). The present chapter deals with the impact of tropospheric O_3 influencing the growth, yield, and metabolic machinery of wheat.

2 Past, Present, and Future Trends of Tropospheric O_3

2.1 *Background Level of Ozone*

The existence of a background level of O_3 in the atmosphere is well established, and its sources are natural and anthropogenic such as:

1. Downwind transport of stratospheric O_3 through the free troposphere to near ground level.

2. O_3 production from methane emitted from swamps and wetlands reacting with natural NOx (from soils, lightning strikes, and downwind transport of nitric oxides (NO) from the stratosphere).
3. Formation of O_3 from reactions of biogenic VOCs with natural NOx.
4. Long-range transport of O_3 from distant pollutant sources.

2.2 Tropospheric O_3 Formation Due to Anthropogenic Component

Ozone is formed in the planetary boundary layer (PBL), the free troposphere, and the stratosphere. In the stratosphere, O_3 is produced mainly due to photolysis of O_2 by ultraviolet radiation into atomic oxygen to form O_3. However, in the troposphere, O_3 formation occurs due to photolysis of NO_2. In the free troposphere, O_3 formation depends on the reaction of methane, CO, and non-methane organic compounds with NOx (Fig. 1). Ozone in the PBL is not emitted as such by any source but has its origin in reactions between the nitrogen and oxygen of the atmosphere at high

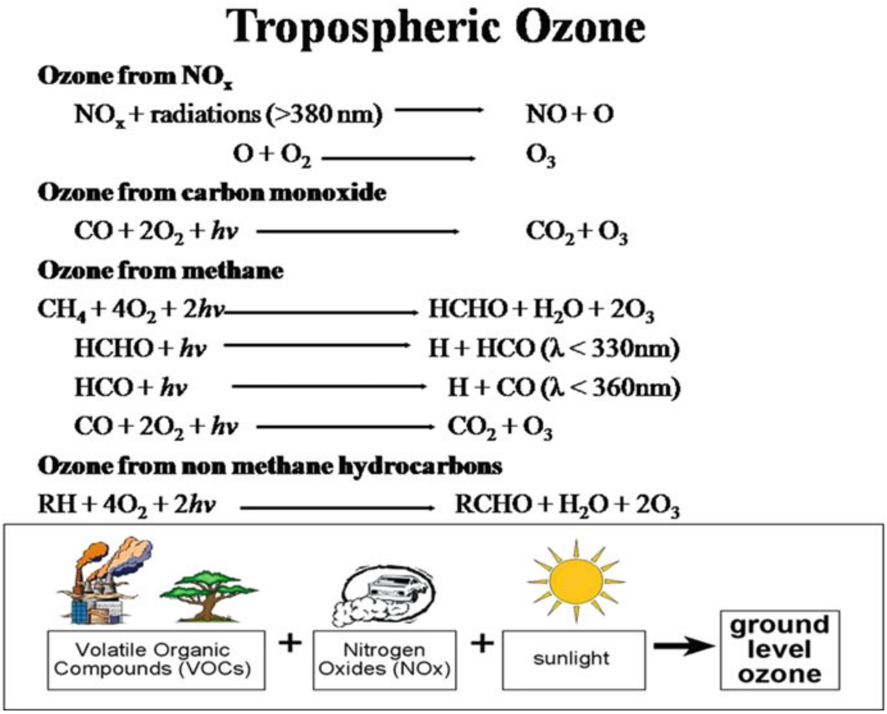


Fig. 1 Chemical reactions showing tropospheric O_3 formation

temperature to form NO, which in turn undergoes chemical transformations in the presence of automobile exhaust to produce O_3 and other oxidants.

HCs

$$2NO + ½\ O_2 \rightarrow 2NO_2$$

Nitrogen dioxide is highly reactive photochemically for the radiations below 380 nm, and the gas dissociates according to the reaction.

$$NO_2 + h\nu \rightarrow NO + O$$

This is one of the most important photochemical reactions in the PBL since this produces the highly active monoatomic oxygen, which on reaction with molecular oxygen produces $O_{3.}$

$$O + O_2 \rightarrow O_3$$

Such reactions may be responsible for elevating the level of O_3 in metropolitan areas during sunny periods; nitrogen dioxide diminishes as O_3 reaches the peak. Highest peaks of ozone concentration are observed during the late morning and early afternoon hours.

In the ambient air, O_3 precursors play an important role during long-range transport, downwind from the sources. Polluted air masses from urban and industrial areas can affect suburban and rural areas. Elevated concentrations of O_3 in urban areas are generally confined to 4- to 6-hour period within a day which represents only 15–25% of the 24-hour cycle; due to this O_3 data are reported in terms of highest 1-hour concentration.

2.3 Trends of O_3 Concentration Across the Globe

Current background O_3 levels have risen by approximately two times from the late nineteenth to early twentieth centuries (Stevenson 2001). Photolytic reactions in the polluted atmosphere are the major sources of phytotoxic levels of ozone. Motor vehicles, space heating, power plants, and industrial processes are major sources of oxidant precursors. Peroxy radicals produced by photochemical degradation of hydrocarbons convert nitric oxide to nitrogen dioxide, which favors more O_3 production during daylight. At night, emissions of nitric oxide into the atmosphere serve as a sink for ozone. The global rise in methane levels has played a major role in the increase in tropospheric ozone (Finlayson-Pitts and Pitts 2000). Fusco and Logan (2003) modeling study suggested that the rise in CH4 levels is responsible for roughly one fifth of the anthropogenically induced increase in tropospheric O_3 at northern mid-latitudes and to a global increase of 3–4% over the past century

Tropospheric O_3 concentrations are persistently increasing worldwide (Mittal et al. 2007; Rai and Agrawal 2012). Concentrations of background O_3 in the mid-latitudes of Northern Hemisphere doubled to about 30–35 ppb and further increased by another 5 ppb reaching up to 35–40 ppb between the late nineteenth century and 1980 (The Royal Society 2008). The peak values of O_3 continued to exceed the WHO guideline value of 50 ppb in many countries, including Latin America, North America, Europe, and Africa (WHO 2006). During the smog episodes in Southern California in the 1960s, even higher levels up to 400 ppb were observed (The Royal Society 2008). In the Southern Hemisphere, an increase of 30 ppb was reported in South America and Africa (Zeng et al. 2008). Springtime ozone increased at the rate of 0.46 ppb year^{-1} during 1985–2007 over the western coastal USA (Cooper et al. 2010). In rural agricultural areas of the USA, the mean O_3 concentration was reported between 50 and 60 ppb. Jaffe and Ray (2007) reported a significant increase in O_3 at a rate of 0.26 ppb year^{-1} at seven rural monitoring sites in the Western USA between the years 1987 and 2004.

Reports have shown reductions in emissions of anthropogenic O_3 precursors but increase in background O_3 in the lower European troposphere (Chevalier et al. 2007). The report published by Royal Society (2008) showed that background O_3 concentrations in Europe are still rising and predicted to rise till 2030 due to the hemispheric transport of O_3 precursors from developing areas of the world. All countries of Europe are experiencing periodic O_3 episode each year with several days of peak O_3 concentrations exceeding 50 ppb and sometimes exceeding 90 ppb (Hayes et al. 2007). Monks (2005) pooled monitoring data as well as modeling studies along the whole of Europe and showed that European emissions of O_3 and its precursors had decreased over the past three decades with larger reductions in Russia. Saitanis et al. (2015) reported frequent exceedance of hourly O_3 concentrations above 70 ppb at Tripolis plateau located in Greece. The highest 1 h O_3 concentration of 240 ppb was observed in France (Pellegrini et al. 2011). From 1987 to 2003, mean O_3 concentration measured increased by 0.49 ppb year^{-1} (Simmonds et al. 2004) and by 0.31 ppb year^{-1} at an Atlantic coastal station (Mace Head) in Ireland from 1987 to 2007 (Derwent et al. 2007). An average increase of 0.14 ppb year^{-1} in O_3 concentration was reported from 13 rural sites in the UK over the period 1990–2006 (Jenkin 2008).

Tienhoven et al. (2006) in modeling study conducted showed that maximum hourly O_3 concentration over 50 ppb is common over central Zimbabwe. Emberson et al. (2009) reported that large parts of South Asia experience up to 50–90 ppb mean 7 h (M 7) O_3 concentration. Results of monitoring studies in several parts of the Asian continent suggested that mean monthly O_3 concentration of 50 ppb occurs frequently during growing period of important crops (EANET 2006; Xu et al. 2008). Concentrations of O_3 varied from 71 ppb in Pakistan (Wahid 2006), 41.7 ppb in China (Pang et al. 2009), and 49.5 ppb in India (Tripathi and Agrawal 2012).

Wang et al. (2009) monitored the variations in O_3 concentrations from 1994 to 2007 at a costal site in Hong Kong and reported a 0.87 ppb year^{-1} increase by comparing mean values of O_3 concentration during 1994–2000 and 2001–2007. In the last two decades, fast industrialization and urbanization have increased O_3

concentration at a higher rate in China than other countries, and the mean of the daily 24 h average O_3 concentration reached more than 50 ppb during the crop growing season in some regions (Zhao et al. 2009; Tang et al. 2013). The daily mean and hourly peak O_3 concentrations recorded at urban and suburban regions in Beijing (China) were 46 and 67 ppb and 181 and 209 ppb, respectively, during May to September in 2010 (Wan et al. 2013). Xu et al. (2008) observed a decrease in the average concentration, but an increase in the daily variations in diurnal O_3 concentration in the Yangtze delta region of China.

Dey et al. (2014) studied O_3 concentrations and reported O_3 concentrations as high as 66.8 ppb at Durgapur, West Bengal, from February 2013 to May 2013. Ganguly (2012) analyzed O_3 concentrations between 1998 and 2008 at five O_3 monitoring stations, namely, New Delhi, Nagpur, Pune, Kodaikanal, and Thiruvananthapuram, stretching across the country. During the study period, the surface O_3 levels at Pune and Thiruvananthapuram indicated a small decreasing trend, while at New Delhi, Nagpur, and Kodaikanal, an increasing trend was observed. From urban and rural sites of Maharashtra, a similar trend of O_3 concentrations was recorded (Debaje and Kakade 2008). Roy et al. (2009) using Regional Chemistry Transport Model (REMO-CTM) monitored high AOT40 values, between November and May, that exceeded the threshold set by WHO for crops (3 ppmh for 3 months).

The average monthly O_3 concentration in India was found to exceed frequently the National Ambient Air Quality Standards of O_3 (NAAQS) as set by the Central Pollution Control Board (CPCB), New Delhi. O_3 monitoring studies conducted at a suburban site in Varanasi 2002 to 2006 were reported by Tiwari et al. (2008), and Gaur et al. (2014) recorded O_3 concentrations at an urban site in Kanpur from 2009 to 2013 which clearly showed significant seasonal and diurnal variations in O_3 concentrations. Seasonal O_3 concentration trend at Varanasi monitoring site showed highest concentrations during summer season followed by winter season and minimum at rainy season during 2002–2006 (Tiwari et al. 2008). Monthly O_3 concentration reported during summer time ranged from 55.21 ppb to 62.2 ppb (Singh et al. 2014; Sarkar et al. 2015) and in the winter season, ranged from 32.33 ppb to 53.2 ppb (Mishra et al. 2013). The rise in O_3 concentrations during summer season can be attributed to its linear relationship with high solar radiation, which directly influences the chemical kinetic rates and mechanism for O_3 production (Pudasainee et al. 2006). The dependence of O_3 concentrations on solar radiations is evident by the positive correlation between the temperature and sunlight (Tiwari et al. 2008).

Various modeling studies have shown O_3 concentration may increase in the future. Dentener et al. (2006) predicted that future surface O_3 may show a decrease of 2 ppb in cleaner areas or an increase of 4 ppb in polluted areas between 2000 and 2030 under current emission rates and legislation scenarios. Global chemical transport models were employed for understanding global future tropospheric O_3 concentrations using future climate and meteorological scenarios and estimates of future emission. Dentener et al. (2006) modeled variations in surface O_3 concentration between 2000 and 2030 using 26 global atmospheric chemistry models under

3 different emission scenarios, viz., CLE scenario (reflects implementation of current air quality legislation), MRC scenario (represents the maximum emission reduction of O_3 precursors), and an intermediate IPCC SRES A2 scenario. By 2030, global O_3 concentration is expected to increase by 1.5 ± 1.2 ppb under CLE scenario and 4.3 ± 2.2 ppb under A2 scenario by 2030 (Dentener et al. 2006). Asian regions are predicted to experience a maximum increase in surface O_3 while a moderate increase in Europe and North America (Dentener et al. 2006). Wilkinson et al. (2012) reported that the background O_3 concentration is further expected to increase at an annual rate of 0.3 ppb year^{-1}. Meehl et al. (2007) have estimated an increase of 20–25% O_3 concentrations by 2050 and 40–60% by 2100. Sicard et al. (2013) reported that changes in surface O_3 by 2100 worldwide range from about 4 to 5 ppb according to the climate model RCP8.5 scenario.

3 Effect of O_3 on Plant Vital Processes

3.1 Ozone Uptake

The reaction of a plant depends on the ambient exposure, the amount of O_3 uptake into the leaves, and the plants' autonomous and environmentally induced resistance (Fig. 2). The open stomata provide the principal route for the entry of O_3 into leaf tissues. Unlike acidic gases and heavy metals, which are absorbed both by the aboveground plant parts and the roots following deposition into the soil, uptake of O_3 is limited essentially to the chlorophyll-containing organs; thus particularly all the absorption occurs within the leaves. Factors that influence stomatal aperture also affect plant response to O_3. The flux of O_3 from the troposphere into the plant depends on different resistances at various levels, i.e., an aerodynamic resistance depending on atmospheric turbulence, a boundary layer resistance caused by the layer of laminar air adjacent to the leaf, the stomatal resistance exerted by the stomatal pores, and an internal resistance in the mesophyll cell of leaves (Guderian et al. 1985). In addition, the boundary layer and stomatal resistance are also important factors that influence O_3 uptake, and also the leaf boundary layer resistance (Rb) also plays an important role. Boundary layer resistance is a function of leaf morphology (size, shape, epidermal characteristics, trichomes, etc.), orientation, and wind speed as at low wind speed, as in exposure chambers, the boundary layer resistance can be appreciable and thus influencing O_3 uptake. High O_3 concentration occurs in spring and summer under atmospheric conditions of high temperature, high irradiance, and low wind speed. Under these conditions, boundary layer and stomatal resistances are (generally) high and thus injury symptoms.

The O_3 flux-based approach is used as an indicator of O_3 damage in Europe (UNECE 2004). Altimir et al. (2006) found 10% less uptake of O_3 in darkened leaves in which stomata were closed than that of recorded in illuminated leaves. The impact of O_3 on plants depends on both the concentration of O_3 and its rate of O_3 uptake by plants (Mills et al. 2011). When stomatal conductance is high, it leads

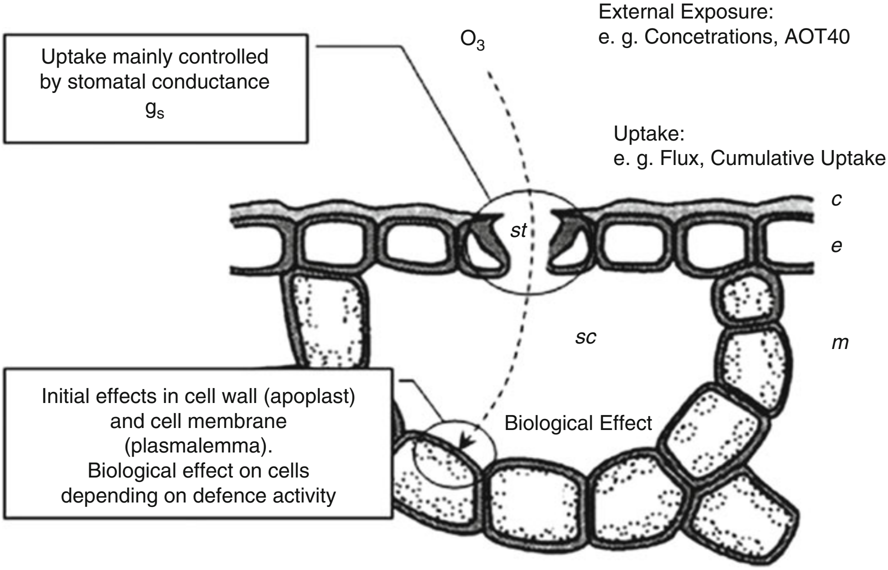


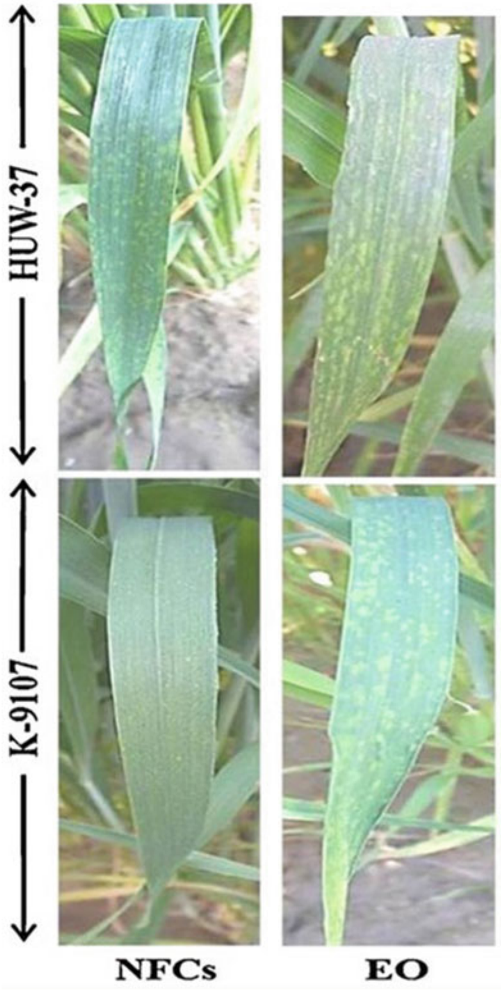
Fig. 2 Schematic presentation of O_3 uptake and biological effect on leaves. st denotes stomata; sc, substomatal cavity; c, cuticle; e, epidermis; m, mesophyll; and g_s, stomatal conductance (Modified from Fuhrer and Booker 2003)

to strong inflow of O_3 inside the leaf which saturates the scavenging potential of the antioxidative defense system of plants (Caregnato et al. 2013). On the basis of known stomatal flux, it is possible to calculate the O_3 dose, which is summation of stomatal flux of stomatal O_3 fluxes (Mills et al. 2011). However in the present scenario, O_3 flux is not considered a suitable damage index as it does not include the detoxification component of plants (Gerosa et al. 2015). UN/ECE scientific community has introduced the term “phytotoxical ozone dose” (POD_1), which is the cumulative O_3 dose over a threshold of 1 nmol O_3 m^{-2} s^{-1} (Mills et al. 2011), and it considers the capacity of the plants to detoxify part of O_3 entering through the stomata.

3.2 Visible Injury

The first incident of photochemical smog injury to vegetation was reported by Middleton (1956). Visible injury from O_3 is normally confined almost extensively to the green foliage of plants, but in few cases, it is found inducing rind discoloration and corkiness of skin on some fruits. A wide variety of visible injury symptoms on wheat foliage are associated with exposure to O_3 depending on the duration of O_3 exposure and maximum concentration during exposure.

Fig. 3 Tropospheric O_3-induced injury in Indian wheat cultivars grown in ambient (NFCs) and elevated O_3 (EO) chambers. (Modified from Mishra et al. 2013)



Chronic symptoms appear due to frequent, relatively low hourly O_3 concentrations and periodic, intermittent peaks of relatively high hourly concentrations. Chronic effects can lead to changes in plant growth, productivity, and quality, and these effects may occur without visible symptoms (Agrawal et al. 2003, 2006). Symptoms develop in the form of chlorosis in wheat leaves, delayed early season growth, premature senescence, and leaf abscission. Pigmentation results in small dot-like lesions or flecks on the upper surface of the leaf (Fig. 3). In chronic injury symptoms, only the palisade cells are injured; the epidermis above the injured palisade parenchyma usually remains uninjured. With repeated exposures, the injured areas may collapse giving the leaf a mottle appearance. On species such as grasses, the injury may occur on either surface, because they lack a well-differentiated mesophyll tissue. Short-term acute exposures destroy the mesophyll tissue between upper and lower epidermis resulting into the bifacial necrosis.

3.3 *ROS Generation and Defense Mechanism*

The main route for O_3 entry into the leaves is through the stomata, which is principally regulated by stomatal conductance (Ainsworth et al. 2012). After its entry into the substomatal chamber, O_3 does not persist in the apoplast for long and immediately breaks down or reacts with the compounds present in cell wall or apoplastic fluid to generate ROS such as superoxide radicals ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^{\bullet}$). Staining by $CeCl_3$ revealed that extracellular H_2O_2 accumulation was one of the earliest detectable responses to O_3 in poplar leaves subjected to 150 ppb O_3 after 1 h exposure (Diara et al. 2005) (Fig. 4). Fatima et al. (2018) also showed localization of O_3-induced H_2O_2 by DAB staining in wheat cultivar.

Among the ROS, $OH^{\bullet}$ radical is the most reactive of oxygen species causing serious damages. The ROS produced act as an early messenger molecules in signaling cascades hence switching on the downstream signaling and also induce

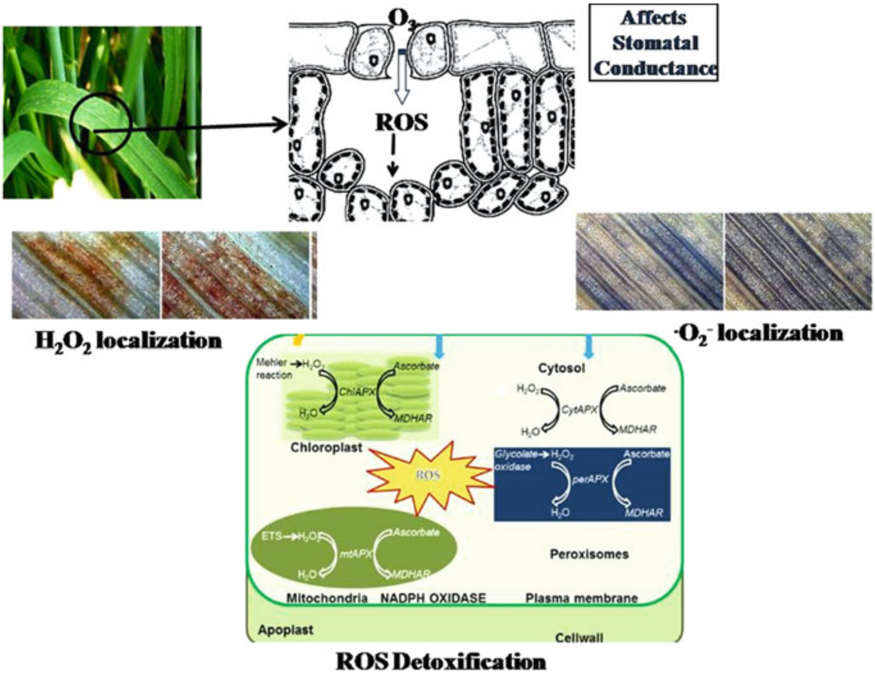


Fig. 4 Diagrammatic presentation of O_3-induced ROS production, localization, and detoxification in wheat leaves. (Modified from Fatima et al. 2018)

defense reactions in apoplast (Vainonen and Kangasjarvi 2014). These signaling molecules are ethylene (ET), salicylic acid (SA), jasmonic acid (JA), and MAP kinase (Matyssek et al. 2008). Ozone is also known to induce Ca^{2+} influx within few seconds, which is required for the activation of MAP kinase and NADPH oxidase, and activated MAP kinase cascade is involved in the upregulation of ET synthesis. In addition to ET, biosynthesis of SA is also induced, which along with ET is required for the development of foliar injury or O_3-induced lesions (Vainonen and Kangasjarvi 2014). Ethylene and NADPH oxidase spread the signal of oxidative burst from the site of lesion initiation to the surrounding cells and lead to cell death. When the cell death occurs, products of lipid peroxidation serve as the substrate for synthesis of JA, which acts antagonistically and to ET and reduces ET-dependent lesion production and hence the spread of cell death (Vainonen and Kangasjarvi 2014). ROS also mediate the abscisic acid (ABA)-induced stomatal closure response.

Ozone-induced lipid peroxidation may also increase production of ROS including. $O_2^{\bullet -}$ and H_2O_2 (Mishra and Agrawal 2015). With respect to photosynthetic apparatus of plants growing under O_3 stress, dysfunctioning of membrane permeability in chloroplast has an adverse effect upon membrane-bound reaction centers in electron transport chain, inactivating the rate of photosynthesis and activating respiration (Foyer and Noctor 2011). Increments in lipid peroxidation upon increased ROS production have been reported in wheat (Rai and Agrawal 2008; Mishra et al. 2013; Fatima et al. 2018). Ozone is known to initiate the expression of lipoxygenase, which targets the lipid ester fraction of biological membranes and plays an important role in determining the O_3 sensitivity of plants (Francini et al. 2007). Lipid peroxidation is measured in terms of malonaldehyde (MDA) content and has been correlated with the degree of injury to the membrane under O_3 exposure (Ranieri et al. 1996). Malonaldehyde is the end product of ROS-induced oxidation of polyunsaturated fatty acids; therefore it is frequently used as a biomarker of oxidative stress (Bhattacharjee 2015). Excess ROS production under O_3 stress hinders the natural potential of specific cell wall components to scavenge the overproduced ROS, leading to damage to the plasma membrane. According to Heath (2008), the peroxidation of lipid components results in solute leakage due to alteration in membrane permeability. Liu et al. (2015) studied the response of wheat to elevated O_3 and observed that MDA content increased by 314.3% and 65% at jointing and heading stages when treated with 120 ppb (4 hd^{-1}) O_3. Rai et al. (2007) reported differential response in wheat cultivars; sensitive M 234 showed higher increase in MDA content (47.4%) at mean O_3 concentration of 41 ppb (Rai et al. 2007) as compared to the increments in comparatively resistant cultivars PBW 343 (34.6%) and M 533 (4.5%) grown at mean O_3 concentration of 53 ppb (Rai and Agrawal 2014), suggesting more lipid peroxidation in sensitive wheat cultivars. Sarkar et al. (2010) observed that lipid peroxidation increased by 24% and 41.4% in wheat cultivars Sonalika and by 44.4% and 51.1% in HUW 510 at mean O_3 concentrations of 50.4 and 54.9 ppb, respectively.

The stress condition generated by O_3 results in an oxidative burst due to enhanced production of ROS, which causes negative effects on cellular components leading to damage to the lipids (peroxidation of unsaturated fatty acids in the membrane), proteins (denaturation), carbohydrates, and nucleic acids (Blokhina et al. 2003). To counteract the stress imposed by ROS, an array of antioxidant molecules are induced (Ashmore 2005; Caregnato et al. 2013) via nonenzymatic antioxidants such as ascorbic acid (AA), flavonoids, phenolics, vitamin E (tocopherol), peptides (glutathiones), carotenoids, polyamines, and organic buffering systems or through enzymatic antioxidants (Blokhina et al. 2003), viz., superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), catalase (CAT), and various types of peroxidases (POD) (Caregnato et al. 2013; Fig. 4).

Among the nonenzymatic antioxidants, AA protects critical macromolecules from oxidative damage by directly reacting with $O_2^{\bullet -}$ and H_2O_2, regenerating α-tocopherol from tocopheroxyl, and removing H_2O_2 via AA-GSH cycle. Increases in AA pool have been observed in wheat cultivars (Singh et al. 2010; Yan et al. 2010; Rai and Agrawal 2014). Rai et al. (2007) reported 11.2% increase in AA content in wheat leaves under ambient O_3 pollution. Increments in the mean value of AA by 40% in 20 wheat cultivars grown in chambers receiving 82 ppb O_3 for 7 h day^{-1} have been reported by Biswas et al. (2008a). The level of total apoplastic AA correlates directly with O_3 tolerance in many plant species (Castagna and Ranieri 2009). Feng et al. (2010) reported that apoplastic ascorbate contributes toward differential response of tolerant cultivar (Y 16) which showed higher ascorbate concentration than sensitive cultivar (Y 2) of wheat exposed to elevated $O_{3.}$

Biswas et al. (2008a) reported that there was a mean increase of 46% in POD activity in 20 wheat varieties at 85 ppb O_3 concentration supplied 7 h d^{-1} for 21 days compared to filtered air. Rai et al. (2007) and Rai and Agrawal (2014) also reported higher POD activity in wheat plants under ambient O_3 compared to filtered air. The constitutive APX activity measured in a resistant wheat with respect to a sensitive one was found to be more, suggesting its possible role in conferring higher tolerance toward O_3 stress (Yadav et al. 2019).

Differences in the antioxidant defense response are often related with the differential O_3 sensitivity in various plants. Feng et al. (2016) have found that differences in O_3 sensitivity between the five varieties of wheat (Yangmai 16, Yangmai 15, Yangfumai 2, Yannong 19, and Jiaxing 002) depended on the differences involved in the maintenance of intracellular redox homeostasis exposed to EO_3 (1.5 times above ambient O_3). Fatima et al. (2018) found differential antioxidative and secondary metabolic responses of three wheat cultivars with differential O_3 sensitivity led to variable yield losses suggesting that the test cultivars ranging from sensitive, intermediately sensitive, and tolerant were manifested with different defense strategies to cope with elevated O_3 exposure. Even variation in induction of enzymatic and nonenzymatic defense response has been observed in wheat cultivars as the early released cultivar, i.e., Kharchiya 65, was manifested with higher nonenzymatic defense capacity and PBW 502 (released in 2003) showed more or less equal contribution of both enzymatic and nonenzymatic antioxidants, while the modern cultivar HD 2987 (sensitive cultivar) reflected a strong manifestation of enzymatic antioxidants along with the enzymes of the phenylpropanoid pathway under O_3-induced oxidative stress.

Along with AA (reduced and oxidized) and APX, another important antioxidant entity, which contributes to the symplastic defense mechanism, is CAT. Catalase is responsible for the scavenging of H_2O_2, which is a powerful oxidant, rapidly oxidizing thiol groups (Garg and Manchanda 2009). CAT has a vital role in the removal of H_2O_2 generated in peroxisomes by oxidases involved in β-oxidation of fatty acids, photorespiration, and purine catabolism. An alternative mode of H_2O_2 destruction within the symplast is by peroxidases, specifically APX. Yadav et al. (2019) found increased CAT activity in sensitive wheat cultivars than tolerant ones under elevated O_3 exposure.

Another enzyme contributing toward the symplastic defense is glutathione reductase (GR), which catalyzes the reduction of GSSH (oxidized glutathione) to GSH (reduced glutathione) (Noctor and Foyer 1998). The GSH/GSSH couple plays a significant role in the regeneration of reduced AA (Foyer and Noctor 2005). Reduced glutathione not only serves as a reducing cofactor for several enzymes involved in ROS detoxification but also conjugates to specific proteins to prevent their oxidation (Rouhier et al. 2004).

3.4 Photosynthesis

Photosynthesis is a core function in the physiology of plants and is most affected by O_3. It consists of light reactions, which generate reducing power and dark reactions where fixation of CO_2 occurs by RuBisCO enzymes. Ozone-related decreases in chlorophyll content strongly correlate with a reduction in photosynthetic rates (Agrawal 1982, Agrawal et al. 2003) (Fig. 5). Prolonged exposure to high ozone concentrations resulted in both decreased chlorophyll content and decreased photosynthetic rates (Agrawal 2005). Ozone reduces assimilation by decreasing leaf longevity and increasing senescence. From a whole plant perspective, decreased leaf longevity decreases the plants “return on investment” since assimilation is a function of rate and duration of photosynthesis.

3.4.1 Dark Reactions

Ozone exposure results in decreased photosynthetic carbon assimilation (Morgan et al. 2003). Loss of assimilation capacity is mainly due to reduced carboxylation efficiency directly related to loss of RuBisCO activity. These losses of activity are attributed to a decrease in RuBisCO concentration in the leaves rather than a decrease in the activation state. O_3 affects assimilation through decreased protein synthesis associated with photosynthetic enzymes (Sarkar et al. 2010). Feng et al. (2016) studied the response of five modern wheat cultivars exposed to 1.5 times the ambient concentration of O_3 and reported that significant losses in RuBisCO

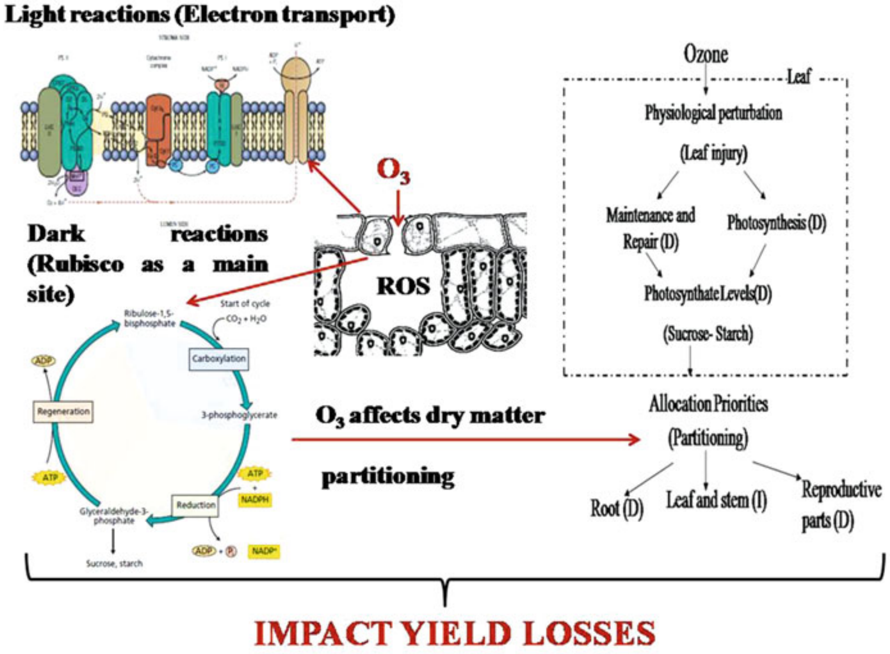


Fig. 5 Diagrammatic presentation of the effect of O_3-induced ROS on photosynthetic machinery, alteration in photosynthate allocation, and yield of wheat crop. (Modified from Rai and Agrawal 2012)

carboxylation efficiency and RuBP 1,5-bisphosphate regeneration were responsible for lower photosynthetic rates.

RuBisCO is regarded as a key protein and is made up of two types of subunits designated as a large subunit (LSU) encoded by chloroplastic DNA and a small subunit (SSU), encoded by nuclear DNA. The reduction in RuBisCO activity may be attributed to declining in RuBisCO quantity which may be due to an increased rate of protein degradation or inhibition of protein synthesis (Heath 2008). Sarkar et al. (2010) observed reductions in the abundance of LSU and SSU in two cultivars of rice, Malviya Dhan 36 and Shivani, through one-dimensional protein profiling. Transcription of chlorophyll a/b binding protein (cab) and glyceraldehyde 3-phosphate dehydrogenase (gap A and gap B) was also reduced in O_3-exposed plants (Glick et al. 1995). O_3-generated ROS affect the permeability of membrane-bound organelles such as chloroplasts leading to the destruction of photosynthetic pigments (Rai and Agrawal 2014).

Highly reactive O_3-induced ROS react with proteins and membrane lipid in the mesophyll cells. Chloroplast degradation occurs through a complex series of events starting with damage to mesophyll plasmalemma and leading to decreased photosynthesis. Calatayud and Barreno (2004) suggested that the significant decrease in chlorophyll a and b and maintenance of low concentration of chlorophyll in leaves were general features of plants subjected to oxidative stress due to O_3. It has been suggested that reduction in the plant's pigment content is an adaptational strategy to protect PS II from photooxidation through a reduction in the number of light-harvesting antennae (Pellegrini et al. 2011; Rainieri et al. 2001). Reduction in chlorophyll content as such is indicative of the effect of O_3 stress on chlorophyll-binding proteins of light-harvesting complexes (LHCs).

O_3 stress also affects the accessory pigments like carotenoids (car). A decrease in the value of chl/car ratio suggests an early stress indicator. This result confirmed the findings of Pellegrini et al. (2011) and established that O_3-treated leaves enhance the need for carotenoid-mediated photoprotection and induce a partial breakdown of chlorophylls.

Ps is a multistep process, and its response to O_3 stress depends upon the fact that which particular event of the entire process is affected. Alteration in *Ps* may be influenced either by changes in internal CO_2 or by variations in the light reactions (light energy utilization and conversion) or dark reaction (carboxylation efficiency of RuBisCO; Table 1).

Table 1 Percent changes in photosynthetic rate (Ps) and stomatal conductance (g_s) in wheat cultivars exposed to tropospheric O_3

Plant	O_3 concentration (ppb)	Percent increment/ decrements in Ps and g_s		References
		Ps	g_s	
Wheat (3 cultivars)	72 ppb 8 h	−20-22	- 7-24	Wahid (2006)
Wheat (12 cultivars)	100 ppb 7 h	−36.9	−11.1	Biswas et al. (2008b)
Wheat (20 cultivars)	$O_3 = 82$ ppb 7 h d^{-1}	−24	−8	Biswas et al. (2008a)
Wheat cultivars HUW 234	42 ppb	−27	−20	Rai and Agrawal (2014)
Meta-analytical study on wheat	$O_3 = 77$ ppb	−40	−31	
Wheat				Adrees et al. (2016)
FH 8203	4612 ppb.h	−36	−15	
FH 7096	291.5 ppb.h	−38	−60	
Wheat	60 ppb	−8.3	+5.4	Akhtar et al. (2010)
Sufi	100 ppb	−16.1	+21.8	
Bijoy	60 ppb	−1	No change	
	100 ppb	−18.4	−15.2	

3.4.2 Light Reactions

Ozone alters light reaction, decreasing the electron transfer between the two photosystems (Pellegrini et al. 2011; Calatayud et al. 2003). The Fv/Fm ratio is reported to be a good indicator of photoinhibitory damage (Bolhar-Nordenkampf et al. 1989). Fv/Fm ratio is generally around 0.8, a value generally accepted for nonstressed conditions. However, a reduction in Fv/Fm ratio indicates photoinhibition of photosynthesis (Baker and Rosenqvist 2004). Reduction in the value of Fv/Fm ratio has been reported in wheat (Sarkar et al. 2010; Rai and Agrawal 2014). Chlorophyll fluorescence techniques have been used to follow the primary processes in photosynthesis (Murchie and Lawson 2013). Barnes et al. (1990) working on old and modern Greek wheat cultivars exposed to O_3 concentration of 90 ppb for 7 h day^{-1} reported that Fv/Fm ratio, which indicates the efficiency of excitation capture of PS II, decreased significantly suggesting that electron transport around PS II has been altered.

The chlorophyll fluorescence kinetics also referred to as Kautsky transient, as explained by Krause and Weis (1991) upon saturated illumination, reveals detailed information not only on the redox state of primary acceptor Q but also on the electron transport beyond QA on the donor side of PS II. The different levels observed in Kautsky transient (Fo and Fm) are used to calculate the electron flow around PS II, and Fv/Fm value gives the maximum quantum yield of PS II (Kitajima and Butler 1975). The decrease in Fm corresponds to a transient reduction in the pool of primary PS II electron receptor, QA, whereas an increase in Fm suggests that reaction centers in electron transport chain remain closed for most of the time and the quantum energy absorbed was mostly dissipated as heat (Singh and Agrawal 2009). O_3-treated leaves also showed a significant increase in Fo which is an indicative of a higher number of deactivated PS II centers and a decrease in photochemical efficiency.

The disruption of light reaction of photosynthesis can also be attributed to the vulnerability of D1 core protein of PS II upon O_3 stress (Adir et al. 2003). Godde and Buchhold (1992) have shown that O_3 exposure stimulates both synthesis and degradation of D1 protein. An imbalance between degradation and de novo synthesis can lead to damage to the photosynthetic apparatus (Yamamoto and Akasada 1995). The light reaction system of photosynthesis is found to be more stable than the dark reaction system under O_3 exposure (Heath 2008).

3.4.3 Stomatal Conductance and Intercellular CO_2

Apart from O_3-induced negative changes in dark and light reactions, numerous studies have proved that the decline in photosynthetic rate in the plants exposed to O_3 stress is associated with damage to photosynthetic machinery (Feng et al. 2016; Guidi and Degl'Innocenti 2008) but biophysical parameters such as stomatal conductance (*gs*) and internal CO_2 (*Ci*) also play significant roles in determining the photosynthetic yield and sensitivity of O_3-exposed plants.

Pleijel et al. (2006) observed the differential response of old and modern wheat cultivars with respect to its stomatal conductance (*gs*) exposed to elevated O_3 (75 ppb). Sarkar et al. (2010) observed reductions in the stomatal conductance of *T. aestivum* L. cvs Sonalika and HUW 510 at O_3 concentration of 36.4–48 ppb. Table 1 shows variations in different physiological parameters upon O_3 exposure.

Stomatal response under O_3 exposure may also be regulated independent of *Ci* response. The damaged photosynthetic machinery reduces the carboxylation efficiency, which increases the concentration of *Ci* in the substomatal cavity, resulting in reduced *gs* in wheat. Elevated O_3 may directly affect the guard cell functioning, leading to stomatal closure (McAinsh et al. 2002). Rai et al. (2011) reported increase in the gas exchange study on wheat cultivar HUW 533 exposed to ambient O_3. Stomatal conductance has an important role in maintaining the ratio of *Ci* to ambient CO_2 concentration (Lambers et al. 2008). Biswas et al. (2008a, b) observed that the sensitivity to O_3 in wheat cultivars progressed with the year of release due to higher *gs* and lower levels of antioxidant capacity of the modern cultivars while studying the response of 20 varieties of wheat to elevated O_3.

4 Growth and Yield of Wheat Cultivars

Disturbances at the metabolic and physiological level are always manifested in terms of growth and yield of wheat crops (Fig. 5). The relative effects on the growth of the different parts of the plants are the result of varied O_3 impacts on the translocation of photoassimilates from the leaves. Ozone stress decreases carbon allocation to roots (Cooley and Manning 1987). Shoot/root ratio often increases under O_3 exposure due to higher reductions in root growth than in shoot growth. Alteration in the shoot/root ratio due to O_3 exposure is an adaptive mechanism within the plant to maintain the relative growth rate in conditions of reduced carbohydrate availability. When concentrations of O_3 are low, such compensatory changes related to carbon allocation maintain growth rate, but at higher concentration, reduction in relative growth rate occurs. The higher retention of C in the leaves may be explained by higher carbon demand for repair of damaged foliage, by reduced assimilate transport in the phloem, or by decreased phloem loading. Impairment of phloem loading due to O_3 occurs due to plasmalemma or plasmodesmatal damage in the mesophyll cells (Grantz and Yang 2000). The source-sink relationship decreased phloem loading, and increased carbohydrate concentrations lead to feedback inhibition of photosynthesis (Koch et al. 1998). This shift in partitioning from storage compounds to soluble carbohydrates and other carbon compounds involved in the repair might be a compensatory response to maintain photosynthetic rates. However, the level of individual sugars such as fructose and sucrose may increase. O_3 exposure in wheat cultivars leads to reduction in starch content as reported by many available reports (Rai and Agrawal 2014; Sarkar and Agrawal 2010; Pleijel et al. 2006).

Ozone generally inhibited both CO_2 fixation and translocation in the primary leaf, which is the main source of photosynthate for root growth. CO_2 fixation in the first trifoliate, which provides photosynthate to immature leaves, was less inhibited than that in other leaves, and translocation to immature leaves increased in some experiments. Consequently, translocation to stem and roots decreased significantly more than the translocation to developing young leaves. In roots, the soluble sugars decline due to O_3 leading to a reduction in root respiration. The production of sucrose and fructose in leaves decreases due to O_3. Variability in growth response exists depending on plant age, species, genotype sensitivity, O_3 dynamics (duration, frequency, and concentration), and concurrent biotic and abiotic stresses.

The damaging effects of O_3 on the biochemical and physiological processes are translated in the yield responses. The grain yield of a cereal stand is a function of a number of factors that are under genetic and environmental control. The potential ear density is mainly dependent on the extent of tillering before ear initiation in combination with the sowing density. The number of spikelet initials per ear and the number of floret initials per spikelet are also determined early during plant development. The floret initiation is already in progress when the ear is at 1 cm, measured from the attachment of the lowest leaves (Tottman and Broad 1987). After anthesis, both the number of ears per unit area, apart from late tillers, which normally only contribute little to the yield, and the maximum number of grains per ear are already fixed. Then, the rate and the duration of the grain-filling processes are the dominant factors influencing the final grain yield, within limits set by the preceding life history of the plant. The maximum grain size is related to the number of endosperm cells in the developing grains, which is determined before starch storage begins, 1–2 weeks after anthesis.

Ozone has been shown to be more important for yield reductions when the exposure is conducted during and after anthesis compared to exposure before anthesis (Pleijel et al. 1998). Thus, the rate and the duration of grain filling seem to be the key processes to study in order to understand the mechanisms behind the ozone-induced reduction of grain yield in wheat. Despite air quality regulations intended to limit O_3 concentration in the troposphere, current ground-level O_3 is sufficiently high to suppress the growth and yield of many agricultural crops (McGrath et al. 2015; Feng et al. 2015; Wilkinson et al. 2012; Ghude et al. 2014; Emberson et al. 2009; Avnery et al. 2011a, b). As per the annual report of IPCC (2013), the most rapid increase in O_3 concentration is currently occurring in South Asia and is also expected to show the maximum increase in the near future. Studies have shown that O_3 exposure reduced yield in grain crops by decreasing assimilate partitioning toward the ear.

Grain yield in cereals is reduced by the effect of O_3 on the rate and the duration of grain filling and due to impairment of production in carbohydrates and translocation of assimilates from the source organs to the grains. Meta-analysis conducted by Feng et al. (2008) reported mean wheat yield reductions of 29% at elevated O_3 with a range of 31–200 ppb collected from database of studies from "Web of Science" and

"AGRICOLA" related to wheat photosynthesis, growth, yield, and its components and grain quality responses between 1980 and 2007. The large yield loss was caused by a combination of a decrease in individual grain weight (−18%), ear number plant^{-1} (−6%), and grain number ear^{-1} (−11%). Results of meta-analysis suggest that among the growth processes, grain filling was most damaged by elevated O_3.

The yield reductions in wheat cv. HP 1209 and M 234 at O_3 concentration of 70 and 100 ppb for 4 h daily for 70 days, respectively, were 8, 4.7, 17, and 15.5% (Rai et al. 2016). Rai et al. (2007) found 20.7% reductions in yield of wheat cv. M 234 grown in chambers ventilated with ambient air (40.6 ppb) as compared to the filtered chamber. Analyzing the cultivar sensitivity response, Sarkar and Agrawal (2010) found reductions of 7, 16.7, and 22% in wheat cv. Sonalika and 8.4, 18.5, and 25% in cultivar HUW 510 grown in NFCs (45.3 ppb), NFCLOs (50.4 ppb), and NFCHOs (55.6 ppb) compared to FCs. Mills et al. (2018) reported on the basis of modeling study from 2010 to 2012 that O_3 impacts on wheat yield are particularly large in humid rain-fed and irrigated areas of major wheat-producing countries (e.g., the USA, France, India, China, and Russia), and it was estimated that ozone reduces wheat yields by a mean 9.9% in the Northern Hemisphere and 6.2% in the Southern Hemisphere, corresponding to some 85 Tg (million tonnes) of lost grain. Total production losses in developing countries receiving official development assistance are 50% higher than those in developed countries. Significant yield reductions in wheat cultivars were exposed to tropospheric O_3 (Singh et al. 2014; Li et al. 2016; Pandey et al. 2018; Fatima et al. 2018; Picchi et al. 2017; Table 2).

Tropospheric O_3 not only affects yield of wheat but also deteriorates wheat quality by decreasing total starch content, amino acid content, and nutrient content (Mg, P, K, and Ca are essential macronutrients, and Fe, Zn, Mn, and Cu are essential micronutrients in crops) and increasing soluble sugar (Li et al. 2016; Singh et al. 2014; Rai et al. 2011).

5 Conclusions and Recommendations

The present chapter concludes that tropospheric O_3 impact harmful effect on wheat physiology, growth, yield, and quality. Plant resistance to O_3 involves a wide array of response ranging from the molecular and cellular level to the whole plant level. Significant effects of O_3 have been observed in a wide range of characteristics such as early leaf senescence, decreased photosynthetic assimilation, altered stomatal behavior, decreased growth and productivity, and reduced carbon allocation to roots. Many metabolic pathways are altered by O_3. Cultivar differences in response to O_3 are related to the stomatal behavior of the leaf surface and the free radical scavenging ability of endogenous antioxidant compounds in the leaf mesophyll cells. In the present scenario, it is utmost important to identify mitigating methods to close yield gaps and provide food security and to eradicate hunger. There should be large-scale screening of local wheat cultivars for their O_3 sensitivity/tolerance.

Table 2 Percent yield losses in wheat cultivars exposed to tropospheric O_3

Location	Method	O_3 concentration (ppb)	Cultivars	Percent reductions	References
China	OTCs	AOT 40 = 17–27 ppmh, 7 h mean = 56–63 ppb O_3	Wheat	20–30	Huixiang et al. (2005)
China	OTCs	FA+ 105 ppb O_3	Wheat	36	Feng et al. (2007)
Pakistan	OTCs	NF (72 ppb O_3)	Inquilab 91	18	Wahid (2006)
			Punjab 96	39	
			Pasban 96	43	
India	OTCs	NFCs (45.3 ppb), NFCs +10 ppb, NFCs+20 ppb	Sonalika	11, 25, 38	Sarkar et al. (2010)
			HUW 510	20, 36, 45	
Bangladesh	OTCs	FC + 60 ppb	Sufi	11.5, 44.5	Akhtar et al. (2010)
		FC + 100 ppb	Bijoy	33.2, 45.6	
India	OTCs	NFCs(48 ppb)	M 234	20.7	Rai and Agrawal (2014)
			PBW 343	16	
			M 533	14	
China	OTCs	AO_3 (35 ppb)	Liangxing 99	42	Li et al. (2016)
		EO_3 (120 ppb)			
India	OTCs	70 ppb O_3 for 8 h daily for 70 days	M 234	15	Singh et al. 2015
			HP 1209	17	
India	OTCs	NFCs (56.5 ppb)	LOK-1	16.3	Singh et al. 2015
			HUW 510	10.1	

Simultaneously, some early and late sown wheat cultivars should be employed to check its sensitivity. In the long-term scenario, farmers may select more O_3-resilient or O_3-tolerant cultivars to minimize the crop losses.

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Abiotic Stress-Induced Oxidative Stress in Wheat

Aditi Shreeya Bali and Gagan Preet Singh Sidhu

Contents

Abstract Wheat is a primary staple food and is ranked third in terms of global production all over the world. It maintains carbohydrate and protein balance in the diet. The unprecedented, fast altering environmental conditions have led to different abiotic stresses in plants such as drought, salinity, heavy metal, and temperature that instigate considerable losses in growth and yield of wheat worldwide. These abiotic stresses cause pollen sterility, disturb photosynthetic apparatus, produce shriveled seeds in wheat, and lead to the exorbitant production of reactive oxygen species (ROS) that pose pessimistic effects on proteins, lipids, carbohydrates, and DNA, eventually inducing oxidative stress in plants. Furthermore, imprudent ROS generation causes oxidative damage, irremediable harm to plant metabolic activities, and ultimately cell death. The systematic scavenging of ROS requires the activity of various enzymatic and nonenzymatic antioxidants in plant tissues. This chapter summarizes (i) the effect of various abiotic stresses on growth and physiology of wheat, (ii) ROS production and its induced oxidative damage in wheat, and (iii) mechanism involved in providing tolerance to wheat.

Keywords Antioxidants · Reactive oxygen species · Oxidative stress · Signaling · Tolerance

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Abbreviations

APX	ascorbate peroxidase
CAT	catalase
DNA	deoxyribonucleic acid
GPX	guaiacol peroxidase
GR	glutathione reductase
H_2O_2	hydrogen peroxide
MDA	malondialdehyde
NUE	nitrogen use efficiency
$^1O_2$	singlet oxygen
$O_2^{\bullet -}$	superoxide radical
$OH^{\bullet}$	hydroxyl radical
RNA	ribonucleic acid
ROS	reactive oxygen species
RuBisCO	ribulose-1,5-bis-phosphate carboxylase/oxygenase
SNP	sodium nitroprusside
SOD	superoxide dismutase

1 Introduction

Wheat (*Triticum aestivum* L.) is ranked third worldwide after maize and rice in terms of production. Being a primary staple food, its annual production reaches more than 600 million tonnes globally per year. According to FAO (2014), wheat occupies an area of approximately 218.5 million hectares, with an average yield of 3.26 t ha^{-1}. During the last 50 years, increased global population and varied consumption predilection have led to the elevated demand for wheat worldwide. The extremely aberrant, rapidly mutating environmental conditions hamper crop production and exhibit serious risk that needs to be handled to retain fruitful production. These changing environmental conditions have led to different abiotic stresses in plants such as drought, salinity, heavy metal, waterlogging, and temperature that abet substantial losses in growth and yield of wheat worldwide (Barlow et al. 2015; Herzog et al. 2016; Rizwan et al. 2016). These abiotic stresses cause pollen sterility (Chakrabarti et al. 2011), disturb photosynthetic apparatus (Brestic et al. 2016), produce shriveled seeds (Rascio et al. 2015) in wheat, and account for the inordinate production of reactive oxygen species (ROS).

Reactive oxygen species are moderately reduced form of oxygen. They culminate from excitation of molecular oxygen (O_2) to form singlet oxygen ($^1O_2$) or transferring electrons to O_2 to form hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet -}$), and hydroxyl radical ($OH^{\bullet}$). In plants, ROS are consistently formed by the imminent flow of electrons from electron transport pathways occurring in chloroplast and mitochondria to oxygen. Abiotic stresses such as drought, temperature, salinity, and heavy metal lead to the elevated generation of ROS in plants due to interruption of cellular homeostasis (Gong et al. 2005; Sairam et al. 2005; Khan et al. 2015; Zang et al. 2017). ROS have a dual role in plants depending upon its concentration. At lower doses it acts as a signaling molecule or secondary messenger (Neill et al. 2002; Yan et al. 2007) and provides tolerance during various environmental stresses; however, it poses fatalistic effects on cellular machinery eventually inducing oxidative stress in plants when present in high concentration. During oxidative stress, ROS targets the proteins, lipids, RNA, and DNA. Furthermore, imprudent generation of ROS causes irremediable harm to plant metabolic activities and ultimately cell death (Petrov et al. 2015).

In order to establish durability, plants have developed competent and systematic antioxidant machinery that requires activity of various enzymatic [superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and glutathione reductase (GR)] and nonenzymatic [ascorbic acid (AA), reduced glutathione (GSH), carotenoids, and flavonoids] antioxidants in plant tissues. They play a major role in scavenging ROS generated under different stressful conditions. Various researchers have reported increased activity of antioxidant enzymes to encounter oxidative stress generated by different abiotic stresses (Sekmen et al. 2014; Al-Issawi et al. 2016; Sidhu et al. 2016, 2017). This chapter summarizes (i) the effect of various abiotic stresses on growth and physiology of wheat, (ii) ROS production and its induced oxidative damage in wheat, and (iii) mechanism involved in providing tolerance to wheat.

2 Various Abiotic Stresses and Their Effect on Wheat

Wheat is the most important food crop of the world, and maximum wheat-growing areas globally encounter various abiotic stresses which include drought and temperature that affect the growth and yield of the crop (Pradhan et al. 2012; Fig. 1). Among the different stages of development of wheat, the reproductive stage is the most susceptible stage to environmental stresses (Prasad et al. 2008; Ji et al. 2010; Lott et al. 2011; Fig. 1). This section gives insight on the effects of different abiotic stresses on growth and physiology of wheat.

2.1 High Temperature Stress/Heat Stress

The continuously increasing climate change has altered the temperature and caused heat stress in the environment. Heat stress is a serious menace to wheat production worldwide, specifically during reproductive stages since it affects both the grain number and dry weight of the crop (Wollenweber et al. 2003). Gibson and Paulsen (1999) observed 3–5 % reduction in yield of wheat with every 1 °C rise in temperature. Earlier reports have documented that heat stress induces pollen sterility,

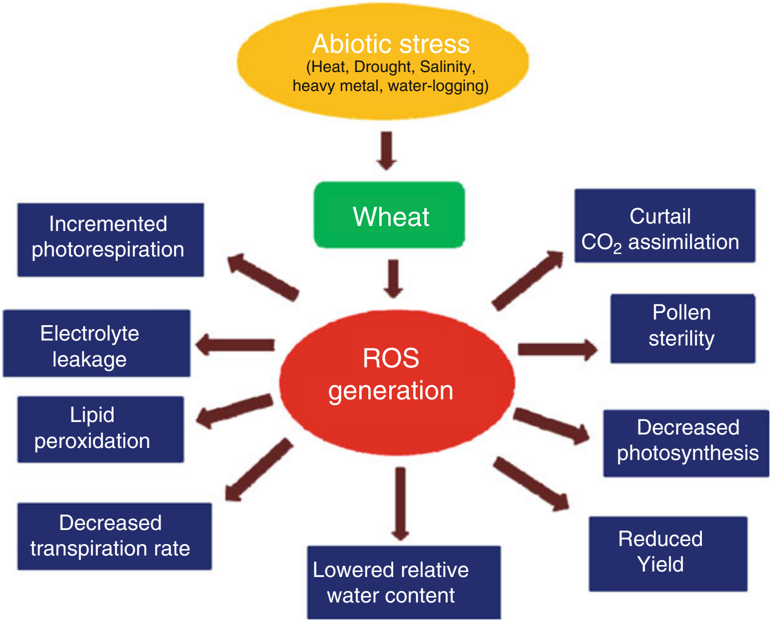

Fig. 1 Abiotic stress-induced ROS generation and its effect on different parameters of wheat

curtails CO_2 assimilation, and elevates photorespiration in wheat (Perdomo et al. 2015; Hlaváčová et al. 2017). Wahid et al. (2007) documented that high temperature severely harms the photosynthesis process that adversely affects the growth and grain yield in wheat (Asseng et al. 2011).

Increased temperature disrupts chloroplast structure, reduces chlorophyll content, and inactivates chloroplast enzymes that may lead to decreased photosynthesis in crops (Farooq et al. 2011). Wang et al. (2010) reported ultrastructural damage to chloroplast and thylakoid lamellae in wheat in response to heat stress. Recently, Khan et al. (2013) observed a reduction in RuBisCO activity, photosynthetic nitrogen use efficiency (NUE), and net photosynthesis in wheat plants subjected to heat stress. High temperature has been reported to inhibit photosystem II thereby hampering the photosynthesis apparatus in wheat (Mathur et al. 2011).

Further, high temperature limits the grain number and size and affects the wheat yield to a large extent (Porter and Semenov 2005). Semenov and Shewry (2011) noticed a substantial reduction in grain number and size in heat-sensitive cultivar of wheat under exposure of heat stress during flowering. The reduced grain yield might be attributed to the effect of heat stress on assimilate availability, reduced translocation of photosynthates to grain, and starch synthesis in developing grain (Modhej et al. 2012). Earlier studies also indicated a reduction in wheat yield in response to heat stress. For example, Mitchell et al. (1993) detected that temperature higher than 27 °C, applied during anthesis (flowering) stage, produced a large number of sterile grains leading to extensive yield loss in wheat. Similarly, Wheeler et al. (1996)

demonstrated that temperature higher than 30 °C before the stage of anthesis considerably decreased grain number and yield in wheat cultivar.

2.2 Heavy Metal Stress

Heavy metal contamination of soils is a major hazard to crops globally (Rizwan et al. 2016). Growing anthropogenic activities like industrialization and urbanization have led to an increase of heavy metal concentration in the soil. Heavy metals present in soil enter the wheat plant through roots alongside nutrients with water and get accumulated in the tissues (Ovečka and Takáč 2014). They induce oxidative stress in the wheat due to excessive generation of ROS (Dimkpa et al. 2012). The increased amount of these compounds causes severe damage to various cellular, biochemical, and physiological mechanisms in wheat (Ci et al. 2010; Yang et al. 2010; Lamhamdi et al. 2011). For example, Athar and Ahmad (2002) conducted a pot experiment to study the toxic effect of different heavy metals on growth and grain yield of wheat. The results exhibited a significant reduction in both parameters in response to metals, viz., Cd (cadmium), Cu (copper), Ni (nickel), Zn (zinc), Pb (lead), and Cr (chromium); however, Cd was found to be the most toxic among all of them. Further, the effect of different concentrations of Pb on seed germination and seedling growth was investigated in wheat, and results revealed significant inhibition in germination and growth of roots and shoots in response to high concentration of Pb (Yang et al. 2010).

Several reports have suggested a toxic effect of heavy metals on biochemical processes occurring in wheat. Gajewska and SkŁodowska (2010) studied the effect of Cu, Cd, and Ni on growth, nonprotein thiols, GSH content, membrane damage, lipid peroxidation, and activities of proteases and peroxidase in shoots and roots of wheat. The results indicated increased lipid peroxidation and electrolyte leakage in wheat tissues that resulted in decreased growth in the plant. Hasanuzzaman and Fujita (2013) studied that exposure of As (arsenic) to wheat seedlings caused a reduction in relative water content and chlorophyll content after 72 h of growth. Moreover, with increasing concentration of As, marked increase in the content of malondialdehyde (MDA) and H_2O_2 and activities of APX and glutathione *S*-transferase (GST) was observed, thus suggesting As-induced oxidative stress in wheat.

The coal mines located near the agriculture fields also affect the growth and yield of the crop. Ma et al. (2015) reported irrigation of wheat fields with mine wastewater reduced activities of soil enzymes, root activity, and net photosynthetic rate of wheat. Further, the level of Cr and Pb increased in wheat grain and significantly affected the yield of the crop. Recently, Rizvi and Khan (2017) demonstrated the phytotoxic effect of Cu, Cd, and Cr on the root morphology of wheat. They found that increasing concentration of metals increased the toxic effect on wheat and hampered the root structure in wheat plants.

2.3 Drought Stress

Drought stress generally leads to a great loss in crop production and is a major threat to world food security. It affects the plant at morphological, physiological, and molecular level. Drought stress restricts photosynthesis, alters chlorophyll content, and causes severe damage to the photosynthetic apparatus in plants (Iturbe-Ormaetxe et al. 2001; Keyvan 2010). Wheat, an important cereal crop, experiences severe stress during crop cycle, which is the main factor that limits the yield of the crop during the grain filling stage. Several reports suggested the growth inhibitory effect of drought stress on different parameters of wheat. For example, Siddique et al. (2000) observed reduced leaf water potential and relative water content in relation to increased drought stress. Further, they observed higher canopy temperature in drought-stressed plants at both vegetative and anthesis growth stages (Siddique et al. 2000). Alexieva et al. (2001) noticed that relative leaf water content is the main factor that is responsible for the decreased growth of wheat in response to drought stress.

Drought stress not only leads to a reduction in relative water content but also decreased the chlorophyll content in the different wheat cultivars as studied by Keyvan (2010). This might be related to the reduction in production potential and storage capacity of wheat (Keyvan 2010). Similarly, Prasad et al. (2011) reported the significant impact of drought stress on physiological, growth, and yield of wheat. The results revealed a decrease in leaf photosynthetic rate, spikelet fertility, grain numbers, and yield in response to increased drought stress (Prasad et al. 2011). Severe drought stress has been reported to adversely affect the wheat plant at different stages of growth. It reduced the assimilation of CO_2, stomatal conductance, transpiration rate, and chlorophyll content that later hamper the grain yield at both tillering and flowering stages (Naveed et al. 2014).

Drought stress hinders wheat performance at all the stages, but it is more crucial during flowering and grain filling phase and causes considerable losses in wheat yield (Farooq et al. 2014). Further, they reported that a significant reduction in yield might be due to the reduced rates of net photosynthesis, stomatal closure, and oxidative damage to chloroplast (Farooq et al. 2014). Further, Ihsan et al. (2016) observed decreased leaf area index, dry matter accumulation, crop growth rate, and net assimilation rate in wheat plants in response to severe drought stress. They later found that this might be due to complete termination of carbohydrate translocation to grains that damages the photosynthetic machinery of the plant (Ihsan et al. 2016).

2.4 Salinity Stress

Salinity stress has been a major threat to agriculture nowadays. The problem has been provoked by the requirement of irrigation for production of crops (Läuchli and Grattan 2007). Läuchli and Epstein (1990) reported that salt stress affects plant in many ways like osmotic effects, ion toxicity, and nutritional disorders. Munns

(2002) described that plants show a two-phase growth response upon exposure to salt stress. Firstly, the plants undergo growth reduction when subjected to salt stress. Secondly, accumulation of salt in the plant causes salt toxicity in the plant that leads to a reduction in photosynthetic rate in plants (Munns 2002). Several reports suggested an adverse effect of salt stress on growth and development of wheat. Extreme salt stress reduced germination percentage in wheat seedlings which might be due to the accumulation of toxic ions in the plant (Almansouri et al. 2001). Soltani et al. (2006) observed reduced seedling growth, seed reserve utilization, and weight in response to salt stress.

Salinity stress decreased relative water content, chlorophyll and carotenoid content, and biomass and grain yield in two wheat cultivars, which might be due to increased oxidative stress in response to stress (Sairam et al. 2002). Further, according to Turan et al. (2007), reduction in chlorophyll content in wheat leaves under salt stress might be attributed to the salt-induced weakening of protein-pigment-lipid complex or increased activity of enzyme chlorophyllase (Turan et al. 2007). Moreover, Ashraf et al. (2010) studied the response of two genetically diverse wheat cultivars to salt stress at various growth stages and found that with increase in concentration of salt, the plant growth decreased which might be related to increased production of MDA content in the plant in response to stress (Ashraf et al. 2010).

2.5 *Waterlogging Stress*

Waterlogging of soils occurs due to excessive rainfall and further depends upon the amount of rain, evapotranspiration, and soil structure (Malik et al. 2002). It results in a reduced gaseous exchange between soil and air (Malik et al. 2002). The amount of O_2 present in soil gradually attenuated resulting in hypoxic or anoxic soil (Malik et al. 2002). Waterlogging of soils severely affects wheat in many ways. For example, Araki et al. (2012) observed reduced root and shoot growth and weight in wheat plants under 8 days of waterlogging stress.

The extreme effect of waterlogging depends on the growth stage of the plant (Davies et al. 2000) and duration of waterlogging (Jackson 1979). Malik et al. (2002) reported reduced leaf nitrogen concentration in wheat due to waterlogging stress. Further, it has been found that waterlogging lowered leaf water potential, stomatal conductance, photosynthesis, chlorophyll content, and shoot and root growth in wheat genotypes (Huang et al. 1994). Dickin and Wright (2008) documented reduced grain yield and length of root in response to waterlogging in wheat.

3 ROS Production Induces Oxidative Damage in Wheat

Different abiotic stresses mentioned above lead to increased production of ROS in plants. They are extremely reactive and toxic compounds that hamper the protein, carbohydrate, and DNA of the plants and conclusively lead to oxidative damage in the plants (Gill and Tuteja 2010). Reactive oxygen species are divided into two types/forms, i.e., free radical [(superoxide radical ($O_2^{\bullet-}$), hydroxyl radical ($OH^{\bullet}$), perhydroxy radical ($HO_2^{\bullet}$)] and non-radical [singlet oxygen ($^1O_2$) and hydrogen peroxide (H_2O_2)]. In plant cells, chloroplast, mitochondria, or peroxisomes are important sources of ROS due to occurrence of high metabolic activity and electron flow pathways in these organelles. Accumulation of ROS results in loss of crop productivity globally (Tuteja 2010).

Several reports suggested increased oxidative damage due to excessive generation of ROS in wheat as a result of various abiotic stresses (Fig. 1). For example, heavy metals when entering the plant cell induce oxidative stress and damage cellular functions of the plant. For example, Hao et al. (2006) reported a significant elevation in the amount of H_2O_2 and $O_2^{\bullet-}$ that further leads to lipid peroxidation in wheat roots due to Ni stress. The amount of MDA content was found to be elevated in wheat seedlings upon exposure to Cd stress (Lin et al. 2007). Further, a high concentration of Zn caused the enhanced level of H_2O_2 and MDA content in wheat leaves (Li et al. 2013).

Similarly, Tambussi et al. (2000) noticed production of ROS in the chloroplast of wheat under water stress, and further it was found that with increased water-stressed conditions, the oxidative damage to the photosynthetic machinery also increased. Recently, Chakraborty and Pradhan (2012) observed the elevated concentration of H_2O_2 and MDA in wheat varieties under drought stress. Nikolaeva et al. (2010) observed increased MDA content that indicates weakened antioxidant defense systems and further enhanced lipid peroxidation in wheat cultivars upon exposure to water stress.

Heat stress generates the production and accumulation of ROS in plants (Farooq et al. 2011). Moreover, Savicka and Škute (2010) reported increased $O_2^{\bullet-}$ production that caused an elevated level of MDA content in the wheat seedlings in response to heat stress. Similarly, Hasanuzzaman et al. (2012) observed increased lipid peroxidation and content of H_2O_2 in response to high temperature stress in wheat. Further, they also documented that increased level of oxidative stress affects the chlorophyll content in the seedlings (Hasanuzzaman et al. 2012).

Further, salt stress or salinity is also a major environmental hazard that impacts the growth and physiology of wheat crops by inducing oxidative damage. For example, Al-Quraan et al. (2013) observed the incremented amount of MDA in the wheat cultivars. Masood et al. (2012) noticed that NaCl application produced more oxidative stress in wheat seedlings as compared to boron. Further, the activity of various antioxidant enzymes was increased in response to elevated salt stress (Masood et al. 2012). Ashraf et al. (2010) noticed a negative correlation between growth and MDA content in the wheat cultivars in response to the high intensity of salt stress. The increased MDA content upon exposure to salt stress might be responsible for the adverse effect on the growth of the plant (Ashraf et al. 2010).

From the above literature, it is evident that the generation of toxic ROS species significantly hampers the growth and development of wheat by causing oxidative damage to the metabolic machinery that can further impact the yield of the plant. Therefore, in order to prevent the loss, plants adapt different tolerance strategies that are studied below that help the plant to survive under extreme environmental conditions.

4 Tolerance Mechanism Operating in Wheat

Exposure of wheat to different environmental stresses such as temperature, heavy metals, drought, waterlogging, and salt stress enhanced the generation of ROS, e.g., $O_2^{\bullet -}$, $OH^{\bullet}$, $HO_2^{\bullet}$, $^1O_2$, and H_2O_2. Wheat plants employ different tolerance mechanisms to protect them against these reactive oxygen intermediates. A substantial amount of research has enlisted that the initiation of antioxidant machinery is crucial for protection against different abiotic stresses. The antioxidant system contains two components, viz., enzymatic and nonenzymatic antioxidants (Gill and Tuteja 2010).

4.1 ROS Scavenging Enzymatic Antioxidants

Enzymatic antioxidants are SOD, CAT, APX, GPX, and GR (Gill and Tuteja 2010). These antioxidants act as a defense mechanism for providing tolerance from various stresses to wheat. For example, high temperature stress triggers the increased activity of SOD, CAT, and APX in wheat (Sairam et al. 2000).

Superoxide dismutase is a powerful enzymatic antioxidant, which is present in all the aerobic organisms within the organelles prone to oxidative stress. Superoxide dismutase provides the first line of defense against increased amount of ROS. It acts on $O_2^{\bullet -}$ and converts it into a reduced form, H_2O_2, and later into O_2. Sairam et al. (2005) observed the increased activity of SOD in salt-tolerant wheat genotype compared to susceptible genotype. The elevated level of SOD in response to salt stress depicts the tolerance mechanism operating in wheat genotypes (Sairam et al. 2005). Similarly, Hameed et al. (2012) reported incremented activity of SOD that helps in scavenging H_2O_2 in wheat plants exposed to heat stress. The exposure of wheat plants to increased concentration of municipal solid waste compost that contains heavy metals like Ni, Pb, Cu, and Zn stimulated the activity of SOD that provides tolerance to the plant under adverse conditions (Lakhdar et al. 2010).

Catalase is a heme-containing enzyme that converts H_2O_2 into H_2O and O_2. It is a crucial enzyme for detoxification of ROS under abiotic stress environments. Hasanuzzaman et al. (2012) studied that exogenous application of nitric oxide reduces heat stress-induced oxidative stress in wheat seedlings by regulating antioxidant defense system. They reported upregulated activity of CAT in wheat plants in response to stress conditions (Hasanuzzaman et al. 2012). Further, treatment of sodium nitroprusside (SNP) mitigates As-induced oxidative stress in wheat by increasing antioxidant defense system particularly the activity of enzymatic antioxidant, CAT (Hasanuzzaman and Fujita 2013). Similarly, Qiu et al. (2014) reported that application of jasmonic acid (JA) increased tolerance of wheat seedlings to salt stress. They found the increased activity of CAT in JA-treated wheat plants that further enhanced the growth of the plant under stressed condition (Qiu et al. 2014).

Enzymatic antioxidants like APX, GPX, and GR also play a significant role in providing stress tolerance in plants. They help in scavenging ROS and protect cells in higher plants. The activity of APX was found to increase with increasing concentration of Fe and Cu stress in wheat seedlings suggesting its role in scavenging H_2O_2 in the plant (Li et al. 2012). Further, Zn stress induced an enhanced level of H_2O_2 and MDA in wheat seedlings that increased the activity of APX and GR in plants pointing their role in ROS scavenging (Li et al. 2013). Moreover, increased activity of GPX was reported in wheat seedlings upon exposure to short-term heat stress providing evidence that wheat plants have an effective antioxidant defense system that provides tolerance under various stressful conditions (Gupta et al. 2013).

4.2 ROS Scavenging Nonenzymatic Antioxidants

Nonenzymatic antioxidants comprise GSH, AA, carotenoids, and tocopherols (Gill and Tuteja 2010). Many reports suggested their increased activity in providing stress tolerance against various stresses in wheat.

Ascorbic acid is a potent, water-soluble antioxidant that prevents damage induced by ROS in plants (Gill and Tuteja 2010). Similarly, α-tocopherol, a lipid-soluble antioxidant, is also an important scavenger of ROS and specifically protects membrane stability (Hollander-Czytko et al. 2005). Leaf senescence, an oxidative process, was reported to get reduced in wheat due to increased activity of AA and α-tocopherol in plants exposed under salt stress (Farouk 2011). They found that with enhanced activity of antioxidant like AA, the concentration of H_2O_2 gets lowered, which might be a major reason for oxidative damage (Farouk 2011).

Carotenoids help in providing protection to photosynthetic apparatus by scavenging ROS and repressing lipid peroxidation (Gill and Tuteja 2010). They are lipid-soluble antioxidant that plays a role in oxidative stress tolerance in plants. It helps in quenching harmful radicals that are formed during the photosynthesis process. A higher level of carotenoids in drought-tolerant genotypes of wheat suggests its role in scavenging $^1O_2$ formed due to oxidative damage caused by stress (Balouchi 2010).

Flavonoids are plant secondary metabolites and neutralize free radicals thereby preventing plants from damage under extreme environmental conditions. Recently, Ma et al. (2014) observed increased expression of flavonoid expression genes and incremented the content of flavonoid in wheat leaves in response to drought stress.

5 Conclusion and Future Prospective

It is well known that different environmental stresses or abiotic stresses cause excessive generation of ROS in wheat that is extremely harmful and leads to oxidative damage. These ROS damage the cell membranes and photosynthetic apparatus and affects growth and productivity of wheat. However, wheat plants have powerful enzymatic and nonenzymatic antioxidants that play a role in imparting tolerance during stressful conditions. Further, research is needed to find the role of various genes that are expressed in wheat that induce defense mechanism under stressed conditions.

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Trending Methods to Enhance Antioxidant Activities in Wheat

Kratika Pathak, Sunita Kataria, and Rekha Gadre

Contents

Abstract Free radicals are defined as any molecular species which are proficient of independent existence and consist of an unpaired electron in their atomic orbital. These free radicals are derived from reactive oxygen or reactive nitrogen species which are generally produced in cellular metabolism and tend to increase under stress conditions. The most vulnerable biological targets of these reactive species include biomolecules such as proteins, lipids, and nucleic acids. To neutralize the adverse effect of free radicals, a strong antioxidant mechanism is required in plant cells. Wheat is one of the major cereals in the world, which is used in food and nonfood products. Wheat is cultivated in tropical and subtropical regions both under rain-fed and irrigated conditions, as it has a high level of adaptation. Wheat has a well-known antioxidant defense mechanism, i.e., enzymatic and nonenzymatic. However, crop production is adversely affected by environmental stresses alone or in combination. These stresses are commonly due to salinity, drought, waterlogging, cold, heavy metals, etc. Recent studies suggest the use of algal consortium in the soil, treatment with external agents like organic acids, signaling molecules, essential elements, seed priming, etc. can lead to a constructive approach toward a high yield of wheat under adverse conditions.

Keywords Antioxidant activity · Algal consortium · Organic acids · Oxidative stress · Seed priming

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Abbreviations

ABA	abscisic acid
APX	ascorbate peroxidase
AsA	ascorbic acid
ATP	adenosine triphosphate
CAT	catalase
CK	cytokinins
CO	carbon monoxide
DHA	dehydroascorbate
DHAR	dehydroascorbate reductase
DMSP	dimethylsulfoniopropionate
GO	glycolate oxidase
GPX	glutathione peroxidase
GR	glutathione reductase
GS	glutathione synthase
GSH	reduced glutathione
GSSG	oxidized glutathione
GST	glutathione S-transferase
HO	heme oxygenase
IAA	indoleacetic acid
MDA	malondialdehyde
MDHA	monodehydroascorbate
MDHAR	monodehydroascorbate reductase
NADH	nicotinamide adenine dinucleotide
NADPH	nicotinamide adenine dinucleotide phosphate
NO	nitric oxide
NOS	nitric oxide synthases
NR	nitrate reductase
PCs	phytochelatins
PEG	polyethylene glycol
POD	guaiacol peroxidase
POX	peroxidases
PSII	photosystem II
ROS	reactive oxygen species
RWC	relative water content
SA	salicylic acid
SHAM	salicylhydroxamic acid
SNP	sodium nitroprusside

1 Introduction

Wheat is a highly adaptive crop which is cultivated mainly in tropical and subtropical regions under rain-fed as well as irrigated cultivation (Rahaie et al. 2013). Wheat is being used in the production of food products such as breads, pasta, noodles, biscuits, beer, etc. (Curtis and Halford 2014). Dietary protein in wheat fulfills up to 82% of the world population demand (Chaves et al. 2013). Moreover, wheat straw is also used in the biofuel generation as biogas (Chandra et al. 2012). Increase in population, colonization, and industrialization by humans have severely affected the environmental condition and crop production as productivity is dependent on soil fertility and climatic conditions. Environmental stress alone or in combination that affects wheat growth includes salt, water deficiency, water excess, cold, UV-B radiation, pathogens, insects, heavy metals, etc. (Mahajan and Tuteja 2005; Cançado 2011). These stresses induce the assimilation of reactive oxygen species (ROS) in the cells, which results in growth inhibition and low grain yield. The process of equilibrium between the production and scavenging of ROS is commonly known as redox homeostasis (Caverzan et al. 2016). However, ROS production under stress conditions disbalances the cellular scavenging capacity, which results in oxidative stress (Mullineaux and Baker 2010; Sharma et al. 2012). Plants have antioxidant mechanisms for scavenging the excess ROS, thus preventing cellular damage. This comprises enzymatic and nonenzymatic components. Plant genes encode different ROS-detoxifying and ROS-producing enzymes, which aid in ROS scavenging in the cell (Mittler et al. 2004). Several enzymes are involved in the detoxification of ROS like ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), glutathione peroxidase (GPX), and superoxide dismutase (SOD). Superoxide dismutase activity is responsible for the degradation of superoxide radicals ($O_2^{\bullet -}$) to produce O_2 and H_2O_2, hence is considered as the first enzyme, which imitates the removal of ROS (Ashraf 2009; Aggarwal et al. 2015). The H_2O_2 generated is utilized by APX and CAT to generate water and oxygen (Mhamdi et al. 2010). Other enzymes that are important in the ROS scavenging system and function in the ascorbate (AsA)-glutathione (GSH) cycle are GR, monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) (Foyer and Noctor 2011; Feki et al. 2016; Fig. 1). Various chemical and biochemical agents are known to enhance antioxidant enzymes under stress condition. This review addresses various methods like treatment with algal consortium, exogenous application of hormones (abscisic acid (ABA) and salicylic acid (SA)), signaling molecules (H_2O_2, H_2S, CO, and NO), use of essential elements (nitrogen, N; sulfur, S; selenium, Se; and silicon, Si), and seed priming, which can be constructive approaches toward high yield of wheat under adverse conditions.

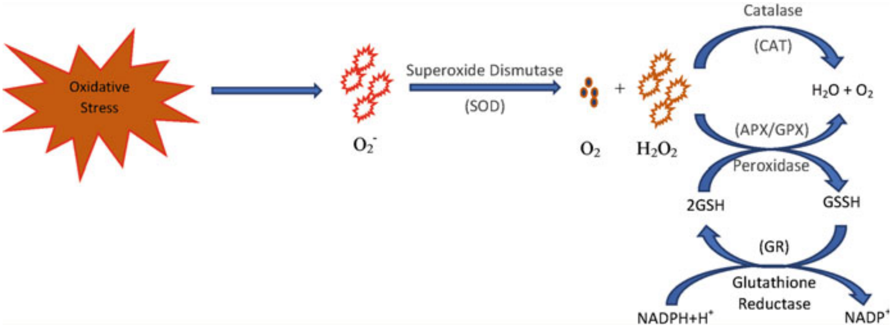

Fig. 1 Overall scheme for antioxidant activity

2 Methods to Enhance Antioxidant Activity

Extensive research has been done which focuses on various methods to enhance antioxidation system in wheat species against a wide spectrum of abiotic as well as biotic stress. These methods are as follows.

2.1 *Algal Remediation*

Algal species consist of a variety of bioactive component such as proline (Pro), betaine, AsA, and GSH, which can potentially participate in alleviating stress condition. Studies conducted by Stamatiadis et al. (2014) suggest that use of *Ascophyllum nodosum* may ameliorate the efficiency of the fertilizer application by improving the development of the root system. Moreover, *Ulva lactuca* (Ibrahim et al. 2014); marine species such as *Caulerpa racemosa*, *Padina pavonica*, *Saragassum muticum*, *Galaxaura obtusata*, *and Laurencia obtusa* (Ibrahim 2016); and extracts of *Chlorella ellipoida* and *Spirulina maxima* (Baky et al. 2008, 2010) can be efficient in inducing salt tolerance in wheat. Furthermore, algal species such as *Azospirillum amazonense* (Boddey et al. 1986) and *Nostoc*, *Anabaena*, and *Cylindrospermum* (Gantar et al. 1991) can also be beneficial in increasing N of the soil and thus can result in better wheat cultivation. According to Nabti et al. (2010), inoculation of *Azospirillum brasilense* with or without algal extracts in wheat under osmotic stress induces the production of indoleacetic acid (IAA), proline (Pro), and total sugar accumulation. Furthermore, *Ulva lactuca* constitute of an efficient source of osmoprotectants for microorganisms under saline stress. This alga contains high levels of various betaines, amino acids, proteins, and dimethylsulfoniopropionate (DMSP) (Nabti et al. 2010). Integration of algal species with wheat is done by various processes. Studies conducted by Nabti et al. (2007, 2010) suggest that the extracts of *Ulva lactuca*, with *A. brasilense NH*, resulted in improved salt tolerance in durum wheat, while Baky et al. (2008) suggest that spraying of algal extracts derived from *Chlorella ellipoida* and *Spirulina maxima* plays a major role in increasing the antioxidant enzyme such as SOD, APX, and guaiacol peroxidase (POD) activity in wheat plant growth under saline conditions. Under salt stress condition, wheat seeds presoaked in seaweed such as *Ulva lactuca* and *Laurencia obtusa* can thereafter grow under salt stress, resulting in the increase of SOD and CAT (Ibrahim et al. 2014; Ibrahim 2016).

2.2 Organic Acids

Naturally occurring acids such as SA and ABA play a vital role in the cellular metabolism of the plant. Under stress condition, these molecules act as antioxidants and help in alleviating antagonistic effects such as cell death and assimilation of malondialdehyde (MDA) and H_2O_2.

2.2.1 Abscisic Acid

Abscisic acid, a plant hormone, functions in many plant developmental processes and is important under stress responses. ABA plays a vital role in alleviating the adverse effect of heat and cold condition. Studies conducted by Lalk and Dorffling (1985) suggest that the application of ABA before freezing condition increases the resistance against cold stress but cannot completely elicit the stress effect; hence, it can be said that ABA plays a role in the initial stages of frost resistance development in wheat cultivar (Veisz et al. 1996). It is observed that application of ABA in plants can also increase the root/shoot ratio. Moreover, it has a synergistic effect on ion and sugar accumulation in roots which suggests that the maintenance of root cell turgor pressure in drought-stressed plants could be mediated by ABA (Jones et al. 1987). According to Agarwal et al. (2005), exogenous application of ABA and SA on wheat cultivar under water stress enhances SOD, APX, CAT, and GR activity while reduces lipid peroxidation and H_2O_2 content. Moreover, ABA also causes an increase in Pro concentration, shoot growth, and dry weight under water stress condition (Nayyar and Walia 2003; Valluru et al. 2016). Exogenous application of ABA has synergistic effects on SOD, POD, CAT activity, IAA concentration, and endosperm cell division but reduced MDA and H_2O_2 concentration (Yang et al. 2014). Recent studies conducted show that drought and cold tolerance in wheat is controlled by two different genes, i.e., *TaNCED2A* homologue (Son et al. 2016) and genes including *CBF14*, *Cor14b*, and *WCS120*, which are associated to chromosome 5A and are involved in the regulation of hormone-related genes and metabolites underlying the freezing tolerance (Kalapos et al. 2017).

2.2.2 Salicylic Acid

Salicylic acid functions as plant hormone and is derived from the metabolism of salicin. It acts as an endogenous growth regulator, participates in the regulation of physiological processes, and protects the plant against biotic and abiotic stress by aiding in the germination of seedling (Jini and Joseph 2017). Salicylic acid has proved to be efficient against abiotic stress such as cold, drought, and salinity when applied in high concentration (Miura and Tada 2014). SA mediates salicylhydroxamic acid (SHAM)-sensitive POD, intracellular ROS accumulation in guard cells, and K^+ ion channel inactivation, thus inducing stomatal closure accompanied by extracellular ROS production. Salicylic acid is also reported to induce antioxidant activity such as SOD (Singh and Usha 2003) and GPX (Abbasi et al. 2015) under drought condition. Studies suggest that high concentration (2–3 mM) of SA suppressed drought tolerance as well as plant growth, whereas plant growth enhanced at low concentration (0.5 mM) of SA (Kang et al. 2013). Moreover, wheat seeds primed by 100 ppm acetyl SA exhibited resistance to salinity-drought stress (Hamada 2001). On the contrary, studies conducted by Singh and Usha (2003) suggest the application of 1–3 mM of SA-induced carboxylase activity of RuBisCo, SOD, and nitrate reductase (NR) activity which remained protected especially at 3 mM concentration. Small dosage SA under saline condition promotes accumulation of ABA and IAA, thus resulting in better yield (Shakirova et al. 2003). Recent studies by Khan et al. (2015a, b) under metal stress suggest that SA also regulates photosynthesis, photosystem II (PSII), photosynthetic pigments, and the activity of enzymes such as RuBisCO and carbonic anhydrase. Moreover, the application of SA under cadmium (Cd) stress in the wheat induced accumulation of ABA but reduced IAA and cytokinin (CK) in stressed plants (Shakirova et al. 2015). Whereas under manganese toxicity, SA application induced antioxidant activity of antioxidants such as SOD, APX, CAT, DHAR, and GR (Sheng et al. 2015).

2.3 Exogenous Application of Plant Nutrients

Incorporation of essential or beneficial nutrients such as N, S, Se, and Si in wheat restores photosynthetic ability and antioxidants capacity and positively affects overall crop productivity.

2.3.1 Nitrogen (N)

Nitrogen plays a key role in the protein content and yield of wheat grains. The quantity, time of application, and source of nitrogen play a key role in its availability to the plant. It is well known that N accumulation during early-to-mid vegetative growth stages affects yield potential. Upon heading in wheat, N availability influences grain protein more than yield (Shapiro and Bavougian 2017). Recent studies by Stumpf et al. (2015) and Ma et al. (2014) suggest that application of N (240–300 kg ha^{-1}) to wheat cultivar has a positive effect on phenolic compounds such as ferulic acid and vanillic acid. Studies have also reported that nitrogen source also affects the antioxidant activity in wheat. It has been reported that the activities of SOD, POD, APX, GR, and CAT in the leaves and roots of NH_4^+-treated plants were significantly higher than in the plants grown in the nitrate medium (Polesskaya et al. 2004).

2.3.2 Sulfur (S)

Sulfur is a fundamental part of certain lipids, amino acids (cysteine and methionine), antioxidant (GSH), coenzymes, prosthetic groups, vitamins, secondary metabolites, and phytochelatins (PCs). Studies conducted by Khan et al. (2007) suggest that S assimilation and enhanced activity of ATP-sulfurylase help in alleviating stress caused due to the cadmium in wheat cultivar. Assimilation of sulfur can induce the production of GSH, PCs, and metal-binding peptides, which can efficiently sequester heavy metals. Moreover, Se and S are reported to modulate ethylene (ET) formation, as well as Pro and antioxidant metabolism under Cd tolerance. Under Cd stress, the application of S and Se to wheat significantly reduces ET level while enhances GR and GPX activity, thereby reducing oxidative stress (Khan et al. 2015a, b).

2.3.3 Selenium (Se)

Selenium is a micronutrient which is essential for human and animal health. Its concentration ranges from 0.1 to more than 2 ppm. Selenium is a dietary element abundant in wheat specifically in grains and is used in the synthesis of selenocysteine and various other selenoproteins, which play an important role in redox function involved in free radical scavenging. Various reports suggest that selenium has an antioxidant, anticancer, and antiviral properties (Lyons et al. 2004; Ducsay and Ložek 2006). Furthermore, high concentration does not result in phytotoxicity (Lyons et al. 2005). The mechanism of selenate uptake by plants has been well known. Selenate persists chemical similarity with sulfate, therefore it is taken up via high-affinity sulfate transporters and is translocated in shoots and xylem sap (Li et al. 2008; Zhu et al. 2009). Various studies conducted on plant-Se interaction suggest that low concentration of Se plays a major role against various abiotic stresses, which include various environmental factor such as salinity, cold, water stress, drought, and heavy metals like arsenic (As), mercury (Hg), lead (Pb), aluminum (Al), cadmium (Cd), zinc (Zn), cupper (Cu), chromium (Cr), etc., by enhancing GSH and SOD, thereby reducing free radical occurred due to stress condition. Studies on Se supplementation suggest that Se is efficient in inhibiting the accumulation of MDA and helps in building ultrastructure of the chloroplast, thus increasing the rate of photosynthesis (Feng et al. 2013).

2.3.4 Silicon (Si)

Silicon is a second major element in the earth's crust and varies considerably from 1% to 45%. Si, in the growth medium, alleviates the adverse effects of various stresses which include drought, salinity, frost, and toxicity due to heavy metals/ metalloids like Al, Cd, and boron (B). Under drought stress, Si stimulates the formation of a double layer of silica cuticle under leaf epidermis, thus decreasing the loss of water in wheat. Moreover, deposition of Si modifies cell wall properties, thereby decreasing stomatal conductance in connection with turgor loss of guard cells. Under salt stress, Si reduces Na^+ uptake, increasing K^+/Na^+ ratio to alleviate salt toxicity effect in a plant. To overcome heavy metal toxicity, it reduces uptake of heavy metal into plant roots via detoxification mechanism. Experiments conducted by Gong et al. (2005) also suggest that Si increases the activities of some antioxidant enzymes, such as SOD, CAT, and GR, with no significant changes in glycolate oxidase (GO), POD, and APX. Similarly, Gong et al. (2008) stated that application of Si increased SOD activity but decreased in POD activity of drought-stressed plants. According to Pei et al. (2010), application of 1 mM Si on stimulated drought condition using PEG-induced GSH production and reduces MDA, H_2O_2, and Pro content. Similar studies conducted by Ma et al. (2015) suggest that application of Si on wheat resulted in induction of SOD, CAT, APX, AsA, GSH, and total phenolic and flavonoid contents under drought conditions. The effect of Si under freezing condition has also been reported. At frosting conditions, application of 0.1–1 mM Si exogenously can prove to be efficient in reducing stress by increasing antioxidant enzyme activities (SOD and CAT) and nonenzymatic antioxidants (i.e., GSH and AsA) in the wheat leaves (Liang et al. 2008). Under ion toxicity, Daoud et al. (2018) reported that application of 0.78 mM sodium metasilicate enhances the activity of SOD and CAT. It also reduced leaf Na^+ content but reported to increase in the K^+ content, which ultimately increased the cytosolic K^+/Na^+ ratio, hence resorting the ion content within the cell. The effect of Si on metal/metalloid toxicity such as B and Cd in wheat has also been reported. According to Shi et al. (2017) and Liu et al. (2017), application of Si on Cd and B toxicity in wheat, respectively, decreases MDA and H_2O_2 contents but increased SOD and POD activity. Moreover, Si also proved to be efficient in removing Cd from the cell as Si significantly inhibits the net Cd^{2+}. Studies conducted by Alzahrani et al. (2018) suggest application of Si ranging between 4 and 6 mM can enhance antioxidant activity such as SOD, POD, and CAT in wheat under salt, drought, as well as under Cd stress wheat cultivar.

2.4 Signaling Molecules

Cell signaling is a communication process that controls cell activity toward microenvironment, cell damage, and to normal tissue homeostasis as well. Cell signaling is regulated by low-molecular-weight molecules which can easily diffuse through the

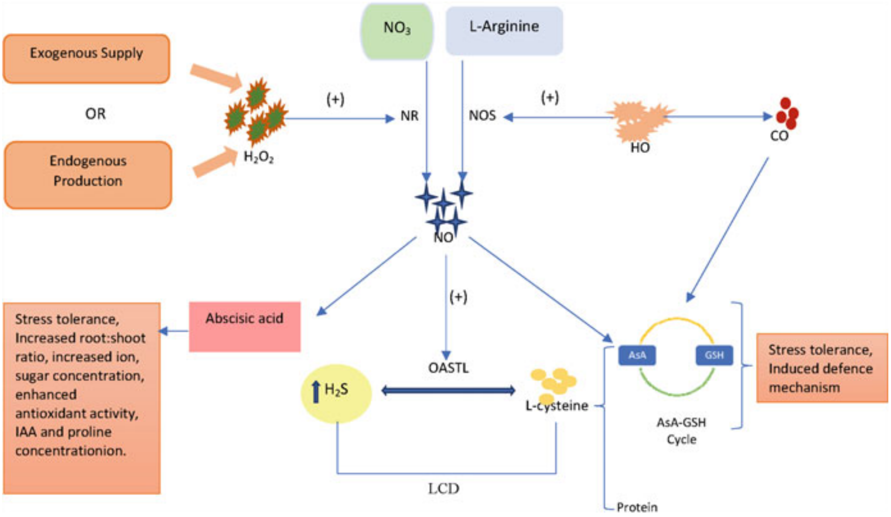

Fig. 2 Interaction between signaling molecules to eliminate the effect of abiotic stresses in wheat

cell membrane. In plants, ROS are known for their concentration-dependent role, i.e., deleterious when exists in excess and beneficial when scanty. Reactive oxygen species as signaling molecules are involved in processes such as growth, cell cycle, development, regulation of gene expression, hormonal signaling cell, stomatal conductance cell senescence, and cell death (Caverzan et al. 2016). This effectiveness of ROS in cell regulation is dependent on the rate of production via oxidant and their subsequent removal (Sharma et al. 2012). In plants, signaling molecules (H_2O_2, CO, NO, H_2S) and their interaction (Fig. 2) play a significant role in cell germination, seed dormancy, and acquisition of stress tolerance as well.

2.4.1 Hydrogen Peroxide (H_2O_2)

Hydrogen peroxide is an abundant molecule, which is highly reactive as well as toxic, found in aerobic biological systems in higher plants. Its effect on the cell is dependent on concentration, site of production, stage of occurrence, and exposure to varying kind of stress (Petrov and Breusegem 2012). Low concentration of H_2O_2 plays a major role in cell signaling. In wheat, endogenous production of H_2O_2 plays a major role in the upregulation of heme oxygeneases by enhancing its mRNA level and protein expression, thus leading to adaptivity to oxidative stress. Moreover, it also enhances the activity of SOD (Chen et al. 2009; Lu et al. 2013). Hydrogen peroxide pre-treatment also improves Al acclimation during subsequent Al exposure in wheat, thereby reducing ROS accumulation (Xu et al. 2011). The exogenous H_2O_2 treatment/pre-treatment also protects wheat seedlings from salt stress, by decreasing the oxidative damage (Wahid et al. 2007; Li et al. 2011).

Moreover, it is observed that seed pre-treatment with H_2O_2 enhances drought tolerance in wheat seedlings (He et al. 2009). Recent studies suggest that H_2O_2 alone or with H_2S regulates AsA-GSH cycle under drought stress as it increased transcript levels and activities of APX, GR, DHAR, and MDHAR (Shan et al. 2018; Shan and Ou 2018).

2.4.2 Hydrogen Sulfide (H_2S)

Hydrogen sulfide has a strong affinity to Fe^{2+}-containing proteins, such as cytochrome oxidase, hemoglobin, and myoglobin, and is thus considered as a toxic intermediate of cell metabolism. In plant cells, H_2S homeostasis is regulated similar to other signal molecules like H_2O_2 and nitric oxide (NO). Hydrogen sulfide homeostasis is closely regulated by L-cysteine desulfhydrase (LCD), D-cysteine desulfhydrase (DCD), sulfite reductase, cyanoalanine synthase, and cysteine synthase. Sodium hydrosulfide (NaHS) is known as a donor for H_2S. A study suggests endogenous generation H_2S at an early stage of osmotic exposure in wheat seedlings is responsible for the rapid increase of dry biomass (Zhang et al. 2010a). The effect of H_2S on heavy metal toxicity has also been studied. Sodium hydrosulfide pre-treatment increased the activities of SOD and CAT but decreased that of lipoxygenase (LOX) in wheat under Cu stress (Zhang et al. 2008). Under Cr stress, exogenous application of NaHS can improve the germination rate and activities of amylase, esterase, as well as antioxidant enzymes such as SOD, CAT, APX, CAT, and GPX whereas reduced the activity of LOX and overproduction of MDA as well as H_2O_2 induced by Cr and sustained higher endogenous H_2S level (Zhang et al. 2010b). Zhang et al. (2010c) also reported that application of NaHS significantly alleviated citrate secretion and oxidative stress under aluminum stress in wheat. Hydrogen sulfide is also reported to induce a response against salt and drought stress. In salt-sensitive wheat cultivar, Bao et al. (2011) showed that wheat seed priming with NaHS could significantly alleviate the inhibition of seed germination and seedling growth induced by 100 mM NaCl. Moreover, exogenously applied NaHS increased the activities of APX, GR, DHAR, and gamma-glutamylcysteine synthetase in wheat seedlings, as well as the contents of reduced AsA and reduced GSH, total AsA, and total GSH under water stress compared to the control without NaHS treatment, which in turn decreased the MDA content and electrolyte leakage induced by water deficiency in wheat seedlings (Shan et al. 2011). Zhang et al. (2010d) found that the germination rate in wheat under osmotic stress can be increased by application of NaHS in a dose-dependent manner. Further experiments showed that NaHS treatment significantly increased CAT and APX activities. Cross studies of NO and H_2S also suggest that application of NO to wheat seedlings, under osmotic stress, considerably enhanced the activities of H_2S-synthesizing enzymes LCD and DCD leading to an enhanced level of endogenous H_2S content. At the same time, exogenous NO also enhanced the activity of cysteine-synthesizing enzyme *O*-acetylserine(thiol)lyase (OAS-TL) and maintained cysteine homeostasis under osmotic stress. Nitric oxide and H_2S together markedly improved the activities of antioxidant enzymes, viz., APX, GR, POX, SOD, and CAT (Khan et al. 2017).

2.4.3 Carbon Monoxide (CO)

Carbon monoxide has been widely explored in biochemistry, pharmacology, toxicology, and medicine. It is a valuable tool for studying the biochemical characteristics and reactions of a variety of heme proteins, most notably hemoglobin, myoglobin, and cytochromes (Piantadosi 2002). High concentration of CO is the most common cause of fatal poisoning in the world. Ling et al. (2009) suggest that 50% CO aqueous solution inhibited the overproduction of superoxide anion, NADPH oxidase activities and its corresponding transcript, SOD activity, and Mn-SOD and Cu/Zn-SOD transcript. On the contrary, small amount of endogenous CO can behave as a signaling molecule in various animal cellular and biological processes. It is being well documented that CO is efficient against the excessive saline condition in wheat. Studies conducted by Sa et al. (2007) and Huang et al. (2006) suggest application of 0.01 μmol/L hematin (CO donor) can potentially alleviate salt-induced oxidative damage in shoots and delay leaf chlorophyll deterioration mediated in the presence of two reactive species, i.e., H_2O_2 and paraquat. Crosstalk studies have also confirmed that small concentration of HO (heme oxygenase, the enzyme responsible for CO generation) helps in upregulation of NOS (Nitric oxide synthases, the enzyme responsible for NO generation) (Hartsfeild 2002). Apparently Xie et al. (2008) suggest that under salt stress condition, application of 50% CO donor, i.e., hematin, and NO donor, i.e., sodium nitroprusside (SNP), upregulates H^+ pump, thus resulting in the increase of K/Na ratio and the alleviation of oxidative damage and significantly increases antioxidant enzyme activities, i.e., APX, GR, SOD, MDHAR, and DHAR. Similar results were observed by Liu et al. (2010) suggesting that HO/CO system regulates NOS/NO system and also induces antioxidant activities in wheat under water-deficit condition as well.

2.4.4 Nitric Oxide (NO)

In nature, nitric oxide exists in interchangeable structures, namely, the nitrosonium cation (NO^+), nitroxyl anion (NO^-), and a nitroxyl radical (NO^-), thus making NO an ideal molecule for paracrine and autocrine signaling. NO is also known to perform posttranslational modification signaling (Saxena and Shekhawat 2013). Nitric oxide is involved in wheat responses to various biotic or abiotic stresses, such as salt stress (Hua et al. 2003; Zheng et al. 2009), cold stress (Esim and Atici 2015), heat stress (Tian and Lie 2006), and nutrient toxicity. Nitric oxide is generated in plants via both nonenzymatic and enzymatic systems. Under various stress conditions in wheat, NO is also known for its downstream regulation of various molecules such as H_2O_2 (Sun et al. 2018), CO (Liu et al. 2010), H_2S (Khan et al. 2017), and ABA (Wu et al. 2017a, b), whereas regulation of NO is dependent on the availability of essential element like molybdenum (Mo) (Wu et al. 2017a, b). Studies conducted by Balotf et al. (2018) suggest that at low N levels, application of NO increased the gene expressions and activities of N assimilation pathway enzymes in two different wheat cultivars, i.e., cv. Spitfire and cv. Westonia. Moreover, application of exogenous NO caused an increase in leaf NO content at the low level of ammonium nitrate, suggesting N assimilation gene expression and enzyme activity showed a clear relationship between exogenous NO, N concentration, and N forms in primary plant nitrogen assimilation. Studies conducted by Hananuzzaman et al. (2011, 2012) and Sun et al. (2014, 2015) on wheat under salinity, drought stress, and aluminum toxicity, respectively, suggest that, under such conditions, exogenous application of NO has a synergistic effect on AsA-GSH cycle, hence upregulating methylglyoxal (MG) detoxification system.

Nitric oxide has been effective in inducing antioxidation mechanism against heavy metal toxicity. Evidence suggest the exogenous application of SA and NO under Ni stress can result in the induction of enzymes like CAT, POD, and SOD and osmoprotectants such as Pro (Siddiqui et al. 2013). Studies conducted by Sun et al. (2014) on Al-resistant and sensitive wheat cultivar suggest that NR-mediated early NO burst in Al-resistant wheat enhances antioxidant mechanism and plays an important role in Al stress. Recent studies also suggest that NO ameliorated Pb-induced membrane damage in wheat roots by altering the SOD and CAT activity (Kaur et al. 2015). Nitric oxide is also reported to reduce the effect of UV-B stress on wheat by inducing antioxidants, such as POD, SOD, APX, and GR (Yan et al. 2016).

2.5 Seed Priming

Pre-treatment of seeds for partial hydration under control condition to enhance the uniform emergence of the seedling is known as seed priming. Seed priming is an effective methodology, which is beneficial in enhancing growth attributes of cereal crops under various stress conditions (Mirza et al. 2016). Priming of wheat seeds (Fig. 3) has been practiced by various researchers. This practice has been reported to alleviate the effect of drought and saline conditions. In wheat, priming is performed by following various processes, which are:

1. Hydro-priming: Soaking seeds using distilled water for few hours is known as hydro-priming (Jafar et al. 2012; Mirza et al. 2016; Hussain et al. 2016; Tabassum et al. 2017).
2. Halo priming: Halo priming corresponds to soaking of seeds using different salts solutions (Mirza et al. 2016).
3. Osmo-priming: It is a pre-treatment of seeds in different solutions consisting of $CaCl_2$, KNO_3, or PEG-KNO_3 (Salehzade et al. 2009; Jafar et al. 2012; Mirza et al. 2016).

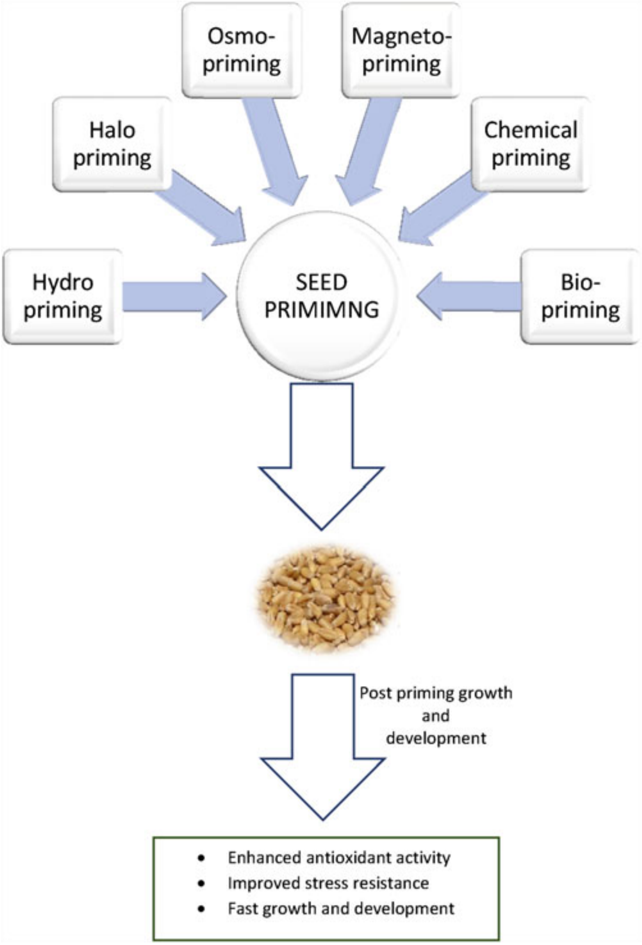

Fig. 3 Seed priming methods in wheat

4. Magneto-priming: It is an emerging method whereby seeds are exposed to the low magnetic field for 3–4 h (Rathod and Anand 2015; Katsenios et al. 2015).
5. Chemical priming (Sher et al. 2017): It comprises of various chemicals such as SNP (Hameed et al. 2015), Si (Ahmed et al. 2013), AsA (Jafar et al. 2012; Fercha et al. 2014), chitosan (Hameed et al. 2014), zinc via zinc sulfate and zinc chloride (Rehman et al. 2015), etc.
6. Bio-priming: It comprises of pre-treatment of seeds via plant extract (Bajwa et al. 2017) or microbial coating by immersing the seed in the culture/slurry followed by soaking for 30 min (Meena et al. 2016).

It is being well documented that priming of wheat seeds can prove to be efficient, as it results in better yield, improves water retention, reduces MDA concentration, and increases antioxidant activity such as SOD that can be useful for plant growth under adverse conditions.

3 Conclusions

Wheat is a versatile crop, which is harvested somewhere, every month in a year in the world. Wheat is cultivated in varieties of irrigation zones at varying climatic as well as geographical condition. In recent years, unhealthy practices by humans have caused damage to environment, henceforth affecting the overall wheat grain productivity. Abiotic stresses alone or in combination result in ion misbalance as well as irregulate metabolic pathways, thereby resulting in enhanced oxidative stress, lipid peroxidation, and H_2O_2 concentration. To cope with such condition, plants have an antioxidation system. In recent year researchers have identified various methods to enhance the activity of the enzymatic as well as nonenzymatic antioxidants. Methods such as seed priming and application of organic acid, essential metal ions, or carrier molecules like NO, CO, H_2S, and H_2O_2 in low concentration have shown their prominent effect on enhancing antioxidant activity in wheat. Selection of potent, robust, and cost-effective method to reduce the antagonistic effect of abiotic stress can prove to be a beneficial step in sustainable technology and agriculture practices in wheat cultivation.

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Abiotic Stress Signaling in Wheat Crop

Sana Tounsi, Kaouthar Feki, and Faiçal Brini

Contents

Abstract Plants have developed different mechanisms to overcome abiotic stresses. These responses induce change in gene expression, regulation of protein amount, alteration of cellular metabolism, and change in ions homeostasis. Cell signaling depends on the sucrose non-fermenting 1-related protein kinase (SnRK) family under environmental and hormonal stresses. Plant SnRKs are key sensors of cellular energy status. Phytohormones play key roles during germination, growth, development, and flowering and coordinate various signal transduction pathways in plants during environmental stresses. Here, we review recent advances in elucidating the signaling pathways for abiotic stresses. We will also focus on how plant SnRK may be related to mechanisms of gene expression, metabolism, physiology, growth, and development in wheat. Finally, the cross talk between signal transduction pathways involving phytohormone is highlighted with a focus on the response of wheat to abiotic stresses.

Keywords Abiotic stress · Phytohormones · Protein kinase · Stress signaling · Wheat

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Abbreviations

ABA	Abscisic acid
AREB/ABF	ABA-responsive element-binding factor/ABRE-binding factor
CDPK	Calcium-dependent protein kinase
DREB/CBF	Drought-responsive element-binding factor/c-repeat-binding factor
HKT	High-affinity K^+ transporter
HSFs	Heat shock factors
HSPs	Heat shock proteins
MAPK	Mitogen-activated protein kinase
MYBRS/MYCRS	MYB recognition site/MYC recognition site
NAC	nam/ataf/cuc
ROS	Reactive oxygen species

1 Introduction

Abiotic stresses such as salinity, drought, and temperature display a negative effect on plant growth and productivity of crops in many regions of the world (Rengasamy 2010; James et al. 2012). To cope with different stresses, plants have evolved a number of intricate mechanisms to protect their cellular activities and maintain plant integrity. These mechanisms include the production of osmoprotectants, regulation of ionic homeostasis, and the control of Na^+ translocation and accumulation (Hasegawa et al. 2000; Kreps et al. 2002; Flowers and Colmer 2008). Two major groups of genes are induced by stress: functional proteins that directly improve plant tolerance to abiotic stresses (such as LEA proteins, aquaporins, and HKT) and regulatory proteins (mainly transcription factors, such as DREBs, AREBs, and NACs) responsible for downstream signal transduction and in the modulation of the expression of functional proteins (Hirayama and Shinozaki 2010; Nakashima et al. 2012). Understanding the molecular basis of the stress signaling and the plant gene regulatory mechanisms involved in stress responses is essential to improve plant stress resistance (Chinnusamy et al. 2005). During the precedent, two decades, publication of complete genome sequences of *Arabidopsis thaliana*, a plant model for dicotyledonous, and rice, a plant model for monocotyledonous, encourages researchers to study plant responses to different environmental conditions including abiotic stresses.

Contrary to *Arabidopsis thaliana* and rice, a complete genome annotation is not available for many cereals like maize, barley, and wheat (Mayer et al. 2012; Eversole et al. 2014). Wheat is one of the most widely grown and consumed cereal in the world. Two types of wheat have a major economical importance: durum wheat (*Triticum turgidum ssp. durum*, AABB) and bread wheat (*Triticum aestivum*, AABBDD). The two major cultivated wheat exhibit different sensitivity to salt stress; durum wheat is more sensitive to salinity (Tounsi et al. 2017). Little reports have been carried out on wheat plants due to few protein sequence databases available. Study of mechanisms conferring plant stress tolerance is of high importance due to the identification and characterization of key genes involved in various stress signaling. The understanding of salt tolerance mechanisms is significantly in progress in particular cell signaling in response to salt and ionic homeostasis (Pardo et al. 2006; Munns and Tester 2008; Kronzucker and Britto 2011; Kosová et al. 2011; Nieves-Cordones et al. 2016).

In this chapter, we discuss about current knowledge of abiotic stress effect on the physiological, molecular, and functional response of wheat. We will also provide new insight into the understanding the signaling pathways for abiotic stresses in wheat.

2 Abiotic Stress Signaling and Gene Expression in Wheat

Wheat is one of three major cereal crops consumed throughout the world. As sessile organisms, plants are constantly exposed to various abiotic stresses in their natural environment. Drought, salt, and temperature stresses are major environmental factors that influence wheat productivity in agriculture. To survive under these conditions, plants exhibit a various range of responses at the cellular, molecular, and functional levels. In consequence, there exist a complex signaling pathway underlying plant adaptation to these abiotic stresses (Zhu 2001; Mahajan and Tuteja 2005; Fujita et al. 2006). The external signals are initially sensed by molecular sensors and sequentially amplified to the nucleus by various second messengers, such as, calcium, phospholipids, reactive oxygen species (ROS), and hormones (Kosová et al. 2015; Fig. 1). These molecules stimulate host receptors and quickly generate an internal signal that triggers early defense responses. The coordination between different cells of plants generates complex mechanisms of signal transduction (Fig. 1). Several transcription factors and regulatory proteins are expressed in order to control plant growth, development, accumulation of ROS, and plant homeostasis underlying an active plant stress response (Mittler 2002; Munns 2005; Almeselmani et al. 2006; Rinalducci et al. 2011; Alvarez et al. 2014).

2.1 *Salt Stress Response*

Salinity is one of the major abiotic stresses causing every year massive losses in plant yield. The overaccumulation of Na^+ in the cytosol causes ion damage, osmotic stress, inhibition of biochemical and physiological processes, and deleterious effects on photosynthetic activity and membrane integrity (Véry and Sentenac 2003; Pardo et al. 2006; Horie et al. 2007; Munns and Tester 2008; Kronzucker and Britto 2011; Nieves-Cordones et al. 2016). Soil salinity results in equally reduced soil water

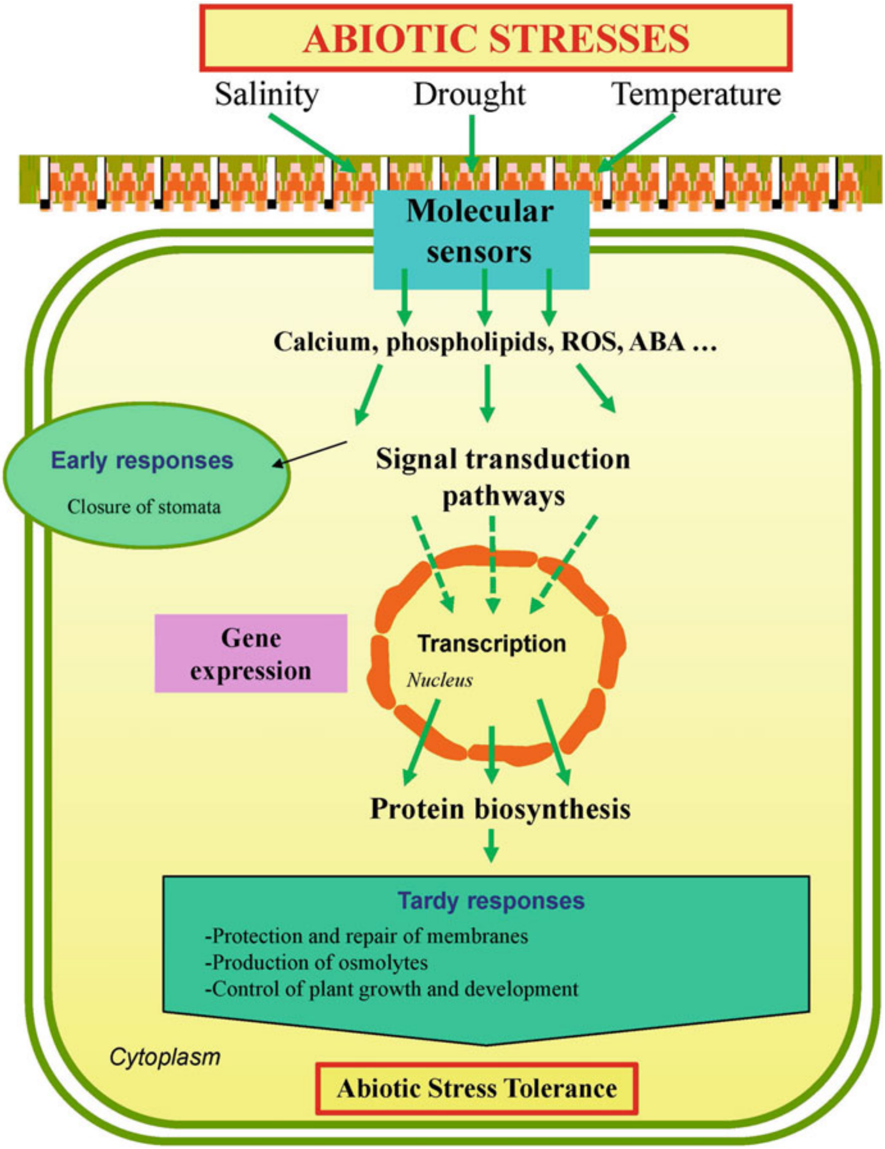

Fig. 1 Schematic representation of plant signal transduction pathways in response to abiotic stress such as salinity, drought, and temperature

accessibility and ionic toxicity. Most crop plants are sensitive to soil salinity, and it is worth noting that Na^+ is the most important cause of the toxicity in most cases. This process of salinization, which already affects 20% of the irrigated lands, would result in loss of 3 ha of arable land from conventional crop farming every minute (Shabala 2013). Plants can be classified into two groups based on the consequence of salt on plant development: Crop species sensitive to soil salinity are named glycophytes, which are sensitive to salt stress and can't thrive in environments, where the concentration of Na^+ is higher than 100 mM, like rice and wheat. Whereas, plants grown in water of high salt concentrations or which can tolerate high salinity are named halophytes, like *Aeluropus littoralis* or the saltbush *Atriplex* (Munns and Tester 2008). It has been reported that maintaining high cytosolic K^+/Na^+ ratios in shoots is crucial for salt tolerance of glycophyte plants (Gorham et al. 1990; Munns and James 2003; Garthwaite et al. 2005; Obata et al. 2007). These glycophytic plants, including the most of crop species, differ significantly in their tolerance to salt stress (Flowers and Colmer 2008). It is also worth noting that the maintenance of ion homeostasis is a die strategy for plants to grow in high salt concentrations. To avoid salt stress, several genes have been shown to play a crucial role in the control of Na^+ movement in the whole plant. Ion transport is the key factor of plant salt tolerance (Clarkson and Hanson 1980; Tester and Davenport 2003). In general, to maintain cellular ion homeostasis, plants have developed three processes that function in a cooperative way, which are (1) control of ion homeostasis to protect different tissues against salt stress via the Salt Overly Sensitive (SOS) signaling pathway, (2) activation of Na^+ exclusion through high-affinity K^+ transporter (HKT), and (3) sequestration of Na^+ in the vacuole through Na^+/H^+ exchanger (NHX) (Tester and Davenport 2003).

2.1.1 Na^+/H^+ Antiporter (SOS1)

The SOS signaling pathway is a key regulatory mechanism for ion homeostasis and Na^+ tolerance (Zhu 2002; Guo et al. 2004; Chinnusamy et al. 2005). Three proteins SOS1, SOS2, and SOS3 are crucial for SOS signal transduction cascade, which mediate cellular signaling under high salt concentration. SOS3 encodes a myristoylated calcium-binding protein that can sense the cytosolic Ca^{2+} signal elicited by salt stress (Quintero et al. 2000, 2011). SOS3 has four EF hands, each of which can bind a Ca^{2+} (Ishitani et al. 2000; Chinnusamy et al. 2005; Fig. 2). Upon binding with Ca^{2+}, SOS3 activates the protein kinase activity of SOS2, which is a Ser/Ther protein kinase belonging to the SNF1-related kinase SnRK3 family (Hongchun et al. 2017). SOS2 has an auto-inhibitory function in controlling the protein kinase activity. In fact, the regulatory region of SOS2 contains a FISL motif that binds to the positive regulator SOS3 and a PPI motif that binds to the negative regulatory type 2C protein phosphatase ABI2 (Guo et al. 2001; Ohta et al. 2003; Sanchez-Barrena et al. 2007; Fig. 2). SOS2 appears to interact with ABI2 (Ohta et al. 2003), suggesting the existence of some cross talk between the SOS and ABA pathways. SOS3/SOS2 complex activates the plasma membrane Na^+/H^+ exchanger SOS1 (Feki et al. 2011, 2014). SOS1 is relieved from auto-inhibition upon phosphorylation of the auto-inhibitory domain by SOS3–SOS2 (Fig. 2).

The role of Na^+/H^+ antiporters in the plasma membrane has been demonstrated in *Arabidopsis*, rice, and wheat under salt stress (Shi et al. 2000; Razzaque et al. 2013; Xu et al. 2008; Feki et al. 2011). A durum wheat plasma membrane Na^+/H^+

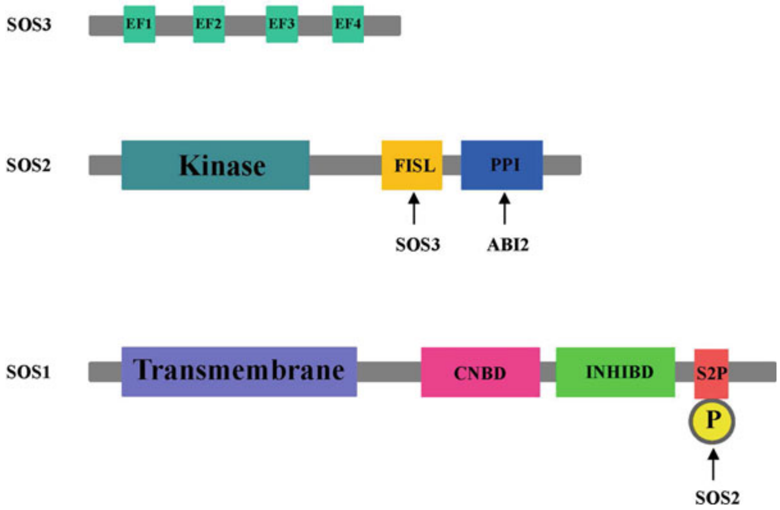

Fig. 2 Domain structure of SOS3, SOS2, and SOS1. SOS3 is formed by four EF hand motifs. SOS3 activates SOS2 by binding to its C-terminal regulatory domain that contains an auto-inhibitory FISL motif. SOS2 activates the antiporter SOS1 by phosphorylation. SOS1 contains 12 transmembrane regions, followed by a putative cyclic nucleotide-binding domain (CNBD), an auto-inhibitory domain (INHIBD), and the SOS2 phosphorylation site (S2P)

exchanger (TdSOS1) was identified by Feki et al. (2011). They demonstrated that TdSOS1 protein can catalyze efficiently both Na^+ efflux and Li^+ efflux in yeast (Feki et al. 2011). The activation mechanism of TdSOS1 protein involves the phosphorylation by the kinase SOS2 and inactivation of an auto-inhibitory domain located at the C-terminal end of this antiporter (Feki et al. 2011). It was reported that the *Arabidopsis thaliana* SOS2–SOS3 proteins complex phosphorylate and activate TdSOS1. A hyperactive form generated from the deletion of the auto-inhibitory domains of TdSOS1 had maximal sodium exclusion activity independent from the regulatory SOS2/SOS3 complex (Feki et al. 2011). It was shown that the hyperactive form of durum wheat SOS1 (TdSOS1Δ972) improves stress tolerance to *Arabidopsis* than the wild-type form (TdSOS1) (Feki et al. 2014, 2016). The SOS signal transduction pathway seems to be crucial for ion homeostasis under salt stress in plants (Zhu 2003; Pardo et al. 2006). The increase in the sensitivity of the mutant plants to salt stress is the result of the dysfunction in any of the SOS genes (Zhu 2000).

2.1.2 HKT Transporters

High-affinity K^+ transporter (HKT) family has been shown to play a crucial role in salinity tolerance (Berthomieu et al. 2003; Ren et al. 2005; Byrt et al. 2007). Based on phylogenetic and functional analyses, HKT genes identified from different plant species were divided into two subfamilies (Platten et al. 2006). A glycine/serine residue in the first pore loop of the protein differs between subfamily 1 and subfamily 2 of HKT genes (Mäser et al. 2002; Horie et al. 2009; Hauser and Horie 2010). Subfamily 1 HKT transporters have a serine residue in the first P-loop region and are only permeable to sodium. However, subfamily 2 comprises transporters that have a glycine in the first P-loop region and are permeable to both sodium and potassium (Rubio et al. 1995; Wang et al. 1998; Mäser et al. 2002; Horie et al. 2009; Jabnoune et al. 2009; Hauser and Horie 2010). The first member of HKT named TaHKT2;1 was isolated from wheat (*Triticum aestivum*) (Schachtman and Schröeder 1994). Heterologous expression in yeast and *Xenopus laevis* oocytes indicated that TaHKT2;1 plays an important role in Na^+ and K^+ transport (Mäser et al. 2002; Platten et al. 2006). Comparison between monocots and dicots indicates that subfamily 1 is present in both dicots and monocots, while the subfamily 2 is present only in monocots. Dicotyledonous species possess a low number of HKT genes than monocotyledonous species (Jabnoune et al. 2009; Yao et al. 2010; Oomen et al. 2012; Sassi et al. 2012). In *Arabidopsis*, a single HKT gene was identified and characterized as a sodium transporter (Uozumi et al. 2000). AtHKT1 transporter has been shown to play an essential role in Na^+ homeostasis in saline conditions by contributing to Na^+ unloading from the ascending xylem sap and to Na^+ loading into descending phloem sap, reducing the net influx of Na^+ in the shoots (Mäser et al. 2002; Berthomieu et al. 2003; Rus et al. 2004; Sunarpi et al. 2005; Plett et al. 2010). *AtHKT1;1* had been expressed in vascular tissues of all *Arabidopsis* organs, more precisely in xylem parenchyma and phloem cells (Berthomieu et al. 2003; Sunarpi et al. 2005). The mutation in HKT1 induces salt stress sensitivity in transpiring plants (Rus et al. 2004). However, it can suppress the salt sensitivity of SOS mutants grown in culture media where there is minimal transpiration (Rus et al. 2004). It seems that HKT seems to restrict Na^+ transport from root to leaves, whereas, SOS1 seems to promote this movement (Zhang et al. 2017).

2.2 Temperature Stress Response

Wheat is particularly sensitive to extreme cold and hot temperatures during the reproductive stage. Heat stress is considered a serious threat to crop production worldwide (Stratonovitch and Semenov 2015; Iqbal et al. 2017). High temperature induces heat stress, which causes a wide range of responses, altering gene expression, cellular metabolism, growth, and development (Qin et al. 2008; Chauhan et al. 2011). Several heat stress-inducible genes were identified in wheat such us heat shock proteins (HSPs), heat shock factors (HSFs), and other transcription factors (Chauhan et al. 2011; Yang et al. 2017). Heat shock factors (HSFs), which are present in all eukaryotes, play a crucial role in the regulation and induction of heat shock proteins (HSPs). The synthesis of HSPs is important in preventing the toxic effect of high temperature. These proteins are known to be part of the stress tolerance strategy to heat stress in plants (Iba 2002; Qing et al. 2017). Several HSPs function as intracellular chaperones for other proteins (Pelham 1985; Randall and Hardy 1986; Murakami et al. 1988). It was reported that HSP transcripts were highly upregulated in response to high temperature in rice (Sarkar et al. 2009). Moreover, the ability of different *Triticum durum* cultivars to acquire thermotolerance and to accumulate HSP transcripts was studied in response to different thermal treatments. It was shown that TdHSP23.5, which encodes a mitochondrial small HSP, is induced by different heat stress conditions (Rampinoa et al. 2009). Understanding the underlying mechanisms of heat tolerance in wheat is crucial to effectively address how heat stress affects wheat production and to provide useful markers and genes for genetic improvement.

2.3 Osmotic Stress Response

Osmotic stress is an important factor limiting growth and productivity of higher plants. In several species, it was shown that MAPK cascades are involved in signaling pathways activated by different environmental conditions like salt, drought, temperature, etc. (Zhou et al. 2016). Mitogen-activated protein kinases (MAPKs) are serine/threonine protein kinases that play a key role in signal transduction under osmotic stress response. A MAPK cascade is the combination of at least three protein kinases: a MAP 3K, a MAPKK, and a MAPK which activate each other via phosphorylation (Colcombet and Hirt 2008; Ichimura et al. 2002). The MAP 3Ks phosphorylate Ser/Thr residues in the activation loop of MAP 2Ks. In turn, MAP 2Ks phosphorylate MAPKs at the conserved Thr-X-Tyr motif in their activation loop (Zhou et al. 2016).

The *Arabidopsis* AtMKP1, the rice OsMKP1, and tobacco NtMKP1 are the most characterized MKP in plants. It has been shown that these MKP1 are required for the control of various stress responses (Ulm et al. 2001, 2002; Bartels et al. 2009; Katou et al. 2007; Yamakawa et al. 2004). Zaidi et al. (2010) have identified in durum wheat the first MKP (TMKP1) highly similar to OsMKP1. They provide evidence that TMKP1 is functionally distinct from its Arabidopsis ortholog, AtMKP1. This data can explain to some extent, the moderate tolerance to salt stress observed in the TMKP1 overexpressors (Zaidi et al. 2010). Osmotic stress signaling seems to be the regulation of the cell cycle via MAPKs as part of the cellular stress response. The precise molecular mechanisms of the pathways downstream of MAPK activity changes to cellular responses are primarily unknown. Additional research on these mechanisms would facilitate an understanding osmotic stress signaling via MAPKs.

2.4 Drought Stress Response

Drought is a major abiotic stress that negatively affects plant growth and productivity of wheat. To avoid drought stress, wheat cultivars have developed diverse drought tolerance mechanisms, including the formation of deeper roots, regulation of ion homeostasis, improvement of osmoprotective and antioxidant response, and regulation of gene expression (Huseynova 2012; Zhang et al. 2012). In general, stress-inducible genes are classified into two important groups, which are functional and regulatory proteins. The first group provides direct tolerance to abiotic stresses like LEA proteins, detoxification enzymes, and proteins involved in osmoprotectant biosynthesis. The second group of drought-inducible genes is responsible for downstream signal transduction and induction of functional proteins including mainly transcription factors, such as DREBs, AREBs, MYB, NACs, and protein kinases and phosphatases (Zaidi et al. 2010; Chipilski et al. 2012; Huseynova 2012; Loutfy et al. 2012). The characterization of key genes implicated in plant responses to drought stress provides a vigorous method to engineer for crop plants with better tolerance to drought stress (Kasuga et al. 1999; Valliyodan and Nguyen 2006). Regulatory proteins act as early responders to abiotic signals and trigger global changes in stress-related genes. Then, regulatory proteins have become an important topic in the study of plant responses to drought stress (Seki et al. 2002a, b). It is worth noting that transcription factors are essential regulatory proteins that control and regulate the expression of target genes by particularly binding to the *cis*-acting elements within the regulatory regions (Valliyodan and Nguyen 2006; Shinozaki and Yamaguchi-Shinozaki 2007; Ashraf 2010; Yang et al. 2010; Deikman et al. 2012; Mwadzingeni et al. 2016).

DREB factors were families of transcription factors responsible for gene regulation under conditions of water deficiency. DREB transcription factors bind to a distinct region in the promoter of target genes known as DRE/CRT sequence, which activates the transcription of genes in response to abiotic stresses (Shinozaki and Yamaguchi-Shinozaki 2000; Terashima and Takumi 2009; Chen et al. 2016). DREB transcription factors activate target genes, like rd29A and cor15A, resulting in enhanced tolerance to drought and high salinity in transgenic plants. Dehydration-responsive element-binding proteins have been identified from numerous plant species such as rice, wheat, diploid wheat (*Triticum monococcum*), barley (*Hordeum vulgare*), and maize (Dubouzet et al. 2003; Shen et al. 2003; Agarwal et al. 2006; Zhao et al. 2009; Sazegari and Niazi 2012). The DREB transcription factors have been divided into two classes: DREB1 is implicated in the signal transduction pathways under low temperature and DREB2 in the signal transduction pathways under dehydration (Fig. 3). It was reported that overexpression of OsDREB1F in transgenic rice and *Arabidopsis* plants demonstrated improved tolerance to salt, drought, and low temperature (Wang et al. 2008).

The *NAC* genes constitute one of the largest families of transcriptional regulators in plants. These transcription factors have been shown to regulate several biological processes in wheat. NAC proteins possess a conserved NAC domain at the N-terminus that consists of approximately 150–160 amino acids and is classified into 5 sub-domains (A to E) (Ooka et al. 2003). Compared with *Arabidopsis* and rice, a small number of NAC transcription factors were identified and characterized from wheat species. In bread wheat (*Triticum aestivum*), a set of NAC transcription factor was characterized under abiotic stresses (Baloglu et al. 2014; Saidi et al. 2017). The wheat genome contains multiple NAC genes with various expression patterns and roles in the responses to environmental conditions (Saidi et al. 2017). It was reported

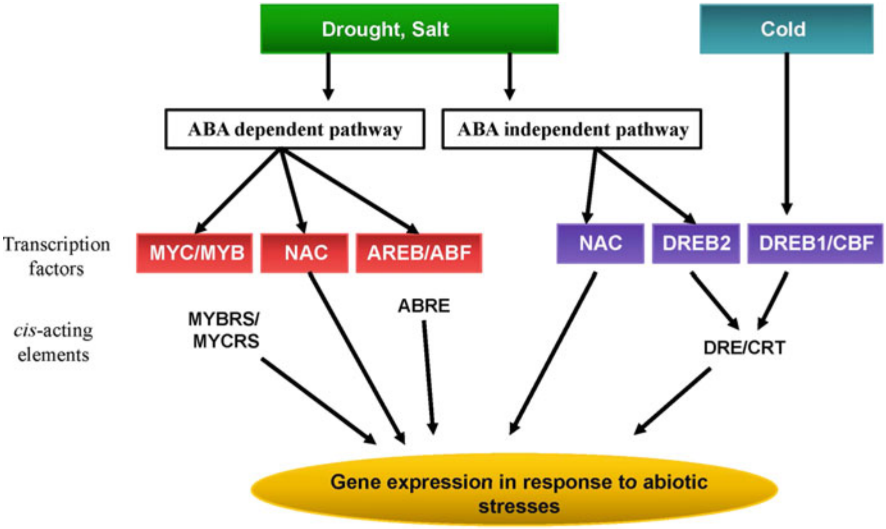

Fig. 3 Regulation of gene expression in response to drought, salt, and cold stresses. The ABA-dependent pathway is activated by AREB, ABA-responsive element-binding protein, and MYC/MYB transcription factors, which recognized the ABRE and MYB/MYC sequences, respectively. The *DRE/CRT cis* elements are recognized by DREB and are involved in the ABA-independent pathway

that the expression of TaNAC2 significantly increased in response to abiotic stresses, and its overexpression in *Arabidopsis* improved tolerance to drought, salt, and freezing stresses (Mao et al. 2012). Recently, 168 NAC genes were identified, in durum wheat (Saidi et al. 2017). Among them, ten genes were selected and analyzed, using qRT-PCR, in two contrasting tolerance cultivars, and evaluated as candidate genes to improve the durum wheat tolerance to drought and salinity (Saidi et al. 2017).

3 Role of SnRK Proteins in the Regulation of Plant Response to Abiotic Stresses

Plant sucrose non-fermenting 1-related protein kinases (SnRKs) represented a major family of signaling proteins and were associated with metabolic regulation and abiotic stress responses (Kobayashi et al. 2004; Boudsocq et al. 2004, 2007). They are grouped into three subfamilies SnRK1, SnRK2, and SnRK3 based on the amino acid sequence identity and expression patterns (Halford 2006). SnRK1 protein kinases were shown to play an important role in the regulation of carbon and nitrogen metabolism, whereas SnRK2 and SnRK3 function principally in stress signaling (Hrabak et al. 2003; Zhang et al. 2016). It is worth noting that SnRK2 and SnRK3 subfamilies are specific to plants (Halford et al. 2003). One of the best-studied members of SnRK3 family is SOS2, which is involved in phosphorylating and activating the plasma membrane Na^+/H^+ exchanger SOS1, in order to regulate ion homeostasis under salt stress condition (Liu et al. 2000; Hey et al. 2010; Guo et al. 2002; Qiu et al. 2002). The SnRK2 family plays diverse roles in response to environmental stresses such as salinity, drought, and cold (Boudsocq et al. 2004; Kobayashi et al. 2004). The amino acid sequences of all SnRK2s contain two regions, the N-terminal highly conserved kinase domain and the regulatory C-terminal containing two sub-domains. The first domain is required for activation by osmotic stress, independently of ABA, whereas the second domain is specific to the ABA-dependent SnRK2s only and is needed for the ABA response (Belin et al. 2006; Kobayashi et al. 2004; Yoshida et al. 2006). Despite the important functions of SnRK2s in plants, knowledge of the molecular mechanism of their activation and their specific functions in wheat is still enigmatic. SnRK2 family contains ten members in *Arabidopsis* and rice (Boudsocq et al. 2004, 2007). In *Arabidopsis*, all members, except AtSnRK2.9, responded to drought and salt stresses, five members (AtSnRK2.2, AtSnRK2.3, AtSnRK2.6, AtSnRK2.7, and AtSnRK2.8) were activated by ABA, and none was induced by low temperature stress (Boudsocq et al. 2004, 2007). In wheat, ten *SnRK2* genes were identified, and all responded to various abiotic stresses (Zhang et al. 2016). It was reported that TaSnRK2.1–3 (subclass II) responded weakly to ABA, TaSnRK2.4–7 (subclass I) were not induced by ABA treatment, and TaSnRK2.8–10 (subclass III) were strongly activated by ABA (Zhang et al. 2016). In general, overexpression of TaSnRK2s enhances plant tolerance to several abiotic stresses like drought, salt, and cold (Zhang et al. 2016, 2017). It was reported that overexpression of TaSnRK2.3, TaSnRK2.4, TaSnRK2.7, and TaSnRK2.8 improves tolerance to abiotic stresses in *Arabidopsis* (Zhang et al. 2010, 2011). The presence of TaSnRK2.8 in the cell membrane, cytoplasm, and nucleus suggested that TaSnRK2.8 plays an important role in wheat. Increasing evidence demonstrates that SnRK2s are a merging point of the ABA-dependent pathway (Ma et al. 2009; Park et al. 2009; Kulik et al. 2011). In the absence of ABA, SnRK2 proteins are inactivated by PP2C (protein phosphatase 2C), which is encoded by abscisic acid insensitive 1 and 2 (ABI1 and ABI2). The PP2C phosphatase will be inactivated by the ABA after its binding to the PYR/PYL/RCAR receptor proteins. Consequently, the transcription factors of the ABF/AREB family will be phosphorylated and activated by SnRK2 kinases relying on ABA signals (Ma et al. 2009; Park et al. 2009).

4 Phytohormones: Key Regulators in Response to Abiotic Stresses

Increasing evidence suggests that phytohormones, like the classical abscisic acid (ABA), auxins (IAA), cytokinins (CKs), ethylene (ET), and salicylic acid (SA), play a crucial role in plant growth and abiotic stress tolerance. Although plant response to abiotic stresses is related to diverse factors, phytohormones are considered the most

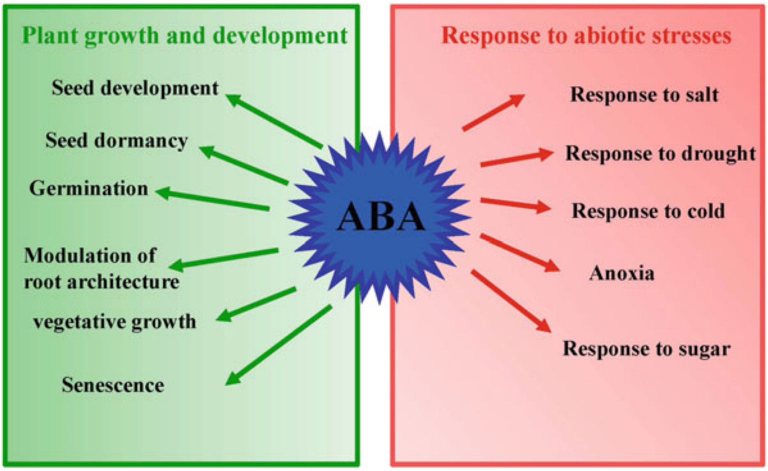

Fig. 4 Physiological response controlled by ABA during plant growth and plant responses to abiotic stresses

important endogenous substances for controlling physiological, molecular, and functional responses in wheat, a critical requirement for plant survival as sessile organisms (Wolters and Jurgens 2009; Peleg and Blumwald 2011; Fahad et al. 2015; Wania et al. 2016).

Abscisic acid is one of the most studied phytohormones, which regulates several physiological processes ranging from stomatal opening to protein storage and improves plant tolerance to various environmental conditions including drought, salt, and cold stresses (Sreenivasulu et al. 2012; Ng et al. 2014; Sah et al. 2016). It is worth noting that ABA is also essential for plant growth and development under non-stress conditions (Fig. 4). The massive production of ABA under drought at the whole plant level is a major contributor to stress responses. These increased levels of endogenous ABA have been reported in many plant species including maize (Beardsell and Cohen 1975), rice (Henson 1984), barley (Stewart and Voetberg 1985; Thameur et al. 2011), and wheat (Guoth et al. 2009). It was reported that 63%, 54%, and 10% of ABA-inducible genes were induced in response to drought, high salinity, and cold treatment, respectively (Seki et al. 2002a, b). Synthesis of ABA is the common dominant factor in the induction of some proteins such as LEA proteins, dehydrin, and lipid transfer proteins (LTP) (Cushman and Bohnert 2000).

It was also reported that ethylene (ET) regulates a large range of plant developmental processes like germination, flowering, senescence, root formation, etc. Importantly, ethylene is produced in response to multiple environmental stresses. Several abiotic stresses including salinity, drought, and low temperature could increase endogenous ET levels in plants (Shi et al. 2012; Klay et al. 2014; Dubois et al. 2018). The ethylene-responsive transcription factor (ERF) family is implicated in numerous processes and considered as one of the most important families of gene regulators in plants (Feng et al. 2005; Sharma et al. 2010; Mizoi et al. 2012). Several

ERF genes were identified in different plant species including *Arabidopsis* (Sakuma et al. 2002), grapevine (Jaillon et al. 2007), poplar (Zhuang et al. 2008), rice (Nakano et al. 2006), and tomato (Pirrello et al. 2012). Recently, a novel ERF gene from durum wheat (TdSHN1) was identified and characterized (Djemal and Khoudi 2015). It was demonstrated that overexpression of TdSHN1 in transgenic tobacco plants improves plant tolerance to salt and drought stresses (Djemal and Khoudi 2016).

Contrary to ABA and ET, little information is available about the role of the plant hormone auxin (IAA) in stress responses. Auxin regulates numerous aspects of plant growth and development such as vascular tissue differentiation, root growth, and flower and fruit development and plays crucial roles in response to abiotic stresses (Zhao 2010; Bouzroud et al. 2018). Three types of transcriptional regulators, auxin/indole-acetic acids (Aux/IAAs), auxin response factors (ARFs), and TOPLESS proteins (TPSs), control cell-specific transcription of auxin response genes (Szemenyei et al. 2008; Causier et al. 2012; Zouine et al. 2014). Among these proteins, ARF family plays crucial roles in controlling the expression of auxin response genes. In rice, it was shown that several OsARFs are involved in salt and drought stress responses (Jain and Khurana 2009). It is worth noting that the role of auxin in gene expression and regulation in many crops is very limited (Di et al. 2015; Li et al. 2016).

5 Conclusion

Plants are sessile, which make them highly subjected to adverse environmental factors and which negatively affect their growth and yield potential. Salinity, water logging, drought, nutritional imbalance, and extreme temperatures are the major abiotic factors that negatively affect crop productivity (Ashraf and Foolad 2007; Mahajan and Tuteja 2005). Among the strategies that plants have developed to adapt to their fluctuating environment, it exists a complex system of signaling networks including reactive oxygen species, phytohormones, ion transport systems, and protein kinases, activated in response to these abiotic stresses (Mahajan and Tuteja 2005). These signaling systems respond to specific stress by up- or downregulating the various genes. Ion channels and transporters play an important role in plant adaptation to abiotic stresses. For example, the TdSOS1 plasma membrane Na^+/H^+ antiporter from wheat is regulated by the CIPK24 kinase and the CBL4 calcium-binding protein complex (Feki et al. 2011). SnRKs are important for plant growth and stress responses. SnRK1s are SNF1/AMPK orthologs that function in regulating metabolism in plants. SnRK2s regulate osmotic stress and ABA signaling, whereas SnRK3s are key regulators of ion homeostasis. The challenge today is the identification of stress sensors for abiotic stress research in plants in order to define the cross talk signaling.

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Molecular and Biotechnological Tools in Developing Abiotic Stress Tolerance in Wheat

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Contents

Abstract Agricultural systems are affected by various abiotic stresses which pose restrictions to the yield and quality of wheat crop. A single crop can be challenged simultaneously by many abiotic stresses. A major target of plant breeding programs globally is the improvement of tolerance to abiotic stresses. The complex nature of abiotic stress tolerance traits and the difficulty in dissecting them into manageable genetic components amenable to molecular breeding are the major challenges. Advances in molecular biology and genomics have had a large impact on the speed of identification and characterization of genes and genetic regions associated with quantitative and qualitative traits in crop breeding programs. To reconstruct the whole cascade of cellular events leading to rapid responses and adaptation to the various abiotic stimuli, researchers have to integrate the various omics approaches. To increase knowledge on the effects of gene expression and to understand whole plant phenotype under stress, a very focused approach combining molecular, physiological, and metabolic aspects of plant stress tolerance is required. The selection of the appropriate promoter or transcription factor to be used for transformation can be done by better understanding of the underlying physiological processes in response to different abiotic stresses. Additionally, genetic and genomic analysis can be utilized to identify DNA molecular markers associated with stress resistance that can facilitate breeding strategies for crop improvement in wheat. In the case of

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abiotic stress tolerance, this approach is particularly useful when target characters are controlled by several genes. To map different QTLs contributing to a given agronomical trait and to identify linked molecular markers, the omics approaches could be combined with the potential which will open the possibility to transfer simultaneously several QTLs and to pyramid QTLs for several agronomical traits in one improved cultivar.

Keywords Abiotic stress · *Triticum aestivum* · QTL · MAS

1 Introduction

All over the world, agriculture face challenges from many abiotic stresses such as drought, salinity, extreme temperatures, chemical toxicity, and oxidative stress that damage the environment. Most major crop plants have decreased in their average yield by almost 50% through these abiotic stresses which are the main cause of crop loss worldwide. Many regions in the world are affected by drought and salinity which by the year 2050 will cause serious salinization of more than 50% of all arable lands. A series of morphological, physiological, biochemical, and molecular changes adversely affecting plant growth and productivity are because of these abiotic stresses such as drought, salinity, extreme temperatures, and oxidative stress which are often interconnected and can induce similar cellular damage. For example, drought and/or salinization results in the disruption of homeostasis and ion distribution in the cell and is manifested primarily as osmotic stress. Oxidative stress may cause denaturation of functional and structural proteins which frequently accompanies high temperature, salinity, or drought stress (Smirnoff 1998). As a result, these different environmental stresses often activate similar cell signaling pathways and cellular responses, like the production of stress proteins, upregulation of anti-oxidants, and accumulation of compatible solutes (Wang et al. 2003).

Many genes and biochemical, molecular mechanisms are involved in the complex plant responses to abiotic stress. The ongoing work on the molecular control mechanisms of abiotic stress tolerance is based on the expression of specific stress-related genes and may result in the use of molecular tools for engineering more tolerant plants. Wang et al. (2003) categorized these genes in three major categories: (i) MyC, MAP kinases and SOS kinase, phospholipases and transcriptional factors like HSF, and the CBF/DREB and ABF/ABAE families which participate in signaling cascades and in transcriptional control; (ii) heat shock proteins (HSPs) and chaperones, late embryogenesis-abundant (LEA) proteins, osmoprotectants, and free radical scavengers which protect membranes and proteins directly; and (iii) aquaporins and ion transporters which are involved in water and ion uptake and transport.

To maintain growth and productivity, plants must adapt to various stress conditions and should exercise specific tolerance mechanisms. Manipulation of those genes that protect and maintain the function and structure of cellular components is responsible for plant modification for enhanced tolerance. The genetically complex responses to abiotic stress conditions are more difficult to control and engineer than most monogenic traits of engineered resistance to pests and herbicides. Engineering strategies presently depend on the transfer of one or several genes which are either involved in signaling and regulatory pathways or encode enzymes present in pathways leading to the synthesis of functional and structural protectants, like osmolytes and antioxidants, or those that encode stress tolerance-conferring proteins. Many important achievements have been made through the current efforts to improve plant stress tolerance by gene transformation, but the nature of the genetically complex mechanisms of abiotic stress tolerance and the potential detrimental side effects make this task extremely difficult (Wang et al. 2003). Multiple, interconnected strategies evolve in higher plants that enable them to survive abiotic stress, but in most agricultural crops, these strategies are not well developed.

Wheat belongs to family *Poaceae* on which most of the world population depends upon as cereal food. Due to its cultivation on a huge area, its potential to give high productivity, and the prominent position in international food grain trade, it is called as the "king of cereals." Three main species of the genus *Triticum* form the majority of the cultivated wheat varieties which are the hexaploid, *Triticum aestivum* L. (bread wheat), and the tetraploid, *T. durum*, *T. dicoccum*, and *T. monococcum*. It has 12.1% protein, 1.8% lipids, 1.8% ash, 2.0% reducing sugars, 6.7% pentosans, 59.2% starch, and 70% total carbohydrates and provides 314 K cal/100 g of food. It also has a good amount of minerals and vitamins like calcium (37 mg/100 g), iron (4.1 mg/100 g), thiamine (0.45 mg/100 g), riboflavin (0.13 mg/100 g), and nicotinic acid (5.4 mg/100 mg) (Iqbal et al. 2017).

Millions of the global population get food and nutritional security by wheat which is a major staple crop of the world and India. The cultivars are being developed to meet the demand for higher productivity and to tolerate the challenges imposed by several abiotic stresses like high temperature, limited access to irrigation water, drought, salinity/alkalinity, waterlogging, mineral deficiency, crop lodging, and preharvest sprouting, although the rate of genetic gain in productivity during the recent years has not been as impressive as in the past. It is essential to integrate the modern approaches with the advances in phenomics, molecular biology, functional genomics, etc. as the conventional methods of wheat improvement will not be sufficient to achieve the productivity targets. In fact, it is essential to stabilize the productivity of wheat through stress mitigation options, particularly through agronomic interventions (Tiwari et al. 2017).

Not much success has been achieved in breeding crop plants with improved stress tolerance by traditional approaches as it is very difficult to do breeding for tolerance traits in traditional breeding programs. In crop species desired traits can be crossed from wild relatives, and extensive abiotic stress tolerance has been identified in screens of landraces and related wild species for the cereals. In modern wheat varieties, only 10–20% of the wild variation has been used. Although not as extreme as in wheat, a similar situation arises in rice and barley. At present a lot of emerging technologies of genomics are being used as a means to identify key loci which control stress tolerance and also as a tool to screen for allelic variation in the wild and landrace gene pools. Although genetic transformation offers more fast option in some circumstances, still outcomes of genomics can be delivered through conventional breeding (Langridge 2006).

Maize, rice, and wheat compete for the number one position in cereals which are our main source of food. The four closely related Triticeae crops, wheat, barley, rye, and triticale, occupy the lower-yielding environments and cover almost twice the area sown with maize or rice. Although wheat, rye, and barley show more tolerance toward many abiotic stresses than maize or rice, there is not much knowledge about the molecular basis for abiotic stress tolerance in these species, and still there is ample scope for improvement. The question arises whether genomics can be a tool for understanding stress tolerance in these species and lead to increased rates of genetic gain for tolerance (Langridge 2006).

Many genes, several regulatory elements, and few transcription factors have been isolated in the past few years through the molecular dissection of the stress response of wheat. But, the molecular basis of stress tolerance is not known. A very fast progress can be made through the genomics approach toward the identification of signal transduction pathway components in the near future. Genomics has revolutionized genetic analysis from microarrays to forward and reverse genetics, shifting the focus from the study of a single gene to a whole genome analysis approach. It is possible to collect information on the expressed portion of the genome through the rapid expansion of EST databases which has opened the way to a better understanding of physiological pathways and to gene discovery. This approach has been successfully applied in the analysis of genes involved in plant response to stress where modification of gene expression is a common feature. A lot of EST databases have been made starting from RNAs of barley or wheat plants which are exposed to different stress conditions. The expression of thousands of genes in a single experiment can be monitored through microarray technology where ESTs are starting points, providing a global perspective of the response to a stress stimulus. A powerful tool for providing correlative evidence on gene functions is the combination of sequence information and RNA expression profiling, although direct demonstration can be only achieved by genetic approaches. New genetic strategies based on the analysis of genotypes in which a given gene is inactivated (loss-of-function approach) are now available in addition to the traditional strategy based on the production of transgenic plants overexpressing the gene of interest (gain-of-function approach). New tools for genetic analysis have been provided by saturating collections of mutants generated by T-DNA or transposon insertional mutagenesis in *Arabidopsis* and maize and the development of posttranscriptional gene silencing techniques in tobacco (Baulcombe 1999). An important step to discover the role of stress-related sequences and their relationship with stress-tolerant loci is the mutant analysis. It will be possible to provide evidence on the importance of stress tolerance genes for crop field performance as soon as the new genetic tools become available for wheat, allowing the design of new breeding strategies for plant improvement (Cattivelli et al. 2002).

Growth and productivity of major crop species like wheat (*Triticum aestivum)* are restricted by many abiotic stresses like extremes in temperature, photon irradiance, and supplies of water and inorganic solutes. It was observed that more than one abiotic stress can occur at one time, and one abiotic stress can reduce a plant's ability to resist a second stress. Most probably low water supply is the most common single abiotic stress which limits the growth of crops worldwide (Araus et al. 2002). Other abiotic stresses like salinity and acidity are also very significant in restricting the growth of both forage kinds of grass and the cereals. Low temperature also restricts plant growth and has a major impact on grasses via vernalization and low-temperature damage at anthesis.

Not much success has been achieved in breeding crop plants with improved abiotic stress tolerances through traditional approaches so far because of a number of contributing factors: (1) there was more focus on yield than specific traits; (2) the difficulties in breeding for tolerance traits like complexities introduced by genotype through environment, or G × E, interactions and the relatively infrequent use of simple physiological traits because measures of tolerance have been potentially less subject to G × E interferences; and (3) desired traits can only be introduced from closely related species.

As most of the cereals are moderately sensitive to various abiotic stresses, and have less variability in their gene pool generally, they provide very few opportunities for major step changes in tolerance. To generate such step changes, genetic manipulation technologies can be utilized which have a potentially larger impact on abiotic stress tolerance. Modest increases in tolerance may be introgressed into commercial lines from tolerant landraces through marker-assisted breeding approaches (Dubcovsky 2004) which are facilitated by recent breakthroughs with positional cloning (e.g., Yan et al. 2003, 2004) enabling identification of extant tolerance genes within cereal germplasms. Not only the sequencing of the rice (*Oryza sativa*) genome has provided an invaluable resource for work on rice but also through exploitation of syntenic alignment with many other kinds of grass (Devos and Gale 2000) facilitated fine mapping in the unsequenced genomes of many other kinds of grass.

The functional genomics approach to the study and manipulation of abiotic stresses in grasses has become increasingly tractable through the exploitation of this latest resource in combination with steadily increasing transformation frequencies for many kinds of grass. Therefore, the need of model plant such as Arabidopsis (*Arabidopsis thaliana*) for such work is steadily decreasing and will continue to do so because the principles uncovered in this model organism are refined or even supplanted by knowledge gained in the plants in which this knowledge needs to be applied primarily in grasses, both cereals and forage species. There are also many fundamental differences in the development and anatomy between monocotyledons and dicotyledons, and many of the mechanisms of tolerance to abiotic stresses have fundamentally different characteristics between these two major plant groups, so transferring knowledge from *Arabidopsis* to the major crops often is not feasible. Many dicotyledonous halophytes accumulate much higher concentrations of Na^+ in their shoots than monocotyledonous halophytes when grown in saline soils. This may be related to succulence which is observed more commonly in dicotyledons than monocotyledons, particularly the grasses.

Although the actual production of transgenic plants with demonstrably improved abiotic stress tolerance has been slow, the possibilities for increasing tolerance to abiotic stresses are enormous. There have been many reports outlining the possibilities for inducing stress tolerance, but only a handful of papers have been published presenting results from transgenic plants. Flowers (2004) found these claims to be rather inadequate due to incomplete implementation of experiments and/or fundamental errors in the design of experiments arising from incomplete knowledge of the basic physiology of salinity tolerance.

The possibilities for increasing tolerance to abiotic stresses are also reviewed by many workers like Taiz and Zeiger (2002), in different conditions such as high Al (Samac and Tesfaye 2003), high Na^+ (Tester and Davenport 2003), low N (Masclaux et al. 2001), low P (Raghothama 1999), low temperature (Thomashow 1999), low water (Shinozaki et al. 2003), ozone, UV-B, etc. (Blokhina et al. 2003). Various workers have correlated particular traits with increased tolerance and probed the possibility of molecular and cellular processes to be involved in adaptive plant responses to abiotic stresses in ongoing reductionist/reverse genetic work. They range from protein structure (Délye et al. 2005) through cell biology (Gilliham and Tester 2005) to whole plant processes (Davenport et al. 2005).

To increase abiotic stress tolerance in commercial lines, knowledge of this work in grasses can be used. An excellent but rare example of the use of new technologies developed from pure plant physiology in otherwise traditional breeding programs to increase abiotic stress tolerance is the use of $\delta^{13}C$ assays for screening wheat lines to generate the new drought-tolerant line Drysdale (Rebetzke et al. 2002). There is also promise in the potential application of these works.

To increase abiotic stress tolerance in grasses, physiological knowledge may also underpin some early breakthroughs using genetic manipulation technologies. The introduction of de novo characteristics that are completely absent from a particular gene pool can give rise to step changes in tolerance such as no wheat variety has the ability to synthesize the sugar alcohol mannitol (Abebe et al. 2003). In some plants it can act as a compatible solute where it is accumulated in large amounts. It reduces the osmotic potential in the cytoplasm and thereby increases the ability of the cytoplasm to retain water in the face of reduced water supply. However, when the bacterial gene which encodes the key enzyme to allow mannitol synthesis was inserted into wheat plants, with expression driven constitutively, it usually caused severe reduction in length of plants and sterility (Abebe et al. 2003). In those lines where very low concentrations of mannitol, i.e., less than 0.7 μmol g^{-1} fresh weight, a level that is osmotically irrelevant, were synthesized, vegetative growth was inhibited less. It could be either by the addition of 150 mM NaCl to the liquid medium in which they were grown or by reduced watering of soil-grown plants. There was no reduction in the growth of these plants in unstressed conditions.

This example involves the manipulation of those processes that limit the damage rather than prevent it. A more appropriate approach for defense against abiotic stress would be the processes involved in the early detection of stress and respond to it. This will also have the benefit of potentially facilitating the coordinated response to a stress because various stresses require more than one response for tolerance to occur. Various abiotic stresses can impinge upon a plant simultaneously that created much interest in investigating the possibility of generating plants with catch-all alterations involving the signaling pathways and their early responses that are common to several abiotic stresses (Seki et al. 2003). This could be done as has been described to some extent in *Arabidopsis* through altering levels or patterns of expression of higher-level transcription factors that are involved in the early responses to stresses (Dubouzet et al. 2003). Placing such genes behind a strong stress-inducible promoter reduced the growth inhibition in unstressed conditions, although increased tolerance was associated with reduced growth in unstressed conditions. Although field trials of wheat expressing DREB1A have been done in Mexico, such an approach has not been extensively tested in grasses. Increased tolerance to NaCl was observed in plants in which expression of a Na^+ transporter, HKT1, was reduced by antisense through use of same rationale of trying to prevent damage from occurring in the first place (Laurie et al. 2002). With this, there was a decrease in net Na^+ influx and root Na^+ concentration. To increase Na^+ tolerance in wheat, this manipulation is significant, especially with the clear empirical observations given by Munns et al. (2003), of Na^+ exclusion being proportional to Na^+ tolerance.

In conditions of reduced stress, some of the alterations described above appear to come with growth and/or yield penalty. To avoid this outcome, expression of these genes should be driven in response to stress by an inducible promoter, as has been done for controlling the expression of a gene that encodes a key pro-synthesizing enzyme in rice (Su and Wu 2004). Such an approach should now be attempted for manipulations in wheat also as this has successfully removed inhibition of growth in low-stress conditions.

Much effort needs to be invested to both complement and guide breeding and genetic manipulation programs because physiological knowledge of the processes of abiotic stress tolerance is still developing. The synergies to be gained by the interfacing of physiological and molecular/genetic research should be exploited further in future work (Tester and Bacic 2005).

2 Abiotic Stress

Any environmental condition, apart from the action of other organisms, which reduce the growth, survival, and/or fecundity of plants such as drought, high soil salinity, floods, extreme temperatures (too high or too low), reduced light level or excess of UV radiation, acidic or alkaline soils, soils poor in nutrients, etc., is called abiotic stress. All important crop plants, and most wild species, are affected by abiotic stress conditions. Through the history of agriculture, the initial domestication and further development of crops by selecting for characters like fast growth, biomass accumulation, fruit and seed production, and so on have not improved stress tolerance. In fact, crop species are probably more sensitive to stress than their wild ancestors due to inhibition of vegetative growth. To survive the adverse environmental conditions, reproductive development is the first and most general response to stress of plants, which invest all their resources (energy, metabolic precursors) (Boscaiu et al. 2008; Serrano and Gaxiola 1994).

3 Types of Abiotic Stress

Constantly changing environments in which plants live are often unfavorable or stressful for growth and development. They can be biotic stress, such as pathogen infection and herbivore attack, and abiotic stress, such as drought, heat, cold, nutrient deficiency, and excess of salt or toxic metals like aluminum, arsenate, and cadmium in the soil. Major environmental factors that affect the geographical distribution of plants in nature, limit plant productivity in agriculture, and threaten food security are drought, salt, and temperature stresses. The adverse effects of these abiotic stresses are aggravated by climatic changes, which result in an increased frequency of extreme weather (Fedoroff et al. 2010). There are some fundamental biological questions like how plants sense stress signals and adapt to adverse environments. It is critical for agricultural productivity and also for environmental sustainability to improve plant stress resistance because crops with poor stress resistance consume too much water and fertilizers and thus greatly burden the environment (Zhu 2016).

3.1 Salt Stress

The cultivated land area of the world is reduced by 2–9% through the effects of climate change (Zhang and Cai 2011). This loss or soil degradation can be increased by soil salinization, due to natural processes and human activities like saline irrigation and land clearing (Zhang and Cai 2011; Horie et al. 2012). It has been estimated that more than 800 million hectares of land including 20% of irrigated area worldwide is affected by salinity (Goyal et al. 2016, Hussain et al. 2015) which significantly decreases wheat growth and development at the seedling stage, resulting in lower grain yield as higher Na + influx causes toxicity and disrupts leaf function (Munns et al. 2012). Moreover, 100–110% extra food will be required by 2050 to feed the growing world population (Tilman et al. 2011). Therefore, it is important for meeting increasing food demand to use saline soils through the development of salt-tolerant and/or climate-resilient wheat. However, comparatively little work has been performed on breeding wheat for salt tolerance despite a major focus on drought (Munns et al. 2006). Due to complexity and severity of salt stress, which occurs in two phases, i.e., osmotic stress and ionic stress (Horie et al. 2012), development of salt-tolerant cultivars is hindered greatly. Water uptake, cell expansion, and development are inhibited by osmotic stress, which results from higher salt concentrations outside the root (Munns et al. 2006). Due to reduced photosynthesis, high Na^+ ion uptake into leaves promotes leaf chlorosis, necrosis, and mortality

(Horie et al. 2012; Munns et al. 2006). Due to the range of interactions between variable Na^+ in the soil profile and differential salt responses depending on genotype, growth stage, and other factors such as high pH and drought, wheat yield data collected from field experiments cannot easily be used as a salt tolerance index (Munns et al. 2006). However, through hydroponics/pot screening performed in greenhouse conditions and physiological studies, it has been indicated that wheat has a significant genetic variation for salt tolerance (Ali et al. 2012; Hussain et al. 2015; Oyiga et al. 2016) which can be exploited for wheat breeding and genetics. Few works have also been directed to explore the physiological and genetic complexity of multigenic and multifaceted salinity-related traits. New horizons and foundations for genetic improvement of complex traits such as drought and salt tolerance have been provided by recent developments in genomic knowledge and technology. To identify and select the preferred genes in breeding populations at a much faster rate than by classical breeding, the combination of genomic tools with MAS can be used (Budak et al. 2004, 2005; Castillo et al. 2008; Vogel et al. 2009; Hussain 2015; Saade et al. 2016). Progress in MAS for wheat was slowed by the limited availability of genomic data, till recently, but advances in genotyping techniques and DNA sequencing have now produced genome datasets that have been used to design sequence-based simple sequence repeats (SSRs) and SNP markers (Filiz et al. 2009; Lucas et al. 2012; Akpinar et al. 2017).

3.2 Drought Stress

The most severe environmental stress among all other stresses is the water deficit which is the major constraint on plant productivity. The losses in crop yield due to water stress probably exceed the loss from all other causes combined. This has an evident effect on plant growth that depends on both the severity and duration of the stress (Araus et al. 2002; Bartels and Souer 2004). Abiotic stress tolerance is a complex phenomenon which comprises a number of physio-biochemical processes at both cellular and whole organism levels activated at different stages of plant development. Drought-tolerant plants adapt various mechanisms to tolerate water stress such as reduction in water loss by raising stomatal resistance, increases of water uptake by developing large and deep root systems, and osmolytes accumulation. The osmolytes which are accumulated include amino acids like proline, glutamate, glycine-betaine, and sugars (mannitol, sorbitol, and trehalose). They play an important role in preventing membrane disintegration and enzyme inactivation in the low water activity environment (Mahajan and Tuteja 2005).

During water deficit, one of the main cellular events is an extensive modification of gene expression resulting in a strict control of all the physiological and biochemical responses to the stress. Several genes have been identified which are specifically involved in stress response. Among them are the genes that encode the so-called LEA proteins. These proteins accumulate under stress conditions like drought, salinity, and low temperatures but also present in ABA-treated vegetative plants. The *DHN* genes belong to this family, which are upregulated during the stress (Zhu et al. 2000). There is association between the accumulation of members of the *DHN* family and tolerance to stresses involving dehydration as shown in several species like sunflower (Cellier et al. 1998), barley (Zhu et al. 2000), and wheat (Lopez et al. 2003). There is variability in the *DHN* gene family in many plant species (Grosselindemann et al. 1998; Morrel et al. 2003; Natali et al. 2003), and there is wide allelic variation found in barley at several *DHN* loci (Close et al. 2000).

According to the genetic background, responses to drought stress are extremely different. Inter- and intraspecies variations are found in drought resistance. The allelic variations of crop species have dramatically been reduced due to early domestication of crop plants and plant breeding which led to an increasing susceptibility of crop plants to environmental stresses, diseases, and pests.

Wild plants rarely die in their environment because of water supply fluctuation, but in many crop species that have been selected for yield potential and other quality characteristics, the potential for drought tolerance appears to be adjusted. Therefore, improvement in drought resistance in cultivated wheat might be achieved using the allelic repertoire offered by wheat wild relatives. Due to this, the existing variability currently available in gene pools must be properly characterized and understood at physiological, morphological, and genetic levels (Robinson et al. 2000; Nevo et al. 2002).

Aegilops, species of the Triticeae genus, are wild winter annuals which are closely related to winter wheat (*Triticum aestivum* L.). They are a possible source of genetic improvement for drought stress resistance as they are distributed in semidesert areas and are adapted to this environmental stress and can hybridize with wheat (Rampino et al. 2006).

3.3 Heat Stress

The rise in soil and air temperature beyond a threshold level for a minimum amount of time such that permanent harm to plant growth and development occur is defined as heat stress. The impact of temperature effects on the yields is highlighted by a detailed multilocation study. Development of drought-prone areas and consequently plant growth and crop productivity of major crops are affected by these adverse conditions (Zhao et al. 2017).

The combined effect of drought and heat is higher than when taken individually; therefore it is important to consider them together (Dreesen et al. 2012). Abiotic stresses including heat and drought are controlled by multiple genes, and the mechanisms controlling them are more complex than other traits like biotic stresses which are generally characterized by monogenic resistance. Other abiotic and/or biotic stresses often have the additive influence to heat and drought response making the study more challenging. Growth and performance of the plants decline rapidly especially in tropical and subtropical environments when water deficit and high temperature occur simultaneously under field conditions (Wahid et al. 2007; De Boeck et al. 2015; Niinemets 2015; Zandalinas et al. 2016, 2017).

The development of thinner leaves with higher leaf area is caused by higher temperature as it affects leaf structure (Loveys et al. 2002; Luomala et al. 2005;

Poorter et al. 2009). These gross morphological changes are due to changes in leaf anatomy. There are smaller cells and higher stomatal density in those leaves which develop under water deficit (Tisne et al. 2010; Shahinnia et al. 2016). Wahid et al. (2007) observed comparable effects of high temperature and water deficit on cell density, but limited data are available with respect to leaf anatomy changes in response to high temperature.

There is decrease in crop productivity and yields because of drought and heat which results in lower income for farmers. There is as much as 40% reduction in yield for maize and 21% for wheat at approximately 40% water reduction (Daryanto et al. 2016). According to the Intergovernmental Panel on Climate Change (IPCC), the air and ocean temperatures have warmed, and the concentrations of greenhouse gases have increased (IPCC 2014) and have direct influences on plant growth and crop yields (Bita and Gerats 2013; Stocker et al. 2013). Land and ocean temperature data from 1880 and 2012 show average global warming of 0.85 °C based on multiple independently produced datasets (Stocker et al. 2013). In the recent years, there is rise in the atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) with net emissions approaching 300 ppm (Stocker et al. 2013). There is impact of climate change on the earth's crust which results in infrequent and erratic precipitations, elevated temperatures, and expansion of affected land areas under flood or water deficit which contributes to the development of drought-prone areas and affects the plant growth and crop productivity. There is lot of debate on the impact of increased CO_2 on crop yield as some researchers argue that elevated CO_2 will increase photosynthesis. However, Gray et al. (2016) observed that rising CO_2 did not counteract the effect of severe drought on photosynthesis and yield.

There are many independent studies which have demonstrated the effects of increased temperature and water stress on crop yields. Like in Canada, the extreme events that occurred during 2001 and 2002 and the droughts and floods during 2010 and 2011 had a devastating impact on crop yield reducing it by as much as 50% (Wheaton et al. 2008). Major US disasters between 1980 and 2016 exceed billion dollars each per year, indicating that when drought and heat are combined, they cause expanded agricultural losses of more than $220 billion (Oceanic Atmospheric Administration website 2015).

The impact of heat and drought is equally significant in developing countries like in Morocco where the economy is largely dependent on agriculture as approximately 40% of the labor force involved. Crop productivity is significantly reduced in years of drought which directly affects the livelihood of farmers and ultimately the economy. Wheat is a staple crop here and is used for bread (hexaploid wheat) and couscous (durum wheat). Wheat productivity significantly affected by the drought like cereal productivity was reduced in 2015–2016 by approx. 50% from 7.5 M tons production on an average year to 3.4 M tons in 2015–2016. In years of significant drought, sub-Saharan countries are also negatively affected. Crop failure due to drought was reported in West Africa, with droughts between 1975 and 1985 resulting in a per capita food production decline of 25% (Epule et al. 2013; Lamaoui et al. 2018).

A universal response to temperature stress being observed in all organisms ranging from bacteria to human beings is the induction of HSPs. Higher plants have at least 20 HSPs, and some species may have up to 40 different HSPs. The adaptation to temperature stress is observed through the wide diversification and abundance of HSPs in plants. They play a primary role in thermotolerance reactions, prevent denaturation or aggregation of target proteins, and facilitate protein refolding (Perez et al. 2009). In response to high temperature in rice, HSP transcripts were highly upregulated (Sarkar et al. 2009). Synthesis of HSPs (100, 78, 70, and 22 kDa) was observed in intact cotton leaves after 1 h at 41 °C (Law et al. 2001). It was also observed that the HSP synthesis was more intense under 24-h heat stress. In wheat leaves under heat stress, probably HSPs with a molecular weight of 70 and 78 kDa play a protective role. In wheat, there was a twofold or higher change in expression of a total of 6560 probe sets following a heat treatment of 34 °C and/or 40 °C. Heat shock proteins in wheat were identified by Xiaozhi et al. (2009), Maestri et al. (2002), Blumenthal et al. (1991), and Iqbal et al. (2017).

3.4 Cold Stress

There is a significant impact on agricultural production by cold and freezing stress which restricts the geographical distribution of plants and reduces crop quality and productivity. There is increased freezing tolerance in response to low but nonfreezing temperatures in many plants from temperate regions which is called as cold acclimation. During cold acclimation many genes with different functions are induced (Seki et al. 2002; Rabbani et al. 2003). Expression of the *Cor* (cold-responsive)/*Lea* (late embryogenesis-abundant) gene family is upregulated particularly under abiotic stress conditions like low temperature, drought, and high salinity, and their gene products function in stress tolerance (Xiong et al. 2002; Kobayashi et al. 2008b). In common wheat, various *Cor*/*Lea* genes have been characterized, of which 5′ upstream sequences were isolated from *Wcs120*, *Wcor15*, *Wdhn13*, *Wrab17*, *Wrab18*, and *Wrab19* (Takumi et al. 2003; Kobayashi et al. 2008a, c). *Wdhn13*, *Wrab17*, *Wrab18*, and *Wrab19* are induced under low temperature, drought, and ABA (Ohno et al. 2003; Kobayashi et al. 2004a, b, 2006; Egawa et al. 2006), and their promoter regions contain ACGT core motifs (Kobayashi et al. 2008a). This is suggested that bZIP-type transcription factors play important roles in the regulation of *Cor*/*Lea* gene expression. Kobayashi et al. (2008b) have isolated a wheat *lip19* homologue, *Wlip19*, and wheat *OBF1* homologue, *TaOBF1*. They have discussed protein-protein interactions and stress tolerance of *Wlip19*-expressing tobacco plants and the development of abiotic stress tolerance through WLIP19-mediated *Cor*/*Lea* expression in two wheat varieties with different levels of stress tolerance on the basis of their expression profiles.

3.5 Heavy Metal Stress

Increased anthropogenic activities, rapid industrialization, and modern agricultural practices have resulted in increased heavy metal contamination in the environment during the last few decades which causes toxicity to the living organisms (Eapen and D'souza 2005; Kavamura and Esposito 2010; Miransari 2011). Due to the use of pesticides, fertilizers, and municipal and compost wastes, and also due to heavy metal release from smelting industries and metalliferous mines, major areas of land have become contaminated with heavy metals (Yang et al. 2005). The problem arises only when these heavy metals are released in excess into the environment due to natural and/or anthropogenic activities as many of them occur naturally in the earth's crust at various levels. The 53 elements that have been categorized as "heavy metals" based on their density (>5 g/cm^3) belong to the d-block (Jarup 2003). Only 19 elements such as C, O, H, Mg, S, N, Ca, P, and K (macronutrients) and Cu, Zn, Mn, Fe, Mo, B, Ni, Co, Cl, and B (micronutrients) were selected for basic metabolism during evolution of angiosperms (Ernst 2006). Si has been reported to be involved in the maintenance of plant structures in some plants as it is also a beneficial element (Epstein 1999). In physiological and biochemical processes of plants such as chlorophyll biosynthesis, photosynthesis, DNA synthesis, protein modifications, redox reactions in the chloroplast and the mitochondrion, sugar metabolism, and nitrogen fixation, these macro- and micronutrients play very important roles. Zn acts as a cofactor for more than 300 enzymes and 200 transcription factors which are associated with the maintenance of membrane integrity, auxin metabolism, and reproduction (Marschner 1995; Barker and Pilbeam 2007; Briat et al. 2007; Williams and Pittman 2010; Prasad 2012; Ricachenevsky et al. 2013). But the uptake and utilization of heavy metals are tightly controlled by the plant cells as at higher concentrations they produce severe toxicity symptoms in plants (Janicka-Russak et al. 2008; Saito et al. 2010; Singh et al. 2012; Srivastava et al. 2012; DalCorso et al. 2013a; Farias et al. 2013; Fidalgo et al. 2013). Some heavy metals like Cd, Cr, Pb, Al, Hg, etc. are nonessential and without physiological function are very toxic even at very low concentrations (Ernst et al. 2008; Janicka-Russak et al. 2008; Garzón et al. 2011; Hayat et al. 2012; Shahid et al. 2012; Chong-qing et al. 2013; Gill et al. 2013). All these essential and nonessential heavy metals generally produce common toxic effects on plants like low biomass accumulation, chlorosis, inhibition of growth and photosynthesis, altered water balance and nutrient assimilation, and senescence, which ultimately cause plant death.

Heavy metals threaten human health due to their persistence in nature in addition to adverse impacts on plants. Pb has soil retention time of 150–5000 years and reported to maintain its concentration high for as long as 150 years and is one of the most toxic heavy metals (Yang et al. 2005). Contamination of food chain occurs because plants growing in heavy metal-contaminated sites generally accumulate higher amounts of heavy metals. Primary route for the entry of heavy metals into animal and human tissues is through contaminated food chain which make them prone to several diseases that range from dermatitis to various types of cancers (McLaughlin et al. 1999). If sufficient measures are not taken at the right time, this problem might worsen more. To decrease the entry of heavy metals in crop plants and to reduce the risk of contamination in animals and human beings, a lot of research in this area is being done (Singh et al. 2016).

These micro- and macronutrients in soils determine plant growth and development. At least some of the soil nutrients will be present at sub-optimal concentrations or will be bound to the soil in such a way as to limit their availability for plant uptake in most cropping systems. For example, most cereal cropping soils in Australia are Zn deficient, while under other stress, they are found to be deficient in Mn, Cu, and Fe. Toxic levels of minerals such as B and Al can restrict the yield potential. Boron is an essential micronutrient particularly relevant in Australia as it is phytotoxic at higher concentrations. Mineral deficiency and toxicity cause important abiotic stresses in crop species. The stresses can often be managed only partly through fertilizer application. When plants are exposed to both simultaneously, mineral stresses can intensify other stresses especially water stress (Langridge 2006).

In plants, various functions of micronutrient minerals have been identified. They act as cofactors for many enzymes (e.g., oxidoreductases), function in light harvesting and carbon assimilation processes in photosynthesis, have a role in pectin structure in cell walls, etc. Plant responses to stress imposed by mineral deficiencies or toxicity are not always well-defined but likely involve, at least partly, changes in specific plasma membrane ion transporting pumps, carriers, and channels (Barbier-Brygoo et al. 2001). The processes that involve the inhibition of plasma membrane H^+-ATPases, the blockage of plasmodesmata, and oxidative damage slow root growth due to toxic levels of Al (Sivaguru et al. 2000; Ezaki et al. 2001). Of the world's 3 billion land, it impairs plant growth in nearly 1 billion hectares of cropland which includes about 35 million hectares in the USA. For adapting wheat to acidic soils, Al tolerance genes from rye may prove useful. Some varieties of rye even can tolerate seven times more Al than wheat (Langridge 2006).

Significant advances can be made in the management of abiotic stresses associated with mineral availability in cereal crops, through a functional genomics approach by the identification of adapted wheat and barley lines, coupled with the molecular mapping of characteristics such as Mn efficiency, Zn efficiency, grain Fe and Zn density, and B toxicity tolerance (Huang et al. 2000; Jefferies et al. 2000; Pallotta et al. 2000; Graham et al. 2001). There is difficulty in achieving good adaptation by empirical breeding methods even though a major locus involved can be understood by poor efficiency of Mn in released cereal cultivars (Pallotta et al. 2000). Genes and gene systems controlling B tolerance and Mn, Zn, and Cu efficiency will be identified first from adapted varieties, wild relatives, and native grasses, with the sole purpose of integrating them into elite varieties of barley and wheat (Langridge 2006).

4 Various Strategies for Developing Abiotic Stress Tolerance in Wheat

Under both natural and agricultural field conditions, plants are constantly exposed to stress conditions (Zhu 2002; Mahmoud and Narisawa 2013). Some of the stresses like air temperature may damage plants within minutes, while some take a couple of days to weeks (e.g., soil water) or even months (mineral nutrients) to become stressful in extreme conditions. A plant generally adapts its metabolism and responds to various physiological and biochemical changes under stressed condition. Major physiological processes like nitrogen fixation, respiration and photosynthesis, and carbohydrate metabolism of genetic material, proteins, and lipids are affected by these stresses. Seed germination, maturation, and senescence stages of plant growth are also affected differentially.

In developing drought-tolerant high-yielding crop varieties, the conventional breeding has contributed significantly since centuries, but the progress in developing new crop cultivars has been relatively slow which restricts the fertility barriers that allow only plants of the same or closely related species for hybridization. Genetic engineering approaches enabled the researchers to overcome all these problems (Bakhsh et al. 2009; Khan et al. 2011). Now, the researchers have understood the changes in cellular, biochemical, and molecular process under stress condition which given a solid background to engineer crop varieties enhances stress tolerance through different plant transformation approaches (Bhatnagar-Mathur et al. 2008). Development of transgenic crops has opened a window of successes for plant biotechnologist through the development of technologies for tissue culture and plant transformation. The production of novel chimeric genes further expanded transgenic plant technologies (Fraley et al. 1983), plant expression vectors (Hoekema et al. 1983; Bevan 1984), and systems of DNA transfer (Draper et al. 1982, Fromm et al. 1985, Sanford et al. 1987), coupled with plant regeneration and transformation methodologies in the 1980s (Zambryski et al. 1983; Shimamoto et al. 1989; Gordon-Kamm et al. 1990). The various transformation methods available can be grouped into direct and indirect transformation methods. Mostly direct methods are microprojectile bombardment or protoplast transformation and do not use bacterial cells as mediators, while the indirect methods involve the introduction of a binary vector which carries the gene of interest into a plant cell via agrobacteria, *Agrobacterium tumefaciens* or *Agrobacterium rhizogenes*. All transformation methods have their own unique advantages, but the transformation using *Agrobacterium* and microprojectile bombardment are the most extensively used methods (Dai et al. 2001). Other most often used methods are infiltration, silicon carbide fiber-mediated transformation, electroporation of cells and tissues, microinjection, liposome-mediated transformation, and transformation via the pollen-tube pathway (Patnaik and Khurana 2001; Rao et al. 2009). Various genes induced under stress circumstances have been identified, characterized, cloned, and used as candidate genes to transform a crop plant encoding stress-related protein. The proteins play important roles in abiotic stress tolerance like LEA (late embryogenesis-abundant) proteins, and other important enzymes that encode for osmolytes production and regulatory proteins are involved in regulation of signal transduction or stress-responsive gene expression such as transcription factors (Shinozaki and Yamaguchi-Shinozaki 2007; Bakhsh and Hussain 2015).

4.1 Conventional Breeding

The majority of the world's wheat areas are very often affected with combinations of several abiotic stresses. Increasing and stabilizing production under these conditions poses one of the greatest challenges for agricultural research in the twenty-first century due to the fragile and highly variable nature of these areas and the continual deterioration of natural resources.

Trends in crop improvement are similar to the magnitude of genetic gains falling as environmental stress increases. These realities imply that over-proportional genetic gains and production increases are required to attain economic production levels and address low and unstable on-farm productivity in stress environments. Production increases can originate from various sources: (1) genetic gains in yield potential; (2) genetic gains in tolerance to abiotic and biotic stresses; (3) productivity gains through improved, sustainable CMR production techniques; and (4) synergistic effects among all these factors. In general, productivity in stressed environments is determined by a combination of tolerances to numerous abiotic and biotic stresses, crop management practices, and production economics. Hence, crop improvement cannot concentrate solely on improving abiotic stress tolerance per se but must consider constellations of adaptive traits under defined environmental conditions including biotic stress tolerance and end-use quality requirements.

Most breeding programs use methodologies designed to improve several traits simultaneously. The target traits are selected based on their relevance to local crop production and their economic value. Existing genetic variation, gene action, trait heritability, associations among traits, available and potential (conventional and molecular) screening techniques, and diagnostic tools are commonly used as criteria to characterize traits and project expected genetic progress. In practice, indirect selection for key constraints is frequently more efficient in raising production than select for yield or the target abiotic stress. Because many biotic and abiotic factors mask or confound the expression of stress tolerance, many earlier attempts to screen for stress tolerance, in particular, drought tolerance, have failed. For example, plants tolerant to nematodes or micronutrient imbalances may be selected as drought tolerant by the plant breeder simply because they have healthier root systems. Thus, breeders often raise productivity by concentrating on improving tolerance to those factors, particularly diseases for which they have known repeatable variation. Progress in crop improvement for abiotically stressed environments is hampered by a number of factors.

Wheat has a large genome size (approximately 17,000 Mb) which makes the improvement process by any method genetically very challenging. Modern bread wheat is still growing in the Middle East and is a true breeding hybrid with its ancestry linked to three wild grass species. It first originated in the "Fertile Crescent," an area in the Middle East, which stretches from Israel and Lebanon into Syria, Turkey, Iraq, and Iran. The earliest and the most primitive type of wheat is diploid einkom, while the hexaploids including the bread wheat, *Triticum aestivum*, constitute the most recent and latest step in the evolution of the wheat complex. The first hybridization event is thought to have occurred millions of years ago when the wild grass *Aegilops speltoides* crossed with the wild diploid wheat, *Triticum monococcum*. The tetraploid emmer wheat, *Triticumdicoccum*, was the resulting hybrid whose domestication led to the evolution of the durum wheat. The origin and evolution of hexaploid wheat about 8000 years ago have taken place by hybridization of tetraploid durum wheat, *Triticum turgidum* var. *durum* ($2n = 28$, AABB), with the diploid wild goat grass, *Aegilops* *tauschii*. Therefore, bread wheat is an allohexaploid which contains three distinct but genetically related (homoeologous) copies of each of the three originally independent haploid genomes, the A, B, and D. Civilizations thrived and spread from the Middle East to new continents with the evolution of wheat which resulted in massive wheat production feeding the growing world population. For wheat improvement by classical breeding approaches, Triticeae comprising over 300 species including wheat, rye, and barley is considered as germplasm source. Rediscovery of Mendel's law at the beginning of this century has led to the development of scientific approaches for crop improvement. Consistently since then, breeders have been searching for technologies and converting this "art" of breeding to a "science." Desirable traits have been introduced by wheat breeders to increase the grain yield and minimize the crop loss. But, conventional breeding techniques which are based on processes of crossing, backcrossing, and selection are time-consuming and, therefore, could hardly keep pace with the rapid coevolution of pathogenic microorganisms and pests. The conventional methods of wheat breeding in generating genetic variability necessary for creating novel cultivars with desirable characters have been complimented by the development of in vitro technologies (Patnaik and Khurana 2001).

One complication limiting progress in stressed environments is the high degree of variability from year to year. The predominant factor influencing yield variability is amount and distribution of rainfall. There was twice variability in those countries where half the wheat was sown in dryland conditions in comparison to those where wheat is grown mostly under well-watered conditions. Yield variability was also tended to be higher in warmer subtropical countries due to heat stress. A dramatic variation in grain yields was shown by a yield simulation model over 50 years for seven rainfed marginal environments. Singh and Byerlee (1990) pointed out that actual grain yields are lower since potential yields are defined by moisture and temperature conditions and are not constrained by other abiotic and biotic stresses such as soil fertility. Plant breeders are confronted with selection environments that vary from year to year. Genotypes selected in 1 year under severe stress, for example, frequently perform poorly in the following year when moderate stress occurs. Consequently, selection gains tend to cancel each other out because genotypes are unlikely to be superior over the wide range of production levels. These changing environmental indices and low trait heritabilities mask genetic potential, while adaptive traits and trait combinations are complex and difficult to identify, and the genetics of abiotic stress tolerance is often poorly understood. To enhance genetic gains and realize production increases in abiotically stressed environments, research should focus on the following activities:

1. Improved characterization and understanding of target environments through the use of physical parameters and probability ranges for climatic variables to identify relevant traits and weighted selection indices.
2. Identification of morphophysiological stress adaptive traits and their associated molecular markers with higher abilities for healing than yield alone.
3. Development of more efficient screening and selection methodologies.
4. Development of sustainable crop management practices to complement crop improvement.

Among the agronomic solutions requiring investigation are the selection and testing of germplasm under moisture conservation practices such as reduced or zero tillage and stubble retention. Tillage regime and genotype interactions are critically important for realizing genetic gains in stress tolerance in fields. Other practices such as shifting cultivation or periods of fallow and water harvesting (collecting runoff after rainfall for irrigation use) also allow better utilization of available moisture.

The existing genetic diversity in wheat for efficiency and/or tolerance to the major nutrient stresses suggests that progress in crop improvement is feasible. Reference was made to the available genetic sources of tolerance/efficiency for the different key nutrient stresses that may be useful in crop improvement. Efficiency or tolerance to several nutrient stresses is controlled by single dominant genes, and relatively "easy" genetic gains from conventional breeding can be projected. However, the more complex inheritance of other nutrients and confounding GxE will slow progress using conventional breeding and will complicate the development and use of molecular markers. Sustainable increases in productivity in areas subject to nutrient stress require a better understanding of the key genetic and environmental determinants of tolerance coupled with the integration of improved crop management practices (Pfeiffer et al. 2005).

4.2 Mutation Breeding

Mutation-based breeding, using both chemicals and radiation, has been available for several decades and is cheap and accessible. It has been successfully used to develop multiple commercial crop varieties with improved abiotic stress tolerance, including wheat, rice, and barley with improved salt, drought, and low-temperature tolerance (Suprasanna et al. 2014). However, a more specific form of mutation breeding known as TILLING (for target-induced local lesions in the genome), which is usually introduced via chemical mutagenesis, has a major advantage over "traditional" mutation breeding in that the requirement for phenotypic screening is reduced. TILLING is a PCR-based methodology that identifies the induced polymorphisms within genes that can be associated with phenotypic variation (Suprasanna et al. 2014). These polymorphisms can lead to new (neomorphic), increased (hypermorphic), or reduced (hypomorphic) gene functions. EcoTILLING and TILLING by sequencing are frequently used in experimental variations. An example of the use of TILLING that is relevant to breeding is the identification of 11 novel single-nucleotide polymorphisms (SNPs) in rice associated with improvements in salt tolerance traits across four genes (including transporters, kinases, and lectins) that are now available for integration into breeding populations (Negrao et al. 2013; Gilliham et al. 2017).

There is a long history of mutation breeding in the cereals as several important varieties result from the selection of mutant phenotypes (Ahloowalia and Maluszynski 2001). But, systematic development of mutant populations as a genomics resource has been done only recently. For mutation screening, a large barley mutant population constructed is based around detection of single-base mismatches (Caldwell et al. 2004). A similar type of population was used to identify a series of mutations in the granule-bound starch synthase I (GBSSI) of wheat (Slade et al. 2005). Wheat is particularly suitable for mutant screening since it is able to carry a very high mutation load due to polyploidy. 246 alleles were identified by Slade et al. (2005) after screening for each homologue in only 1920 mutated individuals. Several projects are being taken around the world to develop mutated populations of both wheat and barley, and diploid progenitors of wheat and many of these will be available as public resources. Work is also being done to develop transposon-tagged populations of barley using the maize Ac/Ds system (Cooper et al. 2004), which will provide an important resource for functional analysis of cloned genes (Langridge 2006).

4.3 Marker-Assisted Breeding

Marker−/genomic-assisted selection, using molecular markers and/or genotyping by sequencing, has been used in recent years, to increase the speed of traditional breeding approaches including the development and evaluation of doubled haploid populations, providing breeders with material 2–3 years faster than with conventional breeding alone (Able et al. 2007, Gupta et al. 2010, Ashraf and Foolad 2013, He et al. 2014). In the case of doubled haploid lines (homozygous lines derived from haploidization and subsequent doubling of the chromosome number), the ability to obtain immediate homozygous lines makes such germplasm very useful for quantitative genetic studies when examining linkage (Gilliham et al. 2017).

Molecular genetic mapping in wheat has been developed since the 1960s when Gary Hart worked on identification and chromosomal mapping of isozymes. Detailed RFLP linkage and physical maps of wheat, comprising more than 2000 DNA markers, have been published covering all 7 homologous groups in wheat. Recent advances in genome mapping techniques based on the polymerase chain reaction (PCR) have accelerated a novel DNA marker system termed SSRs. This is much easier to perform than RFLP analysis and shows much higher levels of polymorphism in hexaploid wheat than any other marker system. In addition, AFLP is more powerful in detecting a large number of loci, producing high complexity DNA fingerprints which can be used for high-resolution mapping and marker-assisted cloning. Nowadays, the availability of detailed linkage maps of molecular markers makes it possible to dissect quantitative traits into discrete genetic factors, called quantitative trait loci (QTL). The genetic analysis of quantitative traits under stressed environments and salt stress, in particular, had little investigation until a few years ago. With this type of work, it is difficult to distinguish between those traits that will improve yields under abiotic stresses and other stress response traits that have no effect on yield. However, QTL analysis can make a considerable contribution to increasing the efficiency of breeding varieties with improved responses to abiotic stresses, e.g., drought and salinity (Dubcovsky et al. 1996). One of the most important goals of QTL mapping is the possibility of using the information obtained on gene number and their effects on plant improvement via marker-assisted selection. Also, this is the area of molecular marker technology which is likely to help bridge the gap between detection and determination of the exact chromosomal location and cloning of a QTL. However, the main factor contributes to the slow progress in mapping QTL for salinity tolerance relaying on the low heritability of yield traits under stress conditions. To map QTL one has to set up a cross between tolerant and susceptible parents, measure the traits of interest, and screen the experimental population for genetic markers (Amin and Diab 2013).

Progress in MAS for wheat was slowed down by the limited availability of genomic data, but recent advances in genotyping techniques and DNA sequencing have produced genome datasets for designing sequence-based simple sequence repeats (SSRs) and SNP markers (Filiz et al. 2009; Lucas et al. 2012; Akpinar et al. 2017). SNPs are increasingly used for germplasm characterization and gene mapping because they provide cost-effective, rapid, and high-throughput genotyping. SNPs are suitable for the dissection of complex traits using highly multiplexed marker microarrays such as the Affymetrix GeneChip because they are codominant, sequence tagged, and highly abundant (Winfield et al. 2016). Recently developed Axiom Wheat Breeders' Genotyping array is a highly efficient system for screening large wheat populations. It a cost-effective high-throughput genotyping method as it contains 35,143 pre-validated SNPs which cover all 21 wheat chromosomes and is capable of genotyping 384 wheat samples simultaneously. For drought-related traits in durum wheat, it has also been used for the construction of a high-density linkage map and subsequent identification of genomic regions (Lucas et al. 2017). To construct high-density linkage maps, which are a prerequisite to mapping the QTLs for agronomically important traits, genotypic data from multiplexed marker assays are used (Peleg et al. 2009, Lorieux 2012, Leonforte et al. 2013, Masoudi et al. 2015). These maps also provide a genomic resource for positional cloning of important genes. They can also be used for comparative genomics to dissect chromosomal organization and evolution due to their construction from sequence-tagged markers (Leonforte et al. 2013). Tags for regions containing QTLs of targeted traits and for several QTLs for salt tolerance which have previously been mapped in wheat have been provided by markers in the linkage map (Genc et al. 2010, Xu et al. 2013, Masoudi et al. 2015). Forty QTLs for seven seedling traits including chlorophyll content, Na^+ and K^+ concentrations in the shoot, and seedling biomass under salinity were mapped by Genc et al. (2010). A NAX QTL interval wPt-3114-wmc170 was mapped on Chromosome 2A, associated with 10% increase in seedling biomass. Two of the five QTLs for NAX were also co-located with seedling biomass QTLs. There is a need for QTL mapping for salt tolerance in more populations to identify other major/novel QTLs as all five QTLs have given rise to only 18% of the seedling biomass phenotypic variation. In addition to NA^+ and K^+, several other factors might be involved in wheat salt tolerance. It has been observed that Mg^{2+} and Ca^{2+} accumulation also influence salt tolerance, and several QTLs for Mg^{2+} and Ca^{2+} concentrations under salinity were identified in wheat (Genc et al. 2014). Genetic bases of other minerals such as P, Zn, Fe, Mn, Cu, S, and boron apart from K^+, Mg^{2+}, and Ca^{2+} have also been investigated under different water regimes, but not under salinity. Two novel major QTLs were identified by Hussain et al. (2017) on wheat chromosome 7A which contributed 11.23 and 15.79% to salt tolerance and 13.69–15.35% to NA^+ in the population, while another major Zn QTL contributed 12.08 and 11.23% to Zn phenotypic variation and salt tolerance, respectively. 11.87% of the observed salt tolerance trait was contributed by a major SCaIC QTL, whereas other novel QTLs have contributed 10.91, 12.96, 11.31, and 14.16% of Ca, Fe, K, and Mn phenotypic variation. Other mapped QTLs represented 2.1–8.98% of the phenotypic variation of different minerals. For MAS breeding for salt tolerance and breeding for biofortification of wheat for Ca, Zn, Mg, Fe, and Mn, these novel QTLs could be used. 1293 segregating SNPs were also annotated that were located within genes for many ion channels, signaling pathways, TFs, metabolic pathways, etc., while 258 of them were differentially expressed under salinity, indicating that they may have a role in salt tolerance. The transcriptome used for this analysis is based on Roche 454-GS FLX sequencing; future transcriptome data from salt-stressed wheat using Illumina technology could help to further the knowledge of gene expression under salinity. The characterization of these annotated genes will help to dissect salt tolerance as well as other stress tolerance mechanisms, guiding future breeding for this important trait (Hussain et al. 2017).

Cytogenetic methods and molecular markers have been used in screening addition, substitution, and recombinant lines. Recently, one of such molecular marker systems called the PCR-based landmark unique gene (PLUG) has been developed in wheat based on intron polymorphism (Ishikawa et al. 2007; 2009). Although homoeologous genes of wheat are highly similar, intron regions have more polymorphism than exon regions (Bryan et al. 1999). Therefore, it is possible to separate PCR products derived from homoeologous genes using electrophoresis. Furthermore, the coding regions of the genes are often highly conserved between species or genera, making the EST-derived markers useful for marker development in wheat relative species such as *Th. bessarabicum*, where whole genome sequences are not yet available (Zeinali et al. 2013).

4.4 Gene Pyramiding

For agronomic traits that are otherwise difficult to tag such as resistance to pathogens, insects, and nematodes, tolerance to abiotic stresses, quality parameters and quantitative traits, and molecular markers are especially advantageous. Molecular marker studies using near-isogenic lines (NILs), bulk segregant analysis, or recombinant inbred lines (RILs) have accelerated the mapping of many genes in different plant species. By using RAPD and RFLP markers in tomato and rice and microsatellite markers in rice, wheat, and cereals, sequence-tagged sites have been developed. Marker-aided selection, which is now more efficient and sophisticated, still mostly based on field selection, and data analysis are practiced more now. But, due to lack of durable resistance effect, many MAS based improved traits have broken up in the past few years. Therefore, it is a challenge now to develop new efficient marker-assisted selection strategies aimed at plant improvement. To attain durable resistance against biotic and abiotic stresses in crops, gene pyramiding holds greater promise. Resistance to different isolates, races, or biotypes is conferred by various resistance genes. In addition to the epistatic effect, the development of pyramid lines is a long and costly affair. But, the pyramiding of genes effectively into a single genetic background could be facilitated by MAS based gene pyramiding. Additional options for pyramiding different resistance gene combinations into different parents also exist, when hybrids crops are the goal.

The strategy in a gene pyramiding scheme is to cumulate into a single genotype those genes that have been identified in multiple parents. The pyramiding process can be sped up by the use of DNA markers, which permits complete gene identification of the progeny at each generation. The gene pyramiding aims at the derivation of an ideal genotype that is homozygous for the favorable alleles at all loci. The gene pyramiding scheme can be distinguished into two parts: the first one is *pedigree*, which aims at cumulating of all target genes in a single genotype called the root genotype, and the second part is called the *fixation step* that fixes the target genes into a homozygous state to derive the ideal genotype from the one single genotype. An intermediate genotype is each node of the tree has two parents. Each of this intermediate genotype variety can resist. Parents in the next cross can also be improved by pyramiding. The intermediate genotype is a particular genotype selected among the offspring in which all parental target genes are present and is not just an arbitrary offspring of a given cross. Several different procedures can be used to undergo fixation in gene pyramiding although the pedigree step may be common. Generation of a population of doubled haploids from the root genotype is a possible procedure for the fixation steps. A population of gametes is obtained from the genotypes, and their genetic material is doubled which leads to a population of fully homozygous individuals among which the ideotype can be found. The ideal genotype can be obtained in just one additional generation by using this process after the root genotype is obtained. Producing a large population of doubled haploid is difficult as well as cumbersome in certain plant species.

To self the root genotype directly to obtain the ideal genotype is a possible alternative to this method. But this selfing the root genotype will result in the breakage of linkage between the desired alleles, and it will be difficult to derive this break as the linkage phase is rarely visible in selfed populations. As a result, it may span too many generations and can stretch the gene pyramiding scheme.

To obtain a genotype carrying all favorable alleles in coupling by crossing the root genotype with a parent containing none of the favorable alleles is another alternative to all these methods which confirms that the linkage phase of the offspring is known and the genotype can be derived without any mixing. After the root genotype, the ideal genotype will be reached within two generations. But a more simplified method would be to cross the root genotype with one of the founding parents instead of crossing with a blank parent. The linkage will still be known in such program, and the selection will be for genotypes that are homozygous for the target gene brought by the founding parent but heterozygous for other regions. In marker-assisted backcross gene pyramiding to increase the probability of getting the ideal genotype, the desired genes need not be fixed subsequently which is the most accepted and efficient method to do the gene pyramiding.

It is now possible for the breeder to conduct many rounds of selections in a year with MAS based gene pyramiding. To allow researchers to access, transfer, and combine genes at a rate and with a precision which was not previously possible, gene pyramiding with marker technology can be integrated into existing plant breeding programs all over the world. Still there are lot of problems in this field, which have to be solved with better scoring methods, larger population sizes, multiple replications and environments, appropriate quantitative genetic analysis, various genetic backgrounds, and independent verification through advanced generations. Tt is not surprising that new or improved selection schemes have been developed and applied as in case of maize because of the number of ongoing experiments and the explosion of new molecular technology (Ribaut et al. 2001), which will help breeders to solve problems related to larger breeding populations and replications in diverse environments and will speed up the development of advanced lines. Much better choices about target traits can be made by improved scoring methods, and screening techniques can be developed and implemented. MAS based gene pyramiding can be made more powerful and effective by new technological developments like automation, allele-specific diagnostics, and diversity array technology (Jaccoud et al. 2001). It is problematic to find out the most suitable way to use the genome information for various biological schemes including MAS based gene pyramiding. The contribution made to improve the food production is measured by the development in plant breeding. Therefore, to implement it successfully in breeding programs, plant breeders must be convinced of the advantages of MAS based gene pyramiding. Recent success in MAS based gene pyramiding was made because of good choice of target traits and availability of information on the mode of inheritance, and protocols to integrate MAS based gene pyramiding technology into breeding programs were developed with a multidisciplinary effort.

When used in conjunction with traditional breeding, MAS based gene pyramiding has the potential to increase the rate of genetic gain. A testimony to this is the adoption of MAS by cereal breeders in Australia and the subsequent commercialization of pyramided lines of cultivars bred. For pyramiding disease resistance genes, the feasibility of gene pyramiding has been demonstrated which was achieved mostly in well-adapted varieties, more or less independent of plant breeders. But, plant breeders simultaneously also came up with new varieties that may be higher yielding, so the pyramided lines did not find their way to the fields even though their yield was at par with the recurrent parents. Now the big question is that how MAS based gene pyramiding can be made operational in the developing world to get maximum benefit from it. As MAS is expensive and breeding programs are mostly funded by the local governments, the national governments can start some MAS based gene pyramiding projects with committed funding. The Indian Council of Agricultural Research (ICAR) in India has already taken the initiative, and MAS based gene pyramiding projects are successfully being done in rice, maize, wheat, etc. which is the integral part of the breeding program. Not many QTLs (especially the productivity-related ones) with tightly linked markers are available; therefore, breeders are not much excited about gene pyramiding for simply inherited traits. It requires a little bit more time for especially the productivity-related QTL from the wild species germplasm to become available to breeders. The efficiency of pyramiding large populations or breeding materials has significantly increased with development and access to reliable PCR-based markers like SSPs and SNPs in several crop plants. Better scoring methods, appropriate quantitative genetic analysis, and independent verifications through parallel populations are needed for QTL pyramiding. To maximize the efficiency of MAS, appropriate DNA markers should be used at a definite stage (Joshi and Nayak 2010).

4.5 *Tissue Culture*

Various biotic and abiotic stresses adversely affect the production and productivity of several crops due to which enormous economic losses occur throughout the world. Traditional breeding technologies and proper management strategies play a very important role in crop improvement. To integrate favorable genes of interest from intercrossing genera and species into the crops to induce stress tolerance, the conventional breeding programs are being employed. But, conventional breeding methods have failed to provide desirable results and achieved little success; therefore, the biotechnological tools are needed for addressing the critical problems of crop improvement for sustainable agriculture. Genetic engineering might prove to be a faster track toward improving crop varieties for developing stress-tolerant plants based on introgression of genes involved in stress response and putative tolerance. For the development of stress-tolerant plants, genetic transformation is now a widely used procedure for introducing genes from distant genepools into many plant species, and considerable efforts have been made to produce stress-tolerant plants by using this technique (Borsani et al. 2003; Yamaguchi and Blumwald 2005). The silencing of the transgene, consequent reduction of gene expression, and low transformation frequency are the major limiting factors in the extension of this technique to several stresses. Therefore for developing stress-tolerant plants in recent years, tissue culture technique has emerged as a feasible and cost-effective alternative tool. It can be used under controlled conditions with limited space and time (Sakhanokho and Kelley 2009) and has the potential for selection of stress-tolerant variants using a low-cost laboratory set up (Rai et al. 2011).

4.5.1 In Vitro Selection

The opportunity to select and regenerate plants with desirable characteristics is offered by in vitro culture of plant cells, tissues, or organs on a medium containing selective agents. It also induces tolerance through the use of some selective agents that permit the preferential survival and growth of desired phenotypes (Purohit et al. 1998). NaCl (for salt tolerance), PEG or mannitol (for drought tolerance), specific fungal culture filtrate (FCF), and phytotoxin such as fusaric acid or the pathogen itself (for disease resistance) are the selecting agents usually employed for in vitro selection. A broad range of these selective agents added to the culture medium to expose the explants to them. Only those explants are selected which are capable of sustaining such environments and survive in the long run. There are two types of selection methods: (a) stepwise long-term treatment, in which cultures are exposed to stress with gradually increasing concentrations of selecting agent, and (b) shock treatment, in which cultures are directly given a shock of high concentration and only those which would tolerate that level will survive. In cultured and regenerated plants, these methods are based on the induction of genetic variation among cells, tissues, and/or organs. Somaclonal variations in regenerated plants are induced by the tissue culture and can result in a range of genetically stable variations which are useful in crop improvement. The time for the selection of desirable traits can be shortened by in vitro selection under selection pressure with minimal environmental interaction which can complement field selection. Development of stress-tolerant plants through in vitro selection despite many advantages has some limitations like loss of regeneration ability during selection, lack of correlation between the mechanisms of tolerance operating in a cultured cell, tissue or organ, and those of the whole plants, and the phenomenon of epigenetic adaptation. Non-tolerant cells sometimes during in vitro selection can undergo an epigenetic adaptation, which means stable epigenetic alterations that are inherited only through mitosis and not through meiosis, to the specific selective agents, thus obscuring the selection of rare mutants with true tolerance, i.e., meiotically inherited. It was observed in numerous studies that altered DNA methylation is a major cause of epigenetic modifications, which are sometimes recorded in cultured tissue experiments (Guo et al. 2007; Li et al. 2007b; Gao et al. 2010). It was suggested by many authors that the problem of epigenetic adaptation during in vitro selection can be overcome by the use of short-term or one-step selection that may prevent the development of epigenetically adapted cells.

Major abiotic stresses including salinity, drought, waterlogging, heat, frost, and mineral toxicities reduce the productivity of several commercial crops. Successful application of biotechnology is restricted by these abiotic constraints in these crops and will require knowledge of good biological information regarding the target species as well as the mechanisms underlying resistance/tolerance to these stresses (Dita et al. 2006). For development of abiotic stress-tolerant plants especially salt and drought, use of in vitro selection has been reported in a wide range of plant species including wheat (Zair et al. 2003; Rai et al. 2011).

4.5.2 Genetic Transformation

Genetic transformation is very important not only to the transfer of novel genes into crop plants but also to the emerging area of functional genomics (Bhalla et al. 2006).

There is introduction of genes most often related to wheat from a foreign source in the wheat transformation. But the successful genetic transformation of wheat remains time-consuming and genotype-dependent (Bhalla et al. 2006). The process of genetic transformation in wheat presently has been successfully carried out either by a gene (biolistic) gun or by the use of a bacterial vector in a dish in a laboratory. There is a tremendous potential for wheat improvement, as biotechnology could be used to add quality, abiotic tolerance, and biotic resistance, including viral disease resistance (Wang et al. 2010).

4.6 Omics Technology

A great deal of research has been carried out in the recent past in the field of plant abiotic stress tolerance encompassing genomics, transcriptomics, proteomics, and metabolomics. These "omics" technologies investigate different facets of a given scientific issue such as abiotic stress tolerance but complement each other. Integration of phenotypic, genetic, transcriptomic, proteomic, and metabolomic data will enable accurate and detailed gene network reconstruction (George et al. 2012).

4.6.1 Transcriptomics

Abiotic stress affects growth, development, and yield of plants worldwide. In the saline-alkali land and water shortage areas, the exploitation and utilization of stress-tolerant plants will become more significant. Identification of beneficial stress-related genes enhances the tolerance of plants to abiotic stresses (Tran et al. 2010; Nakashima et al. 2012). Transcription factors (TFs) are important regulators that are involved in response to abiotic stress, and overexpression of their genes commonly improves a plant's tolerance to abiotic stress (Zhang et al. 2016).

In the cereals, gene number estimates are very similar to other complex organisms like in barley gene number estimates range from around 30,000–50,000 (Zhang et al. 2004). This situation is more complicated by the three genomes of wheat. In polyploids, unusual patterns of gene expression can occur. It was observed by analysis of gene expression in wheat using expressed sequence tag (EST) databases that homologous genes can be expressed in one but are silent in one or both of the remaining genomes (Mochida et al. 2004). Changes may also occur in tissue specificity of expression from homologous genes. As a result, a gene in one genome may be expressed in roots, while the homologues are expressed in leaf tissue. Over 1 million cereal EST sequences are present in the public databases with wheat and barley dominating. "Electronic Northerns" have become a useful method for assessing gene expression due to the large number of ESTs and the diversity of cDNA libraries that have been used to generate the sequences which provides a good first measure of transcript abundance. For the cereals, several microarrays and macroarray platforms have been generated. There are a number of proprietal arrays for wheat and barley as

10,000 cDNA array reported by Leader (2005) only. For both wheat and barley, Affymetrix arrays have been developed (Close et al. 2004). By using a series of well-defined developmental stages in a reference experiment, the 22 K Barley 1 Gene Chip identified 18,481 transcripts showing expression above background. Similarly a reference experiment has been conducted using the Affymetrix Wheat Gene Chip which carries 61,127 probe sets representing 55,052 transcripts. However, it is not yet clear how the remaining probe sets will be used as only fewer than 30,000 are from high-quality sequence data. For studying altered gene expression in response to abiotic stress, there are very few published reports on the use of barley or wheat chips (Hazen et al. 2005; Langridge 2006).

Several major regulons involved in response to abiotic stress have been identified in *Arabidopsis*, while DREB1/CBF, DREB2, AREB/ABF, and NAC regulons have important functions in response to abiotic stresses in rice (Nakashima et al. 2009). In recent years, many important regulatory genes involved in stress responses have been identified which confer abiotic stress tolerance in plants (Galiba et al. 2009). Various TF family members like bZIP, bHLH, WRKY, MYB, and NAC TFs have found to be involved in abiotic stress responses in wheat (Rahaie et al. 2013).

4.6.1.1 bZIP Transcription Factors

The basic region/leucine zipper (bZIP) has a basic region that binds DNA and a leucine zipper dimerization motif. Its domain comprises two structural features present on a contiguous α-helix. There is a basic region of about 16 amino acid residues with a nuclear localization signal, an invariant N-x7-R/K motif to contact the DNA, as well as a heptad repeat of leucines or other bulky hydrophobic amino acids located exactly nine amino acids toward the C-terminus to create an amphipathic helix. Two subunits adhere through interactions of the hydrophobic sides of their helices during binding to DNA which creates a superimposing coiled-coil structure (zipper). Homo- and heterodimers are formed by the electrostatic attraction and repulsion of polar residues adjacent to the hydrophobic interaction surface of the helices. Proteins with bZIP domains are present in all eukaryotes, and bZIP proteins typically bind to DNA sequences with an ACGT core. There are also reports of nonpalindromic binding sites for bZIPs although plant bZIPs bind to the A-box (TACGTA), C-box (GACGTC), and G-box (CACGTG) (Jakoby et al. 2002). 75 bZIP protein members have been divided into 10 subgroups in *Arabidopsis* on the basis of the sequence similarities of common domains (Jakoby et al. 2002, Kobayashi et al. 2008b). bZIP transcription factors present a divergent family of TFs in plants which regulate processes including light and stress signaling, seed maturation, pathogen defense, and flower development (Jakoby et al. 2002, Rahaie et al. 2011).

The plant hormone abscisic acid (ABA) play a very important role in maturation and germination in seeds, as well as in mediating adaptive responses to abiotic environmental stresses. It induces the expression of many genes such as late embryogenesis-abundant (LEA) genes. Expression of one of these LEA genes

HVA1 is also affected by ABA. Keyser (2010) has analyzed the interplay between ABA and TaABF1 as a bZIP factor in the aleurone cells of imbibing wheat grains and observed that the two are not additive in their induction of the *HVA1* promoter. It was observed that TaABF1 may undergo an ABA-induced posttranslational modification. But this conclusion was not supported due to the lack of synergism between ABA and TaABF1 overexpression in *HVA1* induction which indicates that the branch of ABA signaling leading to *HVA1* is more complex (Keyser 2010).

A wheat *lip19* (encoding bZIP-type transcription factors) homologue, *Wlip19*, was isolated by Kobayashi et al. (2008b). They have also analyzed its expression in response to cold stress. It was found that *Wlip19* expression was stimulated by low temperature in seedlings and was higher in a freezing-tolerant wheat cultivar than in a freezing-sensitive variety. Its expression was also activated by drought and exogenous ABA treatment. A significant increase in abiotic stress tolerance especially freezing tolerance is shown by heterologous expression of *Wlip19* in tobacco. It acts as a transcriptional regulator of Cor/Lea genes in the development of abiotic stress tolerance by enhancing expression of four wheat Cor/Lea genes, *Wdhn13*, *Wrab17*, *Wrab18*, and *Wrab19*, in wheat callus and tobacco plants. In direct protein-protein interactions between WLIP19 and another bZIP-type transcription factor in wheat, the OBF1 homologue TaOBF1 was observed indicating that this interaction is conserved in cereals (Kobayashi et al. 2008b; Rahaie et al. 2013).

It was reported by expression analysis of a group of bZIP candidate genes in long-term salinity into contrasting cultivars of wheat by reverse northern blot that *bZIP1* (CN011839) was upregulated in a susceptible variety (Chinese Spring) and downregulated in a tolerant cultivar (Mahouti) during salt stress. Sequence analysis by BLASTx has shown that this gene's protein has two homologues in *Arabidopsis* (AtZIP56, E value = 1e-20) and wheat (TaABF, E value = 6e-5). *TaABF* mRNA accumulates together with *PKABA1* mRNA (an ABA-induced protein kinase) during wheat grain maturation and dormancy acquisition, and *TaABF* transcripts rise transiently during imbibitions of dormant grains, while *TaABF* transcripts are seed specific and were not markedly produced in vegetative tissues in response to ABA application or abiotic stress (Johnson et al. 2002. Rahaie et al. 2011, 2013).

4.6.1.2 bHLH Transcription Factors

A group of diverse transcription factors with highly diverse functions is known as basic helix-loop-helix (bHLH) proteins which are present in both plants and animals. The characteristic of this family is the bHLH domain which consists of about 60 amino acids with two functionally distinct regions. Its basic region at the N-terminal end of the domain is required for DNA binding, while the C-terminal HLH region functions as a dimerization domain. These TFs act as transcriptional regulators in plants which are required for phytochrome signaling, anthocyanin biosynthesis, fruit dehiscence, carpel, and epidermal development, as well as for stress response. The biological function of most members of this gene family in the plant has not been known so far (Li et al. 2007a). It was shown by gene expression analysis through reverse northern blot that two selected candidate wheat bHLHs (*bHLH2*, CA599618, and *bHLH3*, CJ685625) are affected by salt stress in a tolerant wheat cultivar. The results from BLASTx showed that both have a homologue in wheat, *bHLH94* (E value = 5e-85 for bHLH2 and E value = 5e-102 for bHLH3). Another homologue AtAIB for bHLH3 from *Arabidopsis* is involved in the regulation of ABA signaling in *Arabidopsis* and has a role in drought tolerance and ABA treatment response (Li et al. 2007a; Rahaie et al. 2011). The high homology (E value = 2e-51) between these orthologues and the result of reverse northern blot hybridizations indicated that these two bHLH genes may have an important function in tolerance to salt stress in wheat (Rahaie et al. 2011, 2013).

4.6.1.3 WRKY Transcription Factors

In the last two decades, WRKY transcription factors have been studied in plants extensively. It consists of a domain of about 60 amino acids which is a characteristic of WRKY proteins. This domain has the conserved sequence WRKYGQK followed by a zinc finger motif. It binds to the W box ([T][T]TGAC[C/T]) of target gene promoters to modulate transcription (Wu et al. 2008; Chen et al. 2012). The overall structures of WRKY TFs are highly divergent in spite of the strong conservation of their DNA-binding domain. WRKY TF family members are grouped into three distinct groups on the basis of the number and type of the WRKY domains which also represent their different functions (Rahaie et al. 2011). Group I has WRKY TFs with two WRKY domain members of group II, and group III possesses one WRKY domain. Group I and group II have a C2H2 zinc finger motif, while group III has the WRKY domain containing a C2HC motif. Based on their phylogenetic clades, WRKY TFs can then be further classified into different subgroups. It is one of the TF families which has shown the regulatory role in biotic and abiotic stresses in plants like infection of bacteria, fungi, oomycetes, and viruses, treatment with salicylic acid (SA) or H_2O_2, mechanical stimulation, drought, cold, wounding, high salinity, and UV radiation. Most WRKY TFs of group III have a role in plant defense signaling pathways. Some members of the WRKY family may have important functions in plant development like embryo development, fruit maturation, tannin synthesis in the seed coat, maturation of root cells, morphogenesis of trichomes, senescence, and dormancy. Some WRKY family members like OsWRKY71 and OsWRKY51 also have a role in hormone signaling and were ABA-inducible and could repress GA signaling transduction in aleurone cells.

Sequences of 15 wheat cDNAs encoding putative WRKY proteins have been obtained by Wu et al. (2008). It was shown by phylogenetic analysis that the 15 WRKY genes are grouped into 3 major WRKY groups, and expression analysis revealed that most genes were highly expressed in leaves. Few of them like *TaWRKY10* are expressed in the crown intensively, and several genes are strongly upregulated during the senescence of leaves. It was found that eight isolated genes were responsive to high or low temperature, NaCl or PEG (polyethylene glycol) treatment. Differential expression was also measured between wheat hybrids and its parents, and some genes were found to be more responsive to PEG treatment in the hybrid. Actually, the differential expression of these WRKY genes in the hybrid might contribute to heterosis by improving the stress tolerance in hybrids.

It was demonstrated by expression analysis of a group of putative wheat WRKYs through reverse northern blot hybridizations that *WRKY1* (CN009320) and *WRKY2* (CJ873146) were upregulated in a stress-tolerant genotype. A homologue from *Arabidopsis* for WRKY1, AtWRKY75 (E value = 3e-42) is upregulated in response to phosphorus deficit stress (Devaiah et al. 2007; Encinas-villarejo et al. 2009; Rahaie et al. 2011). It also acts as a positive regulator in defense responses to pathogens. It was demonstrated by functional characterization of the WRKY2 homologue in *Arabidopsis*, AtWRKY33 (E value = 4e-18), that its expression in response to salt, mannitol (simulated drought) treatment, and cold stress in shoots and roots increased but was downregulated during heat stress. It is speculated that its expression is independent of SOS signaling and only partly dependent on ABA signaling and forms part of plant responses to microbial infections (Lippok et al. 2007; Jiang and Deyholos 2009; Rahaie et al. 2011, 2013).

4.6.1.4 MYB Transcription Factors

One of the largest transcription factor families in plants is MYB TFs. In genomes of *Arabidopsis* and rice, more than 200 MYB proteins are encoded. One to four imperfect repeats (50–53 amino acids) in their DNA-binding domain (MYB domain) are found in MYB TFs near the N terminus and are grouped into four subfamilies (Rahaie et al. 2010; Zhang et al. 2012).

It was observed that 4R-MYB has four repeats, 3R-MYB (R1R2R3-MYB) has three consecutive repeats, R2R3-MYB has two repeats, and the MYB-related type usually, but not always, has a single repeat according to the number of repeat(s) in the MYB domain (Dubos et al. 2010; Jin and Martin 1999). The MYB repeat is 50–53 amino acids in length and contains three regularly distributed tryptophan (or phenylalanine) residues, which can together form a hydrophobic core. There are three α-helices in each MYB repeat. Two of them that are located at the C-terminus adopt a variation of the helix-turn-helix (HLH) conformation which recognizes and binds to the DNA major groove at the specific recognition site such as C/TAACG/TG.

The expression levels of ten MYB TF genes from wheat (*Triticum aestivum*) in two recombinant inbred lines contrasting in their salt tolerance in response to salt or drought stress via quantitative RT-PCR have been analyzed by Rahaie et al. (2010). In leaves and roots of wheat plants subjected to long-term drought stress, a potential new MYB gene *TaMYBsdu*1 was significantly upregulated. Under salt stress, *TaMYBsdu*1 showed higher transcript abundance in the salt-tolerant genotype than in the susceptible genotype which suggested that it is a potentially important regulator for wheat adaptation to both salt and drought stresses.

Two putative MYB genes, *MYB2* (DQ353858.1) and *MYB3* (CJ920766), were upregulated in a tolerant variety (Mahouti) under salt stress conditions but downregulated in the susceptible cultivar (Chinese Spring), *MYB2*. It was observed through sequence analysis with the BLASTx and Plant Gene Ontology assignment that MYB2 is a part of TaMYB1 (E value = 6e-155). It was demonstrated by Lee et al. (2007) that *TaMYB1* is involved in abiotic stress responses in wheat. The expression of this gene increases oxygen deficiency (flooding), PEG treatment (drought), and salt increases especially in roots. Its transcript gradually also increases in starting ABA and PEG treatments. Comparative transcriptome analysis of salt-tolerant wheat germplasm lines has been studied by Mott and Wang (2007) by using wheat genome arrays and observed that *TaMYB1* was one of the upregulated genes with 34 times higher expression levels under stress condition relative to the control. Through functional analysis of the MYB2 homologue in *Arabidopsis*, AtMYB44 (E value = 1e-59), it was observed that this gene was upregulated in response to drought, salt, cold, and ABA treatments, especially in stomata, guard cells, and vascular tissue. There was more tolerance to mentioned stresses compared to wide-type plants in transgenic plants overexpressing this gene. There is high homology between this gene and *AtMYB59* in *Arabidopsis* (E value = 4e-60) as shown by homology analysis of MYB3 (a member of R2R3MYB). *AtMYB59* expression increases in response to phytohormones including jasmonic acid, SA, gibberellic acid, and ethylene, especially in leaf and stem tissues (Li et al. 2006a; Libault et al. 2007; Rahaie et al. 2011). Its expression level in roots and inflorescences was lower than in other organs, proving its role in hormonal signal pathways in response to biotic stresses and plant defense against pathogen attacks (Li et al. 2006a; Libault et al. 2007; Rahaie et al. 2011, 2013).

In wheat, full-length cDNA is an important resource for isolating the functional genes. A group of MYB genes that respond to one or more stress treatments were analyzed by Zhang et al. (2012a) who isolated 60 full-length cDNA sequences encoding wheat MYB proteins. To examine their evolutionary relationships and the putative functions of wheat MYB proteins based on *Arabidopsis* MYB proteins with known functions, a phylogenetic tree with wheat, rice, and *Arabidopsis* MYB proteins was constructed. To find potential genes that participate in the stress signal transduction pathway, including the analysis of transgenic *Arabidopsis* plants expressing the MYB gene, *TaMYB32* tissue-specific analysis and abiotic stress response expression profiles were carried out.

A new R2R3-type MYB transcription factor gene, *TaMYB33*, from wheat (*T. aestivum*) was identified by Qin et al. (2012). It was induced by ABA, NaCl, and PEG treatments, and its promoter sequence has the putative ABRE, MYB, and other abiotic stress-related cis elements. In *Arabidopsis* ectopic overexpression of this gene significantly enhanced its tolerance in drought and NaCl treatments, but not in LiCl and KCl stresses. In the *TaMYB33*-expressing transgenic *Arabidopsis* lines, the expression of two genes, *AtP5CS* (involved in proline synthesis) and *AtZAT12* (a C2H2 zinc finger transcription factor that is involved in regulating ascorbate peroxidase expression), was induced. It is suggested that TaMYB33 promotes the ability for ROS scavenging and osmotic pressure balance reconstruction. *TaMYB33* overexpression lines that displayed upregulation of *AtAAO3*, along with downregulation of *AtABF3* and *AtABI1*, indicate that ABA synthesis was elevated, while its signaling was constrained. It can be concluded from this that TaMYB33 enhances salt and drought tolerance partially via an improved ability for ROS detoxification and osmotic balance reconstruction. Zhang et al. (2012b) identified *TaMYB56* (on chromosomes 3B and 3D) in wheat as a cold stress-related gene. It was observed that the expression levels of *TaMYB56-B* and *TaMYB56-D* were strongly induced by cold stress but slightly induced by salt stress in wheat. It was revealed by detailed characterization of the *Arabidopsis* transgenic plants that overexpressed *TaMYB56-B* is possibly involved in the responses of plants to freezing and salt stresses. The expression of some cold stress-responsive genes like *DREB1A/CBF3* and *COR15a* was found to be elevated in the *TaMYB56-B*-overexpressing *Arabidopsis* plants in comparison to wild type. Another MYB gene *TaMYB3R1* has been shown to be potentially involved in wheat response to drought, salt, and cold stress. *TaMYB3R1 was cloned* from wheat (*T. aestivum*) by Cai et al. (2011). Its amino acid sequence shares high homology to other plant MYB3R proteins. In onion epidermal cells, subcellular localization experiments proved that TaMYB3R1 was present in the nucleus. It was confirmed by transactivation assays in yeast cells that TaMYB3R1 require the C-terminal region to activate the expression of the reporter gene. The MSA cis-element-binding activity of TaMYB3R1 was shown by DNA-binding tests. Its expression was induced by ABA treatment, and its expression gradually increased until 72 h after salt or cold treatment, while PEG treatment leads to an early expression peak at 6 h after treatment and then gradually decreased.

TaMYB32 has been identified as a salt stress-related gene by Zhang et al. (2009) during the bulk sequencing of full-length cDNAs in wheat (*T. aestivum*). Its sequences were cloned from different varieties of hexaploid wheat and its diploid ancestors. It was indicated by sequence analysis that two types of sequences existed in the diploid ancestors and four in the hexaploid wheat. It was observed that one of the sequences was identical in both diploid and hexaploid wheat which means that TaMYB32 was conserved during the evolution of wheat. After comparison with their cDNA sequences, it was found that the genomic *TaMYB32* sequences are non-intron genes. By using the electronic mapping strategy, it was mapped onto the homoeologous group VI of wheat, and two copies of the gene were found in each genome of hexaploid wheat. It was found through homologous analysis that TaMYB32 had a similarity with some R2R3-MYB proteins from rice (*Oryza sativa* L.) and maize (*Zea mays* L.) as high as 72.4% and 73.7%, respectively. The expression of *TaMYB32* in roots, stems, leaves, pistils, and anthers in wheat was induced by salt stress (Rahaie et al. 2013).

4.6.1.5 NAC Transcription Factors

One of the largest families of plant-specific TFs is NAC protein (Olsen et al. 2005) which are derived from three genes containing particular domains of NAM (no apical meristem), ATAF (*Arabidopsis* transcription activation factor), and CUC (cup-shaped cotyledon) (Souer et al. 1996; Aida et al. 1997). A highly conserved N-terminal NAC domain and a variable C-terminal transcription regulatory (TR) region are found in A NAC transcription factor (Ernst et al. 2004; Olsen et al. 2005). The nuclear localization, DNA binding, and formation of homodimers or heterodimers are caused by the nearly invariable N-terminal NAC domain. This domain has approximately 150 amino acids and is known as an A-E subdomain (Olsen et al. 2005), while the C-terminal region is diverse and can function as a transcriptional activator or repressor (Delessert et al. 2005; Kim et al. 2007; Yamaguchi et al. 2010; Puranik et al. 2011).

It was demonstrated by various reports that NAC TFs are involved in a number of biological processes, like controlling cell division by mediating cytokinin signaling (Kim et al. 2006); regulating the growth of plant cells (Kato et al. 2010), lateral root development (He et al. 2005; Quach et al. 2014), and leaf senescence (Guo and Gan 2006; Yang et al. 2011; Shah et al. 2013); inducing phytoalexin biosynthesis (Saga et al. 2012), formation of secondary walls (Mitsuda et al. 2007; Zhao et al. 2010), and flower formation (Hendelman et al., 2013); and responding to pathogen infection (Voitsik et al. 2013; Yokotani et al. 2014), seed development (Park et al. 2011), and fiber development (Zhao et al. 2014). Many members of the NAC TF family can coordinate the response to abiotic stress. There was increased tolerance to drought and salinity in wheat plants expressing the *SNAC1* gene (Nakashima et al. 2007; Takasaki et al. 2010; Saad et al. 2013; Chen et al. 2014). Similarly, enhanced resistance to both drought and salt stresses was observed in transgenic rice overexpressing *OsNAC045* (Zheng et al. 2009). Due to root-specific overexpression of the *OsNAC9* and *OsNAC10* genes, enlargement in roots and enhancement in the drought tolerance of transgenic rice have taken place that led to significantly increasing the grain yield under field drought conditions (Jeong et al. 2010; Redillas et al. 2012). The characterization of stress-related NAC transcription factor's role has been reported in wheat. It was observed that two genes, *TaNAC4* and *TaNAC8*, were involved in stripe rust pathogen infection and abiotic stresses (Xia et al. 2010a, b). The expression of *TaNAC69* was upregulated by multiple abiotic stresses in wheat, and overexpression of this in transgenic wheat enhanced the expression levels of stress upregulated genes and dehydration tolerance (Xue et al. 2011). Overexpression of *TaNAC2*, *TaNAC2a*, and *TaNAC67* improves the tolerance of transgenic plants to abiotic stresses (Tang et al. 2012; Mao et al. 2012, 2014).

Zhang et al. (2016) characterized an abiotic stress-related gene, *TaNAC47*, from a full-length wheat cDNA library to interpret the possible molecular regulatory mechanisms underlying the plant response to abiotic stress and accelerate the use of the *NAC* gene to facilitate engineering transgenic wheat. In response to polyethylene glycol (PEG), salt, cold, and exogenous ABA treatments, its expression profiles were examined in wheat by using the quantitative real-time PCR (RT-qPCR) approach. By ectopic expression of *TaNAC47* in *Arabidopsis*, its function in abiotic stress tolerance was evaluated. No obvious morphological differences were observed between the transgenic and WT *Arabidopsis* plants under normal growth conditions which indicated that *TaNAC47* is likely a candidate gene that will be useful for improving stress tolerance (Zhang et al. 2016).

It was shown by Rahaie et al. (2011) that *NAC67* (BU672229), a putative member of the NAC family, was upregulated during salt stress treatment. The encoded protein has a close homologue in wheat (TaNAC69, E value = 2e-151) (Rahaie et al. 2011; Xue et al. 2006).

The improvement of abiotic stress resistance can be achieved by genetic manipulation of transcription factors as in the past decade demonstrated by various transgenic plant studies. Many resistant transgenic lines with constitutive overexpression of a transcription factor exhibited a slower rate of growth under nonstress conditions. It was also shown by field trials that some transgenes tend to have a negative effect on grain yield under normal growth conditions (Xiao et al. 2009). This phenomenon may be a result from the following two causes: (i) there is a negative impact on the growth and yield of the genes that are induced during stress and (ii) due to overexpression of a transcription factor, the energetic cost of the stress-related metabolite accumulation. If the crop yield is concerned, expression of a transcription factor needs to be tailored to meet the requirement for plant stress adaptation. Any reduction in crop yield under normal growth conditions could potentially override a marked yield advantage under stress. By using a stress-inducible promoter, the expression of a transcription factor can be tailored to adapt stress. As transgenic *Arabidopsis* plants carrying a drought-inducible promoter-driven *DREB2A* gene show the improved drought resistance with no significant difference in growth rate under normal growth conditions (Sakuma et al. 2006). For consideration of minimizing the negative impact of transgene expression on growth and yield, other aspects include the appropriate expression level of the transgene and cell specificity. A root-specific promoter has been used recently for driving expression of drought-upregulated transcription factors for engineering drought tolerance (Jeong et al. 2010; Redillas et al. 2012). A number of transcription factors have been shown to improve crop yield under field conditions when they are over-expressed in transgenic plants. Genetic manipulation of these stress-responsive transcription factors has the potential for improvement of crop yield in the future, including wheat. Certain stress-induced TF genes play important roles in wheat stress tolerance which enhances our understanding of the mechanisms of responses and tolerance to abiotic stress in wheat. It also provides us with a collection of suitable candidate genes for over- or under-expression studies in transgenic wheat with the aim of achieving increased abiotic stress tolerance.

To elucidate the function of the different stress-responsive TFs and their relationship in transcriptional control in wheat, a systems biology approach using reverse genetics, functional genomics and proteomics, as well as metabonomics during various developmental stages and stress conditions will provide us with critical information in the future.

The verification of abiotic stress tolerance and agronomic traits of transgenic wheat utilizing stress-responsive TF genes should be done under harsh field conditions over several years. With increases in climatic variations, more robust cultivars that withstand a wide variety of stresses are expected which will be superior over those that are high yielding under optimal conditions. In order to fully utilize the potential of transcription factors, it will be essential to clarify the differential function of the individual stress-responsive TF genes from different families of TFs for the control of abiotic stress tolerance and other biological processes including biotic stress tolerance, growth regulation, senescence, and yield (Rahaei et al. 2013).

4.7 Proteomics

In the post-genomic era, proteomics is a well-established technique (Liu et al. 2013). In an organism encoded by its genome, proteomics deals with the study of the large-scale expression of proteins. It not only serves as a powerful tool for describing complete protein changes in any organisms but it can also be used to compare variation in protein profiles at organ, tissue, cell, and organelle levels under various stress conditions including heavy metal stress (Ahsan et al. 2009). Transcriptomic changes in the genome are not always reflected at the protein level, although genomic analysis has enhanced our understanding regarding plant's response to heavy metal toxicity (Gygi et al. 1999; Hossain and Komatsu 2013). Putative Zn and Mg transporter protein MHX was more abundant in *Arabidopsis* even though its corresponding transcript level was not different (Elbaz et al. 2006) which suggested that transcription of any gene is not a guarantee that gene would be translated into a functional protein. This occurs due to the potential impact of posttranscriptional and translational modifications, protein folding, stability and localization, and protein-protein interactions, which are important determinants of a protein function (Dalcorso et al. 2013b). Therefore, in studying complex biological processes and interactions among the possible pathways that involve a network of proteins, depth analyses of proteomics offer a new platform for identifying target proteins (Ahsan et al. 2009).

Proteins directly take part in plant stress responses, and plant adaptations to stress are always accompanied with deep proteomic changes. For deciphering the possible relationships between protein abundance and plant stress adaptation, therefore, the technique of proteomics can be exploited which can contribute to better understanding of physiological mechanisms under abiotic stress like perception of stress and further signaling cascade that leads to changes in the expression of huge numbers of genes at transcriptional level and in metabolite profile, which could be used for an acquisition of an enhanced plant tolerance under heavy metal toxicity (Kosová et al. 2011). It was revealed by various studies that an abundance of defense proteins was increased for scavenging of ROS, and molecular chaperones play a role in re-establishing the conformation of a functional protein which contributes in helping heavy metal-stressed plants to maintain the redox homeostasis (Zhao et al. 2011; Sharmin et al. 2012; Wang et al. 2012). Modulations of various metabolic pathways occur under heavy metal stress like photosynthesis, respiration, nitrogen metabolism, sulfur metabolism, etc. particularly in photosynthesis and mitochondrial respiration that help stressed plants to produce more reducing power such as NADPH, NADH, and $FADH_2$ and assimilatory power ATP to compensate high energy demand of heavy metal-challenged plants (Hossain and Komatsu 2013). An increased abundance of RuBisCO large subunit (LSU)-binding proteins, oxygen-evolving enhancer protein 1 and 2, NAD(P)H-dependent oxidoreductase, and photosystem I- and II-related proteins is an adaptive feature to tolerate heavy metal stress (Semane et al. 2010). The first reactions in the plant cell against heavy metal are the cellular mechanism of stress sensing and further transduction of signals into the cell. An intracellular communication of stress signals plays a basic role in signal transduction pathways under stress, which ultimately activates defense-related genes and thus signaling cascades (Hossain et al. 2012). To decipher an underlying molecular mechanism of alterations in the protein signature of a plant cell in order to withstand stress, a deep study on the cellular as well as organelle proteomics would be of great importance in developing stress-tolerant crops (Singh et al. 2016).

There are no reports on the application of proteomics to the study of abiotic stress tolerance in wheat and barley, but proteome studies have been conducted in wheat leaf (Bahrman et al. 2004), grain (Skylas et al. 2005), and lemma (Woo et al. 2003). They have shown the feasibility of differentiating and identifying large numbers of proteins from defined tissues of wheat. 541 proteins were resolved by the leaf proteome study, of which 55 were sequenced (Rice 2005). Around 3000 proteins could be detected in a single gel, and over 1000 could be quantified in the proteomic study of drought- and salt-stressed rice plants (Salekdeh et al. 2002). It was found that 42 proteins changed abundance or position in response to stress. Several of the important proteins were identified and are the subject of further studies.

4.8 Metabolomics

The identification and quantification of all low-molecular-weight metabolites required by the organisms during developmental stages is known as metabolomics (Arbona et al. 2013). Some metabolites have been reported to be involved under abiotic stress tolerance strategies (Singh et al. 2016).

Detailed metabolite profiling may provide valuable insights into stress response mechanisms. It is a relatively new area of research, and there are no published reports on its application to stress tolerance in cereals. Eighty-eight main metabolites could be successfully quantified from the extract of rice leaves (Sato et al. 2004). These compounds identified covered pathways of sugar and amino acid metabolism which proves that these types of analyses are valuable for assessing stress responses (Langridge 2006).

Some nitrogen-containing metabolites like some peptides (phytochelatins, metallothioneins, and ferritins) have been reported to play an important role under abiotic stress apart from inducing synthesis of amino acids (proline and histidine), amines, organic acids, and plant antioxidant α-tocopherol and glutathione. This recently developed technological tool includes different approaches, namely, targeted analysis, metabolic fingerprinting, and metabolite profiling.

The most developed analytical approach in metabolomics is the targeted analysis (Djoukeng et al. 2008) which is used to estimate the concentration of a limited number of known metabolites precisely, by using either gas chromatography (GC) or liquid chromatography (LC) coupled to mass spectrometry (MS) or nuclear magnetic resonance spectroscopy (NMR).

Metabolic fingerprinting uses signals from hundreds to thousands of metabolites for rapid sample classification via statistical analysis, while other approaches using high-throughput metabolite analysis focus on a subset of useful information and avoid the difficulties of comprehensive metabolite characterization (Chatterjee et al. 2010). Metabolite profiling attempts to identify and quantify a specific class or classes of chemically related metabolites that often share chemical properties which facilitate simultaneous analysis (Seger and Sturm 2007).

The downstream result of gene expression is represented by metabolome and is closer to phenotype than transcript expression or proteins. Assessment of genotypic or phenotypic differences between plant species or among genotypes exhibiting different tolerance to some biotic or abiotic stresses is done by extensive knowledge on metabolic flows. Target metabolites have been analyzed as nutritional and/or agronomical biomarkers to classify different crop cultivars or to optimize growth conditions (Arbona et al. 2010).

Current approaches for metabolite characterization still face significant obstacles in contrast to high-throughput methodology for the analysis of DNA, RNA, and proteins. These challenges are largely coming from high degree of chemical diversity among metabolite pools as well as the complexity of spatial and temporal distribution within living tissues. To address these analytical challenges, plant metabolomics methodology and instrumentation are being developed at very fast speed (Hegeman 2010, Pérez-Clemente et al. 2013).

Metabolomics generates large amounts of data like other functional genomics research. It is a clear challenge for researchers to handle, process, and analyze this data. It requires specialized mathematical, statistical, and bioinformatic tools (Shulaev 2006). Developments in this area require improvements in both analytical science and bioinformatics. Development of new analytical techniques is largely focused on increasing resolution and comprehensiveness and increasing speed and throughput of analytical assays and equipment miniaturization.

4.9 Functional Genomics

In abiotic stress tolerance in germplasm of wheat and its wild relatives, there is ample variation available, but it has been relatively less exploited due to poor understanding of wheat genome and its molecular basis of the stress response. For dissecting abiotic stress response in various crop plants, functional genomics is now widely seen as providing tools. It involves many related approaches like global gene expression profiling and identification of responsive genes/alleles, followed by mutant analysis or transgenic approaches to assign the function of a specific gene or its product protein. Because wheat genome is not sequenced, a genome-wide collection of ESTs and full-length cDNAs are important for the structural and functional analysis of wheat genes responsive to abiotic stresses (Khurana et al. 2012).

5 Genes for Abiotic Stress

Abiotic stresses like drought, salinity, extreme temperatures, chemical toxicity, and oxidative stress are significant causes of crop loss worldwide and pose serious threats to agriculture. All these abiotic stresses are often interconnected and could induce similar cellular damage. Plants must adapt to stressful conditions and exercise specific tolerance mechanisms to maintain growth and productivity. Plant modification for enhanced tolerance is based mostly on the manipulation of those genes that protect and maintain the function and structure of cellular components. Present engineering methods rely on the transfer of one or several genes which are either involved in signaling and regulatory pathways or that encode enzymes present in pathways leading to the synthesis of functional and structural protectants or that encode stress tolerance-conferring proteins (Wang et al. 2003).

5.1 Salinity

Salt inhibits the growth of the plant and reduces its ability to take up water. It can also enter the transpiration stream and eventually damage cells in the transpiring leaves which further reduce growth which is the salt-specific or ion-excess effect of salinity (Munns 2005). Wheat is threatened by salinization and is grown under irrigated and rainfed conditions. The wheat gene pool generally has a low tolerance to salinity which restricts advancement in developing salt-tolerant germplasm (Salam et al. 1999). Some alien species like *Thinopyrum*, *T. turgidum*, *H. marinum*, *Secale cereale*, *Leymus chinensis*, *H. brevisubulatum*, and barley are more salt-tolerant than wheat (Liu et al. 2001; Garthwaite et al. 2003; Colmer et al. 2005; Wang et al. 2007). As a source for improving salt tolerance in wheat, *Thinopyrum* has received the most attention (Colmer et al. 2006). Genes for salinity tolerance from Th. elongatum have already been transferred to wheat (Chen et al. 2000). The salt tolerance of common wheat can be increased by some candidate genes from wheat-related species. These genes control salt uptake and transport, making a plant grow more quickly in the saline soil. They are thought to have an osmotic or protective function. A vacuolar Na^+/H^+ antiporter gene, AeNHX1, was isolated from Th. elongatum and transformed into *Arabidopsis* and *Festuca* plants. The overexpression of this gene could promote salt tolerance of *Arabidopsis* and *Festuca*, which shows that expression of this gene is important in salt tolerance (Qiao et al. 2007). A vacuolar Na^+/H^+ antiporter gene *AtNHX1* from *Arabidopsis thaliana* was expressed in transgenic wheat (Xue et al. 2004). Higher grain yields and heavier and larger grains in the field of saline soils with the electrical conductivity values of soil saturation extracts (ECe) of 10.6 and 13.7 dSm − 1 have been revealed by field trials. The transgenic lines accumulated a lower level of Na^+ and a higher level of K^+ in the leaves than non-transgenic plants under saline conditions (100 and 150 mM NaCl). Therefore these results indicate the feasibility of increasing salt tolerance of wheat and grain yield by enhancing the level of the vacuolar Na^+/H^+ antiporter. A sodium transporter (*HKT7*) is a candidate salt tolerance gene for *Nax1* which reduce Na + concentration in leaf blades by retaining Na^+ in the sheaths in *durum* wheat. *TmHKT7-A2* from *durum* wheat controls Na^+ unloading from xylem in roots and sheaths (Huang et al. 2006). *HVA1*, a barley group III (D-7 family) LEA protein, is related to salt tolerance and highly induced by ABA stress in barley aleurone layers. To enhance the ability of tolerance to salinity and water stress, this barley late embryogenesis-abundant protein gene *HVA1* was successfully transformed into *T. aestivum*, *T. durum*, and mulberry (Patnaik and Khurana 2003).

5.2 Drought

Shortage of water availability is defined as drought and is based on precipitation and soil moisture storage capacity in quantity and distribution during the life cycle of wheat (Mitra 2001). Although wild relatives of wheat have an excellent ability to resist drought, bread wheat has low drought resistance. In a number of wild wheat relatives, genes for drought tolerance have been discovered, and their functions have been investigated. There is good drought tolerance in species of genus *Thinopyrum* (Zhang et al. 2007). The drought tolerance of barley can be improved by the salinity-related gene *HVA1* (Li et al. 2006b). *HVA1* was introduced into spring wheat cultivar Hi-Line using biolistics by Sivamani et al. (2000). Higher water use efficiency values, significantly greater total dry mass, root fresh and dry weights, and shoot dry weight compared to the controls under soil water deficit conditions are observed in the transgenic plants under controlled environmental conditions. Testing of four selected transgenic lines was done in nine field experiments over six cropping seasons, and one promising line was selected for commercialization (Bahieldin et al. 2005). The DHN-5 protein in *durum* wheat is also related to drought tolerance (Brini et al. 2007). A series of highly phosphorylated DHN-5 were detected in the resistant wheat variety, whereas in the sensitive variety, it was weakly detectable. Accumulation of phosphorylated DHN-5 mainly in the resistant wheat variety suggested a role of it in the preservation of cell integrity during late embryogenesis and desiccation.

5.3 Cold

Many plants exhibit an increase in freezing tolerance in response to low, nonfreezing temperatures through a phenomenon known as cold acclimation including Triticeae species. Various physiological, biochemical, and molecular processes involved in the attainment of cold acclimation have been studied extensively, but a complete knowledge of the functions of the various genes induced by low temperature is still lacking. There are a number of genes which respond to cold and freezing temperatures during cold acclimation. It includes *COR* (cold-regulated) genes (Ganeshan et al. 2008). The C-repeat binding factor (CBF)/dehydration-responsive element binding protein 1 (DREB1) regulon is the most important transcriptional unit involved in cold acclimation in plants (Nakashima and Yamaguchi-Shinozaki 2006). Twenty CBF genes were identified in barley, of which 11 were assigned to 2 tandem clusters on chromosome arm 5HL (Skinner et al. 2006). Eleven CBF genes form a cluster within a 0.8 cM region located on chromosome 5Am in diploid wheat (Miller et al. 2006). Screening of a wheat cold-acclimated cDNA library identified a novel cold-regulated gene called *Wcs19*. *Wcs19* homologues and orthologues in barley, rye, and wheat were also characterized in an effort to gain a better insight into the structural and functional features of this gene family. It was revealed by various molecular and biochemical analyses that this gene family encodes chloroplastic proteins related to group III LEA proteins (NDong et al. 2002). Expression of the low-temperature-induced *Wcs120* gene of wheat has been associated with freezing tolerance and was used to study mRNa and protein accumulation in wheat-rye and wheat-crested wheatgrass (*Agropyron cristatum*) interspecific combinations during cold acclimation (NDong et al. 2002). Transgenic wheat lines were produced by Khanna and Daggard (2006) via biolistics using immature embryos of spring wheat cultivar Seri 82 with a recombinant antifreeze gene, *rAFPI*, targeted to the apoplast using a murine leader peptide sequence from the mAb24 light chain for retention in the endoplasmic reticulum using a C-terminus KDEL sequence. Highest levels of antifreeze activity were exhibited by the transgenic wheat line T-8, with apoplast-targeted antifreeze protein, and also provided significant freezing protection even at temperatures as low as −7 °C (Wang et al. 2010).

6 Transgenic Wheat

The introduction of foreign genes encoding for useful agronomic traits into commercial cultivars has saved the precious time required for introgression of the desired trait from the wild relatives by conventional practices and alleviating the degradation of the environment due to the use of hazardous biocides (Patnaik and Khurana 2003). All plants (including wheat) can be changed genetically by using two basic strategies: (1) transformation and (2) by the use of known DNA markers. In transformation, the introduction of genes into a plant from some outside foreign source like a fungal pathogen is done. The trait can be carried into the parent plant by pathogen (Ahmad and Shaikh 2003; Jones 2005). On the other hand, the use of DNA markers allows a gene to be inserted into a plant using the information already known about the chromosomes of a plant through the mapping process. It also allows the "pyramiding" of one trait or another. Presently, the process of transformation in wheat has been carried out most successfully in spring wheat, notably the Bob White variety. Any engineered spring wheat has to be backcrossed into winter wheat. Transformation of wheat is actually carried out either by so-called gene gun or by the use of a bacterial vector (*Agrobacterium*) in a dish in a laboratory. There appears to be a tremendous potential for wheat improvement, as biotechnology could be used to add quality, abiotic tolerance, and biotic resistance. Wheat improvement efforts have therefore focused on raising the yield potential, quality characteristics, resistance to biotic stresses (herbicide resistance, disease resistance, including viral disease resistance, etc.), and tolerance to abiotic stresses (e.g., drought tolerance) and depending on the regional requirement of the crop. To enhance the level of resistance, genetic engineering provides an alternative approach (Mackintosh et al. 2007).

7 Abiotic Stress Resistance Wheat

The genes encoding the late embryogenesis proteins (*LEA*) accumulate during seed desiccation and in vegetative tissues when plants experience water deficiencies and recently emerged as attractive candidates for engineering of drought tolerance (Patnaik and Khurana 2003). This transgenic approach has been used for successfully introducing and overexpressing the barley *HVA1* gene encoding for a late embryogenesis-abundant (*LEA*) protein by Sivamani et al. (2000) into wheat by particle bombardment. When exposed for several weeks to cold temperatures, plants with a winter growth habit flower earlier. This process is called as vernalization. Yan et al. (2004) reported the positional cloning of the wheat vernalization gene *VRN2*, a dominant repressor of flowering that is downregulated by vernalization. Loss of function of VRN2, either through natural mutations or deletions, resulted in spring lines, which do not require vernalization to flower. The flowering time of transgenic winter wheat plants was accelerated by more than a month by reduction in the RNA level of *VRN2* by RNA interference (Yan et al. 2004). The production of transgenic crop plants is an expanding component of agricultural biotechnology. It will be crucial for commercial success that the introduced traits be transmitted faithfully through successive generations in a predictable manner. It has been demonstrated by Zainuddin (2005) that transgenes integrated into transgenic wheat obtained via microprojectile bombardment method could be transmitted and, in most cases, expressed until the third generation. As observed in leaves, microspores, anthers, ovaries, and seeds, the expression of the *GUS* gene was stable. The bar gene appeared to undergo a reduction or disappearance in expression in a number of plants from the first to the third generation (Zainuddin 2005). To ensure transfer of only a single copy of a foreign gene in the plant genome of wheat, Srivastava et al. (1999) used a method based on site-specific recombination. For this, they transform vector consisting of a transgene flanked by recombination sites in an inverted orientation. Recombination between the outermost sites resolves the integrated molecules into a single copy regardless of the number of copies integrated between the outermost transgenes. As the experiments related to transgenics increase, some problems also crop up, but for the sake of food crises, scientists continue try to find out the way. Biotechnology application will thus contribute greatly in improving yield stability by generating plants with improved resistance to biotic and abiotic stresses rather than raising the overall yield. For the genetic improvement of wheat, the coming years will undoubtedly witness an increasing application of biotechnology (Patnaik and Khurana 2001).

8 Conclusions and Future Directions

A most popular research field with lots of possibilities is the study of cereal crops. The development of biotechnology tools has opened a new area for the genetic advancement of wheat crop. A major obstacle in crop improvement is the genetic complexity of wheat, but phylogenic study and genetic engineering make it possible to see the evolutionary relationship between major cereal crops as well as to find out genes related to stress stimulus. There is similarity in wheat genome with chromosome 1 of rice and chromosome 9 of barley. Some nonhomologous genes also exist among these homologous regions, which are conserved and phylogenetically important and are necessary to be identified for better results. Among closely related species, studies of similarity of genomic configuration are also important for the development of transgenic plant and also for developing new cultivation strategy. Most of the transgenic verities in wheat are developed through the insertion of rice genes. For developing transgenic tools, studies of selectable markers are of great importance. Bar and gus genes are used in most cases, but due to its microbial origin, many factors have to be considered before using. Therefore it is needed that more sensitive and easily available markers are considered for selection. Many snags have to overcome to make biotechnological tools more apparent, real buy and cherry pie, although gene transformation techniques combat the challenges related to abiotic and biotic stress for cultivars.

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Wheat Responses to Stress and Biotechnological Approaches for Improvement

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Contents

Abstract In the wheat crop, biotechnological approaches are yielding remarkable results in the area of molecular variability for pathogens, genome mapping and characterization, production of virus-free plants, transgenic plants with improved quality, and stress-tolerant traits plus breeding for elite traits up to micronutrient levels. Tissue culture is the prerequisite approach for almost all of the biotechnological applications. Tissue culture performs an important role in improving wheat for various traits including biotic and abiotic stress resistance. The most widely used approaches of tissue culture reviewed here include in vitro androgenesis, somatic embryogenesis, somaclonal variations, and double haploid production. Among its various applications, tissue culture is now being applied for generating heavy metal-tolerant wheat plants. Genetic engineering is the most promising technique that is currently being applied for resistance against particular fungal diseases and subsequently for increasing crop yield. Among fungal diseases, the main focus has been given to *Fusarium* head blight and powdery mildew diseases. Many resistant genes harbored in suitable constructs have been successfully integrated into the wheat genome via biolistic or *Agrobacterium* transformation approaches. Pathogen-derived resistance has also been observed for producing tolerant wheat cultivars against viral diseases. For managing insect/pest resistance in wheat, resistance genes (R-genes) have been identified in resistant varieties and are effectively incorporated into the wheat cultivars through breeding. They are being used in place of

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conventional and molecular breeding to develop resistant cultivars. The next-generation technology is the foremost technique for identification of not only the target genes but also for the transcription factors or families and miRNA responsible for regulating these genes. Most of the abiotic stress-related transcription factors and genes have been documented, for instance, drought factors and metal toxicity. Here the main focus is on the biotechnological approaches and next-generation sequencing technology used in wheat improvement along with certain factors that affect wheat yield by causing biotic and abiotic stress conditions.

Keywords Wheat tissue culture · Next-generation sequencing · Abiotic stress · Biotic stress · Resistant wheat cultivars · Wheat biotechnological approaches

1 Introduction

Among all the cereal crops, wheat (*Triticum aestivum* L.) is the most vital grain crop, and about 21% of the world's food depends on wheat annually (Enghiad et al. 2017). Wheat crop supplies with more than 20% of the protein and 40% of the calories in the diet for the whole population globally (Braun et al. 2010; Kumar et al. 2015). Therefore, demand and value for intensification of wheat production is widely recognized. With this high demand, wheat still faces annual losses in its total production subjected to various abiotic and biotic stresses caused by virus, fungi, bacteria, nematodes, and insects (Agrios 2005).

Presently, the global wheat yield on an average is about 3.12 metric tonnes for crop year 2016/2017, but there are considerable differences among various areas of the world. The increase in yields is an intricate challenge, difficult to be realized by any one particular approach. Basically, there are three main challenges regarding crop yield: yield potential maximization, yield potential protection, and enhancing resource efficiency for sustainability. These challenges are interrelated, and there is healthy evidence that expansion in the yield potential will often also lead to greater yields even under stress states. The genetic improvement of wheat has received significant consideration over the past decades with the purpose of maximizing the grain yield, to reduce crop productivity due to harsh environmental states, plus damage caused by various pathogens and pests.

Crop losses not only affect the farmer on an individual level but also the whole countries' economy due to biotic and abiotic stresses. Since crop production remains the same, the profit expected to be gained from the crop harvest gets significantly. Each year there is a 34.5% loss of cereals due to pests, and this loss also varies with the abiotic stresses (Agrios 2005).

At the beginning of the 1960s, the targets of genetic manipulation shifted to decrease the yield variability caused by several biotic and abiotic stresses and enhance input use efficiency (Pingali and Rajaram 1999). Subsequently, due to alterations in the world food policy during the last few years, biotechnology approaches offered a plausible solution initially, by reducing the costs of farm-level production by providing the plants tolerant to various biotic and abiotic stresses and furthermore by improving the product quality.

Thus, tissue culture techniques became established that could be routinely utilized for the maximization and improvement of many crop plants. In comparison with dicot plants, the monocotyledons respond poorly to tissue culture, and all the major cereal crops are monocots. It is well established that tissue culture of dicotyledons is simple as compared to monocot crop plants (Reinert and Bajaj 1976; Yildiz 2012). Therefore, extensive research was needed to establish the in vitro culture protocols for these crops. The potential significance of cells, tissue, and anther culture as a technique has been described for improvement of crop plants (Vasil 1987). Remarkably, the regeneration of cereal plant species into the whole plant has become possible today and included maize (Duncan et al. 1985), bread wheat (Redway et al. 1990), rice (Yamada et al. 1986), and barley (Luhrs and Lorz 1987).

Various biotechnological approaches used in wheat improvement like the use of next-generation sequencing in accelerating wheat improvement have been of great focus. For a holistic oversight, certain biotic factors, including bacteria, fungi, viruses, and insects, and abiotic factors, including drought, salinity, extreme temperatures, and heavy metals with a special focus on drought and heavy metals, affecting wheat yield have been discussed here.

2 Problems and Challenges

2.1 *Physical or Abiotic Stresses*

Abiotic stress is a situation based on certain environmental conditions when they deviate from the normal or optimal level. De Leonardis et al. (2007) demonstrated that salinity, temperature intensity, and most importantly drought are some major environmental abiotic stresses affecting plant growth to a large extent often resulting in decreased productivity of crops (Mott and Wang 2007). Mittler and Blumwald (2010) also demonstrated the role played by these abiotic factors in determining the growth of plants and their productivity. As a result of such severe environmental conditions, the plant copes by adapting to these stressed conditions through biochemical, physiological, and morphological changes undertaking certain metabolic strategies occurring as a result of altered gene expression. This involves an intricate regulatory system comprising of stress sensory elements, metabolites, and signaling pathways based on certain protein (Knight and Knight 2001).

Wheat being one of the most important staple crops feeding a large global populace, reduction in its productivity is a serious issue and needs to be handled very efficiently. To focus on its stress tolerance capabilities and to increase its resistance to certain stress conditions, thereby increasing its yield, certain research groups have studied and functionally characterized and analyzed the genes involved in response to stress, with drought and salinity being the major ones that limit the productivity of the crop.

2.1.1 Drought

Khakwani et al. (2012) demonstrated the adverse effects of drought on the metabolism of wheat varieties. This abiotic stress is affecting grain yield in bread wheat, an important cereal crop in Pakistan, which was significantly demonstrated recently in certain genotypes by Khavarinejad and Karimov (2012). Johari and Moharram (2011) evaluated different wheat cultivars under water-deficient conditions. Plaut et al. (2004) and Passioura (2007) also evaluated the conditions created in drought and extreme temperature and their adverse effects on the agricultural environment. Sial et al. (2012) reviewed crop yield lowered by approximately 20–30% globally as a result of the impact of drought, with salinity influencing on 20% irrigated land. This damage will have quite a greater impact on developing countries.

2.1.2 Metal Toxicity

Metals are present in the soil naturally and may be useful or harmful for plants. Metals are usually needed in low amounts for plant growth but when found in excess amounts in the soil cause toxicity and are harmful to plants' growth and inhibit it. The main problem occurs when these ions and toxic metals accumulate in the plant cell. The accumulation of metals in the plant cells depends upon the plant species and their ability to absorb nutrients and the concentration of metals in the soil. The reason for the increase in toxicity in the soil is industrialization. There are some natural resources as well as anthropogenic resources that contribute to metal toxicity. Metal toxicity affects the soil properties. Metals such as iron, aluminum, cadmium, lead, etc. in excess amounts cause metal toxicity (Roy and Kumar 2009).

2.1.2.1 Aluminum Toxicity

Aluminum (Al) is the metal which is found most abundantly in the earth's crust because according to weight if it comprises of an 8% level, its Al toxicity affects 40–70% arable land of the earth. It increases the plant growth when it is in low concentration. Al is found in all soils, but it is generally correlated with low pH (Roy and Kumar 2009). It is found in the form of primary and secondary minerals in the soil. When soil becomes slightly acidic, these primary and secondary minerals release Al in the soil and cause Al toxicity and increase soil acidity. The Al and Fe ions have a major contribution in increasing the soil acidity. In soil solutions, different species of Al occur. The pH and toxicity of various Al species are shown in Table 1.

Table 1 Different species of aluminum and their pH and toxicity

Aluminum species	pH	Toxicity
$Al(OH)^{2+}$	4–5	No toxicity
Al^{3+}	5.5–7	High toxicity
$Al(OH)^{4-}$	7–8	Medium toxicity

Al toxicity is a major factor that limits the growth of the plants. The initial response of the plant to Al toxicity stress occurs in roots progressing to affect the whole root system with the color of roots turning brown and root tips and lateral root becoming thick. Root branches remain underdeveloped; therefore no luxuriant root mass formed. These deformations affect the root function. They became inefficient in functioning to absorb nutrients and water that are essential for the plant growth and survival (Reynolds et al. 2001). In roots, Al toxicity blocks the cell-to-cell movement because of accumulation of the cellulose in the plasmodesmata of the cell wall of the root cells (Panda et al. 2009). It is abiotic stress that in some global locations (Brazil) is a wheat production constraint.

2.1.3 Nutrient Deficiency

Nutrients are essential for plants. These nutrients have many functions in plant growth and development. They have a role in physiological functions. They activate enzymes, regulate their functions, and are important parts of the metabolite complexes or the assembly of macromolecules. Many nutrients in ionic form maintain the osmotic potential of the cells. One nutrient has many functions in the cell, and thus one nutrient is involved in another nutrient's metabolism. For example, in wheat, molybdenum is the part of an enzyme that reduces the amount of nitrate in the wheat plant, and due to deficiency of molybdenum, the amount of nitrate increases and causes toxicity. Deficiency symptoms of nitrogen, phosphorous, and potassium occur in older leaves first (Roy and Kumar 2009).

2.1.3.1 Potassium Deficiency

Potassium (K) is an important mineral for the wheat plant. It plays an important role in the plant growth, photosynthesis, and protein synthesis. Enzymes play a key role in plants, and K has a significant role in their activation. About 67% of the wheat fields are K deficient. The phosphorous and nitrogen are nearly balanced in the fields due to the use of fertilizers, but K often becomes a limiting factor for the wheat yield. It is necessary to improve the K efficiency to increase the yield of wheat (Ruan et al. 2013). K deficiency is difficult to diagnose because symptoms of K resemble that of the injury to the plant from the soil below. It is diagnosed by the sporting tissue test result (Stevens et al. 2002) where leaves become spindly and the growth of the plant is adversely affected before the symptoms appear. Necrosis of the older leaves starts on tips and leaf margins which spread inward on the leaves leaving green arrow-like streaks in the middle of the leaf. The leaves ultimately die out and appear to be drought affected.

2.2 *Biological or Biotic Stresses*

In common terms, a biotic stress is defined as the effect of fungi, bacteria, viruses, pests, and weeds on the plants which hinder its normal production and thus decrease their yield. More than 42% of cereal crop yield is decreasing due to these biotic and abiotic factors. The food production would have to be tripled by now to fulfill the needs of the population throughout the world due to demands of people for food with improved nutritional quality (Vasil 2003). For this purpose, yield potential of cereal crops needs to be increased.

Yield potential is defined as the yield of a crop or a cultivar which is grown in such environments that are fully adaptable to biotic and abiotic stresses, thus maximizing the potential yield of a particular cultivar (Evans and Fischer 1999). There are two methods to acquire yield that can fulfill the future demands, firstly by reducing the production losses due to biotic (pathogens, pests, and weeds) and abiotic losses (drought, salinity, etc.) and secondly by increasing the nutrient usage as well as the photosynthetic efficiency of plants (Sramkova et al. 2009). To attain such increases in yield, conventional breeding and marker-assisted breeding are being used. They have achieved considerable results in improving certain stresses, but due to its slow progress in cereal crop improvement, scientists are working on genetic engineering techniques to swiftly fulfill the rising food demands to integrate genes that can increase yield potential. This chapter discusses the factors associated with wheat biotic and abiotic stresses and how they can be controlled to maximize yield.

The above mentioned strategies have been applied in wheat to increase its yield potential. Methods by which abiotic stresses can be improved have already been mentioned. Some of the abiotic and biotic factors responsible for the decline in wheat crops are mentioned in Fig. 1. However, this part focuses on how biotic stresses in wheat can be controlled by the application of the genetic engineering that can ultimately increase yield. These biotic stresses of wheat include damages caused by fungi, bacteria, viruses, and pests.

2.2.1 Fungal Diseases

There are more than 50 diseases of fungi that affect wheat varieties worldwide. These include diseases affecting spike and grain, diseases affecting leaves, and diseases affecting lower tiller portions and roots. Most common fungal diseases of wheat include Karnal bunt (causing agent: *Neovossia indica*), common root rot (causing agent: *Bipolaris sorokiniana*), leaf rust (causing agent: *Puccinia recondita*/*Puccinia triticina*), stem rust (causing agent: *Puccinia graminis*), stripe

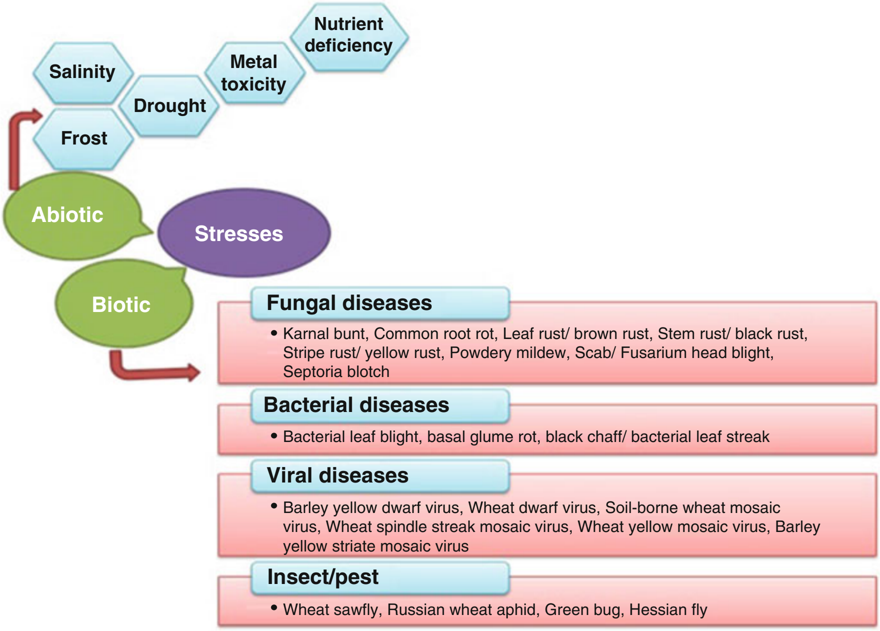

Fig. 1 Abiotic and biotic stresses responsible for the decline in wheat yield

rust (causing agent: *Puccinia striiformis*), powdery mildew (causing agent: *Erysiphe graminis*/*Blumeria graminis*), fusarium head blight or scab (causing agent: *Fusarium graminearum*), and septoria leaf blotch or glume blotch (causing agent: *Septoria tritici*). Therefore, developing resistance to fungal stresses is the major challenge for wheat breeding.

2.2.2 Bacterial Diseases

Bacterial diseases have also been identified in wheat, and most common bacterial diseases include bacterial leaf blight and basal glume rot (*Pseudomonas syringae*) and black chaff or bacterial leaf streak (*Xanthomonas campestris*). However, no significant work on developing resistance against these bacterial diseases through genetic engineering has been reported.

2.2.3 Viral Diseases

Viruses have the ability to infect all the life forms. In plants, the intensity of the viral diseases is associated with the type of crop variety and its location that directly affects the crop by reducing its yield and quality. The range of viral infection also varies in plants from minor or mild to devastating effects (Agrios 2005).

Each year millions of crops are destroyed before reaching the harvesting stage. The main reason for the wheat disease is its susceptibility toward a number of viruses. Among various diseases the following viruses are of importance: *Barley yellow dwarf virus* (*BYDV*), *Wheat dwarf virus*, *Soil-borne wheat mosaic virus* (*SBWMV*), *Wheat spindle streak mosaic virus*, *Wheat yellow mosaic virus*, and *Barley yellow striate mosaic virus* (Agrios 2005).

2.2.3.1 Barley Yellow Striate Mosaic Virus

Barley yellow dwarf virus belongs to *Luteoviridae* and strictly causes diseases in Poaceae family. This virus causes 5–30% losses of wheat and is submitted by aphids including several species of *Sitobion*, notably *S. avenae*, *Rhopalosiphum padi*, and *Metopolophium dirhodum* (McIntosh 1998). It can be controlled in wheat by making the cultivars resistant. Breeding different varieties of cereals to provide tolerance against *BYDV* infection has importance (McIntosh 1998). It is transmitted by plant hopper *Laodelphax striatellus* (Signoret et al. 1977). About 11–12% loss in yield of wheat is observed by this virus in Morocco and Chile (El Yamani and Hill 1990; Ramirez et al. 1992).

2.2.3.2 Soil-Borne Wheat Mosaic Virus

It belongs to *Furovirus* and is transmitted by fungus *Polymyxa graminis*. This virus causes stunting growth and results in 50% wheat yield losses (Campbell and Choy 2005). Recombination breeding of resistant and susceptible wheat can be helpful in preventing *SBWMV*, but effective resistance is not available in wheat (McIntosh 1998).

2.2.3.3 Wheat Spindle Streak Mosaic Virus

It belongs to *Bymovirus* – soilborne. This virus causes 3–87% of loss in wheat; the intensity of disease depends on the wheat variety and climatic conditions, where reduced tillering is the main cause of yield losses. However, crossbreeding can improve the variety (Brunt et al. 1996).

2.2.3.4 Wheat Streak Mosaic Virus (WSMV)

This is one of those viruses that can cause 100% loss in wheat yields (McNeil et al. 1996). It belongs to the genus *Rymovirus* and is transmitted through *eriophyid* mite vector *Aceria tosichella Keifer*. Transgenic crops produced against this virus interrupt with the viral life cycle and maintenance of its regular functions (Sanford and

Johnston 1985). Such type of resistance provided to the crop is derived from the expression of viral genes and is called pathogen-derived resistance (Sanford and Johnston 1985).

2.2.4 Insects/Pests

Insects are major pest in agriculture that were controlled using insecticides (Schoonhoven et al. 2005). But, due to the negative impact of insecticides both on the environment and beneficial insects, other methods for the resistance have been explored. Wheat resistance is important for insect pest management. More than 30 species of aphids are available that cause various damages to wheat (McIntosh 1998). Therefore, crop resistance against insects can be helpful in creating a defense in plants by determining the source of resistance (Schoonhoven et al. 2005).

Various insects coevolved with wheat include Hessian fly and Russian wheat aphid, while those that became pests were the result of cultivation practice. These include greenbug and wheat stem sawfly. Among all these, Hessian fly and wheat stem fly pose a threat to wheat quality and yield (Painter 1951). Synthetic insecticides were introduced in 1940, but to control insects, farmers have relied heavily on plant resistance. There are four types of insects that feed on wheat and cause yield loss each year. They have a short life cycle but are sources of transmitting viral diseases to the crop (Janick and Wiley 2003).

According to Painter (1951), host plant shows resistance to the crop plant by itself using one of the three mechanisms. Antixenosis mechanism of class modalities resists the insect to lay an egg or colonize the plant. The second mechanism is antibiosis that reduces the growth of the insect or causes the death of the insect. This, however, is not a reliable mechanism as if the host plant lacks the resistant genotype, the same insect will result in high damage to the crop. The last mechanism on which the breeders rely is tolerance where wheat grows despite the attack by insects (Janick and Wiley 2003).

2.2.4.1 *Cephus cinctus*

It is also known as wheat sawfly that feeds particularly on wheat among all cereal crops. It infects the solid stems of wheat that are less susceptible. Wheat sawfly causes yellowing and grain shriveling, a common problem in the Mediterranean basin (Prescott 1986). Therefore, for the control of this insect, wheat with solid stems is desirable.

2.2.4.2 Aphids

There are several varieties of aphids that cause damage to wheat including *Rhopalosiphum padi* (bird cherry-oat aphid), *Schizaphis graminum* (greenbug), *R. maidis* (corn leaf aphid), *Metopolophium dirhodum* (rose-grass aphid), *Sitobion* *avenae* (English grain aphid), and *Diuraphis noxia* (Russian wheat aphid). Among these, Russian wheat aphid and greenbug are the most important. They are found to cause damage in all the cereal crops and serve as an important vector for the transmission of *BYDV*. Russian wheat aphid produces leaf rolling, white strips, and sterile heads (Prescott 1986). Resistant wheat has been produced, with six genes responsible for resistance. Greenbug has many biotypes that affect the crop; however, different sources of resistance are also used for control. The greenbug causes necrotic areas along with leaves rolling, whereas other aphids cause yellowing and premature death of leaves (Prescott 1986).

2.2.4.3 Hessian Fly

It is also known as *Mayetiola destructor*. Hessian fly belongs to *Diptera*: *Cecidomyiidae* family of insects that produces galls in infected plants (Foster and Hein 2009). It feeds on a variety of cereals, but in wheat it's highly damaging and presents a common problem in the USA and North Africa. Common symptoms include stunting, reduced yield, and lodging (Prescott 1986). The insect prefers laying eggs in young wheat plants during the fall or in early spring, where the larva feeds permanently and causes damage. The incidence of Hessian fly can be avoided by late plantations, controlling wheat responsible for the spread or using resistant wheat varieties to prevent the loss of yield. Insecticides on Hessian fly are less effective because of its sporadic nature. However, parasitic wasps are used as natural enemies of Hessian fly to prevent the crop from its attack (Foster and Hein 2009).

3 Applications and Approaches in Wheat Biotechnology

Wheat is among the most important cereals, as most of the efforts have been applied to increase the productivity of this crop using conventional methods. But, only minor improvement in productivity of this crop has been achieved (Gupta et al. 2008). The most widely and important applications and approaches employed to improve not only wheat grain quality but also its yield are in vitro tissue culture of wheat, genetic engineering technique to integrate the desired genes, and next-generation sequencing techniques to identify the target genes in the wheat genome accurately with precise timing (Fig. 2).

3.1 In Vitro Tissue Culture of Wheat

La Rue (1949) initiated the first successful in vitro tissue culture exploiting endosperm as explant in cereal crops. Gamborg and Eveleigh (1968) reported the protocol for generating suspension cultures of wheat by employing a defined medium

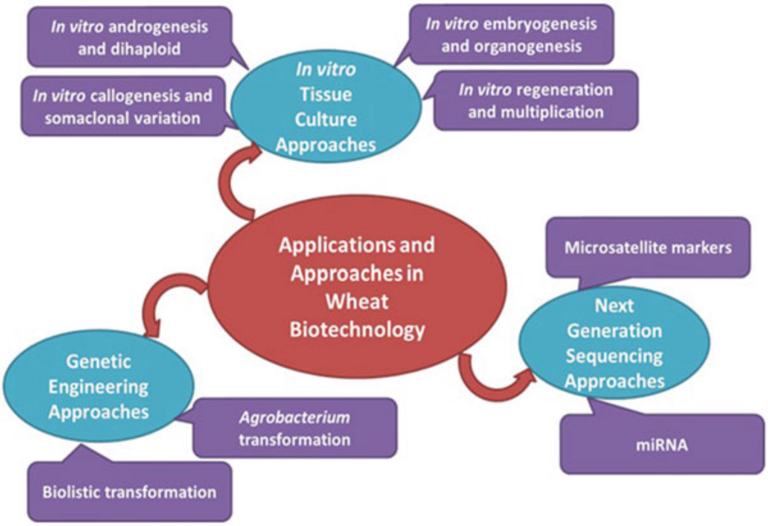

Fig. 2 Approaches and applications in wheat biotechnology

supplemented with mineral salts, sucrose, vitamin B complex, and the auxin 2,4-D (2,4-dichlorophenoxyacetic acid). Shimada et al. (1969) successfully developed callus formation and single cell cultures in wheat crop. Ozgen et al. (1996) reported the study on in vitro culturing of mature and immature embryos from seven different varieties of wheat (winter durum) on MS medium provided with 2,4-D. On the basis of this finding, it was concluded that mature embryos had a lower efficacy of callus production than immature embryo but with high regeneration efficiency. Plant regeneration capacity via embryo culture is affected by regeneration media and the genetic factors that can be regulated and by environmental factors that cannot be controlled (Uppal et al. 1996). The concentrations of plant growth regulators are also a very sensitive factor in the control of explant regeneration and morphogenesis.

The high concentration ratio of auxins and low concentration of cytokinins usually promote profuse cell proliferation in the cultured medium with the formation of callus. Hormone-free medium is better for the shoot regeneration, or it can be supplemented with 2,4-D at low concentration as with BAP and IAA (Chawla and Wenzel 1987). The regeneration of explants can be established either indirectly by adventitious bud or somatic embryogenesis and subsequently shoot and root formation (Bhaskaran and Smith 1990), or sometimes it can be obtained directly through organogenesis (Li et al. 1992). Generally, low light intensity is required for the callus formation, which limits the plantlet regeneration efficiency, the ratio of green plantlets production (Ekiz and Konzak 1993).

These preliminary but important outcomes led to the utilization of in vitro cell and tissue culture for several applications including breeding (Wang and Hu 1984),

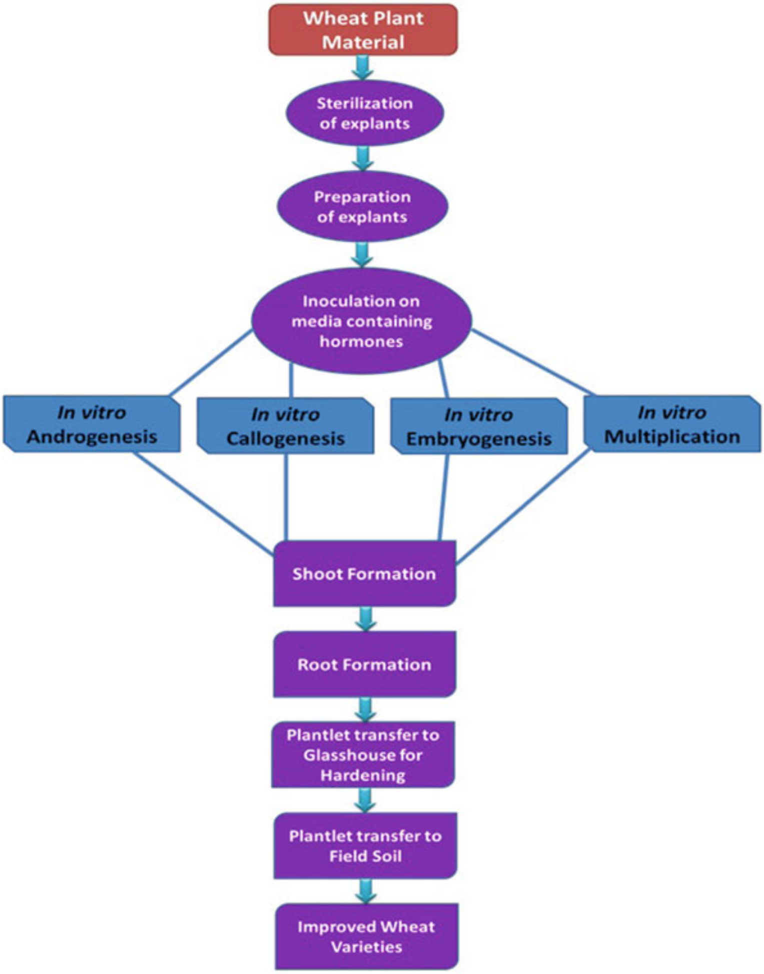

Fig. 3 Wheat tissue culture protocol and its widely used applications

anther and embryo culture (Letarte et al. 2006), the elimination of systemic pathogens (Hafeez et al. 2012) such as viruses, drought resistance (Bajji et al. 2004), and foremost genetic engineering (Vasil 2007) for wheat. The whole procedure and the most widely used application of tissue culture in wheat crops to get the improved and desired variety are demonstrated in Fig. 3.

Pertinent to mention here is the role of embryo culture relative to the innovative aspects that have come on the wheat improvement scene around harnessing the genetic diversity of the wheat families' wild relatives through wide hybridization which encompasses intraspecific, interspecific, and intergeneric hybridization to effect introgression of novel alleles from the related and distant wild species to enrich the wheat genomes. At the initial step when hybrids are produced, embryo culture is crucial since all F1 hybrids from such distant crosses are devoid of endosperm and require nutrient availability to differentiate seedlings from that becoming the stocks that permit alien gene transfers to occur and lead to wheat improvement. This importance and usage has become a standard practice in wheat wide hybridization programs globally and has been reviewed in recent publications of Ogbonnaya et al. 2013 and Mujeeb-Kazi et al. 2013.

3.1.1 In Vitro Androgenesis and Dihaploid Phenomenon in Wheat

For many important cereal crops, including cultivated wheat, specialized tissue culture methods for producing homozygous generations from microspores exploiting in vitro androgenesis have been efficiently used. With the utilization of anther culture in wheat and establishment of homozygous genotypes within a single generation, plant breeders are now proficient to reduce the time span prerequisite for the development of a uniform line from crossing. Moreover, the haploid chromosome numbers revealed that genetic recombination during meiosis and recessive gene effects are exhibited at the plant level. Haploid breeding is the word coined for this technologies' emergence.

Microspore and anther cultures have been the most desired choice of explants to produce double haploids, because of a large number of available microspores within each anther that efficiently produces doubled-haploid plants (Zhou 1996). Procedures for anther culture in wheat are frequently being improved (Hu and Kasha 1997) and obtained a high yield of green plants in some genotypes (Bruins and Snijders 1995). Tuvesson et al. (2000) were successfully optimizing the method for production of wheat and triticale double haploids on a large scale by utilizing a single-anther culture technique. Generally, triticale responds poorly to anther culture (RyoÈppy 1997). The major limitation for the commercially exploitation of anther culture in breeding programs is the genotype effect. The production of double haploids from wheat and triticale was initiated in many breeding combinations but with limited success to raise green plants from anther culture in the F1 and F2 generations. For anther culture the substrate used was 190–2 (Wang and Hu 1984), provided with sucrose (9%), 2,4-D (1.5 mg/l), and kinetin (0.5 mg/l).

The key factors affecting the productivity of anther culture include donor genotype physiology, genotype, anther developmental stages, physical and chemical conditions, and pretreatment conditions for culture initiation and regeneration (Zheng et al. 2001). Liu et al. (2002) successfully improved green plant production through isolated anther culture in bread wheat. Their findings clearly illustrated that providing some nutrients to microspores at the stage when embryogenesis was initiated is a vital factor affecting in vitro regeneration and green plant production for a genotype with a comparatively high tendency for albinism.

Anther pretreatment was also one of the most significant steps. The pretreated techniques include maintaining the spikes in cold temperature about at 4 °C for a week or much longer periods or in high temperature nearly at 33 °C for 2–3 days (Zheng 2003). Other pretreatments have been involved like osmotic shock, microtubule disruption agents, and starvation. Sugar starvation for 4–5 days employing mannitol instead of sucrose is generally used in barley (Cistue et al. 1999). Cistue et al. (1999) were able to produce doubled-haploid plants from durum wheat through the induction of androgenesis employing mannitol as the pretreatment and cocultivated the treated anther with ovaries. With this system, they successfully increased the number of embryoids, and as a result, the figures of green plants regenerated were also improved.

On the other hand, Letarte et al. (2006) established the protocol to improve the induction of embryogenesis in anther culture of wheat with much higher regenerable embryos without the presence of ovaries. They tested arabinogalactan (AG) Larcoll and the arabinogalactan protein (AGP) from gum arabic on two wheat spring genotypes. Their finding showed that Larcoll significantly declined microspore mortality in both genotypes irrespective to ovary presence or absence in the culture. Similarly, gum arabic had a strong influence on the amount of embryos generated and regenerated green plants.

Regarding the androgenic response, the colchicine effects on embryogenesis and frequency of green plant production highly depended on the genotype and the culture methodology. Soriano et al. (2007) found interesting effects of colchicine application on the androgenic response in anther culture and chromosome doubling of different bread wheat genotypes. Colchicine was applied not only over the first hours of anther culture but also at the time of mannitol stress pretreatment. Similarly, Islam (2010) also experimented to compare the impact of colchicine by applying it to the anthers and directly on the isolated microspores. He found that the direct colchicine treatment reduced embryoid induction but significantly improved fertile plant production. Lantos et al. (2013) also demonstrated that anther culture was an important application for crop improvement. Lantos and Pauk (2016) determined the effect of different induction media and genotypes of winter wheat. They analyzed the data on the basis of genotype response, year, and genotype with year interaction employing the numerous embryo-like structures, regenerated plantlets, and albino besides green plantlets, proving that anther culture was an efficient method in winter wheat breeding programs with lower costs than other alternative technologies.

Double haploid production through anther culture facilitates the plant breeders to accelerate breeding cycles and release wheat cultivars with biotic and abiotic stress resistance and good quality flour. In vitro androgenesis is useful not only for accelerating conventional breeding but also helpful for mutation breeding, in vitro selection of elite genotype, and genetic transformation techniques. Furthermore, doubled-haploid lines generated from anther culture facilitate the decent transfer of alleles/genes from exotic stock or alien species into wheat elite varieties. Dihaploids are basically isogenic lines which can be efficiently exploited for gene mapping (Barnabás et al. 2001).

The popularity for dihaploid breeding has thus targeted anther culture as described above. Microspore culture also has tremendous potential as microspores from one wheat spike have the capacity to provide several thousand green plants. This is exactly what is a need in a wheat improvement program: large number of outputs. Unfortunately, neither anther culture nor microspore culture can combat the genotypic constraint that limits haploids to be obtained across all wheat genotypes. The most posing procedure thus so far with 100% success in haploid production for utilization, wheat breeding has been the wheat/maize protocol. Apart from breeding swiftness, the wheat/maize route has varied applications in wheat research, and the details have been elucidated by Mujeeb-Kazi 2006. It would be fair to mention here that so far a better option for haploid breeding in wheat other than wheat/maize has to become available that can provide 100% efficiency and is genotype independent.

3.1.2 In Vitro Callogenesis and Somaclonal Variation in Wheat

During in vitro callogenesis, some genetic and phenotypic variations termed as somaclonal variation in the clonally propagated plants from a single clone are observed (Kaeppler et al. 2000). These somaclonal variations can be established either via meiotically or somatically stable events. Somatically stable variants involve phenotypes such as culture adaptation where the variations physiologically induced are examined among initial clones. This form of variation is generally not transferred to the following generations and has an impact in conditions where the primary clones are the final product, for instance, in ornamental plants being amplified and trees for direct utilization. Meiotically inherited variation is essential where the end products of the tissue culture are proliferated and retailed as seed (Kaeppler et al. 2000). Such types of variations can be adapted to cope with biotic and abiotic stresses in the plant genome.

Some studies on in vivo osmoregulation were reported that it is the vital adaptation to salinity in plants since it involved maintenance of the cell volume and turgor pressure (Ashraf and Waheed 1993). Due to lack of osmotic regulation, osmotic stress causes inhibition in the uptake of water and results in physiological drought causing salt injury to plants. Therefore, water loss or dissolved solute enhancement or both may be observed in the condition of the reduced osmotic potential of plants during salt stress (Carvagel et al. 1998).

Javed (2002) presented the study describing an efficient method to investigate the effect of salt (sodium chloride) stress on in vitro callus tissues of wheat genotypes in relation to water. He concluded that callus tissue of genotypes with more salt tolerance had great potential for osmotic maintenance and water reduction. Similarly, Bajji et al. (2004) experimented to produce improved drought-resistant wheat cultivars by exploiting somaclonal variations as a source of variability and placed explants in regenerated media containing polyethylene glycol. They were selecting tissue culture lines in the following generations and found differences in chlorophyll fluorescence, electrolyte leakage, electrolyte conductance in stomata, and days to heading among parent lines and tissue-cultured cultivars. Hence, somaclonal variations are the source of a wide range of modifications among progeny of drought resistance methodology.

Arun et al. (2003) regenerated immature embryos of spring wheat varieties that generated somaclones resistant for spot blotch disease for up to R2, R3, and R4 generations. They have successfully improved wheat varieties employing somaclonal variation for resistance to spot blotch disease and earliness. The resulting progenies have enhanced yield over the parents. Some of the other osmotic agents include sucrose, sorbitol, and mannitol as they provide carbon and energy in the cereal cell culture media (Al-Khayri and Al-Bahrany 2002) and also act as osmotica in explant organogenesis (Huang and Liu 2002). These were accumulated in plant tissues influenced by environmental stress such as water deficit and perform a role of osmoregulation. Javed and Ikram (2008) researched the response of sucrose that induces osmotic stress on callus development of two wheat genotypes. They used the seed for callus induction and propagated the resulting calli in media containing varying amounts of sucrose (control, 3–5%, and 8%). They conferred that increased sucrose concentration in media resulted in osmotic stress, enhancement of free proline, and total soluble carbohydrates.

Rashid et al. (2009) established a rapid protocol for callus production and regeneration and achieved a maximum of 97% callus induction efficacy using 2,4-D and 87% of regeneration frequency by employing different concentrations of IAA, kinetin, and 2iP. Similarly, Mehmood et al. (2013) obtained the highest callus induction frequency of 90% using 2,4-D and maximum regeneration efficiency of 59% in media supplemented with various concentrations of BAP.

3.1.3 In Vitro Embryogenesis and Organogenesis in Wheat

Among the most important food, wheat is the extensively examined in vitro regeneration employing different explant sources including anthers (Cistué et al. 2006), inflorescences (Ozias-Akins and Vasil 1982), shoot tips (Ahmad et al. 2002), immature embryos (He et al. 1992), and isolated microspores (Liu et al. 2002). These explant tissues have shown variable responses to regeneration into the whole plant during tissue culture system.

Many studies reported in vitro embryogenesis in wheat were either direct in which no callus induction phase or indirect with callus formation stage. Delporte et al. (2001) reported the indirect system for wheat embryogenesis via callus induction phase from exploiting thin mature embryo. The sterilized mature embryos were placed on solid medium supplemented with 2,4-D, and 90% callus formation rate was achieved, followed by 47% embryogenic calli induction frequency with the suppressed amount of 2,4-D. However, Mendoza and Kaeppler (2002) established the protocol for the regeneration of mature embryo with modifying and altering the amount of auxin and sugar for callus induction media. They compared the effects of four auxins, viz., 2,4-D, dicamba, picloram, and 2-MCPP, and sucrose versus with maltose. They found that the effect of the sugar type depended upon the kind of auxin used. The 2,4-D and picloram enhanced callus regeneration on media with maltose. A similar study was performed to investigate the role of plant growth regulators and plant hormones on in vitro somatic embryogenesis (Jiménez 2005). They suggested that endogenous plant hormone and exogenously provided growth regulators could provide evidence of divergent patterns occurring during stages of somatic embryogenesis and in vitro tissue culture.

Reported an efficient plant regeneration method employing mature embryos of ten wheat genotypes that analyzed the influence of auxin type on callus development (Nasircilar et al. 2006). They illustrated that the callus obtained from mature embryos was a good source of somatic embryogenesis and later on organogenesis. A study revealed that in vitro regeneration of mature embryo on media supplied with BAP and TDZ increased shoot production per explant (Ganeshan et al. 2006). The shoot production frequency in winter wheat genotypes ranged between 11 and 25 shoots per explant.

More recently plant genetic engineering has provided several options for improvement of cereal crops, particularly wheat. For the genetic transformation of wheat, an efficient tissue culture protocol is required. Therefore, researchers have routinely attempted different protocols with variable inputs. One such attempt reported a vigorous callus formation and regeneration method using mature embryos as the explant source with various hormonal regimes (Raziuddin et al. 2010; Aydin et al. 2011).

The plant tissue culture technique can be opted to produce plantlet tolerant to stress. One of the earliest efforts was made to generate drought resistance. Farshadfar et al. (2012) provided the experiment to identify in vitro predictors of drought resistance in the wheat landraces employing mature embryo for callus induction on media containing 2,4-D and followed by providing drought stress condition. In one of their studies, they provided PEG and mannitol for callus germination for screening drought-resistant plantlets. PEG has high molecular weight and, therefore, is unable to cross membranes and does not change the osmotic potential of the cell. Hence, it activates water scarcity in in vitro cells.

In wheat, immature embryos are the most extensively used explants for culture induction, but sometimes this is problematic because of its temporary accessibility and culture requirements. On the other side, mature embryos are easily available and stored similar to a seed. However, there are some potential studies conducted to provide a protocol for in vitro culture of an immature embryo. Yasmin et al. (2009) established the protocol for initiation of callus and regeneration in the immature embryo supplied with culture media with auxins and cytokinin. Murín et al. (2012) compared the regeneration efficacy of mature and immature embryo of various wheat genotypes in media containing auxin and found no significant correlation between their growths, hence suggesting different protocols for each regeneration step on media.

Einkorn (*Triticum monococcum* L.) is a recalcitrant diploid wheat, comprised of A-genome, and has a potential to employ as a useful model for understanding the concept of biology and genomics in tribe *Triticeae*. Miroshnichenko et al. (2017) developed a protocol for direct or indirect somatic embryogenesis and organogenesis and found that daminozide together with auxin remarkably improved establishment of morphogenic structures. They also observed that the maximum shoots per initial explant were obtained on medium containing 0.25 mg/L TDZ, 3.0 mg/L dicamba, and 50.0 mg/L daminozide.

In vitro embryogenesis is also exploited to assess disease resistance in wheat genotypes. In the context, Hafeez et al. (2012) selected three wheat landraces that showed leaf rust resistance and regenerated immature embryos on in vitro culture media supplemented with 2,4-D. Maximum regeneration was observed in LLR-16. Similarly, Soliman and Hendawy (2013) exploited the in vitro embryogenesis for producing drought-tolerant plantlets employing immature embryos as the explant source and providing water-deficit conditions with various concentrations of PEG for durum wheat genotypes. RAPD-PCR diagnostics were carried out with four primer pairs to discriminate the plantlets produced from PEG resistant and control plantlets. They found that durum wheat genotypes were differentiated with amplified DNA capacity.

3.1.4 In Vitro Regeneration and Multiplication in Wheat

Much research has been conducted to establish the most rapid and cost-effective protocol in tissue culture employments, but still, the most efficient method is always obscure. In this context, many methodologies have been reported, and some are in progress of completion.

One of the major applications of tissue culture is the production of multiple plantlets to enhance the yield of elite genotypes and eliminate diseases such as viral infections from the plant genome. Besides these applications, one of the recent uses of tissue culture is a requirement of the most flourished in vitro regeneration protocol for the production of transformed plantlets.

Therefore, Ahmad et al. (2002) reported the study to generate multiple shoots and later on somatic embryo formation on media provided with 2,4-D and BA employing 7-days-old shoot apical meristem of four different wheat genotypes as explant source. They achieved multiple shoots that produced fertile plantlets with viable seeds. Another similar approach was the influence of one of the plant regulators where thidiazuron was investigated on in vitro tissue culture of barley and wheat (Shan et al. 2000). They found vigorous shoot formation from callus derived from immature embryos. The highest regeneration frequency of 87% was achieved in wheat. Similarly, Satyavathi et al. (2004) investigated the effect of picloram, 2,4-D, and dicamba on callus formation and regeneration of durum wheat. They ascertained dicamba as the best plant regulator among them. Haliloglu (2006) provided an efficient growth system of two wheat genotypes exploiting leaf base segments, also investigated factors involved in callus initiation and plantlet regeneration. Remarkably, the highest figure of the somatic embryo was observed on media containing NAA and 2,4-D.

Recently, there has been an increase of heavy metal presence because of rapid industrialization that limits plant growth and cereal grain development and affects the chemical composition (Hart et al. 1998). Likewise, a higher amount of cadmium (Cd) in grains are lethal to human being and animals. Ganeshan et al. (2012) proposed an effective study that provides the uptake of Cd in the developing wheat grain via in vitro culture of the immature wheat spike on medium with varying concentration of cadmium chloride as the source of Cd metal. They successfully provided the evidence of grain development in media supplemented with Cd, accumulation of Cd in grain, and expression analysis of the Cd-related genes such as *metallothionein*, *glutathione reductase*, and *phytochelatin synthase* that have been activated in the tissue-cultured grains. AE Saeed et al. (2015) established an *Agrobacterium*-mediated transformation protocol for two wheat cultivars employing mature embryos as explant. They regenerated putative explants in MS medium with some modifications, e.g., for shoot initiation, used 2,4-D (4.0 mg/l); for shoot elongation, also added zeatin (1.0 mg/l); and for plantlet maintenance, used 2,4-D, zeatin, and GA_3 each of 1.0 mg/l in MS medium. The resulting transformation efficiency was 20–23% in both cultivars, and further molecular assays verified successful transformation.

3.2 Post-Sequencing Next-Generation Sequencing Technology

Next-generation sequencing (NGS) tends to be an emerging high-throughput technique for certain post-sequencing approaches and development due to its cost-effective and efficient nature. More recently, the wheat community (IWGSC 2014) has generated complete hexaploid wheat genome (*T. aestivum*) after sequencing diploid donors of A (*T. urartu*) and D (*Aegilops tauschii*) genomes by Ling et al. (2013) and Jia et al. (2013), respectively. Jia et al. (2017) reviewed some of the progress achieved on wheat genomics with assistance of NGS approach which included genomic polymorphism, sequencing of hexaploid wheat whole genome and its donor species, cloning of agronomical significant genes, development of wheat SNP microarrays, dynamics in wheat transcriptomes, and genotyping by sequencing (genome-wide association studies). In this chapter, the use of NGS in identifying certain microsatellite markers and miRNA from wheat has been reviewed.

3.2.1 Microsatellite Markers

Certain conventional methods currently in use for the identification of microsatellites are not so efficient according to the current research pace in the field, and these methods tend to be costly and slow, taking much longer for the identification process. These methods mainly include expressed sequence tag (EST) sequencing and mining of microsatellite libraries. However, Imelfort et al. (2009) demonstrated the promising nature of NGS technology for the purpose of marker development mainly due to being much economical, less time-consuming, impartial, and high throughput in nature. A large amount of work has been done on microsatellite markers in wheat due to their importance and high yield demand. However, no microsatellite markers specific to a single arm of chromosome were developed with the use of next-generation sequencing (NGS) technology until the foremost study regarding identification of microsatellite marker on specific chromosome arms based on the new and advanced technology of NGS was carried out by Nie et al. (2012) on the long arm of chromosome 7D (7DL) of wheat generating Illumina paired-read survey sequence of 7DL. Nie et al. (2012) demonstrated the efficacy of the newly identified chromosome arm-specific markers in various mapping and cloning outcomes such as their assistance in genetic mapping and saturation and positional cloning. On this chromosome, they assembled a sum of 1,61,061 contigs within which they identified 16,315 microsatellites and selected 33 markers, on a random basis, for validation in 20 cultivars of wheat with diversified genomes. For further validation regarding the specific nature of these markers developed by the research group, among the stock, they also screened two nulli-tetrasomic stocks.

In detecting the amplification of microsatellite markers, the primers used by Nie et al. (2012) exhibited a success rate of 79% which is quite high in contrast to 32% in a study carried out by Bryan et al. (1997), 36% in the case of Röder et al. (1995), and 68% with the experiments conducted by Nicot et al. (2004) suggesting detection of higher polymorphic activity using NGS technology than the conventional technologies. Thus the use of NGS technology in survey sequencing proves itself in all aspects to be an optimal approach for microsatellite marker development.

3.2.2 MicroRNA

MicroRNAs (miRNAs) are short, single-stranded, and noncoding RNAs made up of nearly 21 nucleotides. These are a highly conserved entity within the cell of all plant species and play a diverse role in many biochemical processes such as signal transduction, biological and physical stresses, growth and development, environmental adaptation, and protein processing along with their biogenesis. More recently miRNAs have been predicted within wheat genome on chromosomes 1, 6, and 5 of genomes A (long arm), B, and D, respectively (Lucas and Budak 2012; Tanaka et al. 2013; Kurtoglu et al. 2013).

3.2.3 MicroRNAs on Wheat Chromosome 5D

According to one study, out of 48 miRNAs, 36 are predicted to be located on long arm of chromosome 5D and 24 of 42 in short arm of chromosome 5D similarly present in the chromosome 4A of wheat (Kantar et al. 2012). Kurtoglu et al. (2013) used NGS to discover conserved miRNAs systematically for the very first time in wheat chromosome 5 of genome D and identified 55 putative miRNAs inclusive of 14 novels once reported for the first time in wheat. Here 13 miRNA of 55 are located on long arm of chromosome 5D, while 7 are present on the short arm of chromosome

5D. However, the remaining is present on both arms. It is notable that of the total read, long arm of wheat chromosome 5D has shown higher variety than that of the short arm of 5D.

Of these 55 miRNAs, 6 resulted in EST hits via in silico expression analysis after prediction of potential targets. They found three 5D-specific miRNAs in the process of verifying five miRNAs for their presence on chromosome 5D. This study also detailed the expression of one miRNA, miR2118, based on experimental assays. These findings of Kurtoglu and his colleagues are major contributions in wheat miRNA research. The novel 14 putative miRNAs on 5 chromosomes of D genome have been identified, are predicted to be involved in experimentally confirmed targets, and have role in many biological or metabolic functions with different percentages as a whole including binding activity of transcription factors with nucleic acid (miR5205; TC413453), hydrolase enzyme activity (miR3700; TC412324), oxidoreductase enzyme activity (miR482; CO348589), transferase enzyme activity (miR5568; TC446402, TC395950), and binding activity to metal ion (miR6197; AL821953) and respond to stress stimuli such as drought (miR5387; BE637541). Kurtoglu with his colleagues also identified that miR5387, miR6197/miR1118, miR1117/miR437, and miR1133 located on chromosome 5D targeted certain drought-responsive proteins: late embryogenesis abundant (LEA) protein, HVA22, aquaporin, and calmodulin-like protein, respectively.

Similarly, Kantar et al. (2011) identified the presence of certain miRNAs on wheat chromosome 5D including miR160, miR167, miR169, miR1125, and miR398 which were earlier demonstrated to be involved in responding to the drought stress independently in *Arabidopsis* and rice by Liu et al. (2008) and Zhou et al. (2010). Such finding will efficiently contribute to diverse miRNA functions located on wheat chromosomes, and many of similar research are on their way to recognition.

3.3 Identification of Genes and Transcription Factors for Physical Stresses

Purification and characterization of some genes that respond to drought, heat stress, and saline conditions in wheat carried out previously include TNHX1, TVP1 (Brini et al. 2005), TaERF3 (Zhang et al. 2007), SNF1-type S/T protein kinase (Mao et al. 2010), and TaAIDFa (Xu et al. 2008). However, the abiotic stress response of MYB3R proteins was first cloned in wheat by Cai et al. (2011) who isolated TaMYB3R1, a novel transcription factor of the family from bread wheat, performed sequence analysis by constructing alignments, and further performed phylogenetic studies through tree construction. They also performed a transient expression assay in the epidermal cells of onion for elucidating the localization of TaMYB3R1 at the subcellular level, DNA-binding activity, and trans-activation activity via yeast two-hybrid (Y2H). Cai et al. (2011) primarily focused on demonstrating the response of this MYB3R protein to certain stresses under various abiotic conditions including drought, salinity, and low temperature.

Rahaie et al. (2010) performed expression profiling of ten MYB genes in bread wheat against salinity to observe their response in recombinant inbred lines comprising of different levels of resistance to drought and salinity. Among the MYB genes involved in salinity and drought stress characterized by the research group, only one gene TaMYBsdu1 was evaluated to have been upregulated and expressed to a great extent in saline and drought conditions in a salt-tolerant line. Bartels and Sunkar (2005) demonstrated the involvement of certain genes in cell damage protection including the genes that code for reactive oxygen species (ROS) removal, osmolyte synthesis, and dehydrins.

In 2015, Kumar et al. sequenced the whole transcriptome under controlled (22° ± 3 °C) and heat stress (42 °C for 2 h) conditions at the flowering stage of wheat using two platforms, Illumina HiSeq and Roche GS-FLX 454. Their study revealed that under heat-treated condition, out of 1525 transcripts, 27 of them showed very high (>ten-fold) upregulation of gene expression. Moreover, metabolic processes, such as oxidation-reduction, protein phosphorylation, and others, were greatly influenced by heat stress.

Transcriptional regulation plays an important role in the expression of these genes as a coping mechanism against stressful environments created as a result of high salt and low water levels (Zhu 2002). Major transcription factor families that have been reported to respond to abiotic stress conditions include WRKY (Mare et al. 2004), C2H2 zinc finger (Kam et al. 2008), AP2 (Sakuma et al. 2006), basic domain-leucine zipper (bZIP; Uno et al. 2000), NAC (Xue et al. 2006), ethylene-responsive element-binding factors (ERF), and MYB (Jin and Martin 1999; Stracke et al. 2001). Riechmann et al. (2000) and Stracke et al. (2001) characterized the MYB transcription factor (TF) family constituting the MYB DNA-binding domain (MYB domain) of approximately 51–53 amino acids as being among the largest TF families in plants. Jin and Martin (1999) and Rosinski and Atchley (1998) demonstrated that this TF family could be divided into three subfamilies on the basis of the presence of a number of adjacent repeats in the characterizing domain: those with a single repeat in the MYB domain as MYB-1R, two repeat proteins as R2R3MYB, and three repeat proteins as MYB3R (Chen et al. 2005) have similar findings. Dubos et al. (2010) also identified some four repeats containing MYB proteins (MYB4R) in plants, but their detailed functionality in plants is yet to be demonstrated. The largest subfamily in MYB proteins is the R2R3MYB with a major role in responding to biotic and abiotic stress studied extensively in various studies by Abe et al. (2003), Agarwal et al. (2006), Cominelli et al. (2005), Maeda et al. (2005), Mengiste et al. (2003), Miyake et al. (2003), Seo et al. (2009), and Vannini et al. (2004). Although this family comprises of a large number of members in plants with quite divergent functions, drought- and salinity-related stress responsiveness among them has been studied to a very limited extent (Abe et al. 2003).

3.3.1 Drought-Related Genes

Sial et al. (2009) demonstrated the improvement in crop yields under water-deficient conditions, which can be attained by improved germplasm of crops developed to be well suited for conditions of lower water availability.

Sial et al. (2012) screened out the capabilities of a variety of wheat genotypes to tolerate drought stress by reviewing the grain yield in accordance with water availability and development of certain genotypes more capable of higher yield in the more stressed environment. These genotypes can be compared, keeping in view their yield, and can be utilized for developing drought-resistant wheat varieties. The higher the allele number and its stability of expression in the evolved genotype, the better the wheat variety gets in tolerance to drought conditions and performs normally to increase comparative yield. Zhang et al. (2012) reported MYB gene *TaPIMP1* in wheat expressed through overexpression and underexpression and regulated by ABA (abscisic acid) and salicylic acid (SA).

Budak et al. (2013) recently reviewed the drought stress-related genes and QTLs in cultivated (bread and durum) and wild (emmer) wheat over the last 3 years. These include TaPIMP1, TaSRG, TaMYB3R1, TaNAC (NAM/ATAF/CUC), TaMYB33, TaWRKY2, TaWRKY19, TdicDRF1, TaABC1, TaSnRK2.4, TaSnRK2.7, TdTMKP1, TaCHP, TaCP, TaEXPR23, TaL5, TdPIP1;1, TdPIP1;2, TdicATG8, TdicTMPIT1, *Era1*, and *Sal1* (Fig. 4). The role of dehydrin genes (*dhn*, *wcor*, and *dreb*) in two bread wheat cultivars for tolerance in response to drought stress was observed by Hassan et al. (2015). They showed a striking finding of high induction expression of these genes in the leaves of one of the cultivars under water-deficit condition.

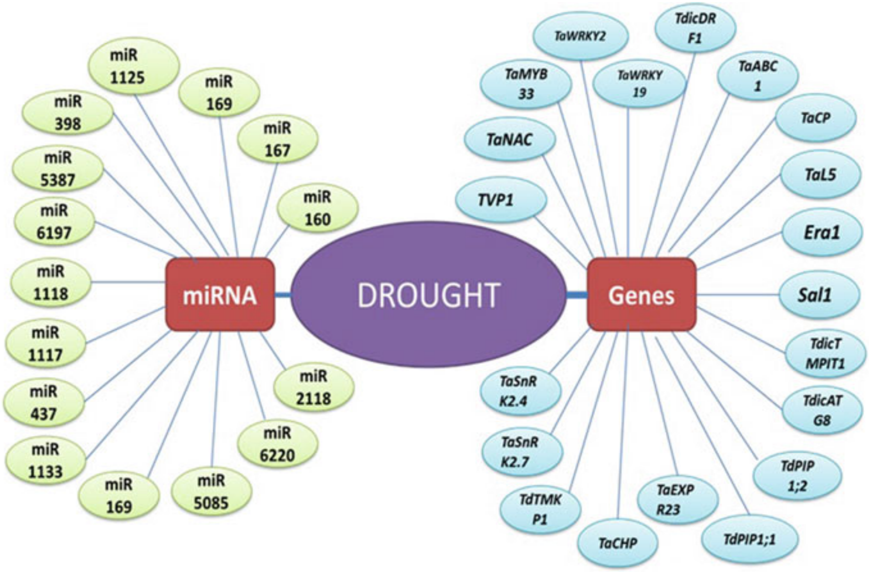

Fig. 4 Different genes and miRNAs activated under drought condition in wheat

Table 2 The miRNAs and their target proteins involved in drought and frost resistance

miRNA	Targeted protein	Possible function
miR6197	Ice recrystallization inhibition protein	Frost resistance?
miR5387	LEA protein	Drought stress-responsive

Table 3 The miRNA and their targeted proteins with various functions (Han et al. 2013)

miRNA	Targeted protein	Function
miR774, miR1436, and miR1439	Zinc finger transcription factors	Plant growth and development, biotic and abiotic stresses
miR1436 and miR5175	Basic/helix-loop-helix (bHLH) transcription factors	Cell proliferation and cell lineage establishment
MiR1439	TetR family proteins	
miR5183	WRKY transcription factor	Germination, senescence, abiotic stresses like drought and cold
MiR5205	CBS domain containing protein	Salinity, drought, cold, high temperature, UV, wounding

3.3.2 Drought-Related miRNA Targets by NGS

MicroRNAs miR169, miR5085, miR6220, and miR2118 also get expressed in wheat tissues in certain environmental stress conditions at different phases during development. The drought- and frost-resistant proteins targeted by certain miRNAs have been represented in Table 2. Han et al. (2013) demonstrated various miRNAs in bread wheat and their target proteins by EST analysis. Some of those involved in certain stress responses are shown in Table 3. miRNA microarray approach has been utilized in order to screen root and leaf of bread wheat cultivar for identification of drought stress-related miRNAs (Akdogan et al. 2015). The results revealed 285 and 244 miRNAs in leaf and root tissues, respectively, among them the expression of miR169, miR172, miR159, miR160, miR166, miR395, miR1858, miR2118, miR396, miR408, miR472, miR477, miR482, and miR5049, differentiated significantly in bread wheat. Moreover, Bakhshi et al. (2017) identified 1813 miRNA belonging to 106 families, 104 of which predicted to be similar to 212 novel miRNA precursors.

3.3.3 Drought-Tolerant Cultivars in Pakistan

Raj is a wheat cultivar tolerant to certain biotic (leaf and yellow rust) and abiotic stresses (mainly drought tolerance) released to be cultivated in rainfed areas of KPK Pakistan (Khan and Khan 2010). Tijaban-10, a wheat variety, tolerant to biotic (yellow rust) and abiotic stresses (mainly drought but also low temperature), developed mainly in the rainfed areas of Baluchistan, Pakistan (Khan et al. 2013). These two major drought-tolerant varieties that have gone through several phases of testing and their main characteristics are summarized in Table 4.

Table 4 Characteristics of drought-tolerant wheat varieties

Variety	Protein content	Gluten content		Potential yield	References
Tijaban-10	13.29%	29.91% (wet)	10.04% (dry)	7000 kg ha-1	Khan et al. (2013)
Raj (DN-10)	11.20	8.98 (dry)		3716 kg ha-1	Khan and Khan (2010)

3.3.4 Transcription Factors in Wheat Plant Response to Aluminum Metal Toxicity

In the acidic soil, Al metal toxicity is one of the major constraints affecting plant yield. Signal transduction pathways conduct the signals within the cell and throughout the plant, and then as a result, gene expression and different cellular functions occur. Al stress leads to cascade pathways. The concentration of calcium ions Ca^{2+} may be affected by the Al toxicity. It increases the Ca ion concentration in the root apex.

Protein phosphorylation has a vital role in the pathway of signal transduction and in the regulation of many biological activities for the mediation of external stimuli into the cells. The major pathway for the signal transmission is the mitogen-activated protein kinase (MAPK) cascade. These pathway signals transduct the signals for light, temperature, nutrient deficiency, and all stress, etc. in yeast, MAP kinase plays a role in Al tolerance. In wheat, it is estimated that the MAP kinase plays a role in Al resistance because in root apex MAP kinase transduces the Al signal and its expressions (Mossor-Pietraszewska 2001).

Al tolerance genes are studied extensively in cereal crops, and the major emphasis is on the wheat. For the manipulation of genes, it is known in which plant and on which chromosome Al-tolerant genes are present (Reynolds et al. 2001). Most of the Al-tolerant genes are the general stress tolerance genes which increase Al tolerance. Al tolerance genetic variation is not only found between the species but also within the species. Major genes are present on the short arm of the 5A chromosome and long arms of 2D and 4D chromosomes in hexaploid wheat. In the wheat plant, root apex is the main site for the accumulation of Al. Ca uptake is affected by the Al toxicity. With the increase in Al, Ca concentration decreases in root and shoot of the plant (Mossor-Pietraszewska 2001).

Al resistance is not controlled by a single gene but is a multigenic trait. On chromosome, 4DL is a locus which controls most of the phenotypic variation as well as the release of malate which is the major Al-activated anion from the root apex. By chelating the Al and making it nontoxic, malate anion protects the root apex. The TaALMT1 gene encodes an anion channel called Al-activated malate transporter. In the promoter region, large tandem repeat sequences are present which increase the expression of TaALMT1. It has been proposed that these tandem repeats enhance the expression of the gene because these sequences have enhancer elements. Thus, by increasing the TaALMT1 expression, Al resistance can be increased (Pereira et al. 2010).

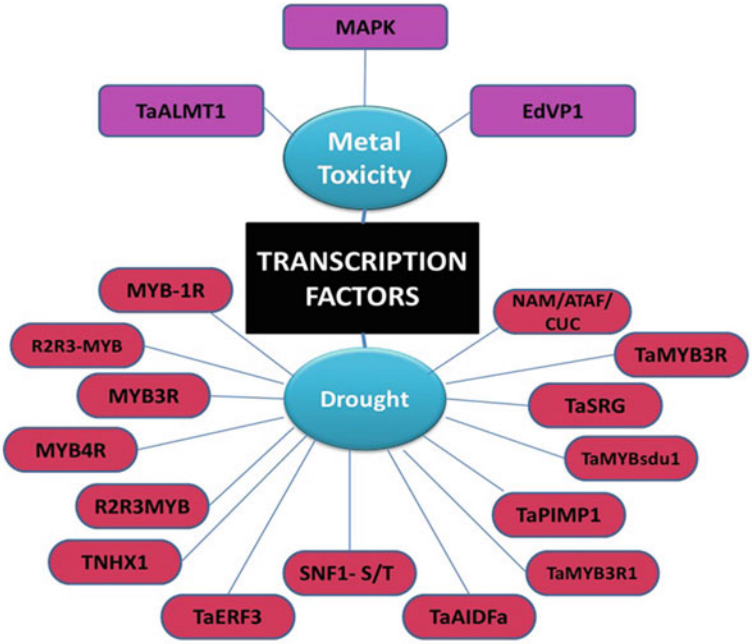

Fig. 5 The transcription factors and families responsible for regulating genes under the state of metal toxicity and drought

3.3.5 Transcription Factors in Wheat Response to Low Potassium

To improve the wheat tolerance to low-K stress in the transgenic plant, an *Elymus dahuricus* H^+-PPase (*EdVP1*) gene is used. It is known that indole acetic acid (IAA) plays a key role in the root development. *EdVP1* gene increases the IAA concentration in the root under low-K stress condition. *EdVP1* also increases the concentration of H^+ and root cation exchange capacity, which increases the ability of K accumulation in *EdVP1* transgenic wheat. Transgenic wheat also releases more organic acids which help in the activation of more soil K, under low-K condition. The *EdVP1* gene increases the ability of wheat to absorb and utilize K; thus this enhances the grain yield of the wheat (Ruan et al. 2013). The transcription factors and families responsible for regulating the metal toxicity as compared to drought in the wheat crop are listed in Fig. 5.

3.4 Genetic Engineering Approaches to Biological Stresses

To overcome these challenges, many approaches have been used including molecular breeding and developing tolerance by use of the D genome wheat synthetic hexaploids and genetic engineering approaches. Wheat is among the last major cereal crops that have been genetically engineered due to its reduced transformation efficiency. However successful wheat transformation studies have been published in the 1990s. Since then scientists have been using *Agrobacterium* as well as biolistic transformation protocols to develop transgenic wheat.

3.4.1 Wheat Transformation with Genes Resistant to Fungal Diseases

Earlier studies were conducted on transgenic wheat varieties against a devastating fungal disease powdery mildew caused by *Erysiphe graminis*. In this study RIP or β-1,3-glucanase genes under the regulation of rice actin 1 promoter and a barley seed *chitinase gene II* under the regulation of maize ubiquitin 1 promoter were transferred into wheat. The transgene was found to be stably expressing in the transgenic lines and showed increased resistance to powdery mildew infection (Bliffeld et al. 1999). The first study conducted to introduce resistance against scab or *Fusarium* head blight (FHB) by using genetic engineering techniques was published in 1999 in which the possibilities of engineering resistance were explored by expression of pathogen-related (PR) genes. In this study thaumatin-like protein (*tlp*) gene and chitinase gene (*chi II*) from rice were introduced in Bobwhite wheat cultivar by biolistic transformation protocol. The expression and integration of transgenes were analyzed by various techniques. However, no significant expression was observed. The inoculation of conidia of *Fusarium graminearum* done on the wheat variety showed that the infection rate was significantly slower in transgenic plants as compared to non-transgenic ones (Chen et al. 1999).

KP4, an antifungal protein from *Ustilago maydis* (corn smut), was genetically engineered to wheat to develop resistance against the stinking smut (*Tilletia tritici*). The transgene regulated by ubiquitin promoter was found to be stable over generations. Out of seven, three transgenic lines showed endogenous resistance against stinking smut disease (Clausen et al. 2000). Slight resistance against powdery mildew was achieved by biolistic transformation of stilbene synthase gene (*vst 1*) obtained from grapevine in T_3 generation of spring wheat Jinghong 5 (Hui et al. 2000). Moderate resistance against powdery mildew was developed by transforming wheat with barley seed ribosome-inactivating protein (RIP) regulated by *cauliflower mosaic virus* 35S promoter. It was found to be stable over four generations. A signal peptide derived from barley seed, that is, *β-1,3-glucanase*, is also engineered which has increased the antifungal properties of RIP (Bieri et al. 2000).

Another study of biolistic transformation was done in which resistance against powdery mildew and leaf rust (*Puccinia recondita*) was developed by transferring antifungal protein Ag-AFP from *Aspergillus giganteus*, *chitinase* gene from barley class II, and RIPs from barley type I under the control of ubiquitin 1 promoter. A significant decrease of about 40–50% in powdery mildew and leaf rust colonies was seen from *afp* and *chitinase II* at an inoculum density of 80–100 spores per cm^3. However, disease resistance by the activity of *RIP-I* expression was not observed (Oldach et al. 2001). A study to develop scab (FHB)-resistant wheat has been done to reduce the effect of DON (deoxynivalenol) that poses a health hazard to humans and animals. An *FsTR1101* gene from *Fusarium sporotrichioides* has been integrated in Bobwhite cultivar of wheat using biolistic transformation technique. *FSTR1101* encodes trichothecene acetyltransferase enzyme that limits FHB pathogen's hyphal spread in wheat. The expression of *FSTR1101* was mostly in endosperm and glume. Greenhouse analysis of transgenics showed an accumulation of acetyltransferase in wheat that gives partial resistance against scab disease (Okubara et al. 2002).

Fusarium graminearum resistance in susceptible spring wheat Bobwhite has been developed by using biolistic transformation method. Pathogen-related (PR) proteins were isolated from *Fusarium graminearum*-resistant cultivar Sumai 3. Transgene expression was observed in four wheat lines. Among them, one wheat line showed co-expression of *chitinase* and *β-1,3-glucanase* genes. When assayed against scab infection under optimum greenhouse conditions, a delay in the spread of infection was observed. A second transgenic wheat line expressing rice thaumatin-like protein gene (*tlp*) showed moderated resistance to scab infection in greenhouse conditions. However, none of the lines were resistant to scab infection under field conditions (Anand et al. 2003). Another study has been done to increase the resistance of a fungal pathogen *Blumeria graminis* that causes powdery mildew diseases. Three gene constructs were designed for this experiment: plasmid A containing barley seed β-1,3-glucanase and chitinase coding sequences, plasmid B containing ribosome-inactivating protein (RIP) expressed with *β-1,3-glucanase* signal peptide, and plasmid C including signal peptides barnase and barstar. Most significant resistance was obtained from RIP expression. Barnase and barstar were less efficient, while lines containing *chitinase* and *β-1,3-glucanase* varied from highly resistant to highly susceptible. Combination of all three constructs did not show any resistance against powdery mildew (Bieri et al. 2003).

Resistance against fungal disease *Puccinia recondita* was developed by the expression of phytoalexins *vst1* and *vst2* obtained from grapevine (*Vitis vinifera*) involved in resveratrol synthase and pss gene from pine (*Pinus sylvestris*) involved in pinosylvan synthase were transformed into the bread wheat. This resulted in the accumulation of stilbene derivative when exposed to UV light and showed a significant reduction of disease ranging from 19 ± 9% to 27 ± 8% as compared to wild types (Serazetdinova et al. 2005). In another study published in 2005, enhanced resistance against powdery mildew disease has been achieved by integrating two defense-related genes *oxalate-oxidase* 9f-2.8 and *TaPERO peroxidase* under the control of Gst AI promoter in combination with WIR1a intron. Biolistic bombardment was used for developing transgenic wheat. The expression of defense-related genes is epidermis-specific. The results showed that TaPERO peroxidase gene had enhanced resistance against powdery mildew, while oxalate-oxidase overexpression did not have any effect (Altpeter et al. 2005).

In another study resistance against *Fusarium* head blight or scab has been developed by *Agrobacterium*-mediated transformation of Chinese cv. Sumai 3 wheat with *Arabidopsis thaliana AtNPR-1* gene which develops a type II resistance to FHB by elevating levels of salicylic acid (SA) pathogenesis-related (PR) genes that cause the expression of antimicrobial proteins, thus regulating systemic acquired resistance in a FHB-susceptible wheat cultivar (Makandar et al. 2006). In 2006 the hexaploid wheat genome was genetically engineered to express the antimicrobial protein Ace-ANP1 obtained from *Allium cepa* (onion) against wheat fungal diseases like Karnal bunt (*Neovossia indica*) and powdery mildew. The transgene was controlled by the maize ubiquitin promoter and *Bar* gene on the medium of phosphinothricin (PPT) as a selectable marker. The expression of Ace-AMP1 was confirmed over two generations. About 50% increase in resistance was observed against powdery mildew disease, while the increase in expression of defense-related genes was observed in Karnal bunt-infected wheat plants (Roy-Barman et al. 2006).

Agrobacterium-mediated transformation of the basal portion of wheat seedlings was done with *β-1,-3-glucanase* gene to develop resistance against powdery mildew. A transformation efficiency of 9.82% was observed. The transgene was stable in the following generations. Study of T_2 generation showed high resistance against powdery mildew as compared to controls showing that the transgene could be efficiently expressed in wheat seedlings when transformed with *Agrobacterium tumefaciens* (Zhao et al. 2006). FHB resistance in wheat was developed by integrating a maize gene b-32 that encodes an RIP (ribosome-inactivating protein) by biolistic transformation and regulated by 35S *CaMV* promoter with the bar gene as a selectable marker. The transgene was stably expressed, and in all transgenic lines, reduction in FHB symptoms was observed from about 20% to 30% as compared to non-transgenic lines (Balconi et al. 2006).

Most of the work using genetic engineering techniques in wheat fungal diseases has been done to develop resistance against scab or FHB. In this study, defense-related genes have been overexpressed, and their effect on FHB-infected wheat under greenhouse and field conditions has been studied. These defense-related genes include *α-1-purothionin*, thaumatin-like protein 1 (*tlp 1*), and *β-1,-3-glucanase*. The wheat variety Bobwhite has been used for checking the expression. Results of this study showed that defense-related genes particularly *β-1,-3-glucanase* had enhanced resistance against FHB in both greenhouse and field conditions (Mackintosh et al. 2007). A similar study was conducted by developing resistance against FHB by transforming Bobwhite wheat variety with barley class II *chitinase* gene using biolistic bombardment, which showed that barley class II *chitinase* exhibited resistance against FHB in greenhouse and field conditions (Shin et al. 2008).

Studies on plant’s natural defense-related mechanism have also been done. One of these mechanisms includes plant’s glycoproteins PGIP (polygalacturonase-inhibiting proteins) that inhibit the activity of fungal endopolygalacturonases (endo-PGs). To access their effectiveness, transgenic wheat lines expressing bean’s PGIP genes have been developed. Results showed that transgenic wheat having *PvPGIP2* accumulation has new PG recognition capabilities and showed increased resistance against *Bipolaris sorokiniana*. About 46–50% reductions in symptoms of fungal pathogens were observed (Janni et al. 2008). Transgenic tetraploid wheat (AABB genome) resistant against leaf rust has been developed. In this study puroindoline gene a (*pin*) that encodes puroindoline protein A (PINA) under the control of maize ubiquitin promoter, along with *nptII* gene (*neomycin phosphotransferase II*) used as a selectable marker, was transformed by biolistic bombardment using gold particles. These proteins located on chromosome 5D are known to have antibacterial and antifungal properties as well as control the grain hardness of wheat. Comparative study of transgenic and non-transgenic wheat varieties was done which showed that PINA protein significantly lowered the growth of *P. triticina* in vivo (Luo et al. 2008).

In another study an antibody fusion protein consisting of a *Fusarium*-specific recombinant antibody obtained from chicken and an antifungal peptide obtained from *Aspergillus giganteus* was transferred in wheat via biolistic bombardment. A significant resistance against types I and II scab diseases (FHB) was observed in T_2 and T_3 generations. This also significantly increased the yield of wheat cultivars demonstrating antibody fusion proteins were effective for scab disease (Li et al. 2008). Resistance against sharp eyespot (*Rhizoctonia cerealis*) is achieved by integrating an ethylene response factor (*ERF*) gene *TiERF1* obtained from *Thinopyrum intermedium* via biolistic bombardment. *TiERF1* was found to be stably expressed even in T_4 generation. *TiEFR1* was found to be increasing the expression of PR (pathogenesis-related) genes such as *chitinase* and *β-1,-3-glucanase* which enhanced the resistance against sharp eyespot in transgenic wheat variety (Chen et al. 2008). A similar study was conducted for developing resistance against common root rot (*B. sorokiniana*) in which an ERF gene, *TaPIEPI*, was integrated in wheat variety using Yangmai 12 biolistic bombardment. The transgenic wheat was found to be stably expressing, conferring enhanced resistance, and was showing accumulation of defense-related genes, e.g., ethylene (ET) and jasmonic acid (JA), which may be useful in crop improvement (Dong et al. 2010).

Transgenic lines resistant to wheat fungal pathogens *B. sorokiniana* (spot blotch) and *F. graminearum* (FHB) were developed by modifying the cell wall pectin methyl esterification. *PMEI* gene which controls pectin methyl esterification has been obtained from *Actinidia chinensis* (i.e., *AcPMEI*). High expression of pectin methyl esterases (*PME*) makes a plant's cell wall less susceptible to hydrolysis of fungal endopolygalacturonases (PG). The transgenic lines showed significant increase in *PME* activity as a result of which high resistance against spot blotch and FHB is seen (Volpi et al. 2011). Resistance to scab (FHB) disease and sharp eyespot (*Rhizoctonia cerealis*) is done by inserting a defensin gene *RsAFP2* obtained from Radish (*Raphanus sativus*). *RsAFP2* is a small cysteine-rich protein gene that exhibits antifungal properties.

Chinese wheat cultivar Yangmai 12 with *RsAFP2* gene was transformed by biolistic bombardment. Four *RsAFP2* gene integrated lines showed enhanced resistance to FHB, while two lines showed resistance to *Rhizoctonia cerealis* (Li et al. 2011). TaWRKY 45 is a wheat transcription factor that shows antifungal properties, so resistance against powdery mildew and leaf rust (*Puccinia triticina*) was obtained by transforming wheat with *TaWRKY45* gene. Its constitutive overexpression was found to be enhancing resistance against both fungal pathogens but different from the expression of *Pm 3* and *Lr34* defense-related genes (Bahrini et al. 2011). Snakin-1 (*SN1*) gene obtained from *Solanum chacoense* is known to show antifungal properties. *SN1* gene showed high properties. *SN1* gene showed high resistance against wheat powdery mildew disease when transformed in a wild-type variety ProINTA Federal (Faccio et al. 2011). R genes specifically

Pm 3 resistance locus was engineered in wheat lines to develop resistance against powdery mildew. *Pm3* wheat multilines including Pm3a, Pm3c, Pm3d, Pm3f, or Pm3g were developed and found to be more resistant than non-transformed wheat lines (Brunner et al. 2011).

Multiple studies were done on scab (FHB) in 2012. Scab disease-resistant transgenic wheat lines have been developed by incorporating *PvPGIP2* (polygalacturonase-inhibiting proteins) gene in wheat's floral tissues (Ferrari et al. 2012). A bovine lactoferrin cDNA known to have antimicrobial properties in wheat was transferred in Bobwhite cultivar which showed high resistance against scab disease (Han et al. 2012). Similarly, resistance to FHB and *Fusarium* seedling blight (FSB) has been achieved by developing transgenic lines expressing two antifungal peptides (AFP) in Yangami 11 wheat cultivar (Liu et al. 2012). Puroindolines *PINA* and *PINB* (*PINs*) have been studied to provide enhanced resistance against *Penicillium* seed rot in wheat. Transgenic wheat seeds having high of *PINA* showed significant fungal growth reduction, while expression of both *PINs* didn't have any effect on pathogen (Kim et al. 2012). *Lr34* naturally shows resistance against wheat leaf rust (*Puccinia triticina*). Transgenic wheat lines with *Lr34* gene were inserted to develop enhanced resistance. The results showed that *Lr34* transgene expression did not regulate PR genes (pathogenesis-related genes). Only one *Lr34*-based transgenic line showed leaf rust resistance in the seedling stage (Risk et al. 2012).

Resistance against *Cochliobolus sativus* and *F. graminearum* was achieved by transferring lipid protein gene *TaLTP5* by particle bombardment in wheat variety Yangami 18 (Zhu et al. 2012). Five winter wheat cultivars were particle bombarded with rice class I *chitinase* gene *RC24* to develop resistance against stripe rust (*P. striiformis*). The transgene was stably integrated in T2 and T3 generations and found to be resistant to stripe rust (Huang et al. 2013). Lastly, resistance against taking all diseases (*Gaeumannomyces graminis*) was established by biolistic transformation. Integration of snakin-1 (*SN1*) gene was obtained from *Solanum tuberosum*. All five transgenic lines showed resistance against all mentioned diseases (Rong et al. 2013). Genes associated to confer resistance against fungal diseases like *Fusarium* head blight, eyespot, powdery mildew, and leaf rust are figured out for better understanding (Fig. 6). Eissa et al. (2017) successfully developed transgenic wheat to combat rust and powdery mildew fungal diseases by harboring barley *chitinase* (*chi26*) gene using biolistic bombardment.

Hence, many studies have been done to develop resistance against fungal diseases by genetic engineering. These techniques can be successfully applied in improving wheat yield and productivity. In vitro growth of *F. graminearum* has also been reduced by seed defensin *MsDef1* obtained from *Medicago sativa* (alfalfa). Hence transgenic wheat, with integrated *MsDef1*, can be used to obtain resistance against scab (FHB) disease (Spelbrink et al. 2004).

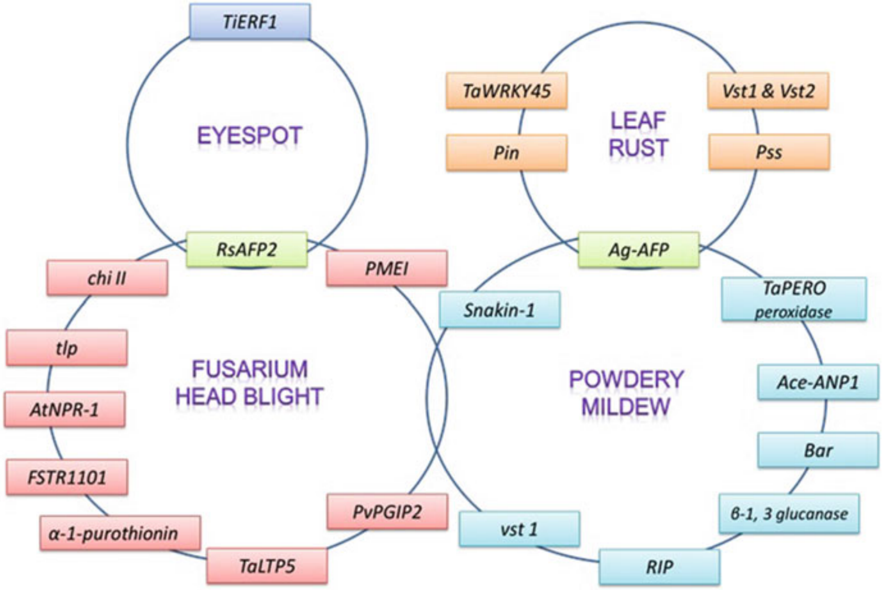

Fig. 6 Some of the transgenes responsible for conferring resistance against fungal diseases in wheat; *RsAFP2* and *Ag-AFP* genes are transformed in wheat for resistance to eyespot and fusarium head blight and leaf rust and powdery mildew, respectively

3.4.2 Wheat Crop Protection Against Viruses

Transformation of a plant with foreign genes does not disturb the plant genome but makes the plant accept the foreign sequence and express it. This technique has helped to make plants more immune to a variety of plant diseases that cause devastating effects on crops and prevent the virus from spreading throughout the plant by interfering with its replication (Agrios 2005). To minimize crop losses, transgenics are playing an important role in making tolerant varieties within high-temperature areas (Fahim et al. 2010).

Many practices have been explored to create virus-resistant plants that include: (1) Creating plants with natural resistant genes that help in virus resistance are extracted and transferred to another plant and (2) Pathogen-derived resistant (genes from viral sequences) (Sanford and Johnston 1985) involve blockage of molecules or interaction between infecting viruses and the plant. Pathogen-derived resistance involves two basic methods: protein-based protection, where viral gene product/coat protein interferes with the virus in providing resistance to plants or referred to as "coat protein-mediated resistance," as they have reserved sequences that help to prevent diseases against a variety of strains of the same species, and nucleic acid-based protection, where the interference exists either at a transcriptional stage called transcriptional gene silencing (PGS) or at a posttranscriptional stage called posttranscriptional gene silencing (PTGS).

3.4.2.1 Pathogen-Derived Resistance

It is the most promising technique for providing resistance to crops against viruses and has proven to be successful in crop protection. Crops can be transformed by the virus to resist against virus vectors. Insect vectors play an important role in the transmission of viruses; thus controlling insect vectors can also broaden the ways of controlling some viral diseases. Serological testing can also be helpful to make sure the mother-plant is virus-free. Another way of improving the crop immunity against viral diseases is by crossing it with crops possessing resistance against viruses.

Scientists have adopted the method of cross-protection which allows the inoculation of crop plants with a mild strain of the same virus that helps in protection by severe strains of the same virus. A recent method for protection involves viral control using coat protein or another segment of the genome. This method is called pathogen-derived resistance that blocks the virus activity and its interaction with the plant. Viral gene silencing is an approach used in pathogen-derived resistance, where a homology inhibitory RNA sequence silences the virus gene and prevents it from causing disease. It is also considered that the plant defense system comprises of gene silencing against foreign material; therefore, to cause infection, virus needs to overcome this barrier (Agrios 2005).

3.4.2.1.1 Resistance Against Wheat Streak Mosaic Virus (WSMV)

Coat protein of *WSMV* is also used to make wheat resistant against the virus, by making CP gene constructs for transformation: pESCP45, pESCP35, and pRQ105 that showed resistance against *Potyviruses* (Smith et al. 1994) with 0.3–0.7% efficiency rates. Two viral transgenes from “Conrad-MT” isolate of *WSMV* were *WSMV-CP* and *WSMV-NIb* genes which are involved in providing resistance. But, resistance due to CP gene provides longer protection than *replicase* gene resistance (Jones et al. 2005). RNAi plays an important role in inhibiting the virus to cause a disease (Waterhouse et al. 1998), where dsRNA, or hpRNA, is sliced into siRNA by an enzyme Dicer (Tougou et al. 2006) and further incorporated into RNA-induced silencing complex (RISC) to find its complementary strand for degradation and to provide resistance to the crop (Campbell and Choy 2005).

Transformed wheat showed immunity against the WSMV and segregates in a Mendelian manner. WSMV can transmit through seed (Jones et al. 2005) or by the vector *Aceria tosichella* – the wheat curl mite – but the use of RNAi construct helps to achieve immunity in wheat even against vector transmission. Recently, a new strategy is adapted to create immunity in wheat against *WSMV* using applicable intron of hpRNA (Fahim et al. 2010) that targets nuclear inclusion protein a (*NIa*) gene of *WSMV*. The genome of *WSMV* undergoes co- and post-translation modification by three genes that cleave the protein including *P1*, *HC-Pro*, and *NIa*. Sivamani et al. (2002) reported that wheat resistance against *WSMV* with the inoculation of *NIb* and CP sense transgene, in comparison to dsRNA, provides more resistance against the virus (Waterhouse et al. 1998).

For wheat transformation hpRNA was created using an amplified clone of *NIa* gene of *WSMV* in vector pSTARGATE with a dehydrogenase kinase (pdk) intron and a polyubiquitin promoter. This method showed 3.5% efficiency when 16 independent T_0 transgenic wheat plants were transformed with hairpin. Furthermore, the transgenic cultivar showed Mendelian segregation, when resistance provided against *WSMV* "Conrad, MT" through isolated gene of *WSMV-NIb* gene by posttranscriptional gene silencing or by the expression of *CP* gene from "Conrad, MT" (Sivamani et al. 2000). Growth of transgenic wheat transformed against *WSMV* with *WSMV-NIb* gene showed disease-free symptoms (Sivamani et al. 2000) where *CP* gene of *Potyviruses* also showed the same results (Smith et al. 1994).

In some cases, wheat can be protected by the pre-resistance state by inoculation and degradation of viral RNA (Sivamani et al. 2000). F2 generations with intensive RNA expression from *WSMV* were intensively resistant. Thus, RNA degradation helps in resistance by activating the suppression mechanism (Waterhouse et al. 1998). As a result, transgenic crop with the transgene RNA has shown high resistance because of a large number of copies that resulted in transcriptional gene silencing.

3.4.2.1.2 Resistance Against Barley Yellow Striate Mosaic Virus (BYDV)

Resistant wheat lines against *BYDV* have been successfully produced. The resistant gene source in the host plant is located in *Bdv1* gene which is linked to *Lr34/Yr18* in the same chromosome; however, this resistant gene was considered ineffective in China (McIntosh 1998). Though a number of translocation wheat lines were produced, using *Agropyron* species was considered as more desirable for resistance to *BYDV* (Sharma et al. 1995) involving 7Ag chromosome exchanges with wheat chromosome 7D. Another resistant wheat line with 2Ag and 7Ag chromosomes was also produced (Sharma et al. 1995). The benefit of producing such resistant lines was to monitor virus attack serologically.

Resistance against *BYDV* in wheat exists in *Thinopyrum intermedium* that has been used for transformation of wheat with *BYDV-PAV* isolate and genotyping by a marker that reduced the infection against the particular strain. To create resistance against *BYDV*, antisense coat protein sequences are inserted using biolistic methods that showed positive results (Ma 2009). A wheat progenitor grass species, *Th. intermedium*, harbors genes for resistance against *BYDV* infection (Sharma et al. 1995). In wheat/*Th. intermedium BYDV* resistance genes were present in the long and short arm of a chromosome. In the wheat line PP9-1, a single gene showed resistance against *BYDV* that was crossed with different varieties to produce stable resistance. The wheat lines *Yw642*, *Yw443*, and *Yw243* WITH resistant gene present in chromosome 7 of *Th. intermedium* resistant against *BYDV* serotypes are *GPV* and *GAV*. This wheat species in next-generation co-segregated with *BYDV* resistance (Xin et al. 2001). Spliceable intron in hpRNA has been shown to induce RNAi efficiently (Smith et al. 2000), against *Barley yellow dwarf virus* in wheat (Wang et al. 2000).

3.4.2.2 Wheat Crop Protection Using Marker-Assisted Selection

Wheat diseases caused by the virus are controlled by establishing tolerant or resistant cultivars. Genes for tolerance or resistance are taken from the infected ones; some cultivars are engineered with the resistant gene against the diseases to show resistance (http://www.apsnet.org/edcenter/intropp/lessons/viruses/Pages/BarleyYelDwarf.aspx). Disease leading to crop losses is a challenge for breeders; therefore, crop highly affected by the disease, the methods for control, and the source of resistance availability and durability is taken under consideration for disease resistance. Marker-assisted selection (MAS) helps in selecting desired makers for molecular breeding (Miedaner and Korzun 2012). So far markers for the resistance of diseases have been available for various types of biotic stresses (Koebner 2003). MAS uses about 50 genes in wheat, because of its high precision and its application in the seedling stage and cost-effectiveness. MAS helps in implementing the resistance into breeding crops because of its feasibility to linked markers (Miedaner and Korzun 2012).

Marker-assisted selection (MAS) is used widely in developed countries to help in the conventional breeding of wheat (Gupta et al. 2009). MAS is used for simple traits instead of complex polygenic traits, for instance, to increase the quality of wheat and to improve crop yields. But for wheat yield maximization, marker-assisted recurrent selection (MARS) and genome-wide selection (GWS) can be used (Bernardo and Yu 2007; Heffner et al. 2009). MAS targets varieties with useful traits, but it is important to consider the MAS nature, as it is preferred for traits that have low heritability, are difficult to phenotype, are recessive, and for disease resistance require gene pyramiding (Gupta et al. 2009). Therefore, for improvisation of wheat, simple traits for disease resistance are targeted. Once resistance against a variety of diseases has been achieved, it is easy to improve the grain including protein content, color, texture, hardness, and gluten strength. In contrast, MAS is also targeted to achieve resistance against abiotic stress protection such as metal toxicity, tolerance to salinity, heat, drought, and waterlogging (Gupta et al. 2009).

3.4.3 Wheat Crop Defense Against Insect/Pest Using Resistant Genes

Resistant wheat with 26 genes for resistance located in 5A chromosome (Ohm et al. 1995) was produced. But the emergence of new biotypes of Hessian fly still poses a threat. In 1955, first three wheat genes resistant to Hessian fly were bred into wheat varieties that had been gaining combat to this pest; but by the following years in 2000, the flies had overcome the resistant wheat varieties due to variations, introduced successfully tolerant against Hessian fly since 1986. Williams et al. (2003) mapped the new wheat genes: *H31* and *H32*. As a result of high variability in the fly genome, more resistant genes are now created to defend the cultivars (USDA/ Agricultural Research Service 2007).

The primary defense of wheat is through antibiosis genes that prevent the survival of larva, although some cultivars will allow the survival of insects that can develop to overcome host resistance (Foster and Hein 2009). However, Hessian fly is the most successful pest that overcame antibiosis genes *H3*, *H5*, and *H6* of the host plant. The host plant resistance gene and virulence gene of the insect coevolved; as the plant resistance increases, insect virulence also increases. An elicitor is a resistant gene product of avirulent insect that triggers defense in plants. Whereas, virulent insects do not produce this product and are not recognized by the host; this strategy is used to make the host resistant (Janick and Wiley 2003). To make plants resistant, an avirulent protein (R-gene) from the insect is inserted to trigger plant defenses against particular insects (Dodds and Rathjen 2010). This wheat/Hessian fly interaction is responsible for provoking a response in wheat, resulting in programmed cell death of the fly (Klingler et al. 2009).

For resistance against Hessian fly, cuticle presence in wheat is vital (Kosma et al. 2010). William et al. (2011) found that the larva of Hessian fly produces saliva that acts on the plant and causes permeability in susceptible plants. However, the resistant plant variety starts producing surface waxes with the cuticle maintaining the integrity of its cell wall. The amount of gene expressing waxes and cuticle was verified using PCR giving evidence that the amount of mRNA helped to determine the gene expression responsible for a wax tissue. The plants were further confirmed by using a red dye that produced slight red spots as compared to the susceptible ones that absorbed the dye since no cuticles were present (Kosma et al. 2010). Recently, certain wheat lines have been produced against Hessian flies that act on the gut of the fly, thus decreasing its ability to absorb nutrients and leading to its death. Such wheat produces large amounts of lectin protein by gene *Hfr1* and lectin-like protein from gene *Hfr-3*. Lectin produced is considered to be toxic for the fly (Shukle et al. 2010) that keeps the crop resistant.

R-gene (resistance gene)-mediated resistance is preferred over backcrossing. Insects have the ability to overcome this type of resistance, as it has been seen that introgression of h-genes in wheat against Hessian fly has failed within 10 years (Cambron et al. 2010). The effectiveness of R-gene can be increased using gene pyramiding (Yencho et al. 2000). Integration of multiple R-genes into cultivars proved useful toward resistance against insect pests. However, plants also consist of susceptible genes that can be switched on by the insects to prevent defense against them (Walling 2008; Giordanengo et al. 2010). Plant susceptibility can be removed, if certain genes are knocked down to increase its resistance against pathogens (Lorang et al. 2007; Pavan et al. 2010). Combination based on biological control and host resistance can be complicated but holds a strong future in preventing crop losses (Allmann and Baldwin 2010). Therefore, for long-lasting resistance, direct resistance can be combined with indirect defense traits that slow direct resistance (Mitchell et al. 2010).

Another method includes insertion of barley trypsin inhibitor CMe (BTI-CMe) in immature embryos of wheat by the biolistic method. Proteinase inhibitors were considered in plant defense against pests that protected the transgenic seeds of wheat from Angoumois grain moth of *Sitotroga cerealella*, Lepidoptera: Gelechiidae.

3.4.3.1 Wheat Crop Breeding for Protection Against Insects/Pests

A resistant crop is bred against a particular pest by keeping its life cycle and heritability of resistance in mind. The source of resistance used for this purpose should have particular resistant genes that can lower crop loss. Some cultivars have resistant genes against pests, but some may require the transfer of resistance from other sources. However, resistance genes transferred to distant cultivars provide very limited resistance and success as a new pest from outside has the potential to develop new biotypes against the resistance variety due to changes in agronomic practices (McIntosh 1998).

Producing insect-resistant varieties paves paths for crop protection instead of using expensive, hazardous pesticides. Insect-resistant varieties are rarely used by the breeders who prefer increasing the quality, quantity, and stability of desired abiotic traits and neglect the importance of insect resistance (William and Bonjean 2011). Insects are becoming virulent because of crop domestication with increased nutrients for insects that have reduced defenses against them. Under such circumstances, resistant varieties against the pests are important especially against Russian wheat aphid and Hessian fly. Although there is a concern of developing resistance against the resistant wheat by these insects, in the future, more than one gene may be required to protect wheat. To create resistant wheat varieties with high expression of the resistant gene, constitutive resistance is enough for protection. The drawback of such cultivars, however, is that they will show resistance against only one insect. This makes the cultivars susceptible to other insects (William and Bonjean 2011).

4 Conclusion and Future Perspectives: Biotechnology, Output Practicality, Vision 2050, and Food Security

Once wheat has been protected by various biotic and abiotic stresses, the yield of wheat increases automatically. Wheat being the source of protein and nutrition is utilized when it is refined into various products, so its grain and texture determine the quality. Wheat yield is directly linked with a number of grains per unit area (Peltonen-Sainio et al. 2007); improvement of grain number and quality increases the yield of wheat.

Controlling viral diseases in wheat can help to improvise its yield by using various methods including genetic modification in wheat at the cellular level to improve its photosynthetic capacity. Among viruses, *BYDV*- and *WSMV*-resistant cultivars have been produced using various methodologies from conventional breeding to the use of genetic engineering. Insect control is significantly important in making wheat resistant and improving its yield and quality. Hessian fly causes drastic damage to the crop that can be prevented by making resistant cultivars. By preventing the disease incidence, crop yield can be improved (McIntosh 1998). Once the disease is under control, various efforts can be made to improve the nutrition level to fulfill the requirement (Foulkes et al. 2011).

For maximization of a crop, factors involved in increasing the productivity of a crop are considered. Crop's response to light duration and the growth inputs also provide high yield (Reynolds et al. 2009). Spike growth and stem elongation in wheat take place in the pre-anthesis period; increasing this duration improves spike dry matter. In the post-anthesis period, photosynthesis increases the strength and high grain numbers (Reynolds et al. 2005; Acreche and Slafer 2009). Improvement in photosynthetic rate increases crop productivity to accommodate grain numbers by developing partitioned spikes (Foulkes et al. 2011). Grain number can be increased by increasing spike development and increasing lodging resistance to improve water productivity and nutrient productivity and by increasing grain size. The quantitative approach in breeding can help to withstand the climatic change and to make faster progress in wheat yield returns (Foulkes et al. 2011).

Tissue culture being a biotechnological approach is very efficient in its applications. A wide range of tissue culture techniques are now worked out, and many more are in place. The scale of tissue culture revolution has initiated to impact over the survival in many ways. Hence civilization is now moving forward into the era of biotechnology. In the beginning, numerous protocols are devised for maximization and accomplishment of elite genotypes in a short period. Other major reasons for tissue culture enhancement are double haploid and somatic embryogenesis during breeding of different parental lines and genotypes. Tissue culture response of the wheat crop can be enhanced by achieving more success in improving and modifying elite genotypes for various agronomic traits. Wheat yield can be achieved, if the crop is protected against various biotic and abiotic environmental factors, but tissue culture and transformation difficulties in wheat pose a hurdle and are still in progress to control the yield. Further research efforts require reducing deleterious somaclonal variations during clonal production and transgenic plant propagation to get higher wheat yields.

Extensive work has been reported in this context. During this channel, some researchers have tried to produce in vitro plantlets with resistance to biotic and abiotic stresses. In this regard, plantlet's ability to cope with abiotic stresses such as drought, salinity, heavy metal, etc. has been remarkably achieved. Similarly, regenerated plants withstand the biological stress condition, for instance, diseases, pathogen, etc., that has been accomplished. Fungal diseases such as scab (FHB), powdery mildew, rusts, smuts, and many others have been improved through genetic engineering. Many in vitro studies have been conducted, and outputs have emerged on achieving fungal stress resistance in fields. The confirmation of resistance in putative tissue culture plantlet is achieved through the molecular marker and target gene-specific primers.

Use of genetic engineering helps in resistance to disease incidence, increasing yield and making the crop more nutritious for use. The use of hpRNA helps to reduce amylose production by changing amylase amylopectin ratio in wheat that can help to reduce heart diseases and colon cancer incidences (Regina et al. 2006), type 2 diabetes, and other types of cancer. These benefits are lost as milling removes fibers, minerals, and phytochemicals present in the embryo aleurone layer and in salts of phytic acid. To make nutritionally improvised wheat, identification of composition source is required along with the development of a high portion of bran and germ. To overcome the problem of nutrition, GE uses the expression of fungal phytase enzyme in grain to reduce the amount of phytates (Brinch-Pedersen et al. 2003).

Genetic engineering is meaningless without the application of tissue culture technique. Therefore, in vitro tissue culture is an important technique and the hour of need that should be routinely practiced to uncover its more usage in across a wide array. However, genetic modification in wheat domestication entails knowledge about the genome of domestic wheat (Avni et al. 2017), particularly wild emmer (*T. turgidum* ssp. *dicoccoides*). This is the reference assemblage and would serve as a huge resource for genome-wide improvement of modern wheat varieties.

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Applications of Molecular Markers to Develop Resistance Against Abiotic Stresses in Wheat

Ali Raza, Sundas Saher Mehmood, Tariq Shah, Xiling Zou, Lv Yan, Xuekun Zhang, and Rao Sohail Ahmad Khan

Contents

Abstract Innovations had come into being in the field of plant breeding with the development and advancement of molecular marker techniques by the end of the twentieth century. Advancement in molecular markers for sequencing techniques has led to improvements in crop production. Amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism, random amplified polymorphic DNA, and microsatellite markers are being used in the fields of molecular characterization, describing hybrid vigor, marker-assisted selection, abiotic stress tolerance, and genetic distance range. Numerous troubles that a user can face throughout marker application gametogenesis have also been discussed. Germplasm characterization and marker-mediated varietal fingerprinting seemed very ordinary and have many prevalent applications with AFLPs and simple sequence repeats (SSRs). SSR markers are known to be applicable and suitable techniques for molecular characterization owing to their low price, simplicity, and the lack of radio-isotope demand. Preventing hybrid vigor seemed very problematic, with a slight victory because of the absence of a simplistic marker technique that may categorically classify the hybrids, community, and offspring. A marker-assisted

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selection of valuable characters is very effective after molecular characterization, whereas for measurable traits, mainly disease-tolerant genes and quantitative trait loci for abiotic stress resistance, the success is inadequate. It is estimated that the implementation of molecular markers will remain limited in such fields until gene-specific markers exist and the price of the markers study is decreased markedly. This chapter discusses the possible responsibility of molecular markers in developing abiotic stress-resistant wheat.

Keywords Abiotic stresses · Molecular markers · PCR · Resistance · Wheat

1 Introduction

Wheat (*Triticum aestivum* L.) is an essential leading crop for almost 36% of the global community and supplies important carbohydrates and proteins in food (Kumar and Rai 2014; Rashed et al. 2017). Wheat was introduced into the central east around 8000 years ago and spread to almost every part of the globe (Hao et al. 2017). Wheat flour can produce a broad range of foods such as bread, noodles, cakes, and cookies owing to its distinctive elastic features (Ibba et al. 2017). The pace of heredity acquired to date has not been as attractive as it was in ancient times. Cultivars with no or less advancement are changes required to cover the need for a high yield along with the problems caused by abiotic stresses such as high temperature, flooding, drought, salinity, nutrients deficiency or availability, crop lodging and pre-harvest sprouting (Tiwari et al. 2017). Agriculture and climate change are internally associated with each other in different aspects,as climate change is the major cause of both biotic and abiotic stresses, which have adverse effects on the agriculture (Raza et al. 2019a).

Plants have adapted to live in such conditions, where they will introduce some stresses in cooperation. Plants exposed to different stresses are very complicated and demand modifications at the transcriptome, cellular, and physiological levels. Fresh proof indicates that plants respond to many stresses in different ways and they have different responses for different stresses by starting a function of gene appearance related to the same climate situations confront. The existence of abiotic stresses can increase or decrease the sensitivity to a living organism (Atkinson and Urwin 2012).

Although wheat quality and yield are enhanced by different abiotic stresses such as flooding, drought, salinity, low/high temperature, nutrients availability/deficiency, etc., recent findings demonstrate that environmental alteration results aggravate the extremities of drought and temperature stress on wheat (Jaggard et al. 2010; Ortiz et al. 2008) and with every degree increase in heat, the world wheat yield decrease by 6% (Asseng et al. 2015). Therefore, it is important to produce abiotic stress resistance wheat cultivars to enhance wheat grain yield for later food safety (Powell et al. 2012).

A molecular marker is known as a part of DNA that is closely related to a specific character or gene of an organism. DNA markers (molecular markers) are powerful tools for evaluating the heredity differences, although there is less of a heredity difference between wheat cultivars than in many self-pollinated plants (Röder et al. 2002). With the help of DNA markers, the breeder can avoid the traditional phenotype-dependent assortment of techniques that include the growth of plants toward maturity and nearly analyzing their actual features to interpret hidden genetic composition.

Different DNA markers can be applied for many purposes such as genetic divergence analysis, genetic variation, marker-assisted breeding, quantitative trait loci (QTLs) mapping, gene identification, genotypic selection, etc. These markers are restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeats (SSRs), inter simple sequence repeats (ISSRs), sequence-related amplified polymorphism (SRAP), single-nucleotide polymorphism (SNP), sequence characterized amplified region (SCAR), sequence tagged sites (STS), cleaved amplified polymorphic sequence (CAPS), etc. Of the many kinds of markers, simple sequence repeats (SSRs) or microsatellites are the most familiar markers for genetic mapping studies (Gajghate et al. 2015).

Relative molecular findings have described that the direct series of DNA markers and genes are preserved in various plant genomes (e.g., rice, wheat, barley, maize, millet, and sorghum) providing an important tool against gene finding in wheat (Choi et al. 2004; Fulton et al. 2002; Gale and Devos 1998; Gupta et al. 2008; Moore et al. 1995; Sorrells et al. 2003). Barley, rice, and maize genome sequences have been used to get markers for powerful map-based study, gene discovery, and similarity-dependent cloning in wheat crops (Bagge et al. 2007; He et al. 2008). In this chapter, the reaction of the different abiotic stresses of wheat is described, involving simple morphological, physiological, and genetic reactions accompanied by hints on how these reactions could be utilized to increase resistance against abiotic stresses.

2 Applications of Various Molecular Markers Used for Gene Identification in Wheat

Knowledge of the hereditary differences that exist among and within many plant communities can be very effective for the consumption of plants (Cole 2003). The history of evolution, the procedure of gene movements, breeding method, and community strength are essential features applied to the determination of the structure and extent of these differences (Hamrick 1989). To measure the genetic divergence and various essential parameters, many kinds of agronomic and morphological tools have been used in the recent past. Throughout almost three decades, the world has noticed the fast increase in information about the sequence of plant genomes, and the physiological and genetic effects of different plant genes; these have reorganized genetics and its importance in plant breeding programs.

2.1 Genetic Markers

These markers are essential progress in plant breeding and genetics (Kebriyaee et al. 2012). Genetic markers are known as an allele or piece of DNA with a familiar chromosome position containing a specific gene or property. These markers can react as an indicator or mark for the relatively similarly aimed genes (Collard et al. 2005), and can be divided into two groups: traditional markers and DNA/molecular markers. Traditional markers cover morphological, cytological, and biochemical markers whereas molecular markers include RFLP, AFLP, SSRs, SNP), and diversity arrays technology markers (Jiang 2013).

2.2 Traditional Markers

2.2.1 Morphological Markers

Morphological markers can be used to analyze the different properties such as seed shape, flower color, mode of germination, and other essential agronomic parameters. These markers are very secure to apply with no need for any mechanisms, and they do not need any specific biochemical and molecular system. Plant breeders in a breeding program for many plants use these markers extensively. There are some drawbacks to using morphological markers: they are restricted in quantity, and are affected by plant germination phases and many natural elements (Eagles et al. 2001). For a long time, scientists have used many morphological markers to analyze the differences among different crops for breeding purposes (Karaköy et al. 2014).

2.2.2 Cytological Markers

Cytological markers are integrated with differences that exist in the digits; combining the structures, magnitude, configuration, sequence, and location of the chromosome. These differences show the variations in the dispersal of euchromatin and heterochromatin. Like G bars are created by Giemsa stain, Q bars are created by quinacrine hydrochloride, and R bars are exchanged by G bands. These chromosome milestones can be applied to measure the differences among typical and evolved chromosomes. Linkage classification and actual mapping can also be identified by using cytological markers (Jiang 2013).

2.2.3 Biochemical Markers

Biochemical markers or isozymes are multimolecular types of enzymes, enclosed by many genes with similar tasks (Tanksley and Orton 1983). There are genetic markers with enzymes, and these genes and genetic distribution can be measured by using biochemical markers. These markers have many applications such as the analysis of genetic divergence, community structure, a gene circulation, and community sub-groups (Mateu-Andres and De Paco 2004). Co-dominant in nature, simple to manipulate, cost-effective with some drawbacks, and low in quantity, they measure the low level of polymorphisms and are affected by many isolation techniques, plant tissues, and various plant germination phases (Mondini et al. 2009).

2.3 Molecular Markers/DNA Markers

Markers of DNA consist of a small piece of nucleotide sequence and can be analyzed with the help of polymorphisms existing among the nucleotide sequence of various members. Inclusion, excision, target variation replication, and translocation are the main sources of such polymorphisms, but they do not automatically influence the activation of alleles. DNA markers should be co-dominant, equally expended over the whole genome, extremely reproducible, and having the capacity to measure the high altitude of polymorphisms (Mateu-Andres and De Paco 2004; Raza et al. 2018).

3 Classification of Molecular Markers

Molecular markers are divided into a few classes based on:

1. Style of gene movement (co-dominant or dominant markers)
2. The technique used for identification (hybridization-based markers or polymerase chain reaction (PCR)-based markers)
3. Style of transferal (paternal organelle inheritance, maternal organelle inheritance, bi-parental nuclear inheritance or maternal nuclear inheritance) (Semagn et al. 2006)

Until now, many kinds of DNA markers have been created and extensively applied in plant breeding and genetic programs for many plant species.

The next part presents some useful knowledge about markers based on their mode of observation. Differences among essential properties of the most regularly implemented DNA markers are described in Table 1.

3.1 Hybridization-Based Markers: Restriction Fragment Length Polymorphism

Based on hybridization, RFLPs were the only marker system and the first molecular marker technique. Characters of similar species show polymorphism because of

Table 1 Comparison of important characteristics of most commonly used molecular markers

Characteristics	RFLP	RAPD	AFLP	ISSR	SSR	SNP
Co-dominant/ dominant	Co-dominant	Dominant	Dominant	Dominant	Co-dominant	Co-dominant
Reproducibility	High	High	Intermediate	Medium–high	High	High
Polymorphism level	Medium	Very high	High	High	High	High
Required DNA quality	High	High	High	Low	Low	High
Required DNA quantity	High	Medium	Low	Low	Low	Low
Marker index	Low	High	Medium	Medium	Medium	High
Genome abundance	High	Very high	Very high	Medium	Medium	Very high
Cost	High	Less	High	High	High	Variable
Sequencing	Yes	No	No	No	Yes	Yes
Status	Past	Past	Past	Present	Present	Present
PCR requirement	No	Yes	Yes	Yes	Yes	Yes
Visualization	Radioactive	Agarose gel	Agarose gel	Agarose gel	Agarose gel	SNP-VISTA
Required DNA (ng)	10,000	20	500–1000	50	50	50

insertion or deletions, extremity modifications, displacement, replication, and reversal. Pure DNA extraction is the primary step in the RFLP technique. With restriction enzymes, this DNA is diverse, isolated from bacteria, and these enzymes are used to cut DNA at the loci (called as recognition sites). This results in many fragments with diverse lengths. Agarose or polyacrylamide gel electrophoresis (PAGE) is used to isolate the fragments to produce a number of bands. All bands produced by these fragments possess diverse length. These differences in the RFLP system are due to removal of base pairs, alterations, reversal, and shifting of chromosome segments. The resultant misplacement and securing of a specific site occurs. Restriction enzymes will not slit the fragments if only one base pair difference occurs in the specific site. Nevertheless, if this specific alteration happens in one chromosome and not in others, this is known as heterozygous to that marker, as another band exists (Madhumati 2014).

3.2 PCR-Based Markers

Cary Mullis in 1983 developed the PCR technique, which may have boosted a minor amount of DNA without the use of any live creatures (Mullis et al. 1986). Denaturation, annealing, and extension are the major imperative steps implicated in the PCR reaction. For additional information about PCR and its arrangement, the reader is referred to the report by Joshi and Deshpande (2010).

3.3 Randomly Amplified Polymorphic DNA

Welsh and McClelland (1990) and Williams et al. (1990) developed this technique independently. Genomic DNA amplification is attained by PCR via single, small (ten nucleotides) and random markers. PCR amplification take place when two DNA strands are comparable with each other but it reverses movement. Amplification of such bands are based on the size and length of the specific DNA and marker (Jiang 2013). The designated marker should have at least 40% guanine-cytosine (GC) content. If the GC content is less than 40%, then this primer will not survive at annealing temperature (72 °C) where DNA prolongation happens via DNA polymerase (Williams et al. 1990). PCR results are isolated on agarose gel marked with ethidium bromide (Wu et al. 1994) for visualization. The level of polymorphisms can be identified by approving the existence and lack of particular fragments on electrophoresis (Jiang 2013). The nature and amount of DNA, PCR reaction buffer, $MgCl_2$ concentration, Taq DNA, and annealing temperature are particular imperative elements that influence the duplication of RAPD primers (Wolff et al. 1993).

3.4 Amplified Fragment Length Polymorphism

The restrictions existing in the RAPD and RFLP systems were outclassed by the creation of AFLP markers (Vos et al. 1995). The AFLP system merges RFLP and PCR machines, where dissolution of DNA occurs and then PCR is accomplished (Lynch and Walsh 1998). AFLP markers are cost-effective and no previous sequence information is required. The AFLP system can be successfully run with good quality and partially decayed DNA. Nevertheless, no restriction enzymes and PCR inhibitors are present in DNA. For further information about this system, the reader is referred to earlier findings (Blears et al. 1998; Ridout and Donini 1999). Two types of restriction enzymes (a repeated cutter and a precious cutter) are used for DNA fragmentation in the AFLP system. Each end of the subsequent fragments is attached to oligonucleotides. Oligonucleotides are small pieces of nucleic acid used for attachment in PCR (Madhumati 2014). One end is definite for the repeated cutter (6 bp identified site) and the second end is for the precious cutter (3 bp identified site). In this case, multiplication of only those pieces that have been cut by these cutters occurred. A familiar sequence of adapters is used to develop the primers. The adapter is a small, enzyme-specific DNA sequence used for the identification of an unidentified DNA part (Vos et al. 1995). PCR results are visualized on agarose or PAGE gel marked with $AgNO_3$ or by autoradiography (Madhumati 2014).

3.5 Simple Sequence Repeats or Microsatellites

Microsatellites (Litt and Luty 1989) are also called SSRs (Tautz 1989), short tandem repeats, or SSRs (Schlotteröer et al. 1991). SSRs are SSR motifs of one to six nucleotides that exist in large quantities in the genome of numerous taxons (Beckmann and Weber 1992). Microsatellite markers can be mononucleotides (A), dinucleotides (GT), trinucleotides (ATT), tetranucleotides (ATCG), pentanucleotides (TAATC), and hexanucleotides (TGTGCA) (Weber 1990). Microsatellites are spread in the genome; nevertheless, they also exist in chloroplast (Provan et al. 2001) and mitochondria (Rajendrakumar et al. 2006). Recent findings have also documented the existence of microsatellites in protein coding genes and expressed sequence tags (ESTs) (Morgante et al. 2002). SSRs characterize the minor repeating per locus with a high level of polymorphism (Zane et al. 2002). This high level of polymorphism is because of the existence of numerous amounts of repeats in microsatellite sites and can be identified with ease by PCR (Kalia et al. 2011). The existence of SSRs may be due to the decrement of single-strand DNA, the combining of double-strand DNA, the transmission of retrotransposons, and discrepancy. Regular motifs existing in SSRs are Mono: A, T; Di: AT, GA; Tri: AGG; Tetra: AAAC. The preserved sequences are mainly used for the creation of primers. For more information associated with the evolution of SSRs, the reader is referred to the article by Kalia et al. (2011). The development of SSR markers comprises SSR library development and the discovery of particular microsatellites. The uncovering of favorable segments for primer synthesis is done and then PCR is accomplished. Clarification and assessment of the bands pattern is achieved and evaluation of PCR results is carried out to study the polymorphisms (Röder et al. 1998). Microsatellite markers are regarded as superior markers owing to their co-dominant nature with excessive duplication and larger genome size; thus, these primers can be applied proficiently to crop survey research (Kalia et al. 2011). These markers are effectively utilized across plantspecies for practical applications as they are co-dominant,locus specific, hypervariable, multiallelic, and robust. Thegenome-wide distribution of SSR markers makes them suitable markers for gene mapping and high-ranked genotyping, and helpful in marker-assisted breeding and gene mapping (Raza et al. 2019b).

3.6 Randomly Amplified Microsatellite Polymorphisms

Simple sequence repeat markers show the superior extent of polymorphisms with the disadvantage of being labor intensive. Whereas RAPDs are cost-effective over microsatellites, the extent of discovery of their polymorphisms is smaller compared with microsatellite markers. To overcome the limitations of these two techniques, randomly amplified microsatellite polymorphism (RAMP) markers emerged (Wu et al. 1994). RAMP markers comprise SSR primer, which is used for genomic DNA amplification in the lack or existence of RAPD primers. SSRs are radiolabeled containing a ‘5’ anchor and ‘3’ repeats. The results are determined via agarose electrophoresis (Li and Quiros 2001). The liquefying temperature of this marker is kept at 10–15 °C, and is greater for the anchored primers compared with the RAPDs, which supports the effective annealing of the anchored primer (Wu et al. 1994). RAMP markers are cost-effective, reveal greater polymorphism, and possess extensive dispersal in the genome. These markers have been effectively used in numerous plants for genomic studies (Li and Quiros 2001; Wu et al. 1994).

3.7 Single-Nucleotide Polymorphism

Single-nucleotide polymorphism (SNP) is referred to as a one-base-pair variation existing in the genome sequence. SNPs may be alterations (C/T or G/A) or reversions (C/A, C/G, A/T or T/G) based on nucleotide exchange. Usually, there is one base modification existing in the mRNA that comprises SNPs, referred to as the addition or deletion of one base. A single nucleotide base is the lowest element of legacy and SNPs can deliver simple or higher numbers of primers. SNPs exist in abundance in crops and animals, the frequency of SNPs in crops varying from one SNP in each 100–300 base pairs (Xu 2010). SNPs are extensively dispersed inside the genome and can be establish in coding and noncoding parts of genes or among two genes (intergenic part) with diverse frequencies (Xu 2010). SNP genotyping consists of a large number of techniques depending on diverse allelic inequality and identified programs. SNP-RFLP is a simple technique and CAPS markers can be used for SNP identification. SNPs can be identified based on the sequence analysis present in databases. Diverse types of SNP genotyping analyses have been created depending on diverse molecular procedures. Among them, marker extention, aggressive breakdown, oligonucleotide joining and distinct allele hybridization are imperative (Sobrino et al. 2005). Numerous new highly efficient genotyping techniques such as next-generation sequencing (NGS), genotyping by sequencing (GBS), chip-based NGS, and allele-specific PCR creates SNPs as highly inviting markers for genotyping (Agarwal et al. 2008).

4 Effects of Abiotic Stresses in Wheat

Drought, submersion, salinity, high or low temperatures, and nutrient deficiency or presence are major abiotic stresses that have an effect on global agriculture and play a major part in the more than 50% loss of the mean yield of vital crops (Wang et al. 2003) and these factors can cause crop desiccation and death alike. According to environmental forecasting, an increase in stress (water deficit, submersion, and high temperatures) occurs throughout the duration of crop development (Bates et al. 2008; Mittler and Blumwald 2010), and the world food yield remains to be disputed. To obtain world food safety, our consideration of crop reactions to abiotic factors is required to be enhanced with the objective of breeding plants that can retain a high photosynthetic pace, excellent maturity, and for which production can be upgraded under abiotic factors.

Losses of major crops occur owing to extreme changes in climate conditions during the last few decades (Bailey-Serres et al. 2012; Boyer et al. 2013), and environmental models forecast an enhancement of the prevalence of flooding (Hirabayashi et al. 2013), droughts (Pryor et al. 2013), and high temperatures (Bita and Gerats 2013; Gourdji et al. 2013). Complete environment alteration causes a decrease in the production of crucial crops such as wheat, rice, and corn, which has a major effect on world food yield (Iizumi et al. 2013; Rosenzweig et al. 2014). Genes that assure production in a demanding climate present inside the genetic resources of crops, their undomesticated cultivars, and species that are adjusted to a severe climate (Mickelbart et al. 2015). Breeders have developed resistance against abiotic stresses via genetic control of transcription factors (TFs), antioxidant proteins, and late embryogenesis abundant (LEA) proteins (Bhatnagar-Mathur et al. 2008; Umezawa et al. 2006). Different significant abiotic stresses (flooding, salinity, water deficit, heating, and nutrients) have different effects on plants.

4.1 Flooding

Flooding is one of the major risky predictable phenomena provoked by ample rain, an immoderate water supply, a lower soil penetration rate, and its prolonged presence can decrease the production of crops in vital cultivated areas of the globe. Ultimately, flooding minimizes shoot and root development and product (Tiryakioğlu et al. 2015). It can also minimize the consumption and movement of ions via roots, resulting in a deficiency of nutrients, element poisoning such as Mn, Na, Al, Fe, and B (Zhang et al. 2011), and movement of superoxide dismutase (Huang et al. 2015). Cell wall proteins are essential to maintain cell shape and reactions to biotic and abiotic factors, mainly waterlogging factors influence the cell wall, which is slackened at the advanced time of plant development (Komatsu and Yanagawa 2013).

There is little evidence for genetic variations in resistance to flooding in wheat (Mano and Oyanagi 2009). Flooding minimizes leaf expansion, photosynthesis, seed number per spike, and ultimately the production of wheat (Alam and Rabbani 2007). Flooding can decrease seed production of the winter crop by almost 32–94% for 20 days (Romina et al. 2014). The decrease in yield is caused by hypoxia and anoxia, disease, minimization of N by denitrification and the leaching phenomenon (Setter et al. 2008). Even a short period of temporary flooding can have a significant impact on germination and the production of dryland plants. Finally, the dry weight yield of roots and shoot decreases (Sauter 2013). The outcomes of an experiment analyzed the results of flooding for 8 days after the grouping of wheat, and showed a reduction of root growth at that stage (Araki et al. 2012).

Research into rockcress (*Arabidopsis thaliana*) (Gonzali et al. 2005) and rice (*Oryza sativa*) (Fukao and Bailey-Serres 2008; Hattori et al. 2009; Singh et al. 2010) has revealed that multiple genes related to flood stress are recommended and that the control of flood resistance in crops is complicated. Some researchers have examined the unrevealed mechanism of reactions to the flood factor by utilizing model plants (Vashisht et al. 2011) and some crop species (Casierra-Posada and Cutler 2017; Rhine et al. 2010), but only a few have analyzed the entire plant and cellular range.

4.2 *Drought*

Drought stress seriously restricts crop production and minimizes the yield and standard of wheat (Ihsan et al. 2016). Significantly, it is envisioned that the drought factor will continue, bringing dangers because of the coming environmental changes, and thus causing significant problems for agricultural products around the globe (Fracasso et al. 2016). Although drought may influence wheat maturation throughout all the phenological phases, the generative and seed-filling stages are most vulnerable (Pradhan et al. 2012). The final stage of drought in wheat is most common in the Mediterranean environment and produces a fundamental decrease in seed production (Araus et al. 2002; Turner 2004). To illustrate, post-anthesis mild drought minimizes the wheat production by about 1–30%; extended mild drought during the seed-filling and flowering stages decreases seed production by 58–92% (Table 2).

The impact of incurable drought on wheat production will probably be enhanced in the coming years (Araus et al. 2002; de Oliveira et al. 2013). Incurable drought minimizes the lifespan and seed-filling time of wheat. Under drought stress, the seed-filling speed is minimized because of decreased photosynthesis, enhanced leaf senescence, and sink restrictions (Wei et al. 2010). An inclusive study about the impact of terminal drought is essential to improve drought tolerance. However, some great studies on crop drought factors are accessible, although there is no complete study on drought stress on wheat throughout the seed-filling and generative stages (Farooq et al. 2014). Thus, the recognition genes associated with drought stress and a review of the genetic procedure to produce tolerance to drought stress is important in improving useful features in wheat (Tables 3 and 4).

4.3 *Temperature*

4.3.1 High Temperature

The main abiotic stress elements that influence germination, development, production, and food security in crop plants are high levels of heat and drought (Bilal et al. 2015; Hasanuzzaman et al. 2012; Lobell et al. 2015). Sometimes these problems happen simultaneously (Pradhan et al. 2012) and are at least related in some areas (Hirschi et al. 2011). The cumulative effects of these two stresses are completely

Table 2 Reductions in grain yield in wheat caused by drought stress

Growth stage	Stress type	Yield reduction (%)	Reference
Booting to maturity	Severe stress	37	Shamsi et al. (2010)
Booting to maturity	Severe stress	27	Shamsi and Kobraee (2011)
Heading	Mild stress	57	Bencze and Veisz (2011)
Heading to maturity	Severe stress	44	Prasad et al. (2011)
Heading and grain-filling	Prolonged mild stress	58–92	Dhanda and Sethi (2002)
Pre-anthesis	Prolonged mild stress	18–53	Majid et al. (2007)
Anthesis	Mild stress	8	Akram (2011)
Anthesis	Mild stress	19	Sangtarash (2010)
Anthesis	Severe stress	11–39	Jatoi et al. (2011)
Anthesis	Severe stress	43–51	Gupta et al. (2001)
Post-anthesis	Mild stress	1–30	Eskandari and Kazemi (2010)
Post-anthesis	Prolonged mild stress	13–38	Majid et al. (2007)
Grain-filling	Severe stress	9–78	Guóth et al. (2009)
Grain-filling to maturity	Severe stress	31	Shamsi et al. (2010)
Grain-filling to maturity	Severe stress	35	Shamsi and Kobraee (2011)

different from individual stress in the form of maturation, evolution, biomass collection, and production (Mittler 2006; Rizhsky et al. 2002). In wheat, the temperature threshold for damage during the flowering stage and grain-filling stage is estimated to be 31 °C and 35 °C respectively (Niwas and Khichar 2016).

During the reproductive stage, wheat is highly vulnerable to high temperatures compared with the vegetative stage (Farooq et al. 2011). It is commonly known that net carbon assimilation is decreased owing to a high temperature that is directly proportional to the rate of mitochondrial respiration (Atkin and Tjoelker 2003) and photorespiration (Sharkey 1988). Increasing photosynthesis by enhancing the capacity to acclimatize to high temperatures is one of the major challenges (Yamori et al. 2014). To meet this challenge, understanding the process behind various heat factors that limits photosynthetic production is very important.

4.3.2 Low Temperature

Low temperature is one of the most critical abiotic stresses and limits the germination and growth of winter wheat (*Triticum aestivum* L.) by suppressing plant maturation and reducing seed-making (Kosová et al. 2013). Wheat has expanded few of its protective protocols to increase its adaptive capacity under stress

Table 3 Abiotic stresses, their constraints, and effective survival strategies

Stress	Constraint	Tolerance and survival strategy	Transient solution	Chronic solution	References
Flooding	Reduced energy owing to lower photosynthesis or low O_2 levels	Energy conservation or expenditure	Growth quiescence	Rapid growth for avoidance	Bailey-Serres et al. (2012)
				Aerenchyma for aeration	
Drought	Low water potential	Limited water loss	Hydrotropism	Deeper roots	Hu and Xiong (2014)
		Improved water uptake	Reduced transpiration	Reduction of leaf area	
				Adjusted osmotic status	
Salinity	Elevated salt levels (e.g., NaCl) cause ion cytotoxicity and reduce osmotic potential	Reduced root ion uptake	Limited ion movement to transpiration stream	Limited root ion flux to shoots	Deinlein et al. (2014), Munns and Tester (2008)
		Vacuolar ion compartmentalization			
		Osmotic adjustment	Reduced shoot growth	Vacuolar ion compartmentalization in shoot cells	
Ion toxicity	Cytotoxicity	Limited uptake	Efflux of organic acids to apoplast and immobilization of ions by chelation	Compartmentalization of ions (e.g., vacuole and apoplast)	Liu et al. (2014), Nable et al. (1997)
		Vacuolar ion compartmentalization	Intracellular chelation	Efflux of organic ions to chelate toxic ions in soil	
Ion deficiency	Inadequate nutrient acquisition	Enhanced uptake by transporters and development adaptations	Transport protein induction and activation	Transport protein function	Jones et al. (2013)
			Reduced growth	Root sensing and architecture remodeling for acquisition	

(continued)

Table 3 (continued)

Stress	Constraint	Tolerance and survival strategy	Transient solution	Chronic solution	References
				Partitioning for storage	
Low and sub-freezing temperatures	Membrane damage	Low-temperature acclimation	Acclimation	Acclimation and dormancy	Yildiz et al. (2015)
	Low water potential		Dormancy	Altered membrane composition	
		Induction of stress protection genes	Osmoprotection	Increased compatible solutes	
High temperature	Reduced photosynthesis	Maintenance of membrane function and reproductive viability	Leaf cooling	Altered membrane composition	Bita and Gerats (2013)
	Reduced transpiration		Molecular chaperones	Molecular chaperones	
	Impaired cellular function				

Table 4 Gene-to-field examples of effective genetic variation in abiotic stress survival strategies

Stress	Gene and locus	Species	Donor	Genetic basis	Gene product function	Functional mechanisms	References
Flooding	SUB1A	*Oryza sativa*	Landrace	NF; CNV; AV	Ethylene-responsive TV (ERF-VII)	Ethylene-promoted inhibition of GA-mediated elongation growth; energy conservation	Fukao and Bailey-Serres (2008), Fukao et al. (2006), Xu et al. (2006)
	SK1 and SK2	*Oryza sativa*	Landrace	P/A; CNV	Ethylene-responsive TF (ETF-VII)	Ethylene-promoted, GA-mediated elongation of stem internodes	Hattori et al. (2009)
Drought	DRO1	*Oryza sativa*	Tolerant genotype	AV	Unknown function	Enhanced deep rooting; auxin-regulated asymmetric root growth	Uga et al. (2011)
Low temperature	*VRN1* at the *FR1* locus	*T. aestivum* *H. vulgare*	Wild relative Tolerant genotype	CNV; AV	MADS box TF	Regulation of vernalization; low-temperature-induced *CBF* and regulation activation; freezing tolerance	Dhillon et al. (2010)
	CBFs at the *FR2* locus	*T. aestivum* *H. vulgare*	Wild relative Tolerant genotype	CNV; AV	CBFs (TFs)	CBF copy number-dependent expression and regulon activation; freezing tolerance	Knox et al. (2010)
Saline soil	*HKT1;5-A* at the *Nax2* locus	*Triticum turgidum ssp. Durum*	*Triticum monococcum*	P/A	Na^+ transporter	Root Na^+ exclusion from xylem vessels	Munns et al. (2012)
	TaHKT1;5	*Triticum aestivum*	*T. aestivum* D genome (origin *Aegilops tauschii*)	AV	Na^+ transporter	Higher K^+/Na^+ in expanding and young leaves	Dubcovsky et al. (1996)
	HKT1;5	*O. sativa* ssp. *Japonica*	Tolerant *O. sativa* ssp. *indica*	AV	Na^+ transporter	Shoot K^+/Na^+ homeostasis	Ren et al. (2005)

(continued)

Table 4 (continued)

Stress	Gene and locus	Species	Donor	Genetic basis	Gene product function	Functional mechanisms	References
High Al^{3+}	*SbMATE* at the Alt_{sb} locus	*Sorghum bicolor*	Tolerant genotype	AV	Root Al^{3+} activated citrate efflux transporter	Citrate chelation of Al^{3+} detoxifies root zone	Magalhaes et al. (2007)
	MATE1	*Zea mays*	Tolerant genotype	CNV; AV	Root Al^{3+} activated citrate efflux transporter	Citrate chelation of Al^{3+} detoxifies root zone	Maron et al. (2013)
	ALMT	*T. aestivum*	*T. aestivum* (origin probably *A. tauschii*)	CNV; AV	Root Al^{3+} activated malate efflux transporter	Malate chelation of Al^{3+} detoxifies root zone	Sasaki et al. (2006)
	NRAT1	*O. sativa*	Tolerant genotype	AV	Root Al^{3+} activated (NRAT1 expression) Nramp Al^{3+} Transporter (plasma membrane) influx	Intracellular Al^{3+} influx decreases toxic build-up in the cell wall and presumably facilitates vacuolar compartmentalization	Li et al. (2014)
High B	*Bot1*	*Hordeum vulgare*	Landrace	CNV; AV	Root B efflux transporter	Restricts net B accumulation	Sutton et al. (2007)
	Bot-B5b	*T. aestivum*	Landrace	AV	Root B efflux transporter	Restricts net B accumulation	Pallotta et al. (2014)
Low P_i	*PSTOL1* at the *Pup1* locus	*O. sativa*	Landrace	P/A; AV	Protein kinase	Enhanced crown root development for improved P_i acquisition	Gamuyao et al. (2012)
Low Fe^{3+} and Zn^{2+}	*NAM-B1*	*T. turgidum* ssp. *Durum*	Related subspecies	AV	NACTF	Accelerates senescence and nutrient remobilization to grain	Uauy et al. (2006)

ALMT Al^{3+}-activated malate transporter, *AV* allelic variation, *CNV* copy number variation, *DRO1* deeper rooting1, *FR* frost resistance, *HKT1* high-affinity K^+ transporter1, *MATE* multidrug and toxic compound extrusion, *NF* neo functionalization, *NRAT1* NRAMP Al^{3+} transporter 1, *P/A* present or absent locus, *PSTOL1* phosphate starvation tolerance1, *Pup1* phosphorus uptake 1, *SK snorkel*, *SUB1 submergence1*, *TF* transcription factor, *VRN1 vernalization1* conditions. An oxygen-scavenging system that starts by freezing helps to enhance cold resistance (Thakur and Nayyar 2013) by inducing metabolic changes, including the demobilization of several metabolic enzymes and the disturbance of the metabolic procedure (Xu et al. 2013).

Acclimatization to cold stress needs a radical alteration of gene appearance, which translates into changes in the configuration of the transcriptome, metabolomics, and proteome (Chinnusamy et al. 2007). It has been proven that alterations in gene appearance at the transcription level were not similar to modifications at the proteomic level (Bogeat-Triboulot et al. 2007). This result helps to realize the responses of wheat under temperature stress and more accurately quantify the effects of a change in the environment on seed production.

4.4 Salinity

Different physiological and biochemical responses, e.g., photosynthesis, maturation, and the development of plants, are induced by some abiotic stresses in which salt stress accounts for the most (Nemoto and Sasakuma 2002). Nearly 20% of submerged area is useless because of soil salinity, which notably lessens the overall crop yields (Qadir et al. 2014). Soil salinity disturbs different functions of plants, including the toxicity induced by excessive sodium ions, in addition to some other ions, and osmotic pressure imposed on roots by salinity.

Two major environmental factors acting as abiotic stresses are salinity and drought, which have a critical effect on the efficiency and overall production of wheat and other plants. Intrinsically, it is necessary to comprehend the reaction of wheat to drought salt stresses and to breed wheat varieties with enhanced salt and drought tolerance.

The response of *Arabidopsis thaliana* against salinity stress has already been intensively studied, which has revealed numerous key pathways, some of which are controlled by the plant hormone abscisic acid (ABA) (Zhu 2001). On exposure of plant cells to salinity, elevated levels of apoplastic salt concentration forces change the thermodynamic equilibrium of aqueous and ionic solutions, which results in hyperosmotic pressure (Chen et al. 1994; Holappa and Walker-Simmons 1995). The level of ABA increases in plants under saline conditions (Gómez et al. 1988), acting as an indication to stimulate tissue adaptation in the plant (Chandler and Robertson 1994).

Many genes related to dehydration are stimulated to express by salinity; these genes also respond to ABA and have been anticipated to play a key role in adaptive immunity against stresses (Nemoto and Sasakuma 2002). Identification of the genes involved in the salt response is very important for the appreciation of plant reactions to salt stress and for the examination of their features with regard to other stress factors.

4.5 Nutrient Deficiency and Availability

With the limited nutrient supply, pigment amount per unit and the overall quantity production per plant were decreased. Fertilizers contain nutrients that play a basic role in structural and functional constituents for photosynthesis in addition to the biogenesis of light-reactive plant pigments. Any deficiency in nutrients causes a reduction in the content of leaf pigmentation, retardation of plant germination, and lowers the total production of plants (Shah et al. 2017).

How plant growth responds to different essential plant nutrients has already been studied. Most of this research was directed at the estimation of the best nutritional management and control practices under normal saline conditions. However, the higher concentrations of salts and nutrient inequities in the root-zone of the plant make it challenging to scrutinize the plant growth response to fertilizers with nutrients under salinity (Semiz et al. 2014). Under saline conditions, different plants have shown a mixed response to fertilizers, and some were reported to have a positive response (Soliman et al. 1992), whereas some plants have shown a negative response (Dhanda and Toky 2010; Patel et al. 2000) or in some cases a negligible response in situations of higher salinity (Semiz et al. 2014). Fertilizers have a great effect on plant germination and growth, even in nutrient-deficient soils, regardless of the salinity conditions.

5 Different Genes Associated with Abiotic Stresses in Wheat and Other Crops

Various abiotic stresses, e.g., high level of salinity, temperature, and drought, are some of the common environmental circumstances that may sometimes affect plant germination and development globally. ABA acts as a vital part in the physiological and developmental responses of plants. This phytohormone also coordinates signal transduction pathways occurring in plants induced by several external abiotic stresses. Dehydration responsive element binding (DREB) plant transcription factors are sensible for the adjustment of stress-inducible gene expression, mostly in an ABA-independent manner. These TFs also improve abiotic stress resistance in plants with the interaction of the dehydration-responsive element (DRE)/C-repeat (CRT) *cis*-element that is present within promotor regions of various genes, and which are responsive to abiotic stress (Lata and Prasad 2011). This interaction of TFs and *cis*-elements is involved in the up-regulation of the appearance of several downriver genes inducing abiotic stress resistance (Agarwal and Jha 2010). Research into *Arabidopsis thaliana* has shown that there are about 1500 TFs, which are supposed to regulate the stress-associated gene appearance (Riechmann et al. 2000).

Transcriptome analyses on a large scale have shown that the genes responsive to abiotic stresses can be categorized into two sets (Fowler and Thomashow 2002; Seki et al. 2002). One category accounts for the genes involved in protein-encoding for the protection of plant cells from the effects of water disturbances. It was suggested that the plant might also be genetically modified, possessing drought or high salinity tolerance, by either introduction or overexpression of the genes that encode proline synthetase, LEA proteins or betaine synthetase, etc. (Cushman and Bohnert 2000).

The second group comprises the genes with the regulatory function of inducing stress indicator transduction and modulating gene expression. This group includes various TFs, e.g., myeloblastosis oncogene (MYB), ATAF, myelocytomatosis oncogene (MYC), basic leucine zipper (bZIP), NAM, DREB, and CUC (NAC), signifying the functions of several transcriptional regulative procedures in the stress indicator transduction pathways: protein kinases (receptor protein kinase, mitogen-activated protein [MAP] kinase, calcium-dependent protein [CDP] kinase, etc.), protein phosphatases, and proteinases (phosphoesterases and phospholipase C, etc.), which induces the procedure of signal transduction and gene appearance as well (Agarwal et al. 2006; Shinozaki and Yamaguchi-Shinozaki 2007).

In wheat, ABA and dehydration stress induced a SnRK2 member, *PKABA1*, whereas it caused repression in the task of gibberellic acid-inducible promotors when rapidly over-expressed in barley aleurone layers (Gómez-Cadenas et al. 1999). In a different research study, it was observed that the wheat *TaSnRK2.4* gene was intense evidence for booting spindles rather than leaves, spikes, and roots, and it was stimulated by different stresses, e.g., drought, salinity, in addition to ABA application. This study also reports that the over-expression of *TaSnRK2.4* results in longer primary roots, delaying seedling establishment with improved resistance to various abiotic stresses in *Arabidopsis thaliana* (Mao et al. 2009). However, it was also revealed that SnRK2s plays a vital role in abiotic stress signaling transduction in plants and has a quick reaction to osmotic pressure. Nevertheless, the specific functions of SnRK2s have not been fully identified (Zhang et al. 2010).

Because of the huge genome size and an excessive percentage (over 80%) of monotonous introns in DNA sequences, it is a major challenge for scientists to comprehend the sequence of the wheat genome. However, a substantial comprehension of the expressed part of the large wheat genome can be expanded through either large-scale generation or analysis of ESTs.

6 Conclusion and Future Prospects

By the end of twentieth century, due to the complexity of wheat genome, DNA marker development and applications were not fully described. The markers already identified in maize, rice, and barley cannot be used to identify diverse physiological characters of wheat genome because of its complexity. Until now, extensive molecular maps have been designed for wheat genome, which have been used to tag and identify many traits. Molecular markers are now extensively being used for comprehensive understanding of trait inheritance as well as structure and organization of wheat genome. Synteny among many grass species has also been identified with the use of molecular markers. With the advancement in molecular marker techniques, individual homoeologous groups in wheat genome or chromosomal specificity has also been analyzed. Consequently, comparative analyses, intraspecific analysis, gene introgression experiments and practical approaches in wheat breeding have been revolutionized with the accessibility of many molecular markers being identified in wheat. Still the application of this technique is in its initial stages for marker-assisted selection in breeding approaches. Breeding approaches together with biotechnological approaches have accelerated the molecular marker-assisted selection techniques in wheat breeding. Advancement in ESTs, SNPs, DNA chips (microarray or MALDI-TOF mass spectrometry) have also brought about innovations in genome mapping in addition to gene tagging in polyploidy crop breeding. In the coming years, revolutions in molecular marker techniques will lead to the further precision and cost-effective, high productivity of polyploid crops in breeding programs.

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Identification of Stress Responsive Genes by Using Molecular Markers to Develop Tolerance in Wheat

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Contents

Abstract Global climate change, which is rising steeply in the world today, has caused further increases in the influence of abiotic stress factors. Abiotic stresses such as drought, high salinity, and high temperatures are common detrimental environmental circumstances that extremely influence growth, cultivation, and productivity worldwide. Traditionally, the varietal selection is based on morphological feature; hence, polygenic characters were very difficult to analyze, and thus such constraints can be overcome by using molecular marker-assisted selection (MAS). As markers are currently available for relatively few traits, MAS must be integrated with the ongoing conventional breeding to maximize its impact. Molecular markers are useful tools to determine the variation in the DNA sequence and eventually the regions of DNA or the genes controlling the qualitative and/or quantitative traits of agronomic significance. The aim of the presented research was to detect the genes and gene loci responsible for the tolerance to salt stress, drought, and high

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temperatures in wheat using various molecular markers. Wheat genotypes with contrasting stress tolerance, architectonics, productivity, and other physiological traits kept in the gene fund of the Research Institute of Crop Husbandry were used as research objects. Plants were cultivated in the Absheron experimental base under natural conditions (Baku, Azerbaijan). Salt tolerance potential of wheat genotypes was examined genetically based on PCR analysis using various molecular markers associated with salt tolerance. According to the results of the molecular analysis performed with RAPD (OPZ 09) markers linked with salt tolerance, expected 590 bp DNA fragments were amplified in 39% of bread wheat and 27% of durum wheat genotypes. At the same time, salt tolerance gene Nax1 was examined with gwm312 primer in durum wheat genotypes. An expected 200 bp amplicon indicating the existence of this gene in the Barakatli 95, Garabag, Shiraslan 23, Sharg, and Gyrmyzy bugda genotypes was successfully amplified. This amplicon was also synthesized in Barakatli 95, Garabag, Shiraslan 23, and Gyrmyzy bugda genotypes using wmc170 primer linked to salt tolerance locus in durum wheat genotypes. The study of physiological senescence of the flag leaf playing the pivotal role in the uptake of solar energy and stipulating plant productivity in wheat is very important for providing high productivity under stress. Therefore, using RAPD OPH13 marker, the existence of a gene locus linked to the physiological life-span of flag leaf was examined in wheat genotypes under drought stress. Based on the analysis of electrophoretic profiles of PCR results, expected 450 bp fragments were synthesized in 30 wheat genotypes. This result confirms the existence of a gene locus providing the physiological youth of flag leaf, which is considered as the drought tolerance indicator in these genotypes. The existence of the studied locus was not confirmed in 19% of the genotypes. Tolerance to heat stress is a complex phenomenon and controlled by multiple genes imparting a number of physiological and biochemical changes. To differentiate the heat-tolerant and heat-susceptible genotypes of wheat, a heat shock protein (HSP16.9) was taken as a target gene, and domestic genotypes were examined using allele-specific PCR primers. The obtained results can be used in wheat breeding programs for developing wheat varieties tolerant to stresses.

Keywords Wheat · Molecular markers · Salinity · Drought · Heat stress · Nax1 · HSP 16.9 · Flag leaf senescence

1 Introduction

Wheat is a crop of global importance because of its adaptability to a wide range of climatic conditions and the quality of the grain, the most suitable for the production of bread flour. The growth of the world population requires at least 70% increase in agricultural production by 2050 (Tester and Langridge 2010; Pardey 2011; http://faostat.fao.org), which makes it necessary to increase wheat production capacity worldwide. However, the actual yield of modern varieties of wheat is largely limited by the influence of abiotic and biotic stresses (Iqbal et al. 2017; Wang and Xia 2017).

Soil salinity is one of the main limiting factors affecting the growth and development of wheat. Wheat grain quality and productivity decline under saline conditions (Turki et al. 2012; Houshmand et al. 2014). Different varieties of the same culture sometimes differ very much in the degree of salt tolerance and preserve this trait in generations. One of the aspects of the crop tolerance is associated with genetic diversity in plant populations, which is the result of qualitative and/or quantitative changes in the polynucleotide sequences of DNA (Cullis 1999; Kumar et al. 2017).

One of the ways to overcome the negative effects of salinity factor is the use of the most salt-tolerant wheat varieties and forms (Sadiq et al. 2018) Selection and the establishment of resistant to salinity genotypes will increase the land available for agricultural use and reduce crop losses.

Drought is one of the main abiotic stress factors affecting wheat production in many regions of the world (Takeda and Matsuoka 2008; Kumar et al. 2018). In spite of the intensive researches performed for maintaining yield under drought conditions, the physiological basis of this process remains unclear (Tuberosa et al. 2007). Drought tolerance is considered to be a quantitative trait with complex phenotypic and genetic control (Mwadzingeni et al. 2016). It is necessary to understand the genetic and physiological bases of drought tolerance in order to develop high-tolerant genotypes through conventional breeding. As water-limited areas have recently increased, selection for field performance and selection for physiological traits related to drought tolerance are essential. One of the main physiological traits in cereals correlated with plant performance under drought is flag leaf senescence (FLS) (Barakat et al. 2013). The duration of flag leaf senescence is a significant qualifier of plant productivity under stress as well as under normal conditions (Verma et al. 2004).

Global warming is one of the world's main ecological problems that adversely affect agriculture. By the end of this century, the temperature increase in the range 1.8–4.0 °C is expected. High temperature causes pernicious influence on plant growth in different stages of development, reduces its harvest, causes protein and membrane damaging, and furthermore inhibits plant respiration and photosynthesis. High temperature has a significant adverse effect on wheat plant (Nandha et al. 2018). High temperature reduces the duration of grain filling and shortens apoptosis period and harvest maturity (Altenbach et al. 2003). Furthermore, it disrupts chloroplast membranes and chlorophyll molecules in wheat plant that respectively leads to permanent browning of leaves (Tack et al. 2015). Heat stress impact on cereal crops such as wheat was observed basically during the reproductive period (Xue et al. 2013). It has an essential negative impact on carbon assimilation and starch synthesis which leads to grain reduction and decreases grain quality (Wardlaw and Wrigley 1994; Skylas et al. 2002). Under high temperature, heat-labile proteins are exposed to denaturation, and a significant increase in the level of harmful reactive oxygen species (ROS) occurs in plant cells (Mittler et al. 2012; Grover et al. 2013). In order to achieve thermotolerance, plants rely on acclimatization to high temperatures, which causes expression of heat protection genes such as heat shock proteins (HSPs) (Pandey et al. 2015). Some reviews show that in wheat plant, different types of HSP are produced in different tissues in response to duration and type of heat stress (Zivy 1987; Weng and Nguyen 1992; Treglia et al. 1999; Rampino et al. 2009; Sharma-Natu et al. 2010; Xu et al. 2011a, b; Wang et al. 2017).

The introduction of the breeding programs of modern biotechnological approaches based on the use of molecular markers may contribute to the solution of these problems (Sharma et al. 2014; Ni et al. 2017). Genetic markers play a crucial role in assessing the genetic constitution of an organism and serve as one of the principal means of selection (Elshafei et al. 2013; Bungartz et al. 2016). Currently, the molecular genetic study in GenBank of plant germplasm is a generally accepted method for studying preservable diversity, enhancing the resolving power of selection and reducing the time of the selection process. Developing the DNA markers of economically valuable characters allowed carrying out a rapid assessment of plants for resistance to the environmental stress factors, to identify varieties with the high genetic potential for productivity. A large number of genes and loci controlling the stability of various cereals to abiotic stresses, features, and quality of grain yield were identified and mapped via DNA markers (Landjeva et al. 2007; Zhang et al. 2018). Molecular markers are widely used to study the wheat genome, to identify and map genes responsible for expression of useful properties, as well as for the isolation and cloning genes for investigating their controlled properties and for transferring them to other varieties (i.e., for genetic transformation).

The aim of the presented research was the testing availability of the *Nax1* locus responsible for salt tolerance in Azerbaijan wheat germplasm, the assessment of salt tolerance potential by applying the RAPD-PCR method, validation of QTL for the flag leaf senescence gene in wheat, and identification of HSP16.9 gene using an allele-specific primer.

2 Plant Materials

Wheat genotypes collected in the gene pool of the Research Institute of Crop Husbandry (Baku) were used as research objects. Plants were cultivated under field conditions.

3 Extraction of Plant DNA

DNA extraction was carried out using the CTAB method with some modifications (Murray and Thompson 1980). Fresh plant tissue as a fragment of the leaf was minced in liquid nitrogen, suspended in 1000 μl of CTAB extraction buffer (100 mM Tris-HCl, pH 8.0; 20 mM EDTA, pH 8.0; 1.4 mM NaCl; 40 mM β-mercaptoethanol), and pre-warmed in a water bath at 60 °C. Homogenization was completed by intense Vortex shaking. Then 400 ml of chloroform (99.8%) was added into each tube, and the tubes were gently mixed. Next, the tubes were placed in a water bath and incubated for 10 min at 60 °C. After incubation, the tubes were centrifuged in an Eppendorf-type benchtop centrifuge (15000 g) for 10 min at room temperature. After centrifugation, the supernatant was carefully selected (taking care not to capture sediment particles) and transferred to clean 1.5 ml Eppendorf-type tubes, and 600 ml of cold isopropanol was added, mixed well, and left at room temperature for 3–5 min. At this stage, the dispersed DNA precipitate can be observed. The tube contents were centrifuged at room temperature in the Eppendorf-type benchtop centrifuge (15000 g) for 10 min.

The precipitate was washed several times with 70% ethanol, dried in a thermostat at 56 °C for 5 min, and dissolved in TE buffer (10 mM Tris-HCl, pH 8; 1 mM EDTA). Samples were left in a refrigerator at 4 °C for the complete dissolution of the DNA in a buffer.

4 DNA Quantification

After the dissolution of the DNA, the quantity was determined by optical density (OD) at $\lambda = 260$ using the ULTROSPEC 3300 PRO spectrophotometer ("Amersham," USA).

The purity of the genomic DNA was determined by the ratio of absorptions A260/A280. Quality of the DNA was checked on the basis of performance of the extracted DNA samples in 0.8% agarose gel stained with 10 mg/mL ethidium bromide in 1 × TBE (Tris base, boric acid, EDTA) buffer. The gel was developed and photographed under ultraviolet light using "Gel Documentation System UVITEK" (UK).

5 DNA Amplification

Polymerase chain reaction was performed according to Williams et al. (1990). DNA amplification was performed in a 25 μl reaction mixture volume, containing 10 × buffer; 20 ng of the genomic DNA; 0.2 μM primer; 200 μM of each of the following, dATP, dCTP, dGTP, and dTTP; 2.5 mM $MgCl_2$; and 0.2 units of Taq polymerase in the incubation buffer. Different primers were used for the test.

PCR was performed in the Thermal Cycler "Applied Biosystems 2720" (Singapore) thermocycler under the following conditions: 1 cycle, 3 min at 94 °C; 38 cycles, 1 min at 94 °C, an annealing step at variable annealing temperatures depending on the primer pairs for 1 min and 2 min at 72 °C; the final elongation cycle was performed at 72 °C for 10 min and then kept at 4 °C.

The reaction products were separated by electrophoresis in a 1.2–2.0% agarose gel in the HR-2025 High Resolution "IBI Scientific" (UK) horizontal electrophoresis machine with the addition of ethidium bromide and documented using Gel Documentation System "UVITEK." Statistical analysis included binary matrix compilation for each of the primers, in which “presence” (1) or “absence” (0) of fragments with an equal molecular mass on the electrophoregram was noted.

6 Availability Testing of the Nax1 Locus in the Genome of Azerbaijan Durum Wheat Varieties

Soil salinity affects large areas of cultivated land, causing significant reductions in crop yield globally. In general, plant species are sensitive to high concentrations of sodium (Na^+), which causes combined Na^+ toxicity and osmotic stress. One of the important mechanisms of salt tolerance is considered to be the ability of plants to maintain ion homeostasis, allowing them to grow and develop under salinity. A mechanism preventing Na^+ intrusion into tissues, most sensitive to salinity, such as apical meristems, leaf blades and generative organs are of great importance for glycophytes (Tester and Davenport 2003; Munns and Tester 2008). Metabolic toxicity of Na^+ is assumed to be the result of its ability to compete with K^+ for binding sites in biopolymers which are important for cell metabolism. Potassium is needed for the activation of more than 50 enzymes and also for tRNA binding to ribosomes and, consequently, for the protein synthesis (Szczerba et al. 2009). So at a high Na^+/K^+ ratio, many enzymatic processes in the cytoplasm can be violated. Therefore, the ability of plant cells to maintain a stable level of cytosolic K^+, in a medium with high concentrations of Na^+, can also be a key factor in determining the ability of plant cells to overcome salt stress. By maintaining a low level of Na^+ in the cytosol, plant cells can perform all the necessary metabolic functions. The study of a large number of crops showed that the more salt-tolerant species have a greater ability to exclude Na^+ from leaf tissues and maintain high levels of K^+ in the cell (Munns et al. 2000; Flowers and Hajibagheri 2001). Maintaining a high ratio of K^+/Na^+ in the cytosol under the influence of salt is considered to be one of the most important indices of tolerant genotype (Hauser and Horie 2010). Among a large number of ion transporters and ion channels, proton pumps and antiporters of plasmalemma and tonoplast (NHX, HKT, SOS1) play an important role in providing this ratio.

Salt tolerance in wheat and many other species is associated with the ability to exclude Na^+ so that high Na^+ concentrations do not occur in leaves, particularly in the leaf blade. Durum wheat is particularly sensitive to salinity and has higher rates of Na^+ accumulation and poor K^+/Na^+ discrimination and is less salt tolerant than bread wheat (Munns et al. 2006).

In order to increase salt tolerance of cereals, many research centers focused their efforts on the study of different germplasm collections of different origin and the identification of new genetic resources. Thus, CSIRO Plant Industry researchers have isolated two salt-tolerant genes (*Nax1* and *Nax2*) from the ancient wild relative of wheat *T. monococcum*. Both genes inhibit the accumulation of Na^+, limiting its transfer from roots to shoots. By introgression of *Nax* genes of *T. monococcum* into bread wheat, the concentration of Na^+ in the leaf blade was reduced to 60% and the portion of Na^+ in the leaf axils increased (James et al. 2011). Based on the field tests, durum wheat lines with *Nax2* gene produce 25% more yield than isogenic lines lacking this locus under saline conditions (Munns et al. 2012). These results indicate that *Nax* genes have the potential to increase salt tolerance of wheat.

As a result of a search in an international collection of durum and durum-related genotypes, a novel source of Na^+ exclusion was found in an unusual genotype named Line 149. Genetic studies indicated that two major loci *Nax*1 and *Nax*2 (Na^+ exclusion loci) controlled leaf blade Na^+ accumulation in Line 149 (Munns et al. 2003). The *Nax* genes are not present in modern wheat (Huang et al. 2008). They were identified as Na^+ transporters of the HKT gene family (James et al. 2011), encoding transporters in the plasma membrane that mediate the uptake of Na^+ or K^+ from the apoplast (Hauser and Horie 2010). Both *Nax* genes appeared to originate from a wheat relative, *T. monococcum* (C68–101), which was crossed with a durum wheat to transfer rust resistance genes, and this cross inadvertently transferred the *Nax* genes into Line 149 as well (James et al. 2006).

This work was carried out for molecular genetic testing of perspective local varieties of *T. durum* for the presence of the marker locus, linked to the gene *Nax1*. The objects of the study were 19 varieties of durum wheat developed in the Azerbaijan Research Institute of Crop Husbandry. The identification of *Nax1* was performed using gwm312 and wmc170 SSR markers, the sequence of which is presented in Table 1. Conditions for the amplification reaction were described previously (Lindsay et al. 2008a, b).

Currently, modern technologies of molecular DNA markers contribute to the effective search for the resistance genes. Using these methods allows identifying specific DNA fragments that are closely linked to specific genes affecting salt tolerance of wheat.

The main gene *Nax1* was mapped as a QTL to the long arm of chromosome 2A of durum wheat Line149, tightly linked to flanking molecular markers, gwm312 and wmc 170 (Lindsay et al. 2004).

These tightly linked markers can be used to the introgression of *Nax* genes into elite varieties to improve their salt tolerance by means of marker-assisted selection. This technique can accelerate breeding by reducing the time to develop new cultivars (Landjeva et al. 2007).

Table 1 Primer sequences for the markers linked to the Nax1 locus

DNA marker	Forward primer (5′→3′)	Reverse primer (5′→3′)
gwm312	ATGGCATGATGCACGTAGAG	ACATGCATGCCTACCTAATGG
wmc170	ACATCCACGTTTATGTTGTTGC	TTGGTTGCTCAACGTTTACTTC

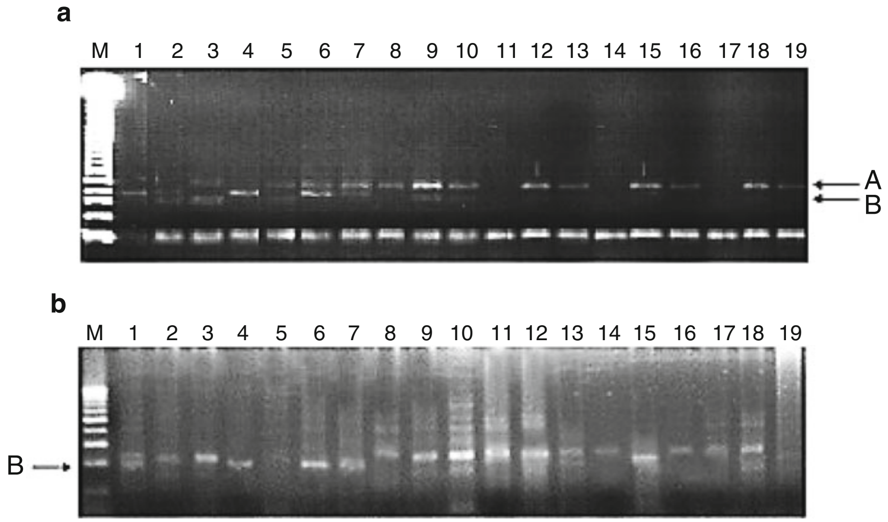

Fig. 1 The results of DNA amplification in durum wheat varieties (**a**) with the gwm312 primer and (**b**) with the wmc170 primer. M, 50 bp (**a**) and 100 bp; (**b**) DNA ladders. A, recessive; B, dominant alleles; lanes 1 to 19, the wheat varieties Barakatli 95, Alinca 84, Garagylchyg 2, Garabag, Tartar, Shiraslan 23, Sharg, Vugar, Shirvan 3, Shirvan 5, Mirvari, Ag bugda, Mirbashir 50, Tartar 2, Gyrmyzy bugda, Yagut, Turan, Mugan, and Kakhraba, respectively

In this study, 19 samples of tetraploid wheat plants were analyzed with the primer pairs gwm312 and wmc170. As seen in Fig. 1a, the studied samples are polymorphic microsatellite repeats on gwm312. Amplification of DNA samples with the primer pair to the gwm312 locus allowed identifying a recessive (A) and a dominant allele (B). The article (Lindsay et al. 2008a, b) indicated that the *Nax1* gene was linked to the allele B of 200 bp. In our studies, this allele has been amplified in the Barakatli 95, Garabagh, Sharg, Shiraslan 23, and Gyrmyzy bugda varieties. In this case, two of them, Barakatli 95 and Garabagh, are homozygous forms for this allele. In the Gyrmyzy bugda, Sharg, and Shiraslan 23, heterozygous spectra have been detected, i.e., spectra in which components of two different alleles are present. Allelic differences between studied samples have been identified using amplification by the wmc170 marker (Fig. 1b).

The results of the DNA amplification with the primer wmc170 coincide with the results of PCR analysis with the primer gwm312. The target amplification fragment of 200 bp has been detected in the abovementioned varieties.

Thus, the allele of 200 bp linked to the genome *Nax1* on two markers gwm312 and wmc170 was found in the varieties Barakatli 95, Garabag, Shiraslan 23, Sharg, and Gyrmyzy bugda. These varieties may be promising for future breeding work as resources of the *Nax1* gene. The molecular markers tested in the present study might facilitate the introgression of *Nax1* gene in Azerbaijan durum wheat varieties.

7 The Assessment of Salt Tolerance Potential in Wheat Varieties by Applying RAPD-PCR Method

Research aimed to evaluate salt tolerance of local and introduced varieties of bread and durum wheat in Azerbaijan using RAPD markers. The materials for the research were 72 samples of *Triticum aestivum* L. and 40 samples of *Triticum durum* Desf. selected from the collection of the gene pool of the Azerbaijan Research Institute of Crop Husbandry (Table 2). We selected five arbitrary decameric primers which were reported previously and initiated DNA fragments associated with the locus controlling the resistance of wheat to salinity. After the amplification of the markers OPA2, OPM13, and OPF13, expected DNA fragments were absent in all the studied samples. When the primer GLE14 was applied, expected DNA fragment of 970 bp was present in all the samples that did not allow differentiating resistant and susceptible samples (data not shown). This suggests that the amplified DNA fragment is not linked to the resistance trait in the tested collection. Thus, the results showed the absence of the efficiency of abovementioned four RAPD markers in the presented collection of samples. From the five tested RAPD primers, only OPZ09 (5′'CACCCCAGTC3′) proved to be informative for the differentiation of resistant and susceptible wheat samples. Examples of profiles obtained using primer OPZ09 are shown in Figs. 2 and 3.

It is evident that among the products of the amplification of the given primer, a polymorphic amplicon of about 590 bp appears which is characteristic for the resistant genotypes. Our results are similar to results obtained by Weng and Chen (2002), who used this marker for their population. This fragment was detected in 39% samples of bread and 27% samples of durum wheat genotypes (Table 2).

Thus, after analyzing all used markers, we found that only one of them, namely, OPZ09, is suitable for the assessment of salt tolerance potential of the studied collection. These data suggest that this marker may be associated with a gene that controls the traits of salt-tolerant wheat. The data allow us to consider RAPD analysis as a promising method to distinguish genotypes for economically important traits. It is known that the RAPD analysis can serve as an express method of detecting genetic polymorphism and a source of unique locus-specific markers, which is especially important for genetic diversity. Especially, the PCR method using RAPD primers is one of the most effective methods for molecular screening of samples (Williams et al. 1990). Important advantages of the RAPD method are the ability to perform simultaneous tests with a large number of loci and conduct a global comparison of the genomes of plants to search for the differences. This advantage of the RAPD analysis is used for searching markers linked to the genes of interest. A huge number of RAPD markers were obtained to identify loci associated with the quantitative traits, so-called QTL.

Table 2 Results of screening of the marker OPZ09 (590 bp) in genomes of different wheat varieties: "+" marker is present; "–"marker is absent

Genotypes	OPZ09 (590 bp)	Genotype	OPZ09 (590 bp)
T. aestivum L.			
Azamatli 95	+	Ruzi 84	–
Murov	+	Murov 2	+
Saratovskaya 29	–	Gunashli	+
Gyrmyzy gul	–	Gobustan	+
Akinchi 84	–	Layagatli 80	+
Saba	–	Aran	+
Shaki 1	–	Shafag 2	–
Sonmaz	–	Agali	+
Farahim 2012	–	Bezostaya	+
Baba 75	–	Gonam	+
Fatima	–	Taraggi	–
Zirva 85	–	Tale	–
Nurlu 99	+	Dagdash	+
Yegana	+	Mirbashir 128	+
Ugur	–	Bayaz	–
Giymatly 2/17	+	Pirshahin	–
Azari	+	Ni477	–
130/21	–	130/32	–
Parvin	–	Gyzyl bugda	–
Parzivan 1	–	Parzivan 2	+
Gilavar	–	Xazri	–
Mironovka	–	Bogdanka	+
Mahmud 80	–	Marxal	–
№4 Pactole	–	№13 F0F02N7N6	+
№14 D8 sechma	–	№15 S4	–
№16 AYTSİR5081	–	№17 first IWWYT-IR	–
№18 3RBWYT	–	№19 15th FAWWON-IR	+
№20 S3	+	№21 F02 N208	+
№22 F0$_2$N2N308	+	№23 S1	+
№24 DDN$_2$	–	№25 THN1	–
№26 F02 N1109	+	№28 30 ESWYT	–
№29 42 IBWSN	+	№32 SFO7N4	–
№33 42 IBWSN	+	№34 17th FAWWON-IR	+
№35 17th FAWWON-IR	–	№36 17th FAWWON-IR	–
№37 17th FAWWON-IR	–	№39 13th FAWWON-IR	–
№44 17th FAWWON-SA	–	№45 S5	–
T. durum Desf.			
Barakatli 95	–	Gyrmyzy bugda	–
Garagylchyg 2	–	Shiraslan 23	+
Tartar	–	Alinca 84	+
Shirvan 3	–	Shirvan 5	–

(continued)

Table 2 (continued)

Genotypes	OPZ09 (590 bp)	Genotype	OPZ09 (590 bp)
T. aestivum L.			
Garabag	+	Yagut	–
Turan	–	Mugan	+
Ag bugda	+	Kakhraba	+
Mirvari	–	Sharg	–
Vugar	+	Mirbashir 50	–
Tartar-2	–	№ 68 33rd IDYT-MD	–
№ 69 33rd IDYT-MD	–	№ 70 33rd IDYT-MD	–
№ 71 SFO_8N_{66}	–	№ 72 34th IDON-MD	–
№ 73 34th IDON-MD	–	№ 74 34th IDON-MD	–
№ 75 34th IDON-MD	–	№ 76 34th IDON-MD	–
№ 77 34th IDON-MD	+	№ 78 34th IDON-MD	+
№ 79 34th IDON-MD	–	№ 80 34th IDON-MD	–
№ 81 34th IDON-MD	–	№ 82 34th IDON-MD	–
№ 83 34th IDON-MD	+	№ 84 34th IDON-MD	–
№ 85 34th IDYT-MD	–	№ 86 34th IDYT-MD	–
№ 87 34th IDYT-MD	+	№ 88 34th IDYT-MD	–

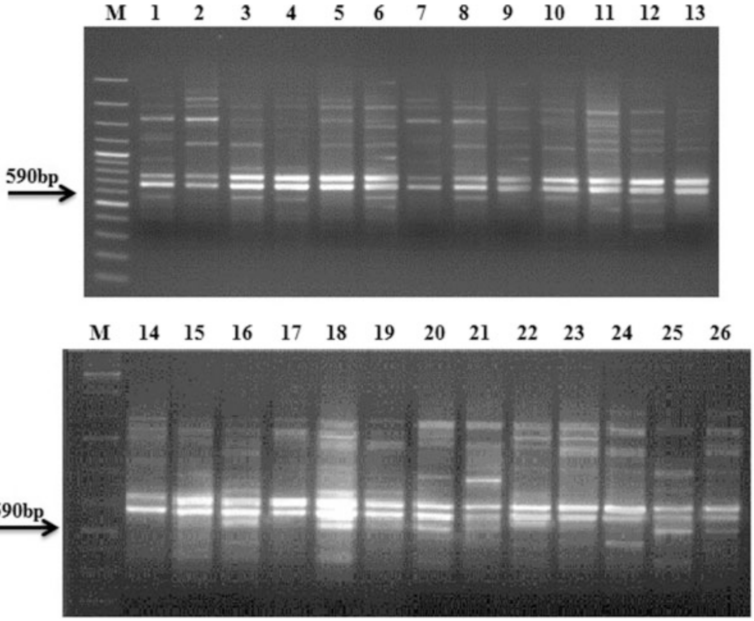

Fig. 2 RAPD profiles of bread wheat genotypes with primer OPZ09. M, 100 bp DNA ladder. 1, Azamatli 95; 2, Ruzi 84; 3, Murov; 4, Murov 2; 5, Saratovskaya 29; 6, Gunashli; 7, Qyrmyzy gul 1; 8, Gobustan; 9, Akinchi-84; 10, Layagatli 80; 11, Saba; 12, Aran; 13, Shaki1; 14, Shafag; 15, Sonmaz; 16, Agali; 17, Farahim 2012; 18, Bezostaya; 19, Baba 75; 20, Gonam; 21, Fatima; 22, Taraggi; 23, Zirva 85; 24, Tale 38; 25, Nurlu 99; 26, Dagdash. Arrow shows ~ 590 bp band present in salt-tolerant (absent in others) genotypes

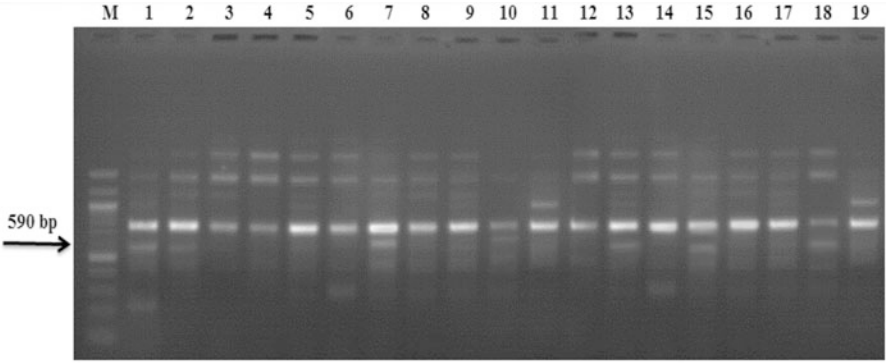

Fig. 3 RAPD profiles of durum wheat genotypes with primer OPZ09. M, 100 bp DNA ladder. 1, Alinca 84; 2, Garabag; 3, Barakatli 95; 4, Gyrmyzy bugda; 5, Garagylchyg 2; 6, Yagut; 7, Ag bugda; 8, Tartar; 9, Tartar 2; 10, Mugan; 11, Mirbashir 50; 12, Sharg; 13, Shiraslan 23; 14, Mirvari; 15, Kakhraba; 16, Shirvan 3; 17, Shirvan 5; 18, Vugar; 19, Turan. Arrow shows ~ 590 bp band present in salt-tolerant (absent in others) genotypes

8 Validation of QTL for the Flag Leaf Senescence in Wheat

High temperature and drought stress are the main factors affecting grain yield and leaf senescence in wheat. Leaf senescence is a biological and physiological event which occurs at the leaf development level and lasts until the death of the plant. It causes significant changes in the cellular, tissue, organ, and organism levels. The environmental factors such as high or low temperature, drought, ozone, nutrient deficiency, pathogen infection, and shading, etc. impact on leaf senescence. Furthermore, it is an active and controlled degeneration process, which leads to great changes in cell structure, metabolism, and gene expression. The most obvious modification in cell structure is the disruption of the chloroplast, the organelle that accounts up to 70% of the leaf protein. Leaf senescence is a combined response of leaf cells to age information and other internal and environmental signals (Lim et al. 2007). The upper three leaves and basically flag leaf which is located at the top of cereals have been identified as the main sources of the photo-assimilate gathered in the grain. In wheat (*Triticum aestivum* L.), flag leaf senescence is closely associated with periodic redistribution of resources from the source to the sink during the grain filling (Verma 2003). Wheat leaf photosynthesis involves about 30–50% of assimilates for grain filling (Sylvester-Bradley et al. 1990), and the rate of senescence is the characteristic pattern for determining product potential.

The main purpose of this work was to identify QTL for flag leaf senescence under drought stress using RAPD marker. Fifty-seven wheat genotypes collected in the gene pool of the Research Institute of Crop Husbandry acted as research objects. Thirty-eight of them were bread wheat, and 19 were durum wheat genotypes. Plants were cultivated under field conditions. RAPD marker OPH13

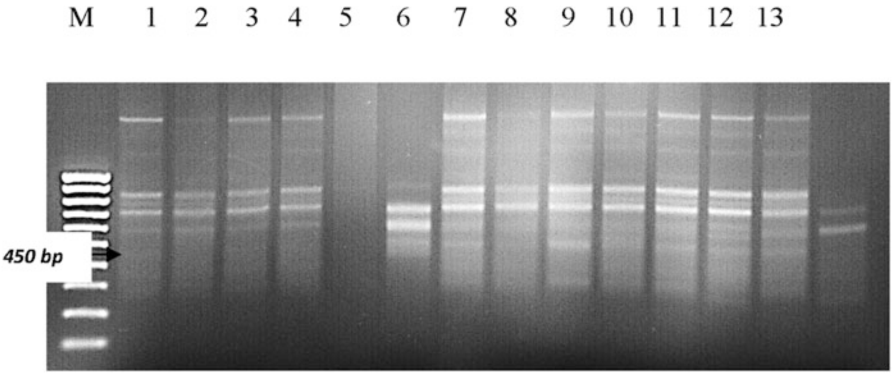

Fig. 4 PCR profiles of wheat genotypes for RAPD OPH13. M, 100 bp DNA ladder. 1, Gilavar; 2, Sevinj; 3, Gyzyl bugda; 4, Garabagh; 5, Garagylchyg 2; 6, Yagut; 7, Shirvan 3; 8, Tartar; 9, Parvin; 10, Saba; 11, Ugur; 12, Aran; 13, Shiraslan 23. Arrow shows ~ 450 bp band

(5′GACGCCACAC3´) linked to the QTL for flag leaf senescence (Milad et al. 2011) was used for the screening (Fig. 4).

As can be seen in Table 3, RAPD OPH13 gives a positive result in 46 genotypes; this is approximately 81% of all genotypes used for this analysis. To put it in more detail, 450 bp diagnostic fragments were identified in 31 bread wheat and 15 durum wheat genotypes. This result shows that there is a gene locus that provides physiological rejuvenation of the flag leaf, which is an indicator of the resistance to drought stress in those genotypes. Amplification products were absent in 11 genotypes: 7 samples among them were bread wheat; the remaining 4 were durum wheat.

Wheat flag leaf has a key role during photosynthesis in absorption solar energy, and, therefore, researching of flag leaf senescence is one of the main parameters to provide high productivity. Leaf senescence is induced not only by hormonal factors due to plant aging, external environmental factors, such as high temperature and drought, can only be the reason for premature senescence (Chandler 2001). Biochemical and physiological events lead to leaf senescence, which is the final stage of leaf development. In wheat flag, leaf senescence occurs when redistributing resources from the source to the sink during grain filling. The onset and rate of senescence are main determinants of yield potential (Evans 1993) because flag leaf photosynthesis in wheat contributes about 30–50% of the assimilates for grain filling (Sylvester-Bradley et al. 1990). Four classes of late senescence or "stay green" were described by Thomas and Smart (1993). Two of these classes relate to the delayed onset of senescence or slower rate in progress of senescence, and the remaining two relate to cosmetic effects that lack the photosynthetic capability. There were some reports on the inheritance of flag leaf senescence in wheat under optimal conditions, where additive gene effects were demonstrated (Simon 1999). It was found that delayed onset of leaf senescence in sorghum (*Sorghum bicolor* L.) (Borrell et al. 2000a, b), maize (*Zea mays* L.) (Baenziger et al. 1999), and durum wheat (*T. durum* L.) (Benbella and Paulsen 1998; Hafsi et al. 2000) increased plant productivity under

Table 3 Results of PCR analysis using RAPD markers OPH13. [+], presence of the expected locus; [−], absence of this locus

Genotypes	OPH13 (450 bp)	Genotypes	OPH13 (450 bp)
T. aestivum L.			
Parvin	+	Dagdash	+
Gilavar	−	Giymatli 2/17	+
Saba	+	Farandole	+
Layaqatli 80	+	Saratovskaya 29	+
Bayaz	+	Tale 38	+
Mahmud 80	+	A2	+
Murov 2	+	Miranovka	+
Pirshahin	+	Ruzi 84	+
Aran	+	1st WWEERYT	+
Ugur	+	Mirbashir 128	+
Zirva 85	+	Renan	+
Nurlu 99	+	11th FAWWON	−
№97 12th FAWWON	−	Gyrmyzy gul 1	+
№50 4th FEFWSN	−	Akinchi 84	+
Parzivan	−	Azamatli 95	+
Fatima	+	Murov	+
Shaki 1	+	Sevinj	−
Farahim 2012	+	Gyzyl bugda	−
Qualite	+	Fransa	+
T. durum Desf.			
Shirvan 3	−	Tigre	+
Mirvari	+	Gyrmyzy bugda	+
Turan	+	Garabagh	−
Vugar	+	Sharg	+
Tartar	+	Ag bugda	+
Yagut	+	Kakhraba	+
Mirbashir 50	+	Garagylchyg 2	+
Mugan	+	Shiraslan 23	−
Asgaran	+	Sarychanak 98	+
Barakatli 95	−		

water-stressed conditions. In sorghum, a slower rate of senescence was also associated with increases in genetic yield under drought (Borrell et al. 2000a, b).

It is necessary for plant breeders to understand the genetics of leaf senescence for increasing yield under drought. Moreover, this would allow the scientist to elucidate how genes and biochemical pathways controlling leaf senescence are regulated.

9 Identification of HSP16.9 Gene Using an Allele-Specific Primer

Nowadays extreme temperature becomes a frequent and long-lasting process than it was in recent years. It adversely affects plant pollination and reproductive processes, hampers seed germination, and decreases moisture level (Klein et al. 2007; Sacks and Kucharik 2011). High temperature causes water loss which leads to growth reduction. Another reason for growth reduction is decreasing of net assimilation rate (NAR) (Hasanuzzaman et al. 2013). Extreme heat can also cause cellular damage or fatal outcome of the whole plant. In the germination stage of growth, plants are more sensitive to heat stress. The high temperature in some plant species leads to significant prolongation of stems; expanding of leaves also reduces total biomass. Reduced numbers of tillers were observed in wheat plants under heat stress conditions. In order to survive in these conditions, plants evolved molecular, biochemical, and physiological response mechanisms. Plant response to heat stress alters with the degree and duration of stress also depends on plant species. Heat stress influences in different ways on membrane and protein stability and RNA species and also affects enzymatic reactions in a cell by creating metabolic disbalance. During heat stress, as a defense mechanism, plants close their stomata to stop water loss which leads to decreasing transpiration level. Another defense mechanism is the root growth of more moisture parts of soil. Plants exposed to a high temperature usually are impaired and attract pests and diseases, and that is why immature fruit or seeds can drop before maturing.

HSP is a family of proteins that are elaborated by cells as a response to high temperature. HSP synthesis is a non-specific cellular response to stress, and according to modern reviews, there was not found any kind of stress at which the production of HSP did not occur. These proteins were identified almost in all organisms from primitive bacteria up to humans (Bharti and Nover 2002). Regardless of stress conditions, they are produced in all cellular nuclear and major intracellular structures (cytoplasm, nucleus, endoplasmic reticulum, mitochondria) and even account for about 2% of all cellular proteins. In cells exposed to heat shock, the content of these proteins can reach up to 20% of all cellular proteins.

In wheat genotype, exposed to high temperature, groups of low-molecular-weight HSPs were identified (Nguyen et al. 1994). The main goal of the present study was to determine the presence of HSP16.9 gene in the genome of local wheat varieties. An allele-specific primer pair indicated in Table 4 was used for HSP16.9 gene screening.

Table 4 Primer sequences for the markers linked to the HSP16.9 gene

DNA marker	Nucleotide sequences (5′ → 3′)	Expected fragment, bp
HSP16.9F	CAGCAATCAACACCACGATG	290
HSP16.9R	TGCCACTTGTCGTTCTTGTC	

Table 5 Results of the PCR analysis for HSP16.9 gene. [+], presence of the expected locus; [–], absence of this locus

Genotypes	HSP16.9 (197 bp)	Genotypes	HSP16.9(197 bp)
T. aestivum L.			
Dagdash	+	Pirshahin 1	+
Gyrmyzy gul 1	–	Parzivan 2	+
Sevinj	–	Gyzyl bugda	–
Fatima	+	1st WWEERYT4	+
11th Fawwon N22	+	12th Fawwon	+
Farandole	+	Azamatli 95	+
Azeri	+	4th FEFWSN	+
Parzivan 1	–	Murov 2	+
Tale 38	+	Qualite	+
Nurlu 99	+	Gunashli	+
Taraggi	+	Ruzi 84	+
Shaki 1	+	Ugur	+
Agali	+	Mirbashir 128	+
Renan	+	Aran	–
Saratovskaya 29	+	Farahim 2012	–
Zirva 85	+	Shafag 2	–
Layagatli 80	+	Fransa	–
Murov	+	A2	+
T. durum Desf.			
Sharg	–	Shiraslan 23	+
Mirbashir 50	+	Vugar	–
Barakatli 95	–	Ag bugda	+
Gyrmyzy bugda	–	Tigre	+
Shirvan 3	+	Garagylchyg 2	–
Alinja 84	+	Turan	+
Kakhraba	+	Mugan	–
Garabagh	+		

The objects of the screening were 51 genotypes, including 36 of bread and 15 of durum wheat genotypes (Table 5). In PCR profiles of 73% genotypes (9 of them are durum and 28 bread wheat genotypes), 197 bp fragments were detected (Fig. 5), suggesting the presence of the gene HSP16.9 in germplasm of these genotypes. In 27% of genotypes (6 samples of durum and 9 of bread wheat genotypes), the expected fragment was not amplified.

In plants HSPs are divided into five classes according to their molecular weight and activity: HSP100, HSP90, HSP70, HSPs60, and small heat shock proteins (sHSPs) with the molecular weight of 15–42 (Schlesinger 1990; Schöffl et al. 1998; Kotak et al. 2007; Al-Whaibi, 2011). Another survey (Gupta et al. 2010) classified HSPs based on their molecular weight and amino acid sequence. More than 20 types of HSPs were identified in higher plants (Vierling 1991). One of them

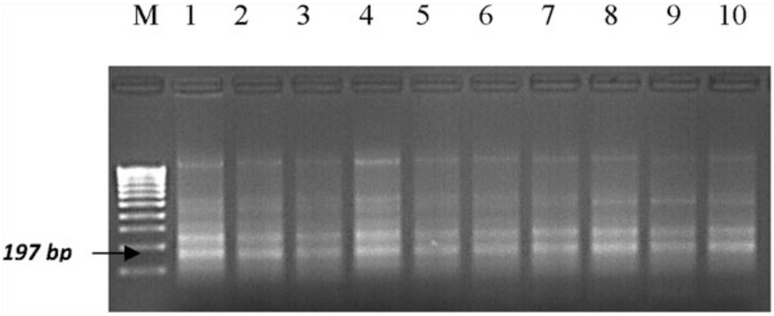

Fig. 5 PCR profiles of wheat plants for HSP16.9 gene. M, 100 bp DNA ladder. 1, Dagdash; 2, Farandole; 3, Azeri; 4, Tale 38; 5, Nurlu 99; 6, Garabagh; 7, Ag bugda; 8, Tigre; 9, Agali; 10, Renan; 11, Zirva 85; 12, Layagatli 80; 13, Murov. Arrow shows ~ 197 bp band

is the HSP16.9 gene (Garg et al. 2012). Under physiological conditions, HSPs were detected in stress periods, including drought, salinity, high temperature, etc. (Löw et al. 2000; Hamilton and Heckathorn 2001; Scharf et al. 2001; Zhang et al. 2008). It suggests that abundance in variety of HSPs intends the adaptation of plants to stress conditions (Waters et al. 1996).

The main role of HSPs is to function as molecular chaperones. Chaperones are the proteins which regulate protein folding, assist to newly synthesized proteins achieve their native state, they prevent protein non-specific aggregation, and take part in protein refolding under thermal stress conditions (Feder and Hofmann 1999; Schulze-Lefert 2004; Panaretou and Zhai 2008; Gupta et al. 2010). Presence of a carboxyl terminal called heat shock domain is a characteristic pattern of these proteins (Helm et al. 1993). There are six classes of genes that encode HSPs. The classification was according to sequence similarity and the location of these proteins in the cell. In cytoplasm, two classes of proteins were identified which are encoded by two group of genes (Vierling 1991; Waters et al. 1996). Under non-stress conditions, expression of these genes is limited and appears at embryogenesis, germination stage of development, also during the development of pollen grains, and fruit ripening (Sun et al. 2002). Expression of these genes is regulated by proteins called heat shock factors (HSFs) which are present in the cytoplasm in an inactive form. These factors are the transcriptional activators for HSPs (Baniwal et al. 2004; Hu et al. 2009).

10 Conclusion

The major aim of wheat breeding programs is developing high productive wheat cultivars tolerant to abiotic stresses. Understanding the genetic, physiological, and molecular basis of the traits including interactions among the different component traits with the environment is required when breeding for complex traits (Dubcovsky

2004; Tester and Langridge 2010). Problems associated with genotype/environment interactions may be solved by marker-assisted selection, which contributes to the improvement of the selection efficiency and combining different tolerance traits into a single efficient genotype. Molecular markers are a useful tool in plant breeding as they are closely linked with target alleles and help to identify the tolerant genes without field evaluations. It also allows screening a lot of breeding materials at early growth stages and in a short period of time (Barakat et al. 2011).

The search is required for efficient donors in durum and bread wheat collections as well as among other species and genera of cereals in order to select and improve economically useful indices of perspective wheat varieties regionalized in Azerbaijan. As the promising approach for the solution of this problem, molecular markers closely linked to the genes that control the traits important for selection were used. These markers will allow us to estimate the genetic potential of varieties to abiotic stress and reveal resources of genes for used in breeding programs.

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Omics Approaches for Developing Abiotic Stress Tolerance in Wheat

Heba T. Ebeed

Contents

Abstract Wheat yield is greatly influenced by the environmental factors such as drought, salt, and high or low temperature. Understanding the molecular mechanisms of stress tolerance effectively requires information at the genomic, proteomic, and transcriptomic levels. The continuous progress in the analytical and the experimental technologies resulted in the development of many experimental approaches that can identify the cellular molecules. These technologies called "omics technologies." Most of them are high throughput with very fast rates of data generation and huge outputs. They are based on bioinformatics, statistical and computational tools. These technologies have made obvious contributions to the current progressions in our understanding of plant biology as a whole or in particular plant stress tolerance. In this chapter, I will present the foremost omics technologies in the view of conventional and modern approaches being used to dissect abiotic stress tolerance in wheat.

Keywords Abiotic stress · Genome · Metabolome · Proteome · Transcriptome · Wheat

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1 Introduction

Wheat is an important cereal crop which provide proteins, energy, minerals, and vitamins to most of the world population. The wheat productivity declines mainly due to yellow rust, drought, and heat stresses associated with climate change. The major challenge for scientists in the current century is to increase the crop production in those areas with a highly variable climatic change (Mahajan and Tuteja 2005). Increasing crop productivity demands extensive programs of breeding for the development the local cultivars (Grainger and Rajcan 2014). The widely used approach is the direct selection for yield stability based on multilocation trials adapted to adverse environmental conditions. This approach is a time-consuming, labor-intensive process and more challenging for abiotic stress-related traits because of low heritability and high influence of various environmental conditions (Manavalan et al. 2009). The alternative option is the planned marker-assisted breeding which can proficiently accelerate the development of tolerant cultivars; nevertheless, it also requires knowledge about genomic loci controling the traits and the availability of related molecular markers (Xu et al. 2012b). The progress in the molecular markers has been accelerated with the accessibility of sequenced genomes and organelles in plants. The uncompleted wheat genome sequence and genome complexity make understanding and identifying the function of many genes challenging. Thus, making it difficult to characterize and manipulate complex traits of interest for the development of improved varieties. Genetic resources have been used for crop improvement efforts in cases where information regarding complex traits are not readily known, the information may then be inferred from closely related species (Shewry 2009).

Omics is a multidisciplinary study that refers to studies in applied biology that end with the term “omics”, including but not limited to genomics, transcriptomics, proteomics, metabolomics, epigenomics, nutrigenomics, metagenomics, and various others. These studies are mainly performed through the application of several high-throughput technologies that mainly involve qualitative and/or quantitative detection of novel or previously identified genes, transcripts or transcription factors, proteins, and metabolites and other parameters through genomics, transcriptomics, proteomics, and metabolomics, respectively (Kato et al. 2011; Kulski 2016).

The era of omics technologies has largely added to our current knowledge of biological functions of many traits in various crops including wheat. This has led to development of crops with improved traits of interest. Consequently, there is a need to merge selected omic technologies to advance our current understanding of many important traits. The integration of these technologies would aid in identifying novel genes or pathways that could be activated to improve desired traits in wheat. This chapter briefly describes about the latest investigations on wheat omics and pinpoints the progress and challenges encountered in attempts to improve wheat traits.

2 Wheat and Abiotic Stresses

Wheat is grown globally under spring, winter, and facultative environmental habitats. Modern wheat cultivation started 9000-11,000 years ago in the Middle East. Because of increased geographical farming, bread wheat became a common staple food from east to west. Wheat resembles the sole source of energy for nearly 35% of the world population (Dreisigacker 2005). Wheat has two important characteristics that allow it to be blended with rye or oats flours for specific purposes, these are its gluten content and low amylase activity (Tatham and Shewry 2008). Wheat varieties are varied in hardness, kernel colors, and their planting time; however, each wheat class has its own characteristics suitable to milling, baking, or other food use (Taylor et al. 2005). Wheat is classified into six groups such as hard red winter wheat, hard red spring wheat, hard white wheat, soft white wheat, soft red winter wheat and durum wheat.

Drought, salinity, low or high temperatures, floods, pollutants, and radiation are environmental factors delimit wheat yield augmented by the adverse effect on growth, metabolism, and yield (Lawlor and Cornic 2002). Under field conditions responses of wheat plants to a certain type of abiotic stress can be synergistically or antagonistically modified by the superimposition of other stresses. Mainly, salinity and drought are two major factors that limit crop yield (Misra et al. 2002). The most promising fact is the sufficient genetic variation in the wheat gene pool that can be ensured for continued development of wheat adaptation to abiotic stress (Trethowan and Mujeeb-Kazi 2008).

Plants respond to environmental factors in time-course phases. The stress-responsive genes can be classified into early and delayed responsive genes. The early responsive genes are induced quickly and transiently, whereas the delayed responsive genes are activated more slowly, and their expression is continued. The early responsive genes encode transcription factors that activate downstream delayed response. This induction does not require new protein synthesis, because all signaling components are already in place. There is an evidence indicating that some abiotic stress types as salt or drought stress induce a complex response and complex gene regulation.

All abiotic stresses never work separetely but various environmental factors interact and contribute at varying degrees to the overall stress. The transduction pathways for stress responses are likely to be very complicated and will involve signalling molecules such as ABA. Thus, the precise mechanism(s) by which plants respond to drought or salinity remains vague. Therefore, engineering genes that protect and maintain the function and structure of cellular components can improve tolerance to stress. At the molecular level, most of the changes are likely the result of alterations in the expression of genes. Thus, it is essential to identify the relevant genes and characterize their regulation in response to stress (Liu and Baird 2003).

The molecular data based on the high-throughput technological are quite powerful, comprehensive and may be complex in other cases. This makes the integration of omics data challenging if the experimental analyses were not designed to contribute to downstream data analyses. The integration of omics data would provide a comprehensive overview of data on various biological variables, herewith allowing researchers to have a comprehensive manner in which they could study relationships among biological variables within a biological system. Thus, it would be possible for researchers to predict the quantitative and qualitative effect of a desired component in the gene network or pathway within a biological system. Also, these technologies would enable researchers to determine which gene region could be targeted to improve the levels of a desirable metabolite without affecting other biological systems.

3 Genomic Resources for Developing Abiotic Stress Tolerance in Wheat

For many years, there were several efforts to sequence and assemble the hexaploid (AABBDD) bread wheat genome, *Triticum aestivum*. The first try to sequence the wheat genome published in 2012 by Brenchley et al. (2012), by using an earlier generation of sequencing technology and only assembled 5.42 billion bases (Gbp), which approximately resemble one-third of the genome. The second try was two years later when the international wheat consortium published the results of one chromosome sequence using deep coverage in 100-bp Illumina reads (International Wheat Genome Sequencing 2014). This gave rise to a genome assembly of 10.2 billion bases of sequence which approximately resembles two-thirds of the wheat genome. The third assembly of wheat genome was published 2017 and estimated to represent 78% of the genome (Clavijo et al. 2017). This assembly contained 12.7 billion bases of sequence, but it was highly fragmented. The wheat genome complexity and the challenge for assembly not only owing to its large size (5 times the size of the human genome) but also to its very high proportion of relatively long, repetitive repeats (Li et al. 2004). Because these repeats are much longer than the length of Illumina reads, tries to assemble the genome using Illumina data had been unable to be resolved.

Another major challenge in assembling the wheat genome is that polyploidy, because its three genome components, wheat A, B, and D, each comprising seven chromosomes and share many regions of high similarity. Genome assembly programs are thus faced with a doubly complex problem; which is repetitiveness and existence of each chromosome in six copies with varying degrees of similarity. All data for this assembly were generated from the Chinese spring variety (CS42, accession Dv418) of *T. aestivum*, which is highly inbred and thus nearly haploid, effectively reducing the number of copies of each chromosome from six to three.

The true genome size of bread wheat has been estimated by flow cytometry to be close to 16 Gb (Arumuganathan and Earle 1991); based on this estimate, assembly contains 96% of the genome sequence (Zimin et al. 2017). Here are some of the most powerful genomic resources that have been used for developing abiotic stress tolerance in wheat.

3.1 Molecular Markers Selection

Molecular markers are specifically important for genomic traits that are difficult to tag such as resistance to pathogen or insects, tolerances to abiotic stresses, quality parameters and quantitative traits. Recent development in genomic knowledge and technology has provided new horizons and basis for genetic improvement of complex traits such as drought and salt tolerance. The merging of genomic tools with molecular assisted selection (MAS) can be used to characterize and select the preferred genes in breeding populations at a much faster rate than by classical breeding. Too many molecular markers are now available to detect polymorphism, each of which has advantages and disadvantages. These are RFLP (restriction fragment length polymorphism), RAPD (random amplified polymorphic DNA), AFLP (amplified fragment length polymorphism), SSR (simple sequence repeat), SNP (single nucleotide polymorphism), and STS (sequence-tagged sites).

RFLP is the basic molecular markers detect polymorphism on the differences in restriction fragment length (Botstein et al. 1980). These differences may be due to mutations or insertion-deletion, which can create or delete restriction endonuclease recognition sites. Until recently, progress in MAS for wheat was slowed by the limited availability of genomic data, but advances in genotyping techniques and DNA sequencing have now produced genome datasets that have been used to design sequence-based simple sequence repeats (SSRs) and SNP markers (Filiz et al. 2009; Akpinar et al. 2017). These markers can be used across a wide range of related species. In wheat mapping probes from wheat, rye, barley, and oats are widely used. Further, wheat sequences successfully hybridize to genomic DNA from other grass species such as rice, maize, and sorghum. RFLPs have disadvantages such as inefficiency due to low multiplicity ratio, low genotyping throughput, high labor intensity, and the requirement for the large amounts of high-quality template DNA.

RAPD is a PCR-based technique that was generated by using random primers in the range of 10–20 nucleotides to detect complementary sites across relatively short distances within the genome (Williams et al. 1990). While AFLP assays are based on a combination of restriction digestion and PCR amplification. One of the principal applications of AFLP is the genetic mapping, either in map construction or identifying linkages using bulk segregate analysis (Vos et al. 1995). AFLP also is a robust and reliable technique that is rapidly becoming the preferred molecular technique established across the vast majority of cereals. AFLP polymorphism observed in durum wheat (Lotti et al. 2000) and in bread wheat (Chalmers et al. 2001). AFLP loci appear to be evenly distributed across the A and B genomes, but there is a significant reduction in the level of polymorphisms that detected in the D genome of hexaploid wheat (Röder et al. 1998).

SSR markers, or microsatellite, are short mono-, di-, tri-, and tetranucleotide tandem repeats although more complex repeats have been detected. SSRs are highly abundant and randomly dispersed throughout most genomes, and many SSRs are available for wheat (Röder et al. 1998). SNPs are increasingly used for germplasm characterization and gene mapping as they provide cost-effective, rapid, and high-throughput genotyping (Akpinar et al. 2017). As SNPs are codominant, sequence-tagged, and highly abundant, they are suitable for the dissection of complex traits using highly multiplexed marker microarrays such as the Affymetrix GeneChip (Winfield et al. 2016).

3.2 Quantitative Trait Loci (QTL) Mapping

Genetic fingerprinting, linkage mapping, and QTL mapping are marker-based applications that have become more progressed with the accessibility of different genotyping platforms. Accordingly, too many studies have been made to recognize QTL for abiotic stress tolerance in wheat (Table 1) in spite of the complex inheritance of abiotic stress tolerance that has identified unstable QTL across different environmental conditions. Further imposition of QTL information for candidate gene identification or marker-assisted breeding has become more difficult due to this complexity. Statistical tools such as “Meta-QTL analysis” have been advanced that gather QTL data from different experiments together on the same linkage map for identification of accurate QTL region (Deshmukh et al. 2012) using a statistical technique to analyze the data on the same topic; however they are still required exclusively for abiotic traits (Goffinet and Gerber 2000). Meta-analysis has been used to study different agronomically important traits in various crop species. In wheat, meta-analysis has been applied to study the *Fusarium* head blight resistance (Liu et al. 2009; Löffler et al. 2009), identification of quantitative traits such as grain protein content, preharvest sprouting tolerance, grain weight (Pushpendra et al. 2007), seed dormancy (Tyagi and Gupta 2012), earliness traits (Hanocq et al. 2007), and QTL related to yield and yield components (Zhang et al. 2010).

Table 1 QTL studies performed for different traits in wheat

No	Trait	Type[a]	References
1	ABA accumulation under drought stress	F4	Barakat et al. (2015)
2	Drought resistance by several physiological traits	RIL	Kumar et al. (2012)
4	Growth transpiration and yield under stress	RIL	Parent et al. (2015)
5	Stomatal density and size under drought stress		Wang et al. (2016a)
6	Osmoregulation under drought	RIL	Morgan and Tan (1996)
7	Stress resistance and potential yield	DH	Bennett et al. (2012)
9	Drought-responsive agronomic traits		Gahlaut et al. (2017)
10	1000 kernel weight under stress and non-stress conditions	F2:3	Nezhad et al. (2012)
11	The relationship between drought/ salinity and agronomic and physiological traits		Fan et al. (2015)
12	Yield and its components under drought	F3-F4	Golabadi et al. (2011)
13	Yield components and drought/heat responses		Acuña-Galindo et al. (2015)
14	Yield stability under drought stress	BC isolines	Merchuk-Ovnat et al. (2016)
15	Yield under drought stress	RIL	Shukla et al. (2015)
16	Flooding survival	RIL	Burgos et al. (2001)
17	Salinity tolerance	RIL	Ma et al. (2007)
18	Salt tolerance and micronutrient concentrations at seedling stage	F2	Hussain et al. (2017)
19	Seedling salinity tolerance	RIL	Xu et al. (2012a, 2013b) and Ghaedrahmati et al. (2014)
20	Frost tolerance in European wheat		Zhao et al. (2013)
21	Chlorophyll fluorescence under heat stress	DH	Azam et al. (2015)
22	Heat stress tolerance		Kumari and Maria (2018)
23	Heat tolerance for grain quality	RIL	Beecher et al. (2012)
24	Heat tolerance for several traits	BIL	Awlachew et al. (2016) and Ali et al. (2013)
25	Heat tolerance in grain filling	F1-F2-F3	Yang et al. (2002)
26	Heat tolerance in terms of spike productivity	RIL	Mason et al. (2011)
27	Heat tolerance in yield components and canopy temperature	DHL	Tiwari et al. (2013)
28	Heat tolerance in yield components over years	RIL	Mason et al. (2010)

(continued)

Table 1 (continued)

No	Trait	Type[a]	References
29	Maintaining grain filling duration under heat stress	RIL	Sharma et al. (2016)
30	Senescence under drought and optimal conditions	DHL	Verma et al. (2004)
31	Grain size and quality under nitrogen stress	RIL	Cui et al. (2016)
32	Phosphorus deficiency tolerance in seedling	RIL/ DHL	Ryan et al. (2015) and Zhang and Wang (2015)
33	Aluminum tolerance	RIL	Riede and Anderson (1996), Ma et al. (2005), Cai et al. (2008), Navakode et al. (2009) and Dai et al. (2013)
34	Copper tolerance	RIL	Bálint et al. (2007)

[a] *DHL* doubled haploid, *RIL* recombinant inbred lines, *BC* backcross, *BIL* backcross recombinant inbred lines

3.3 Whole Genome Association Studies (WGAS)

QTL mapping has limitations owing to the restricted allelic diversity and genomic resolution in the bi-parental populations. The allelic diversity can be increased to some extent by using multi-parental crosses. In contrast, whole genome association study (WGAS) or the genome-wide association study (GWAS) approach provides prospects to discover the tremendous allelic diversity existing in natural germplasm. Mapping resolution of GWAS is also higher since millions of crossing events have been accumulated in the germplasm during evolution. GWAS facilitates understanding of the genetic basis and analysis of complex genes controlling important traits such as drought tolerance. The goal of GWAS is to discern genomic regions that could either be markers, genes, or QTL associated with key agro-morphological traits for marker-assisted breeding, gene discovery, or gene introgression (Tester and Langridge 2010).

GWAS for quantitative traits like disease resistance of stem rust, powdery mildew, Fusarium head blight or nematode was reported in many studies (Arruda et al. 2016; Pariyar et al. 2016; Liu et al. 2017; Mourad et al. 2018) while GWAS mapping for abiotic stress tolerance in wheat is very limited compared to other crops. These limited studies in wheat under stressed conditions include studying of drought-tolerance breeding (Mwadzingeni et al. 2017), spike ethylene under heat stress (Valluru et al. 2017), and yield traits in durum wheat under drought and heat stress (Sukumaran et al. 2018).

4 Transcriptome Profiling for Developing Abiotic Stress Tolerance in Wheat

Plants, including wheat, respond to external environments in a very complex manner. Abiotic stress imposes a defense mechanism that develops tolerance or adapted mechanism against adversative conditions to avoid damage imposed by these stresses. The first step in stress response is stress signal recognition then the signal transduction that activate subsequent molecular, biochemical, and physiological responses (Komatsu et al. 2009; Ge et al. 2010). Understanding such responses is very effective in developing our knowledge about abiotic stress tolerance mechanism. Transcriptome profiling provides great opportunity to study the regulation of plant response and to recognize genes involved in stress tolerance mechanisms. Approaches like expressed sequence tags (ESTs) and suppression subtractive hybridization (SSH) technique have been used earlier for identifying the differentially expressed ESTs in thermotolerant wheat cultivar (Goswami et al. 2016). Then, several high-throughput techniques have been developed for transcriptome analysis due to the progress in sequencing technology. These platforms have been widely used for transcriptome profiling to analyze abiotic stress tolerance mechanisms in wheat (Table 2). Microarray is a high-throughput technology where thousands of probes representing different genes are hybridized with RNA samples. Genes expression is calculated using the hybridization signal level. The Affymetrix GeneChip representing 61 K probe sets is routinely being used for transcriptome profiling of wheat under different abiotic stresses. The microarray data represents various tissues, developmental stages, and environmental conditions are listed in (Table 2).

Cost-effective and high-throughput sequencing technologies make analyzing the transcriptomes sequencing known as RNA-seq is possible. The RNA-seq approach has several advances over the microarray technique that using the available genomic information in designing probe sets. RNA-seq does not require gene information and can identify novel transcripts and provides prospects to analyze noncoding RNAs. The relative accuracy of microarrays and RNA-seq has been evaluated using proteomics that proved that RNA-seq offers a better estimation to absolute expression levels (Fu et al. 2009). Applications of RNA-seq can be expanded further with an increased understanding of molecular regulations. RNA-seq studies on abiotic stress tolerance mechanisms in wheat are listed in (Table 2).

5 Proteomics for Developing Abiotic Stress Tolerance in Wheat

Proteomics deals with structural and functional features of all the proteins in an organism. Understanding complex biological mechanisms including the plant responses to abiotic stress is very important. During stress response, unexpected

Table 2 Major transcriptomic analysis of the abiotic stress tolerance in wheat using different technological platforms

No	Study	Platform	References[a]
1	Deep sequencing of wheat sRNA transcriptome in response to heat, light, and UV	Illumina HiSeq 2000	Ragupathy et al. (2016)
2	Comparative transcriptome analysis of wheat embryo and endosperm response to ABA and H_2O_2 stresses during seed germination	Affymetrix Wheat Genome Array	Yu et al. (2016)
3	Genome-wide study on tissue- and abiotic stress-specific miRNAs in *Triticum aestivum*	Illumina Genome Analyzer IIx	Pandey et al. (2014)
4	Differential gene expression during cold acclimation in barley, wheat, and rye	IPK *Hordeum vulgare* 12 k SEED2	GSE47882
5	Wheat freeze tolerance	Affymetrix Barley Genome Array	GSE2166
6	Wheat grain transcriptome response to high temperature	NimbleGen *Triticum aestivum* array	GSE100642
7	Aluminum stress study in wheat and wheat-rye	Agilent-022297 Wheat Gene Expression Microarray	Salvador-Moreno et al. (2018)
8	Identification of circular RNAs and their targets in leaves of *Triticum aestivum* L. under dehydration stress	Illumina HiSeq 2000 *Triticum aestivum*	Yuexia Wang et al. (2017)
9	Transcriptome analysis in nutrient deficient wheat roots	Affymetrix Wheat Genome Array	GSE61679
10	Wheat drought responses	Affymetrix Wheat Genome Array	Placido et al. (2013)
11	Transcriptome profiling of flag leaves of wheat susceptible and tolerant parents and RILs under drought	Affymetrix Wheat Genome Array	Placido et al. (2013)
12	RNA-mediated responses to cold stress in wheat thermosensitive genic male sterile line	Illumina Genome Analyzer (*Triticum aestivum*)	Tang et al. (2012)
13	Embryos of wheat seeds: temperature effect	Agilent-015520 Custom wheat 38 k array	Nakamura et al. (2011)
14	Drought stress in wheat at grain filling stage	Affymetrix Wheat Genome Array	Aprile et al. (2009)
15	Heat priming induces transgeneration thermotolerance	Affymetrix Wheat Genome Array	Botstein et al. (1980)
16	Early seed development in wheat under control and drought stress	Affymetrix Wheat Genome Array	Begcy and Walia (2015)
17	Expression data from cold-treated wheat cultivars	Affymetrix Wheat Genome Array	Winfield et al. (2009)
18	Expression profile in response to salt treatment in wheat	Wheat 11 k	Kawaura et al. (2008)

[a] GEO accession number provided for unpublished studies

levels of changes occure in the wheat proteome which can lead to different defense mechanisms. Differential expression observed at the transcriptional level need not be translated into differential amounts of protein. So, investigating the post-translational changes are important in understanding plant responses to abiotic stresses. Also, a single gene can be translated into several different proteins, and a few genes can lead to a diverse proteome. To address this, several proteomic studies have been performed to understand abiotic stress tolerance mechanisms in wheat (Table 3). Recently, a database for wheat proteome has been developed to contain reference maps of the wheat proteome that collected from several organs, tissues, and organelles (Table 3).

6 Metabolomics Advances for Abiotic Stress Tolerance in Wheat

The entire set of metabolites synthesized in plants under normal or stressed conditions is defined as the plant's metabolome, which may be viewed as the biochemical phenotype of a given plant tissue. In plants, metabolomics helps in detecting a vast array of metabolites from a single sample, thus allowing speedy and accurate analysis of metabolites. In other words, metabolomics offers a comprehensive view of cellular metabolites that participate in different cellular processes, thus representing the absolute physiological state of a cell. Therefore, metabolomics provides a better understanding of the biochemical pathways and molecular mechanisms. Metabolite profiling has become a standard tool for highly-throughput investigations such as analysis of traits as the responses to herbicides (Schauer and Fernie 2006). The complete understanding of the biological processes was not possible using knowledge of genes, transcripts, and proteins only until knowledge of metabolites that are involved becomes available. In recent years, the metabolite profiling of mutants and transgenic lines offers potential to understand the metabolic networks and to identify the underlying candidate gene(s) (Schauer and Fernie 2006; Nguyen et al. 2016). Combining the advances in metabolomics with the accessibility of whole genome sequence, genome-wide genetic alternates, and cost-effective genotyping analyses resemble exciting prospect to effectively integrate metabolomics in crop breeding programs (Schauer and Fernie 2006).

Gas or liquid chromatography-mass spectrometry (GC-MS and LC-MS), capillary electrophoresis-mass spectrometry (CE-MS), and nuclear magnetic resonance (NMR) are routinely used in plant sciences (Putri et al. 2013). Several statistical models and bioinformatics programs have been established to analyze the metabolome in an interactive means (Fernie et al. 2011; Putri et al. 2013).

More and more researchers focus on linking metabolome with genomic segments to discover genetic factors of regulatory pathways to enhance quality of crops species. Recent advances have revealed an association of genetic variants with metabolites that could be used for metabolic engineering across various plant species such as rice and tomato (Schauer et al. 2006; Kusano et al. 2007). Additionally, the genome-wide metabolomic survey of the ancestral species led to the identification of important compounds which led researchers to link the differential expression of

Table 3 Proteomic analysis of the abiotic stress tolerance in wheat using different techniques

No	Study	Technique	References
1	Quantitative proteomics of the root of transgenic wheat expressing TaBWPR-1.2 genes in response to waterlogging	Nano-liquid chromatography (LC)-MS/MS	Haque et al. (2014)
2	Tolerance to waterlogging stress	Two-dimensional gel electrophoresis	Wang et al. (2016a, b)
3	Salicylic acid-mediated growth, physiological and proteomic responses in two wheat varieties under drought stress	Two-dimensional gel electrophoresis - MALDI TOF/TOF Analyzer	Sharma et al. (2017)
4	Comparative proteomic analysis of Cd-responsive proteins in wheat roots	Two-dimensional gel electrophoresis	Yun Wang et al. (2011)
5	Characterizing physiological and proteomic analysis of the action of H_2S to mitigate drought stress in young seedling of wheat	Nano-LC-MS/MS	Ding et al. (2018)
6	Cold acclimation in under field conditions	Two-dimensional gel electrophoresis	Janmohammadi et al. (2014)
7	Proteomic analysis of wheat seed in response to drought stress	Two-dimensional gel electrophoresis	Zhang et al. (2014)
8	Comparative response to low temperature stress in two winter wheat cultivars differing in low temperature tolerance	Two-dimensional gel electrophoresis	Xu et al. (2013a)
9	Proteomic analysis of spring freeze-stress-responsive proteins in leaves of bread wheat	Two-dimensional gel electrophoresis	Han et al. (2013)
10	Comparative proteomic analysis of salt response proteins in seedling roots of two wheat varieties	Two-dimensional gel electrophoresis	Guo et al. (2012)
11	Response to salinity and drought stress	Two-dimensional gel electrophoresis	Peng et al. (2009)
12	Quantitative proteomic analysis of drought stress-responsive late embryogenesis abundant proteins in the seedling leaves of two wheat genotypes	LC-MS/MS	Li et al. (2018)
13	Physiological, proteomic, and transcriptional responses of wheat to a combination of drought or waterlogging with late spring low temperature	Two-dimensional gel electrophoresis	Li et al. (2014)
14	Proteomic analysis of leaves and roots under copper-stress conditions	Two-dimensional gel electrophoresis	Li et al. (2013)
15	Comparative proteomic analysis of grain development in two spring wheat varieties under drought stress	Two-dimensional gel electrophoresis	Ge et al. (2012)
16	Comparative proteomic analysis of flag leaves reveals new insight into wheat heat adaptation	LC-MS/MS	Lu et al. (2017)
17	Proteomic insight into the mitigation of wheat root drought stress by arbuscular mycorrhizae	Shotgun tandem MS approach	Bernardo et al. (2017)

(continued)

Table 3 (continued)

No	Study	Technique	References
18	Proteomic response to ABA in roots of drought-sensitive and drought-tolerant wheat varieties	LC-MS/MS	Alvarez et al. (2014)
19	Quantitative proteomics analysis reveals the tolerance of wheat to salt stress	LC-MS/MS	Singh et al. (2017)
20	Identification of differentially expressed heat-responsive proteins	Two-dimensional gel electrophoresis	Kumar et al. (2014)

metabolites with important cellular pathways as photosynthesis and photorespiration. Likewise, metabolic profiling of aneuploid wheat highlighted the genes regulating variation in the amino acids structure and trehalose accumulation in mature grain (Li et al. 2015).

Emerging trends of metabolomics have enabled in greater insights regarding survival mechanisms in response to abiotic stress at metabolite level. So far, metabolomics has been very limitedly exploited in clarifying the abiotic stress tolerance mechanisms/adaptation in wheat. Ullah et al. (2017) compared the metabolite profiling of seven *Triticeae* with different drought tolerance/susceptibility levels in root and leaves tissues by GC-MS technique. Additionally, the effect of different nitrogen supply on the wheat leaf metabolome during grain filling was studied (Heyneke et al. 2017). Recently, leaf metabolomic and proteomic responses to drought stress in spring-wheat were reported (Michaletti et al. 2018). Likely, the metabolic responses to drought stress was studied in tolerant and sensitive wheat genotypes by GC-MS (Guo et al. 2018).

7 Integrating Multi-omics Platforms

The recent progress in the omic platforms has generated enormous information which has been used to encourage research activities in all possible scopes. The interactome network studies aiming to reveal molecular interactions between biomolecules (nucleic acid, proteins, amino acids, carbohydrates, lipids, etc.) and expand our knowledge to the genotype-phenotype relationship. Exploitation of available information has become possible due to the computational resources that help to list, store, and analyze available data and make it easily accessible through user-friendly interfaces that called "databases". A comprehensive approach accommodating inferences from genomics, transcriptomics, proteomics, and metabolomics will allow researchers to explore the gene networks that probably would improve the current understanding of important traits, allowing us to develop new strategies for plant improvement. In this regard, several databases have been developed for wheat are listed here in (Table 4).

Table 4 Online databases exclusively developed for wheat studies generated from different omics platforms

No	Database	Features
1	Wheat protein database, http://www.wheatproteome.org/overview	Wheat sub-proteomes grouped by function or tissue
2	MASWheat, http://maswheat.ucdavis.edu/	Marker-assisted selection
3	dbWFA: A Wheat Functional Annotation Database, https://urgi.versailles.inra.fr/dbWFA/	Gene ontology, metabolic pathways, EC reactions, wheat transcription factors
4	The Wheat (*Triticum aestivum*) Transcription Factor Database	predicted transcription factors (TFs)
5	GrainGenes wEST (wheat Expressed Sequence Tag), https://wheat.pw.usda.gov/wEST/	EST, Contig, and Mapping information
6	Wheat URGI, https://wheat-urgi.versailles.inra.fr/	Gene sequence, physical maps, genetic maps, markers, QTLs, MetaQTLs, SNPs
7	Wheat genome database, http://www.wheatgenome.info/wheat_genome_databases.php	Wheat genome assembly
8	The wheat tilling database, http://www.wheat-tilling.com/	TILLING populations
9	Wheat Expression Database, https://dubcovskylab.ucdavis.edu/wheat-expression-database	RNA-seq datasets
10	WheatNet, https://www.inetbio.org/wheatnet/	Functional gene network

8 Conclusion

Different omics tools have been employed to understand how wheat plants respond to abiotic stress conditions. In wheat, genomics, transcriptomics, and proteomics have progressed but the other major omic branches like metabolomics and phenomics are still lagging behind. These omic branches are equally important to get a clear picture of the wheat biological system under abiotic stress.

A major challenge in wheat research is that research is mainly conducted independently across the world which makes it difficult to turnover data which are obtained. Consequently, this leaves a gap in several research areas where some research aspects of the same research focused and some other are left uncovered, which make obtaining a whole overview of the data generated is challenging. Thus, researchers form consolidated consortiums should allow data manipulations for other researcher. Besides, special attention should be paid to sampling omics data for analysis because different crop developmental stages display different sensitivity to drought. For example, wheat is particularly susceptible to drought during flowering time. A drought stress imposed at flowering may result in the widely variance of entries in time to flowering, thus the most "tolerant" may simply be those that flower earlier than the mean. Given the significant changes in protein composition under various abiotic stresses, proteomics can throw new insights into proteins responsible for stress acclimation in plants.

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Use of Phytohormones to Improve Abiotic Stress Tolerance in Wheat

Mahnoor Asif, Hafiz Muhammad Ansab Jamil, Malik Tahir Hayat, Qaisar Mahmood, and Shafaqat Ali

Contents

Abstract Abiotic stress like drought, salinity, heat, and UV radiation results in a reduction of crop growth and yield that threatens the food security at the global level. Different mechanisms has been developed by wheat plant to tackle these abiotic stresses and maintain their growth and yield under harsh conditions. Phytohormones are diverse group of molecules synthesized by plants like abscisic acid (ABA), ethylene (ET), and jasmonate (JA) which are found to be involved in regulation of the protective responses under various abiotic and biotic stress conditions. Exogenous application of phytohormones especially salicylic acid helps wheat crop to cope with abiotic stresses.

Keywords Abiotic stress · Phytohormones · Reactive oxygen species · Stress tolerance · Wheat growth

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1 Introduction: Abiotic Stress

Abiotic stress in plants results in the increased production of reactive oxygen species (ROS) producing oxidative stress (Fig. 1). ROS are highly toxic and reactive and results in damage to carbohydrates, proteins, lipids, and DNA. ROS consists of free radicals like O_2^-, OH^-, superoxide radicals, and hydroxyl radical and non-radical forms like singlet oxygen, H_2O_2, hydrogen peroxide, and singlet oxygen (Gill and Tuteja 2010). Plants have the ability to deal with various abiotic and biotic stresses by different mechanisms (Fujita et al. 2006). Major abiotic stresses include ozone, UV radiation, heat, salinity, drought, freezing, and chemicals that affect the productivity of crops (Fig. 1). The stress response is influenced by the development and period of stress, plant growth stage, and abiotic and biotic factors that can affect the stress response. Tolerance to various stresses varies among different genotypes of crops (Wani et al. 2016). Any plant developmental stage can be affected by abiotic stress, but the reproductive stage is the most crucial. If the plant is exposed to abiotic stress at the reproductive stage, it could destroy the plant and decrease crop yield (Zinn et al. 2010).

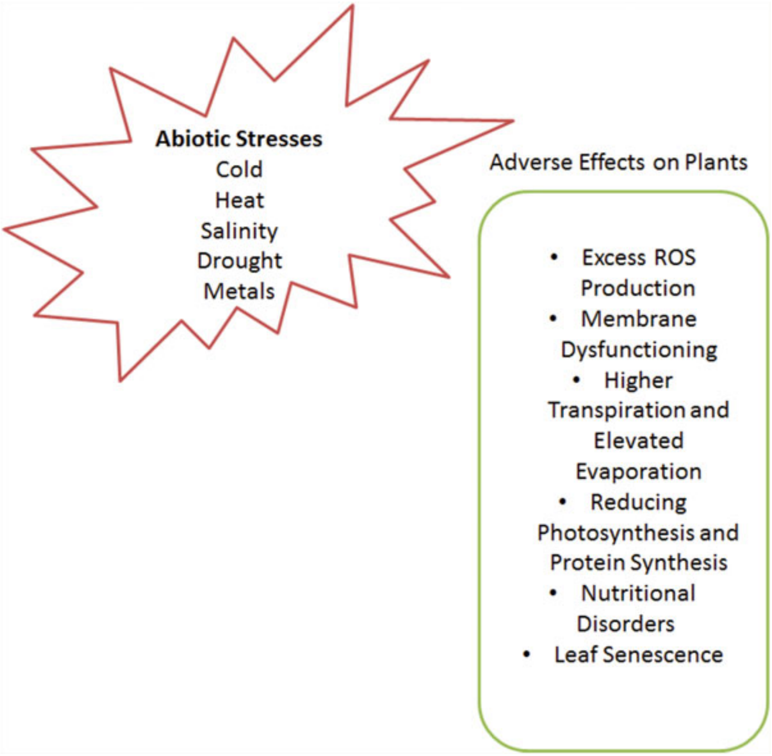

Fig. 1 Abiotic stresses and their negative impacts on plants

2 Phytohormones

Phytohormones are a diverse group of molecules synthesized by plants in small quantities involved in regulating growth and development of plants (Voß et al. 2014; Fahad et al. 2015). Phytohormones like abscisic acid (ABA), salicylic acid (SA), and ethylene (ET) are small molecules with low molecular weight synthesized by plants that are involved in regulation of the protective responses under various abiotic and biotic stress conditions (Bostock 2005).

According to Peleg and Blumwald (2011), the phenotypes of *Arabidopsis thaliana* mutant provides evidence that hormone cross talk. Hormones worked either synergistically or antagonistically and synchronized hormone regulation that plays a crucial role in plant adaptation to various stresses (Peleg and Blumwald 2011). It was found that not only ABA is involved in stomatal movement but also other hormones like ethylene (ET), cytokinin (CK), jasmonate (JA), brassinosteroids (BR), salicylic acid (SA), and nitric oxide (NO) (Acharya and Assmann 2009). Studies suggest that ethylene regulates many genes involved in the synthesis of auxin (Stepanova and Alonso 2009).

2.1 Auxin

Auxin (Aux) is a plant hormone involved in the stimulation of differential growth in response to light or gravity stimuli. It is an important phytohormone involved in cell elongation, apical dominance, vascular tissue development, organogenesis (Lau et al. 2008), flower development, and seedling growth (Zhao 2010). Aux signaling is divided into three parts: its biosynthesis that involves spatiotemporal pattern, its directional transport, and responses that are cell- or tissue-specific (Lau et al. 2008). Environmental as well as developmental signals result in regulation of Aux biosynthesis, i.e., Aux biosynthesis is upregulated when a plant is moved from normal light to shade conditions (Tao et al. 2008). Dunlap and Binzel (1996) found 75% reduction in levels of auxin by salinity stress in tomato plant. Plant growth and development are reduced under stress conditions that may be due to changed auxin accumulation and redistribution (Lau et al. 2008). Genes that are involved in growth and development and stress tolerance in rice and *Arabidopsis* are auxin-response genes, auxin/indole-3-acetic acid (Aux/IAA), auxin-response factor (ARF), lateral organ boundaries (LBD), small auxin-up RNAs, and Gretchen Hagen3 (GH3) (Wang et al. 2010).

2.2 Abscisic Acid

Abscisic acid (ABA) plays a significant role in various stresses (Tuteja 2007). It is named due to its part in abscission of plant leaves, and maximum studies were done on this phytohormone because it plays a major role in the adaptation of plant to different stress conditions (Sreenivasulu et al. 2010). Plants synthesize ABA to regulate germination of seed and other developmental stages. ABA main target is guard cells that induce stomatal closure and also transmit signals to adjust water shortage. The major function of ABA is in the adjustment of water balance and osmotic stress tolerance. ABA is induced by different stresses; that is why it is known as plant stress hormone. Gene expression of ABA-responsive genes is regulated by different transcription factors. ABA is involved in seed dormancy, leaf senescence, production of storage lipids and proteins, stomatal closure under severe water shortage, prevention of the advanced germination of premature embryos, and morphogenesis of embryos (Tuteja 2007). ABA is found to play a major role in plant responses to stress conditions like drought and salinity stress (Javid et al. 2011).

2.3 Cytokinin

Cytokinin (CK) plays a major role in the development of plants such as apical dominance, cell division, biogenesis of chloroplast (Ryu and Cho 2015), delay of leaf senescence (Zwack and Rashotte 2013), synthesis of anthocyanin, movement of nutrients (Ryu and Cho 2015), differentiation of vascular tissues (Bishopp et al. 2011), and increased stress tolerance under abiotic stress. CK is produced in root tips and transported through xylem to shoots (Ryu and Cho 2015). In *Arabidopsis thaliana*, it was found that AHK2, AHK3, and CRE1/AHK4 are histidine kinases involved in the signal perception of cytokinin and all organs of the plant contain mRNA of these three receptor genes, but having a diverse abundance (Riefler et al. 2006). The research indicates that variable and context-specific interactions occur between components of the signaling pathway of CK and different stress responses (Zwack and Rashotte 2015).

2.4 Gibberellin

Gibberellins (GAs) have several physiological roles in the plant development such as seed germination, cell elongation, starch metabolism (Graebe 1987), and obstruction of leaf senescence (Fletcher and Osborne 1965). GAs are a group of tetracyclic diterpenoid carboxylic acids that work as growth-enhancing hormones in higher plants. The major biologically active types are GA_1 and GA_4 (Sponsel and Hedden 2010). Under stress conditions these work to enhance the growth of plant organs through improved cell division and cell elongation. These also stimulate developmental period changes such as those between seed dormancy and seed germination, young and adult growth phases, and reproductive and vegetative development. Jasmonates also affect different plant processes such as ripening of fruit, root growth, pollen development, and anther dehiscence (Sanders et al. 2000). As GA working is essential for appropriate development, the seedlings that lack the ability to synthesize GAs will undergo inadequate development (Griffiths et al. 2006).

2.5 Salicylic Acid

Salicylic acid (SA) was first linked with starting of pathogenesis-related (PR) proteins and the formation of systemic acquired resistance (Ryals et al. 1996). SA also results in the production of the hypersensitive response (HR)-associated resistance by certain processes that contain initiation of ROS production and ultimately cell death (Mur et al. 2000).

2.6 Jasmonate

Jasmonate (JA) is a portion of a huge family of oxylipin products (Schaller et al. 2004). JA is essential for the initiation of stress response such as wounded molecules (Doares et al. 1995), drought (Sugano et al. 2003), and ozone and UV exposure (Overmyer et al. 2000) and defense mechanism against insects and pathogens (Kloek et al. 2001). JA also produces protective alkaloid molecules in cell cultures of *Eschscholzia californica* (Byun 2000). JA, JA precursor 12-oxophytodienoic acid (OPDA) and methyl jasmonate, initiates a large number of wound-inducible genes like proteinase inhibitors (PI) (Ryan 1990) as well as antifungal proteins (Penninckx et al. 1998; Vignutelli et al. 1998). Usage of JA also enhances the oxidative burst (Kauss et al. 1994).

2.7 Brassinosteroids

In plants, different structurally and functionally related steroids have been found. They are called brassinosteroids (BR) (Khripach et al. 2000). BR is a group of phytohormones which plays a vital role in plant development (Chory and Li 1997). They play an important role in cell enlargement by having effects on enzymatic activity and gene expression, are also involved in increasing crop yield, and help plants to cope with unfavorable conditions, like drought, salinity, and low and high temperatures (Khripach et al. 2000). It was found that in rice, BR affects leaf erectness and plant height. *Arabidopsis thaliana* BRASSINOSTEROID INSENSITIVE1 (bri1) mutants, lacking the brassinosteroid receptor, result in severe dwarf phenotype (Sakamoto et al. 2006). Maize seedling treated with BR showed enhanced growth recovery when exposed to 0–3 °C for increasing number of days (He et al. 1991). When sugar beet plants are exposed to drought stress, it results in a reduction in taproot mass. However, when sugar beet roots treated with BR recompensed, biomass reduction results in drought stress (Schilling et al. 1991). Various studies of the BR gene regulation and signaling pathway show that there is cross talk between BR and other hormones, such as ET, ABA, JA, abscisic acid, and jasmonic acid (Krishna 2003).

2.8 Ethylene

Ethylene (ET) is considered as a multifunctional hormone which controls plant growth as well as senescence. It enhances or hinders growth as well as senescence processes which depend on its amount, application timing, and the species of plant. The usage of ethephon, which is an ET-releasing compound, improved ethylene development and enhanced leaf area of mustard at a small concentration (Khan et al. 2008). ET determines the growth and development of leaves, flowers, and fruits. It also enhances or hinders senescence based on the optimal or sub-optimal ET concentration (Pierik et al. 2006). ET role in growth and development of leaf has been shown physiologically by the use of ethylene inhibitors, and it has been shown genetically by the use of ethylene-insensitive mutants or transgenic plants that do not possess the major enzymes for biosynthesis of ethylene (Bleecker et al. 1988). It has been shown that ETHYLENE RESPONSE FACTOR 5 (ERF5) and ERF6 in plants such as in *Arabidopsis* enhanced growth and development of leaf despite environmental challenges (Dubois et al. 2015). ET also has a significant role in the generation of leaf senescence. ET is also important for many other developmental processes and has a major role in responses to biotic and abiotic stress in plants (Mizoi et al. 2012).

3 Hormones Response to Abiotic Stress

Phytohormones are chemical messengers that are synthesized in one part of the plant and transferred to the other parts and play a vital role in the regulation of response to stress environment (Javid et al. 2011). Phytohormones help the plant to cope with abiotic stresses by regulating a variety of adaptive responses to a different environment (Fig. 2). Most of the studies associated to plant response to abiotic stress are related to ABA signaling and ABA-responsive genes. But the role of CK, Aux, and BR during stress conditions is developing (Peleg and Blumwald 2011). In cold stress, expression of multiple type-A *ARRs* is upregulated, and on the contrary, it downregulates the expression of all receptors of CK (Argueso et al. 2009). Under drought stress, low level of CK in the xylem sap of a plant has been noticed (Bano et al. 1994). It has been found that cross talk between phytohormones involves antagonistic or synergetic interactions that play an important role under abiotic stress environment (Peleg and Blumwald 2011). CK is an antagonist to ABA, and when plants are exposed to water-deficient conditions, it results in decreased CK level (Argueso et al. 2009). GA and BR are important in the regulation of many physiological activities in plants. Studies show that OsGSR1, a member of GA-stimulated transcript gene family, plays an important role in both BR and GA signaling pathways and mediating cross talk between them (Wang et al. 2009). ABA inhibits the responses induced by BR during abiotic stress conditions (Divi et al. 2010). Studies show that cross talk between BR and GA, ET, Aux, ABA, and JA results in modification of the expression of hormone biosynthetic genes and signaling intermediates (Bouquin et al. 2001).

There exists a relationship between expression profiles and the 5′ regulatory motifs of stress-regulated genes. This shows that a complicated regulatory network is involved in the regulation of stress genes. This network is based on transcriptome data using various theoretical approaches (Ma and Bohnert 2007). There are many transcription factors that play a role in stress responses. DREB1/CBF family consists of APETALA2 (AP2) type transcription factors which identify DRE/CRT and involve in cold stress response. *DREB1A*/*CBF3* or *DREB1C*/*CBF2* expression is regulated at the transcriptional level by INDUCER OF CBF EXPRESSION 1 (ICE1) or calmodulin-binding transcription activator (CAMTA) (Agarwal et al. 2006) (Fig. 2).

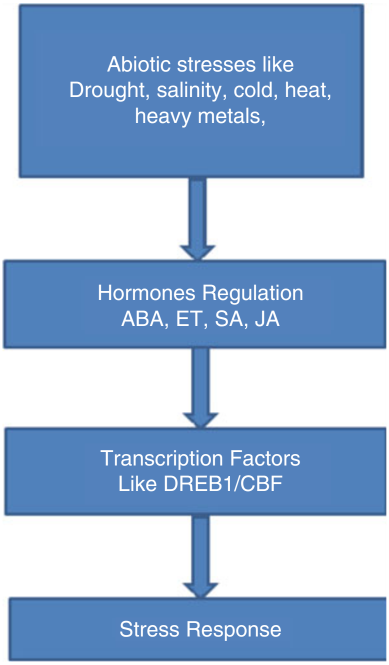

Fig. 2 Phytohormones regulation in response to abiotic stress in plant

4 Response of Phytohormones in Abiotic Stress

Plants respond to the external environment by using a succession of complex response processes. In multiple signal pathways, phytohormones are of utmost importance; they work antagonistically as well as synergistically for regulation of plant growth, development, and defense response, mostly by enhancing gene expression. Mostly genes that are induced by these hormones help plants to adjust to stress environment, and they work in producing stress resistance. Past studies proposed that expression of expansin was regulated by the plant hormones. MaExp1 from banana ripening was upregulated by ET (Trivedi and Nath 2004). IAA enhances expansin gene expression including EXP-A and EXP-B (Ding et al. 2008). Azeez et al. (2010) found that GA-responsive expansin gene is GgEXPA1. Wheat is the most important crop in the world. Cell elongation can be investigated best from wheat coleoptile because cell division does not often take place in coleoptile growth and its elongation is mainly ascribed to its cell expansion. Yang Han et al. (2012) studied the role of expansin genes in stress resistance and regulation of hormone by cloning TaEXPB23 from wheat crop and transforming it into tobacco and concluded that regulation of transcripts of TaEXPB23 was enhanced by NaCl and MeJA but decreased by high temperature, ET, and a-naphthylacetic acid. It was found that overexpression of TaEXPB23 results in changing root growth of transgenic tobacco seedlings and enhances salinity tolerance but not high temperature tolerance.

5 Regulation of TaEXPB23 Transcription by Phytohormones

Expansins belong to a large superfamily. They have a complex gene regulation mechanism. Increased regulation of the expansin gene by ethylene was found in tomato during fruit ripening (Rose et al. 2000). Similarly, expression of expansin genes was upregulated by indole-a-butyric acid (IBA), and ET was induced by RdEXP1 in *Regnellidium diphyllum* (Hutchison et al. 1999). RT-PCR results show that TaEXPB23 have variable responses to different hormones like was downregulated by ABA, upregulated by MeJA, and downregulated by Aux, ET, GA3, and NAA.

5.1 Role of Abscisic Acid

ABA performs some protective functions in cold stress conditions like membrane stabilization, protection against oxidative stress, stomatal closure, and water status enhancement by elevating root hydraulic conductivity. The role of ABA in the initial stage of the cold stress overlaps with transient enhancement of levels of ABA during cold stress (Galiba et al. 1993; Veisz et al. 1996). One of the quick responses of the plant to abiotic stress is the production of ABA by increasing ABA-responsive gene expression (Peleg and Blumwald 2011). It was found that under osmotic stress expression of some ABA biosynthesis, genes are increased like *MOLYBDENUM COFACTOR SULFURASE* gene (*MCSU*), *ALDEHYDE OXIDASE* gene (*AAO3*), *ZEAXANTHIN EPOXIDASE* gene (*ZEP)*, and *9-CIS-EPOXYCAROTENOID DIOXYGENASE* gene (*NCED3*) (Zhu 2002).

5.2 Role of Cytokinin

CK also plays an important role in plants under stress conditions. However, CK is usually thought to have a negative role in plants under stress, but studies are present that shows that CK has both negative and positive effects under stress conditions (Zwack and Rashotte 2015). It was found that when CK is applied to bean plants before drought stress, it enhanced the tolerance of plants while had negative effect on sugar beet tolerance and had no effect on maize plant tolerance (Pospíšilová and Baťkova 2004). Changes in endogenous CK levels under stress shows that CK is involved in stress responses. Under drought stress, there is a decrease in concentration and transport of trans-zeatin riboside in plants but increase in ABA level (Davies et al. 2005). When partial root zone drying was performed in tomato plant, there was decrease in CK levels while increase in ABA levels (Kudoyarova et al. 2006). This shows that local stress applied to the root might result in modifications in the CK levels in various plant parts (Schachtman and Goodger 2008).

5.3 Role of Ethylene

ET is involved in developmental processes as well as stress responses (Zhai et al. 2013) and is involved in freezing tolerance. ET role in stress conditions is facilitated by a downstream transcription factor of the ET signaling cascade, ethylene-insensitive 3 (EIN3). EIN3 decreases the expression of C-repeat/dehydration-responsive element-binding factor (*CBF1*), *CBF2*, and *CBF3* genes and also CK signaling repressors *ARR5*, *ARR7*, and *ARR15* (Shi et al. 2012). ET also interferes with CK signaling output, and CK also affects its pathway. The initiation of both CK and ET signaling in the presence of selenite-induced stress using the ARR5 and ACS8 markers and a decrease in the auxin levels provide evidence of complicated regulatory system under stress (Lehotai et al. 2012). The signaling of ET and its response to stress consist of the pathway that includes ethylene response factors (ERFs). It has been known that ERFs controls response to the pathogen attack. However, the latest studies show that various ERFs attach with dehydration-responsive elements and work to show responses to abiotic stresses. In spite of its simple structure, ET acts as a major mediator of stress factors. Ethylene response factor (ERF) is found to play a significant role in plant response to various stresses (Mizoi et al. 2012).

5.4 Role of Salicylic Acid

SA improves the plant tolerance to abiotic stress conditions like salinity, heat, chemicals, and drought. SA when exogenously applied to plants through seed application, foliar application, adding to the nutrient solution and irrigation, results in abiotic stress resistance (Khan et al. 2015). When SA is applied to *H. vulgare* under drought stress, it results in enhanced CO_2 assimilation rate because of increased stomatal conductance and plant dry mass (Habibi 2012). SA helps *Hordeum vulgare to cope with salinity stress by lowering* malondialdehyde (MDA) and ROS production (Khan et al. 2014).

6 Role of Phytohormones in Wheat Under Abiotic Stress

Wheat (*Triticum aestivum* L.) is a staple food crop and is a part of the diet of the maximum population in the world. Wheat productivity is very sensitive to environmental variations like high- and low-temperature stresses, thus leading to a reduction of yield ranging from 40 to 50% in most of the cases. Negative impacts of environmental conditions on physiological and biochemical properties, cell development, various metabolic processes, and enzymatic functioning at various stages of plant development result in low grain yield of wheat (Ashraf 2010).

Singh and Usha (2003) studied the impact of SA on growth and metabolic profile of wheat crop under drought stress and found that SA enhances dry mass, moisture content, chlorophyll content, and superoxide dismutase (SOD) activity in wheat under stress compared to control.

Shakirova et al. (2003) found fast temporary modifications in the balance of hormones in wheat under SA influences with Aux and ABA accumulation; however, there were no obvious changes in cytokinin level. Growth enhancement of wheat seedlings is due to increase in Aux. ABA accumulation produced no negative effects on seedling growth. Plants treated with SA have a high growth rate as compared to control.

Bano and Yasmeen (2010) studied the role of phytohormones in wheat under drought stress and found that drought stress reduces GA and IAA content while proline and ABA in spikes and leaves increases. Results showed that BA was effective in the early stages of growth while ABA was effective in later stages.

Egamberdieva (2009) have studied the impact of phytohormones producing bacteria on wheat plant under high salt concentration. He found that IAA producing bacteria *Pseudomonas extremorientalis* TSAU20, *Pseudomonas aurantiaca* TSAU22, and *Pseudomonas extremorientalis* TSAU6 enhances the root growth of seedling up to 25% in nonsaline conditions and 52% at saline conditions as compared to control plants and the germination was increased by Aux, GA, ethephon, and zeatin. This shows that phytohormones significantly lessened the salinity-induced dormancy of wheat seeds.

Noreen et al. (2017) conducted various pot culture studies to measure the effectiveness of exogenously applied salicylic acid on wheat under water-deficient conditions and found that various physiological parameters of wheat were improved by SA treatment under drought conditions.

Shakirova et al. (2017) found the role of rapid reversible accumulation of ABA in wheat when treated with salicylic acid and also high level of ABA is maintained in salicyclic acid treated seedlings subjected to Cd stress. Dehydrins, wheat germ agglutinin, and RAB (responsive to ABA) proteins play an important role in resistance of wheat to water-deficient conditions (Shakirova et al. 2017).

7 Conclusion

Plants are exposed to various abiotic stresses that result in the overproduction of reactive oxygen species (ROS) resulting in oxidative stress. Plants exhibit different responses to these stresses. Phytohormones like ABA, JA, SA, and ET are also involved in the regulation of the protective responses under various abiotic stresses, and these responses usually involve modifications in levels of these phytohormones. Cross talk between BR and GA, ET, Aux, ABA, and JA exists. Wheat is an important staple food crop throughout the world. Abiotic stresses especially drought and salinity are major constraints to wheat production. Phytohormones like SA are found to play a significant role in helping wheat crop to cope with abiotic stresses.

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Use of Plant Nutrients in Improving Abiotic Stress Tolerance in Wheat

Mahmoud F. Seleiman

Contents

Abstract Drought and salinity stresses are serious threat limitations for crop growth, productivity and consequently for sustainable of agriculture. The adversative impacts of drought and salinity stresses can be alleviated via different agricultural practices such as application of crop establishment or application of plant nutrients for maintaining a suitable level of water in plant leaves due to osmotic adjustment and stomatal conductance performance, consequently improving plant growth and productivity. Therefore, the aim of the present chapter is to make a review of the abiotic stress effects on wheat growth and yield and how to ameliorate the abiotic stress in wheat through plant nutrient applications.

Keywords Soil fertility · Micronutrients · Ion transport · Fertilizer management · ROS

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1 Introduction

Wheat is categorized as one of the greatest essential cereals worldwide with annual productivity of about 718 Mt, and it is used as nutrition for approximately 20.0% of global population (Nations 2014). To achieve and meet the demands of rapidly increasing global population, productivity of wheat has to be doubled up by year 2050 (Foresight 2011). Wheat crop is one of the highest strategic crops for human beings and is cultivated in the arid and semiarid regions with about 70.0% (Wei et al. 1997). Investigation of drought, salt and heat stresses effects as well as fertility on wheat crop are considered very important target to find a suitable option for food supplies.

A significant success of crop yield improvement programs, agriculturalists and farmers can lose about 20.0–70.0% of their prospective crop productivity as a result of abiotic and biotic stresses (Berry et al. 2013). Abiotic stresses are considered main challenges for growth and crop yield in arable lands, because the assessed yearly loss in crop yields can reach billions of dollars (Pareek et al. 2009; Pereira 2016). Drought stress is a threat for wheat productivity on the global scale (Langridge and Reynolds 2015). Mostly, the episodic drought existence is stated in over 50.0% of the cultivated lands with wheat on the global scale (Ashraf and Harris 2005), generally in the arid and semiarid regions.

The most major environmental factors (i.e., abiotic stresses), for instance, drought, salinity, and heat, can have an overwhelming impacts on growth and productivity of plants in field conditions; consequently they can cause constraints to food security worldwide (Seleiman and Kheir 2018a). The most harmful abiotic stresses that can cause major damage for different plant species in the field were investigated (Ashraf and Harris 2005; Cakmak 2005; Liang et al. 2007; Munns and Tester 2008; Chinnusamy and Zhu 2009; Pareek et al. 2009; Mittler and Blumwald 2010; Pereira 2016). However, open-field conditions are dissimilar to the glasshouse or laboratory that has controlled conditions. Investigations on climate change models expect that the incidence of abiotic stresses (i.e., drought and/or heat stress) will rise in the upcoming decades and will cause decrease in productivity in agricultural sector (IPCC 2007, 2008). Worldwide, food safety is being haunted via the quick growth in population and severe variations in the climate change (Foresight Final Project Report 2011; Lesk et al. 2016; Seleiman and Kheir 2018b). Therefore, to achieve the worldwide food demand for future populations, it is necessitous to improve plant species with enhanced tolerance to those harmful stresses (i.e., drought, heat stress, and salinity). In addition, it is actually important to know and recognize the physiological, ecological, and biochemical interferences associated with these abiotic stresses for better management of plant growth and production of plants.

Remarkably, reproductive skins seem to be more sensitive and susceptible than vegetative parts and tissues to abiotic stresses such as drought and heat stress. Both drought and heat stress can impact the reproductive processes; however they affect the reproductive sink traits contrarily (Westgate 1994; Barnabas et al. 2008). For instance, drought stress prevents ovule functions and development of pistillate flower and reduces GI (grain index), while heat stress reduces pollen fertility and grain number in spring wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) (Westgate 1994; Prasad et al. 2011). These results propose that different traits and growth inhibition patterns as a result of drought and heat stress can arise at the same time with both stress combination, producing high severe harm for plant species growth, particularly toward the reproductive stage. Drought and/or heat stress impacts on growth parameters in cereal crops such as barley (*Hordeum vulgare* L.) were observed (Rollins et al. 2013). In this investigation, the drought stress caused a significant reduction in plant height, spike numbers, and biomass production, while heat stress did not result in a significant effect for these parameters. However, heat stress significantly improved aborted spike number and lessened grain weight, but drought stress did not have a significant effect on these parameters.

Photosynthesis is one of the most physiological traits that can be affected by drought and/or heat stress. Stomatal closure inhibits a limitation on photosynthesis via reducing the CO_2 availability, when plants grow under drought conditions (Chaves et al. 2003). On contrary, heat stress imposed photosynthesis mostly via the alterations in non-stomatal parameters, for instance, Rubisco activity and electron transport capacity (Salvucci and Crafts-Brandner 2004a, b; Way and Oren 2010).

2 Effect of Drought Stress on Plant Growth, Physiological, and Yield Traits

Plant species are exposed to the drought when there is a limitation in the water supply into the roots or there is a loss of the water via the high transpiration (Anjum et al. 2011). The relentlessness of the damage that can be caused via the drought stress is usually variable, since it can occur through different factors such as water losses through evapotranspiration, moisture holding capacity of the soil and rainfall patterns. The reaction of plant species into drought stress can vary from species to others according to growth stage of the plant as well as other environmental influences (Demirevska et al. 2009). The initial negative impact of drought stress on plant is a reduction in the germination percentage and seedling growth (Kaya et al. 2006; Farooq et al. 2009). The lessening in germination percentage and growth traits (i.e., seedling growth, dry weight of plant root and shoot, vegetative growth) of crops have been investigated in field such as growth of rice (*Oryza sativa* L.) with drought stress (Manikavelu et al. 2006). Drought can result in a substantial reduction in crop yield via negative effects on plant growth, physiology, and reproduction traits (Yordanov et al. 2000; Barnabas et al. 2008; Hafez and Seleiman 2017; Seleiman and Abdel-Aal 2018). Drought stress is predictable to initiate plant growth and productivity problems for more than 50.0% of the cultivated arable lands by the end of 2050 (Ashraf 1994; Vinocur and Altman 2005; Kasim et al. 2013). Recently, Daryanto et al. (2016) analyzed the results of published investigations during the period of 1980–2015, and reported a reduction of about 40 and 21% for maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) yield, respectively, as a result of drought stress on the universal scale.

Drought impairs cell division and elongation; consequently this can result in bad plant growth (Hussain et al. 2008). The negative impacts of drought on the process of cell growth can be mainly a result of the turgor loss (Taiz and Zeiger 2006). In addition, it can be as a result of the slow water movement from xylem to the close plant cells (Nonami 1998). Moreover, the drought stress decreased the leaf number per plant and their size as a result of the reduction in the turgor pressure, the slow rate of photosynthesis, as well as the supply of assimilates (Rucker et al. 1995). Biomass production is also severely decreased when plants were exposed to the water-deficit conditions (Zhao et al. 2006).

Exposed wheat plants into drought conditions throughout the early vegetative growth can limit traits such as shoot elongation, tillering, and plant leaf area. This is probably due to the reduction in carbon dioxide assimilation, stomatal conductance and transpiration (Cossani and Reynolds 2012). Nevertheless, exposed wheat plants into drought stress during the reproductive stages can result in pollen and spikelet abortion (Dolferus et al. 2011). Drought stress can facilitate high abscisic acid in plants (Powell et al. 2012) causing the lowest pollen viability and early or delayed flowering for wheat plants (Cattivelli et al. 2008). Also, it can lessen grain number per each spike and GI in wheat (Praba et al. 2009). The adversities of drought stress could be reduced through crop management practices such as seed priming (Sharma and Bhardwaj 2014).

Photosynthesis is one of the most physiological phenomena that mainly can be affected by drought. This is due to the reduction in leaf expansion and indecorous effective of the photosynthetic machinery as well as leaf senescence of plants (Wahid et al. 2007). Under drought stress, stomatal closure lessens the availability of CO_2, and this can make the plant species more inclined to the photo damage (Lawlor and Cornic 2002). Exposure of plants to drought stress causes negative effects for leaf water potential (Ψ_w), stomatal conductance, leaf and canopy temperature, and transpiration rate (Farooq et al. 2009). A major decrease in the leaf Ψ_w, as well as transpiration rate, was reported when plants were exposed to the drought stress which eventually augmented the leaf and canopy temperature of plants (Turner et al. 2001). Moreover, water use efficiency (WUE), which is a ratio of accumulated DM (i.e., dry matter) to the consumed water by the plants during the different growth and reproductive stages (Monclus et al. 2006), was higher in the efficient wheat cultivars grown under drought stress (Abbate et al. 2004). This can be mainly because of the dry matter accumulation via consuming less amount of water as a result of stomata closing and the reduction in transpiration rate. Different vital nutrients such as nitrogen (N), silicon (Si), magnesium (Mg), and calcium (Ca), which are taken up by plant roots along with water, can be limited in the movement via diffusion and mass under the drought stress, and this can lead to retarded plant growth (Barber 1995).

Water stress causes an oxidative stress leading to changes in carbon (C) and N metabolic activities, photosynthetic activity, and disturbed water relations in plant species (Tawfik 2008). For example, the effect of drought stress at anthesis stage can lessen the pollination and consequently can lead to a decrease in the number of grains/spike and finally decrease the grain yield of wheat (Nawaz et al. 2012). Suitable water supply at anthesis stage or after that improves not only photosynthetic rate but also improves and increases grain filling period (GFP) (Zhang et al. 1998), and subsequently increases grain yield of crop (Inoue et al. 2004). Several nutrients have been recognized to act as stress ameliorants, for instance, N (Gevrek and Atasoy 2012), phosphorus (P) (Kaya et al. 2001), potassium (K) (Raza et al. 2012), selenium (Se) (Nawaz et al. 2013), zinc (Zn) (Weisany et al. 2012), and salicylic acid (Waseem et al. 2006).

Cereals exposed to drought at the pre-anthesis stage had the shortest time up to anthesis, while exposing them to drought after anthesis reduced the GFP (Estrada-Campuzano et al. 2008). A reduction in the activity of those enzymes has been obtained when wheat plants were exposed to the droughts which have an undesirable effect on the grain yield (Ahmadi and Baker 2001). This reduction in the grain yield can be due to different factors, for example, a reduction in photosynthesis rate (Flexas et al. 2004) and slow flag leaf development of plants (Rucker et al. 1995). Also, a major reduction in the barley grain yield was reported when plants were exposed to drought conditions as a result of a low number of fertile tillers and grains as well as the lowest weight of grain index (Samarah 2005). The negative effects of drought on the crop yield generally rely on the harshness of the drought and the plant growth stage. A significant reduction (57.0%) in grain yield of wheat was revealed by Balla et al. (2011) due to the drought stress.

3 The Role of Silicon on Growth and Yield of Wheat Grown under Drought Stress

In numerous issues, the stimulation of growth is because of the protection that silicon affords plant species against the harmful impacts of abiotic and biotic stresses. In addition, silicon can control some disease on plant growth (Elawad et al. 1982; Raid et al. 1992), control pest (Elawad et al. 1985; Pan et al. 1979), lessen the toxicity of some metals (Neumann and zur Nieden 2001), and relieve salt stress (Ulloa and Anderson 1991; Liang 1999; Yeo et al. 1999) as well as drought stress. Silicon is considered one of the most abundant elements on the earth surface. However, it is not an essential or a vital element, particularly for higher plants (Neumann and zur Nieden 2001). Silicon in soil is presented as monosilicic acid (H_4SiO_4) at a concentration of 0.1–0.6 mM, and it is taken up via the roots of plants in the form of monosilicic acid (Epstein 1994; Ma and Takahashi 2002). It accumulates, after plant uptake, on the epidermis of different tissues mostly as a polymer of hydrated amorphous silica. Generally, plant biomass contain silicon (0.1–10%) though the content of silicon differs considerably from species to another species (Ma and Takahashi 2002).

Seed priming is a technique that includes specific treatments that have an effect on metabolic and biochemical process as well as on enzyme activities of seed; therefore it can play a vital role in the biological functions, for instance, early germination and seedling establishment (Demir and Mavi 2004), in particular under water-deficit conditions (Rahimi 2013). Seed priming is likewise known to enhance proline, total soluble sugar, and protein when plants were exposed to water-deficit conditions compared to untreated seeds (Sun et al. 2010). Thus, seed priming treatment is highly recommended for farmers and agriculturist to improve the productivity of crops under water stress fields. The seed priming techniques comprise thermo-priming (i.e., seed or grain treatment with low or high temperatures), hydro-priming (i.e., soaking seed or grains in water), halo-priming (i.e., soaking seeds or grains in salt media), osmopriming (i.e., soaking seeds or grains in osmotic solutions, e.g., sugars, glycerol, polyethylene glycol, or sorbitol), priming seeds or grains with hormones of plant growth, and bio-priming (i.e., with bacteria or fungi). Silicon (Si) is one of the plentiful elements with about 31.0% of its mass in different soils and can be used in the form of silicic acid through the plant species (Ma et al. 2001). Consequently, Si can be used as seed priming since it has a vital role to alleviate the lethal significances of drought stress on plant growth in addition to the development of different plants, and finally it is available plentifully in the soils. Also, Si enhanced germination percentage and growth of barley grown under chromium stress, as well as it enhanced the antioxidant activities, for instance, catalase and peroxidase enzymes (Ali et al. 2013). It reduced the oxidative damage through improving the membrane stability under water-deficit condition (Pei et al. 2010) and increased the antioxidant production (Gong et al. 2005).

There is an indication that Si is not only a cell wall incrustation, which is responsible for the severity of plant leaves in monocots, but is also involved in some growth and physiological processes (Epstein 1999; Savant et al. 1999). Different investigations have reported that Si indorses the plant growth (Sistani et al. 1997; Alvarez and Datnoff 2001). Silicon is a nonessential plant nutrient; however, it can improve plant species resistance and tolerance against the different factors of abiotic stresses (Ahmed et al. 2011). It benefits in the maintenance of high leaf Ψ_w in plant species grown under water stress conditions (Lux et al. 2002). Moreover, Si is recognized to improve plant resistance against drought stress through improving sustaining water equilibrium and straightness of leaves in plants as well as improving photosynthetic efficiency (Yin et al. 2013).

Silicon can result in improvement of the drought tolerance of different plants (Savant et al. 1999; Ma et al. 2001; Xia et al. 2001). Gong et al. (2003) reported that Si application can improve dry matter (DM) of wheat grown in well-watering conditions, as well as it also improves wheat growth under drought stress through maintaining high leaf areas (LA) to cover high assimilatory ability, thickening leaves which can be valuable for lessening the transpirational damage of water. Thus, Si fertilization can be a strategic pathway for increasing the wheat crop production, particularly in regions that are arid and/or semiarid. Bukhari et al. (2015) investigated the effective methods of Si application such as Si seed priming, Si fertigation, and Si foliar spray for improving the drought resistance into wheat plants. The data of this investigation revealed that water stress can pose a significant reduction in plant-water relations as well as the uptake of P, K, Mg, and Zn in wheat plants. However, Si application significantly improved the wheat plants' capability of water stress via the increase of Si uptake and improvement in the ascorbate peroxidase, peroxidase, and catalase enzyme activities. Also, foliar spray application of Si was the best method and effective in alleviating the adverse effects of drought stress on wheat plants. The authors of this study recommended the application of Si fertilizer at tillering stage in comparison to anthesis stage for maintenance the turgor pressure of plants and better uptake of different nutrients under well watered and/or stressed wheat plants.

Foliar Si application was indicated as the optimal method which could be attributed to readily availability to the mesophyll tissues (Bukhari et al. 2015). They reported that the foliar spray of Si increased Ψ_w of wheat plants under water stress. This might be because of the accumulation of solutes; thus the water can easily move from surroundings into the cell, and eventually plants can maintain their turgor pressure and fuss their metabolic activities (Subbarao et al. 2000). The enhancement in drought resistance via Si application might be correlated with the improvement of high level of water uptake from the soil solution into the plant issues (Hattori et al. 2005, 2007). Ahmad and Haddad (2011) revealed that application of Si (2 mM of sodium silicate kg^{-1} soil, Na_2SiO_3) into wheat plants grown in drought stress conditions significantly improved the activities of catalase and peroxidase enzymes. Furthermore, Si application via soil (0.1167 $g\ m^{-2}$ as Na_2SiO_3) improved the activity of peroxidase enzyme in wheat plants at booting stage in comparison to grain filling stage under drought stress (Gong et al. 2008).

4 The Role of Potassium on Growth and Yield of Wheat Grown under Drought Stress

Potassium (K) application into plants exposed to the drought stress can enhance the resistance of plants into different types of abiotic stress conditions, and it likewise enhanced successive plant growth and its yield. K improved physiological traits through the plant turgor pressure regulations and photosynthesis, in addition to the imporovement of enzymes activity (Mengel and Kirkby 2001). While, plants that suffer from drought stress require more internal potassium (Cakmak 2005). Raza et al. (2013) studied the influence of bread wheat plants grown under drought stress conditions into the foliar K application at the rate of 1% at three various plant growth stages (i.e., tillering, flower initiation, and grain filling). They reported that exposing plants into drought stress during the three wheat growth stages resulted in harmful negative impact on plant's nutrient uptake, water potential ($\boldsymbol{\Psi}_w$), osmotic potential ($\boldsymbol{\Psi}_s$), and turgor pressure potential ($\boldsymbol{\Psi}_p$). However, the exogenous K application into plants exposed to drought stress at these three wheat growth stages improved the resistance of plants into drought through lessening toxic elements uptake and enhancing the physiological efficiency. In addition, maximum improvement in investigated nutrient uptake and plant physiological traits was obtained when potassium was added at the grain filling stage.

Foliar application of K to wheat grown with water stress at any of the following growth stages (i.e., tillering, flower initiation and grain filling stages) significantly enhanced different nutrient uptake as well as enhanced water ($\boldsymbol{\Psi}_{\mathrm{w}}$), osmotic ($\boldsymbol{\Psi}_{\mathrm{s}}$), and turgor ($\boldsymbol{\Psi}_{\mathrm{t}}$) potential of wheat plants. Such reduction in water, osmotic, and turgor pressure potential was attributed to the reduction in plant leaves water potential under drought stress. On the other hand, the reducing leaf area that caused by drought stress can result in a decrease in photosynthesis and thus in crop productivity (Karamer 1983). It has been reported that K accumulation in the inorganic form can sustain the internal water balance, turgor pressure, and osmotic adjustments as well as physiological traits such as stomatal opening and the photosynthesis of plants which are exposed to water stress (Serraj and Sinclair 2002).

Potassium exogenous application decreased the negative effects of drought stress through lessening the uptake of sodium (Na) by the plant species under drought stress. Potassium foliar application sustained the turgor pressure and internal water balance of plant leaves. Potassium exogenous foliar on plants grown in drought stress conditions, particularly at grain filling stage, was most operative, and it lessened the uptake of sodium by about 23% and enhanced the uptake of nitrogen (N) and K by about 10% and 24%, respectively. Finally, foliar K application improved the adversative impacts of drought stress on plants and enhanced the phosphorus (P) uptake by 36% and calcium (Ca) by 18% in plants grown with water-deficit conditions at grain filling stage.

5 The Role of Boron, Zinc, and Copper in Lessening Abiotic Stresses

Boron (B) is included in cell wall functioning via enabling the cross-linking of pectic polysaccharides. It can play an important function in the cytoskeleton structural integrity (Miwa and Fujiwara 2010). The main function of B in plant species comprises floral organs, flower male fertility, and growth of pollen tube as well as carbohydrate utilization (Blevins and Lukaszewski 1998). Hence, the inaccessibility of B throughout grain filling stage can result in unsuitable anther and pollen formation (Cheng and Rerkasem 1993) and poor grains consequently very low starch content (Dell and Huang 1997). In the open field, sexual reproduction can be easily influenced by the low level of B and consequently a significant reduction in the yield without visual symptoms expressed during the vegetative growth stage. Abdel-Motagally and El-Zohri (2018) reported that application of B significantly improved and enhanced growth traits of wheat grown under water stress (50% of the recommended water application for wheat) in comparison to untreated plants with B. They also reported that foliar B application at the booting stage of wheat resulted in the highest plant pigment contents under normal water application (100% of recommended water for wheat). The lessening of stress markers such as proline and H_2O_2 as well as the improvement of plant pigment content under water-deficit conditions through foliar application of B can be an indicator for the alleviating effects of water stress.

Zinc (Zn) was shown to moderate the activity of some enzymes under abiotic stress conditions. For example, it has a great role in the membrane-bound NADPH oxidase (Cakmak 2000) that is included in the reactive oxygen species (ROS) homeostasis. In an agronomic investigation, wheat grown with sufficient N and P (70 N:70 P, kg ha^{-1}) and insufficient water supply could reduce the production of wheat grain yield by about 25%; however, the addition of foliar application of Zn by 23 kg ha^{-1} can enhance and increase the grain yield of wheat by about 16% (Bagci et al. 2007). Therefore, Zn fertilization can reduce the loss in grain yield by 25–13% when plants exposed to water deficiency. Copper (Cu) is particularly necessary for the metabolism of carbohydrate, and it is also very important for the lignin synthesis that is required for plant cell wall establishment (Yruela 2009; Ryan et al. 2013a, b). Its role in the strengthening of cell wall can have inferences for the plant's survival when it is exposed to the abiotic stress conditions.

6 The Role of Silicon on Growth and Yield of Wheat Grown Under Salt Stress Conditions

Numerous potential mechanisms have been reported that Si can enhance and improve plant resistance in contradiction of salinity impact which is considered the major deteriorating influence for a yield of crops in arid and semiarid counties (Rios et al. 2014). Silicon application resulted in an improvement in physiology of wheat and its resistance in contradiction of biotic stress (Yin et al. 2014). Silicon has been recognized to be an effective element in lessening the opposing results of edaphic and epiedaphic stresses, for example, drought stress (Hattori et al. 2005; Sacala 2009), waterlogging (Sacala 2009), soil salinity (Romero-Aranda et al. 2006), toxicities of different heavy metals (Gunes et al. 2008; Sarwar et al. 2010), and heating or chilling and/or frost (Savant et al. 1999; Ma et al. 2004). It decreases the lethal impacts of the ROS via antioxidant system activation in plant species (Liang et al. 2007; Gunes et al. 2008).

The useful effect of Si on plants grown under salt stress has been observed in wheat (Ahmad et al. 1992), rice (Matoh et al. 1986; Yeo et al. 1999), and barley crop (Liang et al. 1996). Root and shoot traits of rice plants were inhibited by about 60% at 100 mM NaCl for 3 weeks; nonetheless, Si application significantly alleviated salt-induced injury (Matoh et al. 1986). The Na content in plant shoots was reduced to about 50% by Si application. This function of Si might be attributed to the Si-induced reduction of transpiration rate (Matoh et al. 1986).

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Use of Osmolytes in Improving Abiotic Stress Tolerance to Wheat (*Triticum aestivum* L.)

Fahim Nawaz, Sadia Majeed, Khawaja Shafique Ahmad, Abdul Hamid, Rana Nauman Shabbir, Muhammad Aqib, and Rao Muhammad Ikram

Contents

Abstract Wheat is an important food crop that provides vital calories and nutrients essential for human health. However, climate extremities threaten wheat yields and hence food security around the globe. Improving wheat productivity under changing climate scenario is one of the major challenges of agriculturists and plant scientists. Environmental stresses further aggravate the situation. Wheat responds to oxidative stresses through regulation of a series of mechanisms at morphological, physiological, and molecular levels. Accumulation of low molecular weight organic solutes, known as osmolytes, is one of the prime defense strategies to reduce oxidative stress-induced damages in wheat. This chapter would appraise new insights into osmotic adjustment strategies of wheat against various abiotic stresses. In addition, recent studies on the role of exogenously applied osmoprotectants in improving abiotic stress tolerance of wheat are also discussed.

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Abbreviations

AAO	Ascorbic acid oxidase
ABA	Abscisic acid
APX	Ascorbate peroxidase
Arg	Arginine
As	Arsenic
AsA	Ascorbic acid
CAT	Catalase
Cd	Cadmium
Cr	Chromium
Cu	Copper
DAO	Diamine oxidase
GABA	Gamma-aminobutyric acid
GB	Glycine betaine
Hg	Mercury
HMs	Heavy metals
MDA	Malondialdehyde
MEL	Melatonin
MPI	Mannose-6-phosphate isomerase
MPP	Mannose-1-phosphate phosphatase
MPR	Mannose-6-phosphate reductase
Ni	Nickel
NO	Nitric oxide
PAL	Phenylalanine ammonia lyase
PAO	Polyamine oxidase
PAs	Polyamines
PPO	Polyphenol oxidase
Proline	Proline
Put	Putrescine
ROS	Reactive oxygen species
Spd	Spermidine
Spm	Spermine
TPP	Trehalose-6-phosphate phosphatase
TPS	Trehalose-6-phosphate synthase

1 Introduction

Wheat is the base of human civilization and has a significant role in improving food security by feeding the hungry world. The most significant step in converting mankind from hunters to farmers was the domestication of wheat, which started about 10,000 years ago in the Fertile Crescent. Wheat is probably one of the major and most important cereals in the world providing approximately 85% calories and 82% protein to the world population (Chaves et al. 2013). It contributes 21% to the global food requirements (FAO 2014–2015). Central and West Asia and North Africa (CWANA region) are the top user and consumer of wheat (Braun et al. 2010). As the population of the world has almost doubled in the last 50 years, the demand for wheat has also increased along with per capita consumption (Shabbir et al. 2016). Due to urbanization and modernization, global demand for wheat has increased because of its unique feature to produce fortified and economical products. Gluten in wheat allows the processing to produce bread, porridge, crackers, biscuits, Muesli, pancakes, pies, pastries, cakes, cookies, muffins, rolls, doughnuts, and breakfast cereals. These products are easy to consume than the traditional products.

Wheat is cultivated in almost every region due to its wide adaptability, but its production is adversely affected by various biotic and abiotic stresses (Rahaie et al. 2013). Moreover, the adverse effects of stresses are maximized when they occur in combination. Climate change along with global warming has increased the incidence of biotic and abiotic stresses that alter plant growth and development at cellular and molecular levels (Mahalingam 2015; Pandey et al. 2015; Ramegowda and Senthil-Kumar 2015). Plants, in order to cope with these changes, adopt a strategy known as "osmotic adjustment" in which plant accumulates osmolytes (small organic molecules) to protect its cellular processes against disrupting environmental changes (Yancey 2005; Chen and Jiang 2010; Liang et al. 2013). Plant metabolism undergoes several changes including synthesis of compatible solutes to stabilize proteins and structure of the cell, to scavenge ROS, and to maintain cell turgor by osmotic adjustment (Chinnusamy and Zhu 2009; Janská et al. 2010; Krasensky and Jonak 2012). Osmotic adjustments have proven to be a successful strategy in tolerating stress, and plant response by accumulating osmoprotectants like glycine betaine (GB), melatonin (MEL), proline (Pro), and sugars has been detected in several plant systems (Ashraf and Foolad 2007; Chen and Jiang 2010). Organic osmolytes produced by plants include amino acids (Pro and glutamate), low molecular weight compounds (sugar and sugar alcohols), and methylated tertiary N compounds (GB) along with several other low molecular weight metabolites (Chen and Jiang 2010). Other than protecting osmotically, osmolytes can protect plants in several other ways by involving in unique reactions (Yancey 2005). In this chapter, we provide an elaborate and recent literature on different types of osmolytes, their roles, and their mechanism in improving abiotic stress tolerance in wheat.

2 Osmolyte Synthesis and Accumulation in Plants

Accumulation of a wide range of low molecular weight osmoprotective compounds such as carbohydrates (glucose, sucrose, fructose, raffinose, trehalose), sugar alcohols (glycerol, sorbitol, mannitol, inositol), amino acids (pipecolic acid, Pro), and betaines (glycine betaine, hydroxyproline betaine) is considered prime defense mechanism of plants against various environmental stresses (Fig. 1). Synthesis of

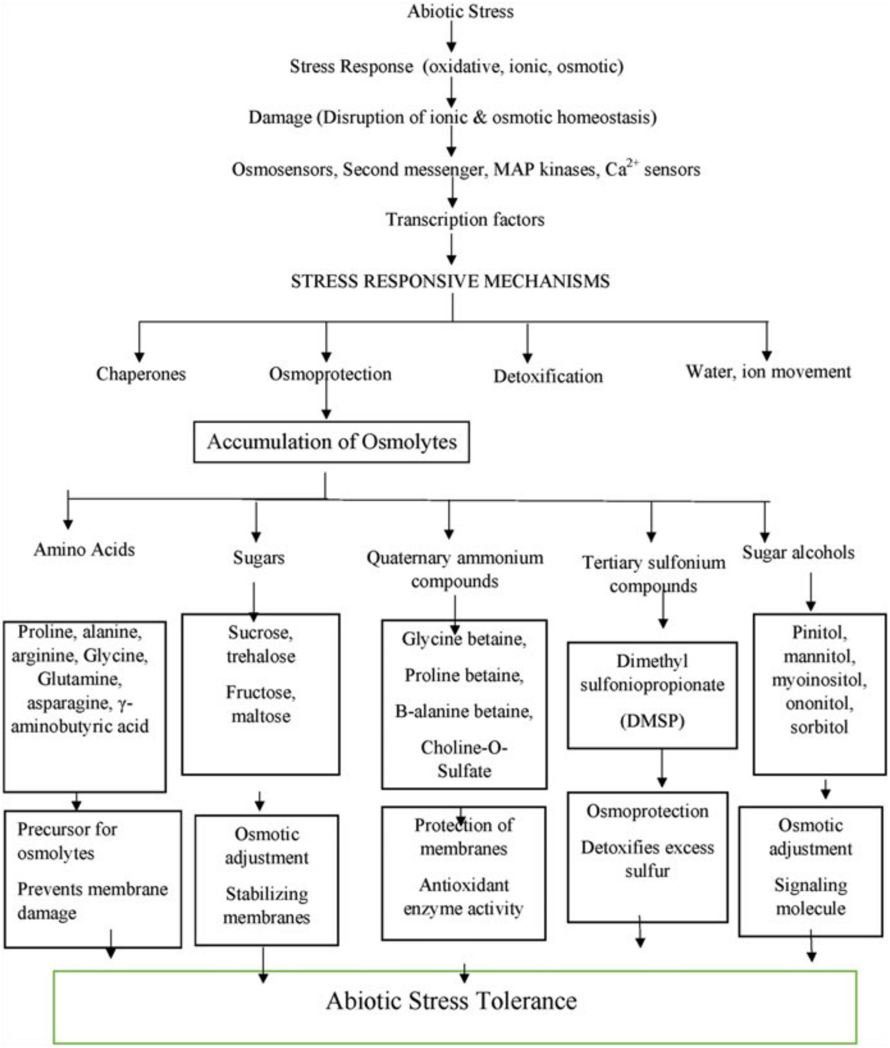

Fig. 1 Schematic overview of the role of various osmoprotectants in improving abiotic stress tolerance in wheat

these noncompatible solutes requires energy and causes no harm to normal metabolic functions even at high cellular concentrations (Salama et al. 2015).

Amino acids such as glycine, arginine (Arg), and proline (Pro) play a central role in improving plant tolerance against various abiotic stresses. Synthesis of Pro involves glutamate and ornithine pathways; however, major Pro accumulation involves glutamate pathway under stress conditions (Ashraf and Foolad 2007). The biosynthetic enzymes involved in Pro synthesis are located in the cytosol of plant cells, whereas the enzymes involved in the catabolism of Pro are localized in mitochondria (Szabados and Savoure 2010). Pro not only serves as an osmolyte but also acts as a protein-compatible hydrotrope to stabilize subcellular structures such as membranes and proteins (Ashraf and Foolad 2007). The positive role of Pro as an antioxidant and ROS scavenger has also been suggested in various studies (Hayat et al. 2012; Hatami et al. 2017). Arginine is involved in nitrogen storage and transport in plants (Witte 2011). The degradation of Arg by arginase induces nitrogen mobilization from source tissues during germination and senescence (Hildebrandt et al. 2015). Decarboxylation of arginine and ornithine results in the synthesis of polyamines (PAs) such as spermine (Spm), spermidine (Spd), and putrescine (Put) involved in specific stress responses in plants (Minocha et al. 2014).

PAs are small, organic molecules that are ubiquitously distributed in all cellular compartments (Minocha et al. 2014). The biosynthesis and catabolism of these metabolites cause major shifts in cellular homeostasis under stress conditions. Increased plant tolerance to a variety of stresses has been linked with enhanced enzymatic activity and overexpression of genes associated with polyamine biosynthesis (Hussain et al. 2011; Shi and Chan 2014). The protective role of PAs is not limited to their function as a compatible solute along with Pro, GB, and polyols (Alet et al. 2011; Gupta et al. 2013). They also interact with translational and transcriptional complexes to stabilize them and are directly involved in the scavenging of reactive oxygen species (ROS) by promoting the activity of antioxidant enzymes (Shi and Chan 2014).

Hydroxyproline betaine, proline betaine, GB, and β-alanine betaine are important quaternary ammonium compounds involved in increasing stress tolerance in plants exposed to drought, salinity, or high temperature stress (Salama et al. 2015). GB is synthesized mainly through the choline pathway that involves the enzymatic action of choline monooxygenase to convert choline to betaine aldehyde, which is then converted to GB by another enzyme, viz., betaine aldehyde dehydrogenase (Fitzgerald et al. 2009). β-Alanine betaine is produced as a consequence of *S*-adenosyl methionine-dependent *N*-methylation of ubiquitous primary metabolite β-alanine (Duhazé et al. 2003). Synthesis of β-alanine betaine from β-alanine has been proposed to be an evolutionary strategy to avoid metabolic competition for choline (Salama et al. 2015). Proline betaine, also called stachydrine, is a dimethyl Pro that accumulates in response to salinization and serves as an effective osmoprotectant (Hanson et al. 1994). Accumulation of methylated Pro in halophytic species of Leguminosae, Capparidaceae, Rutaceae, Myrtaceae, and Plumbaginaceae suggests the protective role of proline betaine in plants (Rhodes and Hanson 1993; Carter et al. 2006).

Disaccharides such as sucrose and trehalose are important water-soluble carbohydrates involved in osmotic adjustment and several other regulatory functions in plants. Sucrose is the main product of photosynthesis and regarded as the key sugar involved in growth, development, and stress acclimation in plants (Keunen et al. 2013). The metabolism of sugars under abiotic stress conditions involves the post-translational upregulation of sucrose-synthesizing enzymes, activation of antioxidant enzymes, and decreased activity of enzymes involved in sucrose-starch partitioning (Rosa et al. 2009). The metabolic pathways involved in trehalose synthesis in plants are characterized by the enzymatic activity of trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP) to synthesize trehalose-6-phosphate and trehalose, respectively (Iordachescu and Imai 2008). Overexpression of trehalose biosynthetic genes (TPS and TPP) has been linked to abiotic stress tolerance in rice (Shima et al. 2007), tobacco (Karim et al. 2007), and *Arabidopsis* (Miranda et al. 2007).

Mannitol and pinitol are important sugar alcohols that not only facilitate osmotic adjustment but also help in redox control. The biosynthesis of mannitol from fructose 6-phosphate involves the subsequent enzymatic activity of mannose-6-phosphate isomerase (MPI), mannose-6-phosphate reductase (MPR), and mannose-1-phosphate phosphatase (MPP) (Loescher et al. 1992). Pinitol is derived from methylation of myoinositol by inositol-*O*-methyltransferase and subsequent epimerization of ononitol by the action of ononitol epimerase (Sureshan et al. 2009).

3 Effect of Exogenous Application of Osmolytes in Wheat Under Abiotic Stresses

Environmental stresses impede wheat performance at morphological, physiological, and molecular level. Alleviation of the negative impact of abiotic stresses in wheat has been a key area of research for agronomists, plant physiologists, and breeders. Many studies have been performed to evaluate the effects of exogenous application of osmolytes in wheat exposed to various abiotic stresses (Table 1). Here, we discuss the potential use of osmolytes in improving abiotic stress tolerance in wheat.

3.1 Drought

Drought stress is one of the major environmental constraints responsible for the decline in wheat productivity, particularly in arid and semiarid regions of the world (Shabbir et al. 2016). Osmotic regulations in wheat during drought stress are associated with increased accumulation of osmoprotective compounds or osmolytes (Farooq et al. 2013; Abid et al. 2018). A sharp increase in Pro contents was correlated with the enhanced activity of antioxidants such as peroxidase (POD),

Table 1 Summary of representative reports on the exogenous application of osmoprotectants in mitigation of various abiotic stresses in wheat

Abiotic stress	Osmolyte (s)	Dose of the osmolyte	Method of application	Effects	References
Drought	Proline	20 and 40 mM	Seed priming	Improved biomass and grain yield	Kamran et al. (2009)
		150 mg L^{-1}	Foliar spray	Enhanced total phenolics, endogenous proline content, and grain yield	Farooq et al. (2017)
	Glycine betaine	50,100, and 150 mM	Foliar spray	Increased water status and yield attributes	Raza et al. (2015)
		10 mM	Foliar spray	Improved yield and total protein, amino acid, and carbohydrate content in grain	Aldesuquy et al. (2012)
	Trehalose	1.5 mM	Foliar spray	Upregulated POX, AAO, and PAL activities	Aldesuquy and Ghanem (2015)
		10 mM	Foliar spray	Increased endogenous proline, total soluble sugars, flavonoids, amino acids, and phenolic content	Ibrahim and Abdellatif (2016)
	Mannitol	10 mM	Seed priming	Increased reducing sugars, relative water contents, and POX activity	Hameed and Iqbal (2014)
	Maltose	10 mM	Foliar spray	Decreased MDA and upregulated POX, PAL, and CAT activities to improve grain yield	Ibrahim and Abdellatif (2016)
	Spermine and putrescine	100 µM	Seed priming and foliar spray	The foliar spray was more effective than seed priming to increase cell water status and upregulate the expression of expression of PA biosynthetic genes	Ebeed et al. (2017)
Salinity	Proline	50 and 100 mM	Foliar spray	Improved biomass, photosynthetic pigments, and endogenous content of proline, glycine betaine, and total soluble sugars	Mahboob et al. (2016)
		50 and 100 mM	Foliar spray	Increased germination percentage, growth, and pigments	Talat et al. (2013)
	Glycine betaine	25, 50, and 100 mM	Seed priming	Decreased MDA and proline content	Salama et al. (2015)
		100 mM	Fertigation	Increased stomatal conductance and net CO_2 assimilation to improve photosynthetic capacity	Khan et al. (2006)

(continued)

Table 1 (continued)

Abiotic stress	Osmolyte (s)	Dose of the osmolyte	Method of application	Effects	References
	Choline	5 and 10 mM	Seed priming	Maintained plasma membrane stability, fluidity, and therefore ion homeostasis	Salama and Mansour (2015)
		5 and 10 mM	Seed priming	Increased glycine betaine, K^{+}, and Ca^{2+} concentrations in roots and shoots to maintain membrane integrity	Salama et al. (2011)
	Spermine	10 mg L^{-1}	Seed priming	Enhanced antioxidant enzyme activities to improve yield	Sakr and El-Metwally (2009)
	Mannitol	100 mM	Seed priming	Increased root length and ROS scavenging	Seckin et al. (2009)
	Gamma-aminobutyric acid	0.5 mM	Foliar spray	Improved germination, photosynthetic capacity, and antioxidant enzyme activities	Li et al. (2016)
Cd toxicity	Proline	1, 5 and 10 mmol L^{-1}	Foliar spray	Increased plant biomass and photosynthetic pigments	Song et al. (2013)
		80 mM	Foliar spray	ROS scavenging and enhanced photochemical quenching, electron transport rate, and productivity of PSII	Noreen et al. (2018)
	Glycine betaine	20 mM	Foliar spray	Increased phenolic content and plant biomass	Rasheed et al. (2014)
		50, 100 mM	Foliar spray	Enhanced photosynthetic pigments and Na^{+} and K^{+} content	Bhatti et al. (2013)
	Spermine and spermidine	2 mM each	Seed priming	Increased starch, proteins, glutathione, and ascorbic acid content and activated antioxidant machinery	Rady and Hemida (2015)
	Melatonin	50 mM	Fertigation	Promoted primary root growth and enhanced the capacity of roots to degrade hydrogen peroxide	Ni et al. (2018)
Cr toxicity	Mannitol	100 mM	Foliar spray	Increased antioxidant enzyme activities to reduce Cr uptake and translocation	Adrees et al. (2015)

Ni toxicity	Glycine, glutamine, and histidine	50 and 100 μM each	Nutrient media	Glycine and glutamine were more effective than histidine to retain Ni in apoplastic or symplastic spaces of roots	Dalir and Khoshgoftarmanesh (2014)
Pb toxicity	Spermine, spermidine, and putrescine	0.25, 0.50, and 1.0 mM, respectively	Seed priming	Putrescine was more effective than other polyamine to improve relative water contents, photosynthetic pigments, and yield attributes	Rady et al. (2016)
High temperature	Arginine and putrescine	1.25 and 2.5 mM each	Foliar spray	Decreased NH^{+4} and ethylene contents and increased the endogenous spermine, putrescine, and total amino acid content	Hassanein et al. (2013)
		1.25 and 2.5 mM each	Foliar spray	Increased antioxidant activities and nucleic acid content	Khalil et al. (2009)
	Putrescine	1.25 and 2.5 mM	Foliar spray	Increased antioxidant activities, tocopherol and ascorbate content in grains	Asthir et al. (2012)
	Trehalose	10 mM	Foliar spray	Increased nonphotochemical quenching (NPQ), β-carotene content, and degree of de-epoxidation (DEPS) of xanthophyll cycle pigments	Luo et al. (2014)
	Citric and oxalic acid	100 and 200 mg L^{-1} each	Foliar spray	Increased indole acetic acid, cytokinin, gibberellic acid, and nucleic acid content	Sadak and Orabi (2015)
Low temperature	Spermidine	0.5, 1.0 and 2.0 mM	Foliar spray	Increased antioxidant enzyme activities to decrease lipid peroxidation, H_2O_2 content, and electrolyte leakage	Abdel Kader et al. (2011)
	Putrescine	0.1, 1.0 and 10 mM	Foliar spray	Enhanced the activities of apoplastic antioxidant enzymes	Çakmak and Atici (2009)
	Gamma-aminobutyric acid	100, 250, 500, and 750 μM L^{-1}		Reduced lipid peroxidation through increased activities of antioxidant enzymes	Malekzadeh et al. (2012)

superoxide dismutase (SOD), and catalase (CAT) to improve drought tolerance in wheat seedlings (Simova et al. 2008). Nazarli and Faraji (2011) observed a significant increase in Pro content of wheat plants grown at 25% field capacity, whereas little or no change was observed in plants at 100% field capacity. Maleki et al. (2010) reported that Pro content in wheat leaves is regulated by genes with additive effects. Intensive Pro accumulation in leaves under stress conditions is correlated with rapid degradation of proteins as well as the conversion of some amino acids such as Arg, glutamic, and ornithine to Pro (Chaitante et al. 1999).

Exogenously applied osmoprotectants regulate endogenous osmolyte concentrations to stabilize proteins and protect cellular compartments from drought-induced oxidative damage (Singh et al. 2015). Pre-sowing treatment of wheat seed with Pro was found effective in improving biomass and yield of different wheat cultivars (Kamran et al. 2009). Recently, Farooq et al. (2017) reported that foliage-applied Pro and gamma-aminobutyric acid (GABA) at pre-optimized rates of 150 and 100 mgL^{-1}, respectively, significantly improved total phenolics, chlorophyll, and Pro content, which helped to maintain grain number and grain weight under drought stress. GABA accumulation facilitates signal transduction with trichloroacetic acid (TCA) cycle, regulates cytosolic pH, and increases antioxidant activity to improve drought tolerance in plants (Yong et al. 2017). Gupta et al. (2014) observed that foliar treatment with GB stimulated the accumulation of Pro, choline, and sucrose in various wheat genotypes. However, accumulation of these metabolites was not correlated with relative water content and stress tolerance index suggesting that osmolyte accumulation could not be considered as a selection tool for drought tolerance. In another study, they reported that exogenous GB application increased total soluble sugars but caused a sharp decline in sucrose synthase and sucrose phosphate synthase activities of wheat genotypes exposed to prolonged field drought stress (Gupta and Thind 2015). Contrarily, Mwadzingeni et al. (2017) demonstrated a positive correlation between wheat grain yield and Pro contents. In a study involving 96 diverse wheat genotypes, higher Pro accumulation in drought-tolerant than drought-sensitive genotypes was positively correlated with stress tolerance index providing evidence that Pro may serve as an effective marker for screening of drought-tolerant genotypes. Likewise, Saeedipour (2013) compared Pro accumulation in drought-tolerant and drought-sensitive wheat genotypes and found that Pro content was higher in drought-tolerant than drought-sensitive genotypes under drought stress suggesting the key role of Pro in breeding for drought tolerance. Raza et al. (2015) observed that combined application of GB with potassium at the milking stage was more effective than each individual application to improve yield attributes of wheat under drought stress. Similarly, Aldesuquy et al. (2012) recommended the combined application of GB and salicylic acid to improve yield and biochemical aspects of wheat grain under water-deficit conditions.

Trehalose is a nonreducing disaccharide that helps to maintain osmotic balance and stabilizes lipid membranes, dehydrated enzymes, and proteins (Alam et al. 2014). Foliar application of trehalose during grain filling stage of wheat induced a significant increase in peroxidase, ascorbic acid oxidase, and phenylalanine ammonia lyase activities to reduce oxidative damage in water-stressed wheat plants

(Aldesuquy and Ghanem 2015). Exogenous application of trehalose and maltose stimulated accumulation of Pro, total soluble sugars, flavonoids, amino acids, and phenolic compounds to improve drought tolerance in wheat. However, supplementation of these osmoprotectants did not influence catalase and phenylalanine ammonia lyase activities (Ibrahim and Abdellatif 2016). An increase in reducing sugar content in wheat leaves raised from seeds primed with mannose and mannitol was reported as an important strategy for osmotic adjustment under drought stress (Hameed and Iqbal 2014). Liu et al. (2016) investigated the effects of exogenous PA supply on hormonal levels of wheat under drought stress. They observed that Put decreased, while free Spm and Spd content increased in grains of water-stressed wheat plants. Additionally, Spm and Spd markedly increased the endogenous ethylene, zeatin + zeatin riboside, and abscisic acid content and decreased ethylene evolution rate to promote grain filling in wheat under drought stress. Hence, it may be concluded that PAs interact with hormones to regulate grain filling in wheat under water-limited environment. Ebeed et al. (2017) showed that seed priming or foliar spray with PAs increased cell water status and upregulated the expression of expression of PA’s biosynthetic genes, viz., *S*-adenosyl methionine decarboxylase, arginine decarboxylase, ornithine decarboxylase, and deoxyhypusine synthase, to improve drought tolerance in wheat. They suggested that foliar spray of Spm and Spm + Put was more effective than seed priming to regulate biosynthetic gene expression in water-stressed wheat seedlings.

3.2 Salinity

Salinity stress is one of the major threats to crop production covering more than 20% of the total irrigated land around the globe (Munns and Tester 2008). It imparts substantial damage to crop plants by decreasing water status, imbalancing ions, degrading proteins, and disrupting membrane integrity (Hasanuzzaman et al. 2013; Kusvuran 2012). Wheat production suffers a significant loss under saline conditions, mainly due to poor germination, reduced availability of nutrients, and poor water status of plants (Oyiga et al. 2016). Plants synthesize and accumulate osmolytes that help to stabilize proteins and maintain osmotic balance under salt stress (Nahar et al. 2016a, b). Improving wheat yields in saline areas is a big challenge for researchers and plant breeders; hence, exogenous application of nontoxic, highly soluble organic compounds commonly known as osmoprotectants is considered as a shotgun, effective strategy to alleviate the damaging effects of salt stress in wheat.

Pro serves as a free radical scavenger, reduces protein carbonylation, and stabilizes membranes under saline conditions (Hoque et al. 2008; Ahmad et al. 2010). Foliar spray of Pro was reported to enhance growth, physiological, and biochemical attributes in two wheat genotypes exposed to saline stress (Mahboob et al. 2016). Pro-induced acclimation to salt tolerance was attributed to improvement in root and shoot length, seedling fresh and dry weight, photosynthetic pigments, as well as K^+ contents and K^+/Na^+ ratio. Moreover, an increase in antioxidant enzyme activity and phenolic content also contributed to tolerance against salinity stress. According to Talat et al. (2013), salt stress significantly reduced photosynthetic pigments, photosynthetic rate, transpiration rate, and stomatal conductance of two wheat genotypes, viz., Sehar-2006 and Lasani-2008. Exogenous Pro application provided protection against salinity-induced oxidative damage by increasing chlorophyll content and net CO_2 assimilation rate in leaves. Pro protects functional units of electron transport chain to enhance the photosynthetic rate and serves as an oxygen radical scavenger to stabilize enzymes such as RuBisCO (Hamilton and Heckathorn 2001).

GB promotes the absorption and translocation of monovalent cations to reduce the toxic effects of salt stress in plants (Cha-Um and Kirdmanee 2010). It plays a key role to reduce Na^+ accumulation and maintain K^+ concentration, thereby improving the surviving percentage of salt-affected plants (Nahar et al. 2016a, b). Wheat seedlings raised from the seeds treated with GB exhibited low MDA and Pro contents and showed elevated levels of glutathione and GB to maintain ion homeostasis under saline conditions (Salama et al. 2015). GB application decreased plasma membrane permeability and cell solute potential to increase salt tolerance in wheat. Khan et al. (2006) reported that exogenous GB application reduces Pro accumulation that contributes to the maintenance of water status and photosynthetic pigments in wheat under salinity stress. Salt stress disturbed the photosynthetic rate and leaf turgor potential of two contrasting wheat genotypes grown in pots. Exogenous GB application increased stomatal conductance and net CO_2 assimilation to improve photosynthetic capacity under salt stress. An increment in K^+ and endogenous GB levels also contributed to osmotic adjustment in salt-affected plants (Raza et al. 2006). In another study, they reported the effects of GB application on the antioxidant machinery of wheat under salinity stress. Foliar spray of GB upregulated the activities of SOD, CAT, and POD to alleviate ROS-induced damages in wheat under saline conditions (Raza et al. 2007).

Choline is an important osmoprotectant that serves as a precursor for phosphatidylcholine, a constituent of membrane phospholipids involved in regulation of ion transport across membranes. Salama and Mansour (2015) found that NaCl affected plasma membrane total lipids, sterol, and phospholipids of salt-sensitive wheat plants. Pretreatment with choline was observed to mitigate NaCl-induced damages on plasma membrane sterol/phospholipid ratio, plasma membrane phosphatidylcholine, phosphatidylglycerol, and diphosphatidylglycerol that helped to maintain plasma membrane stability, fluidity, and therefore ion homeostasis under saline conditions. Wheat seedlings exposed to salt stress significantly reduced fresh mass, dry mass, and relative growth rates. Exogenous choline treatment decreased endogenous Pro, MDA, and glutathione content and increased GB, K^+, and Ca^{2+} concentrations in roots and shoots to maintain membrane integrity in salt-stressed wheat plants (Salama et al. 2011).

The participation of elevated endogenous PA concentrations in improving salt stress tolerance in plants is well reported (Ben Hassine et al. 2009; Alet et al. 2012). Contrasting reports indicating a decrease in PA levels under salt stress are also present (Legocka and Sobieszczuk-Nowicka 2012). Evidence suggests that saline conditions influence endogenous PA concentrations depending on the plant genotype, the developmental stage of tissues, and the duration and intensity of stress treatment (Liu et al. 2007). Mansour et al. (2002) examined the effects of PA pretreatment on salt-stressed wheat plants and found Put- and Spd-mediated decrease in saturated fatty acids and ratio of membrane sterol/phospholipids that significantly contributed to the maintenance of plasma membrane stability. The effects of exogenous spermine on growth and yield of wheat were investigated during salinity stress (Sakr and El-Metwally 2009). Spermine application alleviated the negative effects of salt stress, mainly due to increased protein and endogenous PA content. The conversion of Put to Spm and Spd increases H^+-PPase and H^+-ATPase activities in roots to improve salt tolerance in plants (Liu et al. 2006). Catabolism of Put to GABA influences PA biosynthetic enzymes involved in increasing abiotic stress tolerance in plants (Shelp et al. 2012). The synthesis and accumulation of GABA played a protective role in plants against various stresses by increasing the stability of plasma membranes and upregulation of antioxidant machinery. Li et al. (2016) showed that foliar spray of GABA increased germination rate, photosynthetic activity, and activities of antioxidant enzymes in wheat seedlings grown under saline conditions. GABA-induced reduction in malondialdehyde (MDA) contents and electrolyte leakage helped to maintain phospholipids and plasma membrane stability. A marked increase in root length and antioxidant enzyme activities was also recorded in wheat seedlings raised from mannitol-treated seeds (Seckin et al. 2009). The authors suggested that mannitol acts as a stress-induced ROS scavenger to increase salt stress tolerance in plants.

3.3 Metal Toxicity

Heavy metal (HM) toxicity imparts severe damage to wheat at the physiological, biochemical, and cellular level. It induces chlorosis in young leaf tissues, impairs photosynthesis, damages root cells, and disrupts enzymatic functions (Panda and Choudhury 2005). Overproduction of ROS in metal-stressed plants results in peroxidation of various cell constituents, consequently damaging macromolecules such as proteins, lipids, and nucleic acid (Singh et al. 2016). Although wheat is not recommended for phytoextraction of HMs (Brunetti et al. 2012), the uptake and accumulation of HMs such as chromium (Cr), arsenic (As), cadmium (Cd), mercury (Hg), copper (Cu), and nickel (Ni) in wheat pose serious health risks to humans consuming agricultural products (Khan et al. 2015). The highest levels of HMs in wheat had been observed in roots, followed by the leaves and stem (Al-Othman et al. 2016).

It is well reported that exogenous application of osmolytes plays a critical role to prevent denaturation of proteins, stabilize enzymes, and maintain membrane integrity in plants exposed to metals toxicity (Szabados and Savoure 2010; Aggarwal et al. 2011). A gradual increase in plant biomass, leaf chlorophyll, and carotenoid contents was reported in wheat seedlings sprayed with Pro under Cd stress (Song et al. 2013). The enhanced tolerance to Cd toxicity was attributed to Pro-induced increase in SOD activity that markedly reduced lipid peroxidation and Cd accumulation in leaves. Foliar treatment of wheat with Pro reduced the generation of ROS and enhanced the photochemical quenching, electron transport rate, and productivity of PSII under Cd stress. Accumulation of endogenous Pro and activation of antioxidant enzymes helped to protect cellular proteins in wheat plants exposed to Cd toxicity (Noreen et al. 2018). Rasheed et al. (2014) reported a marked increase in plant biomass and phenolic content in Cd-stressed wheat seedlings treated with Pro and GB. It was observed that foliar spray of Pro was more effective than GB to reduce degradation of photosynthetic pigments and cellular proteins. In a study involving two wheat genotypes, viz., Sehar 2006 and Chakwal-97 subjected to Cd toxicity, foliar application of GB significantly enhanced photosynthetic pigments and Na^+ and K^+ content to alleviate the damaging effects of Cd in wheat seedlings (Bhatti et al. 2013). In a greenhouse study, foliar application of ascorbic acid was observed to significantly increase the photosynthetic pigments, seed weight, and seed yield of wheat plants exposed to Cd toxicity (Reza and Moghadam 2016). Wang et al. (2017) reported that ascorbic acid-mediated endogenous NO production stimulated root length to enhance tolerance in wheat seedlings exposed to cadmium stress.

Amino acids serve as chelating agents to form complexes with metal ions at root-soil interface. These complexes, formed mainly through carboxylate (–COO) and amine ($–NH_2$) groups, significantly affect the bioavailability of metals to plants (Nowack et al. 2006). Exogenous application of amino acids (glycine, glutamine, and histidine) retained or immobilized large proportion of Ni in apoplastic or symplastic space of wheat roots exposed to Ni (Dalir and Khoshgoftarmanesh 2014). It was observed that histidine resulted in more root to shoot translocation of Ni compared to other amino acids, whereas glycine and glutamine were more effective than histidine to retain Ni in apoplastic or symplastic spaces of roots. Glycine cysteine, glutamate, and phenylalanine act as signaling amino acids to enhance the activities of resistance enzyme such as polyphenol oxidase and phenylalanine ammonia lyase (Teixeira et al. 2012).

The antagonistic effects of PAs on metal ions are extensively reported in the literature (Wang et al. 2007; Hussain et al. 2011). Exogenous application of Spm and Spd was reported to enhance Cd tolerance in wheat through increased water status, maintenance of membrane integrity, and activation of antioxidant machinery. Moreover, increased concentrations of starch, proteins, glutathione, and ascorbic acid were also recorded in seedlings treated with either Spm or Spd (Rady and Hemida 2015). Aldesuquy et al. (2014) found that Spm + Spd treatment was more effective than their applications to increase water use efficiency and yield attributes in wheat irrigated with wastewater. The combined application of these PAs also mitigated the HM-induced reduction in phosphorus, proteins, and starch content in wheat grains. Rady et al. (2016) conducted a comparative study involving pretreatment of wheat seeds with Spm, Spd, and Put to improve tolerance against Pb stress. Although soaking of seeds in different PA solutions markedly improved relative water contents, photosynthetic pigments, and yield attributes, Put seed priming was more effective than other PAs to confer tolerance against Pb stress.

MEL is a pleiotropic molecule that acts as a bio-stimulator to regulate plant growth under various environmental stresses (Li et al. 2016; Ding et al. 2017). Recently, Ni et al. (2018) reported the protective role of MEL in the regulation of antioxidant enzymes to counterbalance the hydrogen peroxide homeostasis in Cd-stressed wheat plants. MEL application not only promoted primary root growth but also enhanced the capacity of roots to degrade hydrogen peroxide. Similarly, mannitol is a low molecular weight osmolyte that is well known for its ability to search free radicals to reduce oxidative stress in plants except for wheat, which normally cannot synthesize mannitol (Mitoi et al. 2009; Khare et al. 2010). Exogenous mannitol application, however, has been reported to alleviate Cr toxicity in wheat (Adrees et al. 2015). It was observed that foliar spray of mannitol markedly decreased Cr uptake and translocation through increased activities of antioxidant enzymes in 4-week-old wheat seedlings.

3.4 High or Low Temperature

Wheat productivity is limited in areas of high temperature due to its sensitivity to elevated temperatures (Modarresi et al. 2010). Exposure to high temperature at the vegetative stage causes reduction in CO_2 assimilation and degradation of photosynthetic pigments. At reproductive stage, it leads to floral abortion or early floral initiation, early spike development with less number of spikelets, and reduced grain size that ultimately affects the crop yield (Wahid et al. 2007). The sensitivity of photosynthetic pigments and inhibition of chloroplast functioning at high temperature are considered to be the main reason for reduced seedling growth and leaf development in wheat at elevated temperature (Efeoglu and Terzioglu 2009).

Accumulation of compatible solutes is one of the prime defense strategies of wheat to organize proteins and other cellular structures in response to high or low temperature stress. Exogenous application of osmolytes with growth-promoting and antioxidative properties has been shown beneficial to reduce the damaging effects of temperature injury in wheat. Foliar treatment of wheat with Arg or Put reduced the injurious effects of heat stress by decreasing the NH^{4+} and ethylene contents and increased the endogenous Spd, Put total amino acids, and total PAs compared to untreated plants (Hassanein et al. 2013). Khalil et al. (2009) reported increased antioxidant activities and nucleic acid content in wheat plants treated with Put or Arg before exposure to a high temperature of 35 °C. High temperature-induced catabolism of PAs increased endogenous Spm and Spd content and reduced Put levels in five wheat genotypes. Increased antioxidant activities correlated with higher Pro content in shoots than roots of wheat plants exposed to heat stress (Goyal and Asthir 2010). In a later study, they found that application of Put to wheat seedlings or detached tillers exposed to an elevated temperature of 45 °C enhanced peroxidase (POX) and superoxide dismutase (SOD) activities and increased tocopherol and ascorbate content in grains. Higher SOD and POX activities were recorded in roots, whereas CAT, polyamine oxidase (PO), and diamine oxidase (DAO) activities were higher in shoots (Asthir et al. 2012).

Maltose accumulation during grain filling stages facilitates phenylalanine ammonia lyase (PAL), and polyphenol oxidase (PPO) activates to reduce stress injury in plants (Ibrahim and Abdellatif 2016). Induction of β-amylase stimulates maltose accumulation to stabilize proteins and membranes and protect electron transport chain in the chloroplast stroma in response to heat stress (Kaplan and Guy 2004). Luo et al. (2014) reported the protective role of trehalose pretreatment for thylakoid membrane proteins and photosynthetic capacity of wheat seedlings subjected to heat stress. They observed trehalose-induced increase in nonphotochemical quenching (NPQ), β-carotene content, and degree of de-epoxidation (DEPS) of xanthophyll cycle pigments in wheat seedlings exposed to high temperature of 40 °C. Interestingly, trehalose application decreased chlorophyll content and did not affect maximum chlorophyll *a* fluorescence ratio (F_v/F_m) of wheat. Exogenous application of citric or oxalic acid was observed to improve thermo-tolerance in wheat by increasing indole acetic acid, cytokinin, gibberellic acid, and nucleic acid content (Sadak and Orabi 2015).

Low temperature stress, on the other hand, induces oxidative damage to proteins, lipids, and other macromolecules (Çakmak and Atici 2009). Chilling injury alters membrane structure and lipid composition, stimulates the production of ROS, and induces cellular leakage of amino acids and electrolytes (Abdel Kader et al. 2011). Reports regarding the effects of exogenously applied osmoprotectants to improve cold stress tolerance in wheat are scant. Abdel Kader et al. (2011) studied the effects of exogenous spermidine in two wheat cultivars subjected to chilling stress. They found that spermidine pretreatment counteracted the chilling-induced damages through enhanced activities of SOD, CAT, POD, and APX to decrease lipid peroxidation, H_2O_2 content, and electrolyte leakage. Similarly, Çakmak and Atici (2009) reported that Put application markedly increased the activities of apoplastic antioxidant enzymes in wheat exposed to cold stress. Exogenous GABA treatment reduced the negative effects of chilling stress in wheat. High antioxidant enzyme activities and reduced lipid peroxidation contributed to improved tolerance against cold stress (Malekzadeh et al. 2012).

4 Conclusion

In spite of many studies on the protective role of osmolytes in crop plants exposed to stressful conditions, our understanding of the use of osmolytes in improving abiotic stress tolerance in wheat largely remains mysterious. This book chapter is an attempt to address the regulatory mechanisms mediated by the exogenous application of osmolytes in wheat. We have tried to uncover the role of these low molecular weight organic compounds in upregulating antioxidant machinery and improving the endogenous content of other protective compounds. Undoubtedly, our understanding of osmoprotectant-mediated defense mechanisms has increased in the past decade; further studies are needed to explore their interplay with stress signaling molecules like NO and H_2O_2. Moreover, the identification of novel genes expressed by these osmolytes in plants exposed to a combination of stresses, such as those in field environments, is crucial to properly explain the regulatory mechanisms of these protective compounds. Future studies in this direction will no doubt reveal novel regulatory mechanisms for osmolytes and their interaction with stress signaling molecules and phytohormones; hence the future of osmolyte research is very promising.

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Induction of Wheat Plant Resistance to Stressors by Donors of Nitric Oxide and Hydrogen Sulfide

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Contents

Abstract The phenomenology and mechanisms of induction of resistance of wheat plants against stress temperatures, drought, salinity, and other adverse abiotic factors by the action of donors of signal molecules – nitric oxide (NO) and hydrogen sulfide (H_2S) – are considered. The ways of synthesis of NO and H_2S in plant cells are briefly described. The participation of other signal mediators (in particular, reactive oxygen species (ROS) and calcium ions) is analyzed in the realization of stress-protective effects of exogenous NO and H_2S. The data on change in the endogenous content of NO and H_2S in plants under the action of stressors are analyzed. Attention is focused on the effect of these signal molecules on the state of antioxidant and osmoprotective systems, activation of which defines the development of resistance of wheat plants to stressors of different natures.

Keywords *Triticum* · Nitric oxide · Hydrogen sulfide · Reactive oxygen species · Abiotic stress · Signaling · Antioxidant system · Adaptation

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Abbreviations

ABA	abscisic acid
APX	ascorbate peroxidase;
CAT	catalase
cGMP	cyclic guanosine monophosphate
DMTU	dimethylthiourea
EGTA	ethylene glycol-bis(2-aminoethyl ether)-N,N,N′,N′-tetraacetic acid
FAD	flavin adenine dinucleotide
FMN	flavin mononucleotide
$GS(O)NH_2$	glutathione sulfonamide
GSH	reduced glutathione
GSNO	S-nitrosoglutathione
GSSG	oxidized glutathione
H_2S	hydrogen sulfide
L-NAME	N^G-nitro-L-arginine methyl ester
MAP kinase	mitogen-activated protein kinase
MDA	malondialdehyde
NADH	nicotinamide adenine dinucleotide
NADPH	nicotinamide adenine dinucleotide phosphate
NO	nitric oxide;
NOS	nitric oxide synthase
$ONOO^-$	peroxynitrite
PEG	polyethylene glycol
POX	peroxidase
PTIO	2-phenyl-4,4,5,5-tetramethylimidazoline-l-oxyl-3-oxide
RNS	reactive nitrogen species
ROS	reactive oxygen species
SNP	sodium nitroprusside
SOD	superoxide dismutase

1 Introduction

To increase the resistance of cultivated plants to the action of adverse factors of different nature (stressors), along with the methods of classical breeding and genetic engineering, in recent decades, the method of prestress treatment with compounds that induce protective systems has become increasingly popular. This approach is called "priming" (synonym for sensitization). Priming produces effects that are largely similar, for example, to natural plant hardening processes, which allow them to adapt to extreme temperatures and other adverse factors (Savvides et al. 2016). After exposure to priming compounds, the plant turns in the condition when the activation of protective responses to stress factors occurs faster and/or is shown more considerably than in non-primed plants (Filippou et al. 2013). The mechanisms of these phenomena are not yet fully understood, but on the whole, they are due to the activation of the signal network preceding the action of the stressor.

For priming, various compounds and ions, involved in the cellular signaling, can be used: signal mediators (Ca^{2+}, hydrogen peroxide (H_2O_2), nitric oxide (NO), hydrogen sulfide (H_2S), etc.) (Jiang and Huang 2001; Song et al. 2006; Savvides et al. 2016), stress phytohormones (salicylic acid, jasmonic acid, brassinosteroids, etc.) (Gémes et al. 2011; Wasternack and Hause 2013; Fariduddin et al. 2014), and some metabolites (e.g., polyamines) (Tanou et al. 2014).

In recent years, considerable attention is paid to the investigation of the physiological role of so-called signal gasotransmitters – gaseous signal molecules that can be perceived by cells and also participate in transduction of signals from the environment in different groups of organisms, including plants (Jin et al. 2016; Zhang 2016). This group of molecules includes carbon monoxide (CO), NO, and H_2S. The study of physiological effects of the last two gasotransmitters is of particular interest both for understanding the fundamental mechanisms of formation of adaptive plant responses and for developing practical methods for priming plants since there are stable and inexpensive donors of these compounds.

At present, the nature of some protective reactions, developing with the participation of NO and H_2S in plants of different species, has been established. The main amount of information on the mechanisms of transduction of stress signals of these mediators was obtained in experiments using *Arabidopsis*. At the same time, it seems obvious that physiological responses associated with resistance are quantitatively and qualitatively unequal in plants of different species. As is known, synthesis of nitrogen oxide in plants is carried out in several ways (Mur et al. 2013), wherein their contribution essentially depends on the specific features of plants. Synthesis of H_2S and transduction of its signal into genetic apparatus have been studied mainly in *Arabidopsis* and tobacco plants (L'eon et al. 2002; Lisjak et al. 2013; Guo et al. 2016). The peculiarities of its action in monocotyledonous and, in particular, in wheat, are of practical interest as well as fundamental.

In connection with the preceding, the purpose of our work was to analyze and summarize the information available in the literature, as well as our data on the mechanisms of stress-protective action of nitrogen oxide and H_2S in wheat plants. The connection of these gasotransmitters with other signal mediators is considered, specific protective reactions induced by NO and H_2S donors, and their contribution to the formation of resistance to abiotic stressors are characterized.

2 Nitric Oxide

Nitrogen monoxide (NO) – a lipophilic molecule that can easily diffuse through membranes – is the main representative of reactive nitrogen species (RNS). As a free radical, NO has a high reactivity and can be converted to other RNS – NO^- (nitroxyl anion), NO^+ (nitrosonium cation), $ONOO^-$ (peroxynitrite), ONOOH (peroxynitrous acid), NO_2^- (nitrite anion), NO_3^- (nitrate anion), N_xO_x (various non-radical nitric oxides), and also products of nitrosylation and nitration, which are included into the group of reactive nitrogen species too (del Rio 2015). A feature of NO action in biological systems is a posttranslational modification of proteins: tyrosine nitration and S-nitrosylation (Antoniou et al. 2016; Farnese et al. 2016). The proteins of signaling systems, enzymes regulating the content of ROS and the RNS in cells, various protein kinases and protein phosphatases, and transcriptional factors can be targets of such modifications.

NO functions in plants have been specifically studied since 1998 (Delledonne et al. 1998; Durner et al. 1998). It has been established that as an important intra- and intercellular signaling molecule, NO participates in regulation of cell cycle of plant cells, seed germination processes, de-etiolation, rhizogenesis (Correa-Aragunde et al. 2004; Wilson et al. 2008), and plant interactions with symbionts (Glyan'ko and Vasil'eva 2010; del Giudice et al. 2011) and pathogens (Mamaeva et al. 2015). It is shown that NO is involved in transduction of signals stimulating synthesis of phytohormones, in particular, ethylene (Wilson et al. 2008), abscisic acid (ABA) (Xing et al. 2004), and auxin (Tewari et al. 2008). Recently the special role is assigned to NO in the processes of adaptation of plants to the action of abiotic stressors of various natures, including hypo- and hyperthermia, excessive lightning, ultraviolet, salinity, and heavy metals (Zhang et al. 2006; Xu et al. 2010; Krasylenko et al. 2012; Karpets et al. 2015a).

2.1 Nitric Oxide Synthesis in Plants

Synthesis of NO in plants is still the subject of discussion (Mur et al. 2013). L-arginine and nitrate/nitrite-dependent are considered as the main pathways (Glyan'ko et al. 2012; Mur et al. 2013) (Fig. 1). It is assumed that the L-arginine-dependent pathway of NO synthesis is analogous to that in animal cells. However, until now, the homologues of animal NO synthase (NOS) have been detected only in green algae but not in higher plants (Roszer 2014). At the same time, there is a reason to believe that higher plants have proteins that can generate NO in cooperation, using L-arginine as a substrate. This reaction, as well as catalyzed by animal NO synthase, occurs in the presence of NADPH, FMN, FAD, calmodulin, and calcium ions (Corpas and Barroso 2017).

In favor of the existence of L-arginine-dependent NO formation in plants, a lot of facts are evidenced about the inhibition of its synthesis and many NO-dependent processes by inhibitors of NOS in plants (Crawford 2005). There are experimental data indicating the presence of an enzymatic system similar to animal NOS in chloroplasts, mitochondria, and peroxisomes (Farnese et al. 2016).

Some indirect information was obtained indicating the presence of L-arginine-dependent NO formation in wheat plants too. An increase in NO content in roots of wheat seedlings, induced by the influence of short-term high temperature or by treatment with H_2O_2, was suppressed by the inhibitor of animal NO synthase

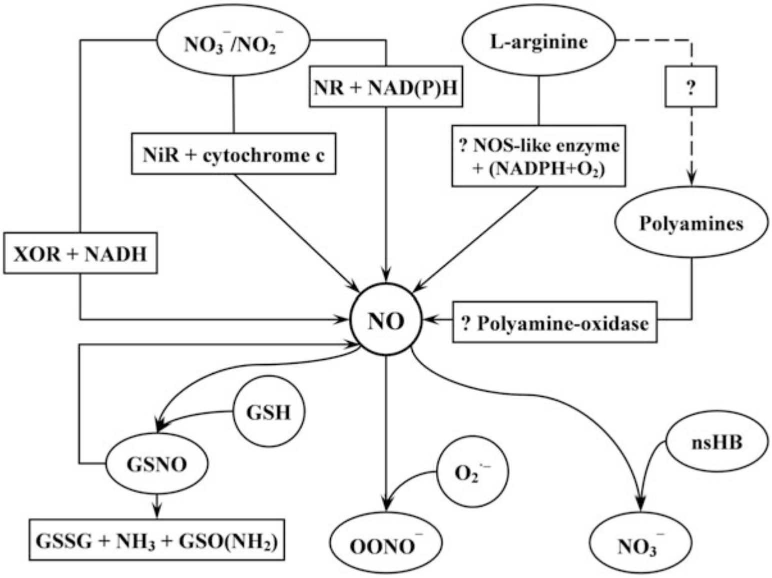


Fig. 1 Possible pathways of synthesis and scavenging of nitric oxide in plants. GSH, reduced glutathione; GSSG, oxidized glutathione; GSNO, S-nitrosoglutathione; GS(O)NH_2, glutathione sulfonamide; NADH, nicotinamide adenine dinucleotide; NADPH, nicotinamide adenine dinucleotide phosphate; NiR, nitrite reductase; NOS, nitric oxide synthase; NR, nitrate reductase; nsHB, nonsymbiotic hemoglobin; $ONOO^-$, peroxynitrite; XOR, xanthine oxidase reductase

L-NAME (N^G-nitro-L-arginine methyl ester) (Karpets et al. 2015a, 2016). However, these results cannot be unambiguously associated with the formation of NO precisely as a result of L-arginine oxidation by the enzyme with activity similar to animal NOS. Thus, polyamine oxidase, which is involved in the degradation of polyamines, is considered one of the possible enzymes that catalyze the formation of NO. Its activity in *Arabidopsis* plants decreased in the presence of NOS inhibitor L-NAME (Flores et al. 2008).

The treatment of wheat roots with L-arginine caused the increase of the content of NO in them. This effect was eliminated by pre-treatment of seedlings with L-NAME (Karpets et al. 2018). However, this result cannot also be interpreted as the proof of formation of NO directly due to the oxidation of L-arginine, since it is shown that in leaves of wheat plants L-arginine can be converted into polyamines, which are considered as one of possible sources of NO (Rosales et al. 2012) (Fig. 1). Polyamines can be oxidized to NO by polyamine oxidase, which, as already noted, is sensitive to the action of L-NAME (Flores et al. 2008). Thus, the mechanism of formation of NO from L-arginine in higher plants is not completely known.

At the same time, the experimental data are obtained on the significant (possibly dominant) contribution of the pathway of nitrate reduction with the participation of nitrate reductase in the NO synthesis (Shi and Li 2008; Mur et al. 2013). The nitrate reductase activity, involved in the synthesis of NO in plant cells, is mainly found in the cytosol (Farnese et al. 2016).

An increase in the content of NO, dependent on the activity of nitrate reductase, in leaves (Galeeva et al. 2012) and roots (Karpets et al. 2018) of wheat is shown. This effect is caused by the processing of plant objects with exogenous nitrate or nitrite.

Nitrite-NO-reductase, found in the plasma membrane, can be another source of nitrogen monoxide in plant cells (Fig. 1). This enzyme, unlike nitrate reductase, uses not NADPH as a cofactor but cytochrome c as an electron donor and functions in the relatively narrow pH range (Neill et al. 2008). Its physiological role and genetic identity are not yet known. Also, its role in the synthesis of NO in wheat has not been studied. NO synthesis can also be carried out by xanthine oxidoreductase localized in peroxisomes (Corpas et al. 2008). However, there is no information on its role in the synthesis of NO in wheat plants.

Between different ways of synthesis of NO, a complex functional interaction is present. Thus, the stimulating effect of inhibitors of NO production, dependent on L-arginine (L-NAME and D-arginine), on nitrate reductase activity in wheat leaf segments was shown (Rosales et al. 2011). In our experiments, the leveling of the physiological effects of nitrate and L-arginine by the joint treatment of wheat seedlings was demonstrated. L-arginine significantly reduced the nitrate-induced increase in nitrate reductase activity and NO content in roots (Karpets et al. 2018).

The content of NO in plant cells depends not only on its synthesis but also on the functioning of utilization mechanisms (Fig. 1). The most significant pool of NO is S-nitrosoglutathione (GSNO). NO can react with glutathione (GSH) with the formation of GSNO, which in turn can again serve as an NO donor in the cell. GSNO content is regulated by S-nitrosoglutathione reductase, reducing GSNO to glutathione sulfinamide (GS(O)NH_2) using NADH (Gupta et al. 2011) (Fig. 1). The binding of NO nonsymbiotic forms of hemoglobin and transformation into nitrate is considered as one more effective process of its excess neutralizing (Corpas et al. 2008). Also, the part of NO pool can react with superoxide anion radical and turn into toxic peroxynitrite ($OONO^-$) (Freschi 2013) (Fig. 1).

2.2 *Nitric Oxide Signal Transduction*

The mechanisms of transduction of NO signal in plant cells are not completely understood. It is believed that in them, as it is in animal cells, cGMP appears as one of the signal mediators between NO and genome (Wilson et al. 2008). It is formed from GTP with the help of soluble cytoplasmic heterodimeric guanylate cyclase. About 15 years ago, there was information about the presence of soluble protein AtGC1 (Guanylyl Cyclase1) in *Arabidopsis* with the sites that are typical for the catalytic domains of soluble guanylate cyclase of cyanobacteria and higher and lower eukaryotes (Ludidi and Gehring 2003). However, despite the structural similarity to the soluble guanylate cyclase of animals and bacteria, the AtGC1 protein does not have the ability to bind NO (Ludidi and Gehring 2003). A later homologue

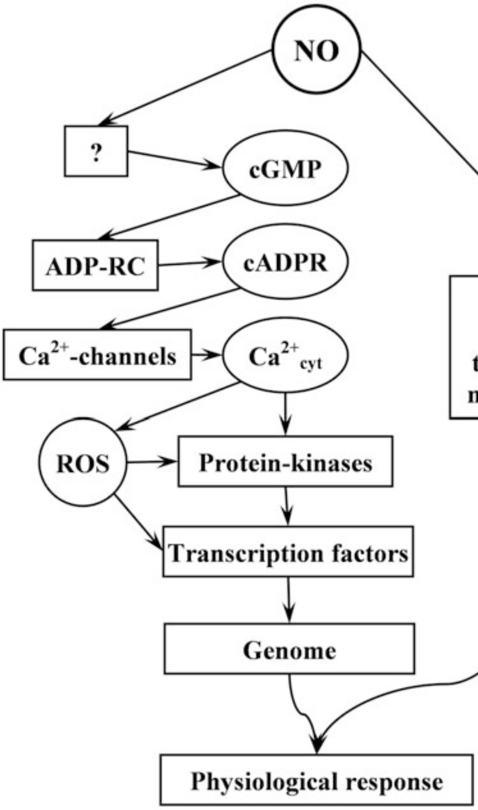


Fig. 2 NO signal transduction into genetic apparatus in plant cells. ADP-RC, ADP-ribosyl cyclase; cADPR, cADP-ryboze; cGMP, cyclic guanosine monophosphate; ROS, reactive oxygen species

of soluble guanylate cyclase was detected in green alga *Chlamydomonas reinhardtii* (de Montaigu et al. 2010), but attempts to identify it in higher plants have not yet succeeded (Baudouin 2011). However, many studies, in particular, those performed with inhibitor analysis, have shown a link between NO and cGMP as components of signal transduction in plants (Bakakina et al. 2011; Baudouin 2011) (Fig. 2). However, the mechanisms of this connection are still unknown.

An accumulation of cGMP induces activation of ADP-ribosyl cyclase and increase in cells of another signal mediator, cADPR, whose action is associated with stimulation of intracellular calcium channels and an increase of calcium influx into the cytosol, which leads to activation of calcium-dependent protein kinases (Neill et al. 2008) (Fig. 2). It is shown that NO donors promote to increase the content of cytosolic calcium in plant cells (Lamotte et al. 2004). It is assumed that in this effect the different calcium pools and different types of calcium channels can be involved, since calcium “peaks” were suppressed to varying degrees by treatment of plant cells with external calcium chelator EGTA, blockers of calcium channel sensitive to inositol-1,4,5-phosphate, and calcium channels regulated by cADP-ribose (Lamotte et al. 2006).

The effect of NO on the content of cGMP and calcium ions as possible mediators in cells was studied mainly using *Arabidopsis* and tobacco plants. However, indirect data indicating the involvement of intracellular calcium into the realization of NO effects have also been obtained in wheat plants. Thus, it was shown that the increase in the formation of H_2O_2 in wheat root cells induced by the donor of NO SNP was partially inhibited by external calcium chelator EGTA, an inhibitor of phosphatidylinositol-specific phospholipase C neomycin, and inhibitor of ADP-ribosyl cyclase nicotinamide (Karpets et al. 2016). These compounds to some extent leveled the effect of increasing the heat resistance of wheat seedlings caused by SNP treatment. Thus, it is possible to assume the participation of calcium, entering the cytosol from both external and intracellular compartments, in the realization of physiological effects of NO.

ROS, in particular, H_2O_2, generation of which, as noted above, is enhanced in plant cells under the influence of exogenous NO (Fig. 2), are necessary for the realization of its stress-protective action. Antioxidants dimethylthiourea (DMTU) and butylhydroxytoluene prevented the appearance of the protective effect of SNP on wheat seedlings under heat stress (Karpets et al. 2016). Thus, it can be assumed that ROS are components in the system of NO signal transduction (Fig. 2).

One of the mechanisms for the realization of signal functions of NO can be its direct interaction with proteins (Fig. 2). Protein modifications, caused by NO, include mainly *S*-nitrosylation, nitration of tyrosine residues, and metal-nitrosylation (Astier and Lindermayr 2012).

S-Nitrosylation is the reversible binding of NO with a sulfur atom, resulting in the formation of S-nitrosothiol (–SNO) (Fig. 3). This process is non-enzymatic, and the degree of S-nitrosylation depends on the reactivity of nitrosylating agent and oxidation-reduction potential of microenvironment (Arora et al. 2016). It is very selective, usually limited to specific cysteine residues, a posttranslational modification of proteins. It is believed that it is one of the mechanisms for the rapid perception of cellular signals and adaptation to the changes in environmental conditions (Arora and Bhatla 2015).

Protein tyrosine nitration consists in the addition of a nitro group ($–NO_2$) into tyrosine residue (usually in *ortho*-position of the phenolic hydroxyl group), which leads to the formation of 3-nitrotyrosine (Radi 2004) (Fig. 3). Peroxynitrite, which is synthesized in the reaction of NO with superoxide anion radical, appears as a nitration agent (Freschi 2013). Tyrosine nitration of proteins can lead to both activation and inhibition of target protein activity (Arora et al. 2016).

Nitrosylation of metal-containing proteins occurs during an interaction of NO with ions of transition metals in metalloproteins and leads to the formation of metal-nitrosyl complexes (Fig. 3). NO can bind to various metal centers (Fe, Cu, Zn) of metalloproteins (Ford 2010; Arora et al. 2016). Formation of metal-nitrosyl complexes causes reversible conformational changes in proteins and changes their structure and/or functional activity (Cooper 1999; Kaur and Kaur 2018).

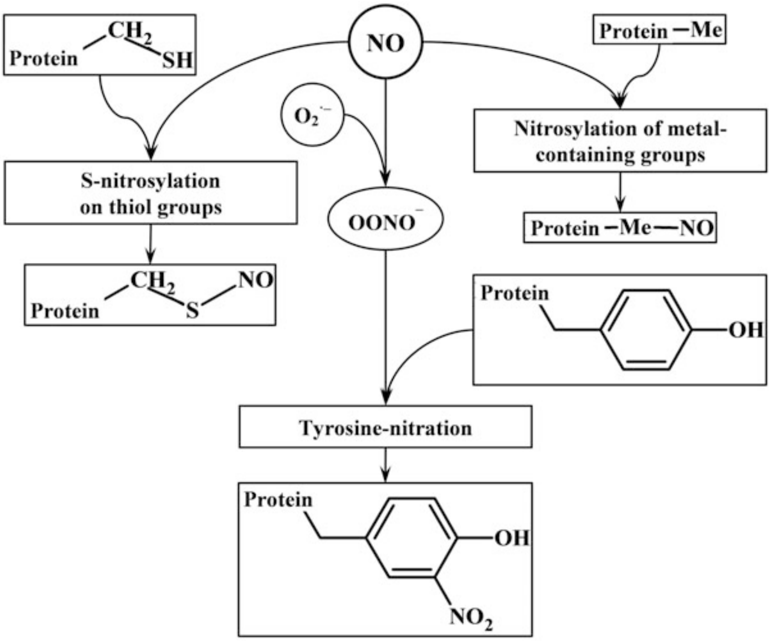


Fig. 3 Posttranslation modification of proteins with the participation of nitric oxide and ROS

2.3 *Changes in Nitric Oxide Content in Wheat Plants Under the Action of Abiotic Stressors*

In a number of studies, the increase in endogenous NO content in plants of different species, including wheat, was recorded in response to stressors of various natures. Thus, the increase in NO content in wheat roots was observed under the conditions of moderate osmotic stress caused by PEG treatment (Kolbert et al. 2005). Short-term heating of wheat seedlings (42 °C, 1 min), which induces the subsequent increase in their resistance to damaging influence, also caused the increase in NO content in roots within 2 hours (Karpets et al. 2015a). At the same time, the content of H_2O_2 also increased in the roots of seedlings (during the first 30 min after heating). The increase in NO content in roots after heat hardening was eliminated by their treatment with antioxidants (butylhydroxytoluene and DMTU) (Karpets et al. 2015a). The amount of NO in roots of wheat plants also increased in response to the action of aluminum salts (Sun et al. 2018). This effect also appeared to be dependent on a preliminary increase in H_2O_2 content in cells. It can be assumed that H_2O_2 in signal transduction network is located upstream in point of NO. However, the increase in H_2O_2 content in wheat roots caused by heat hardening was leveled by their treatment with NO scavenger PTIO and NOS inhibitor L-NAME (Karpets et al. 2015a). In this connection, it can be assumed that at least some effects of NO and H_2O_2 are realized cooperatively.

A lot of effects of increasing of NO content under the action of stressors of different nature were shown for plants of other species. Thus, under the influence of dehydration, the content of NO increased in mesophyll cells of maize leaves (Sang et al. 2008) and in roots of parsley and pea (Kolbert et al. 2005).

The increase in NO content in cells caused by the moderate action of stressors, generally, is reversible, which corresponds to the perception of NO as a signal molecule.

2.4 Effect of Nitric Oxide Donors on Resistance of Wheat Plants to Abiotic Stressors

The action of exogenous NO donors on resistance of plants of different taxonomic groups has been actively studied for almost two decades. A lot of effects have been studied with the use of wheat plants or their isolated organs. Thus, it has been shown that soaking of seeds of spring wheat with 0.1 mM SNP solutions caused an increase in their resistance to hypothermia (Bibi et al. 2017). Treatment of 8-day wheat plants with 0.25 mM SNP increased their resistance to subsequent heat stress (Hasanuzzaman et al. 2012). The effects of increasing resistance to damaging heating by incubation in solutions of SNP were also shown in experiments with etiolated seedlings and isolated wheat coleoptiles (Karpets et al. 2011, 2016).

In many studies, an increase in resistance of wheat plants to osmotic stress was shown under the influence of NO donors. Thus, the resistance of young wheat plants to osmotic stress caused by PEG increased under the influence of SNP and GSNO (Tan et al. 2008; Khan et al. 2014). Also, the ability of SNP (0.5 mM) to enhance germination of wheat seeds in a medium supplemented with PEG (Zhang et al. 2003) was also revealed.

The effect of NO donors on resistance to drought in conditions close to natural remains less investigated. We have shown the easing of growth inhibitory effect of soil drought on wheat plants by the spraying with 0.5 or 2 mM solutions of NO donor SNP (Kolupaev et al. 2018).

Quite a lot of works are devoted to the study of inducing salt tolerance of wheat plants by NO donors. Treatment with SNP (through the roots) significantly reduced the inhibition of growth of wheat plants under conditions of 150 and 300 mM NaCl (Hasanuzzaman et al. 2011). The positive effect of spraying plants with SNP on the photosynthetic activity of wheat under salt stress was shown (Kausar and Shahbaz 2013). There is evidence of an increase in wheat resistance to salt stress at the presowing SNP treatment of seeds (Ali et al. 2017). Finally, the positive effect of plants spraying with SNP on yield under salt stress was shown (Kausar et al. 2013).

A number of studies have documented the positive effect of SNP treatment on resistance of wheat plants to the action of heavy metals and aluminum ions. Thus, the treatment with SNP increased the growth of organs of young wheat plants under the action of lead (Kaur and Zhawar 2017). SNP also improved germination of wheat seeds under the action of copper ions (Hu et al. 2007) and aluminum (Zhang et al. 2008). A decrease in the oxidative damage of wheat plants in a variant with SNP was observed when they were treated with cadmium salts (Singh et al. 2008).

Treatment with SNP reduced the manifestation of oxidative damage of wheat plants and also promoted the preservation of photosynthetic activity and productivity under the action of ozone (Li et al. 2018). It is reported also about the increase in resistance of wheat plants to hypoxia under the influence of SNP, which contributed to the development of aerenchyma (Wany and Gupta 2017).

So, wheat plants are responsive to the action of exogenous NO. Under the influence of this signal molecule under stress conditions of various natures, the integrated indices of plants (photosynthetic activity, growth, productivity) are improved. Below we consider the possible contribution of various protective systems into resistance of wheat plants to various stressors, induced by NO.

2.5 Adaptive Reactions Induced by the Action of Nitric Oxide

2.5.1 Antioxidant System Activation

Oxidative stress, which implies the imbalance between prooxidants and antioxidants, is the consequence of the influence of a wide range of adverse factors on living organisms (Suzuki and Mittler 2006; Gautam et al. 2017; Pradedova et al. 2017). Such imbalance can be due to both the increase in the formation of reactive oxygen species (ROS) caused by stress factors and the oxidation damage of components of antioxidant protection system (Foyer and Shigeoka 2011; Hajiboland 2014).

In order to prevent oxidative damage to biomacromolecules and membrane complexes by ROS, a very perfect antioxidant system (AOS) has developed in plant cells in the course of evolution. It includes antioxidant enzymes, non-enzymatic antioxidants, and metabolites, which can directly or indirectly participate in antioxidant protection, so-called "non-specialized" antioxidants such as proline or polyols (Parida and Das 2005; Hossain et al. 2014). Induction of AOS by various actions causes an increase in plant resistance to stress factors.

The effect of exogenous NO on the functioning of AOS in plants under the action of stressors has been studied quite well. However, the mechanisms of these effects are very difficult depending on the conditions; NO can both increase activity of antioxidant enzymes and reduce it. The effects of NO can be due to direct posttranslational modification of molecules of enzymatic proteins and influence on the expression of the corresponding genes. As already noted, NO-induced protein modifications can include S-nitrosylation, nitration of tyrosine residues, and metal-nitrosylation (Astier and Lindermayr 2012). These mechanisms of NO effect on proteins also apply to antioxidant enzymes whose activity is altered by the interaction of NO with thiol groups or transition metals that are part of active sites, especially with heme (Brown 1995).

Superoxide dismutase (SOD) is the only one enzymatic antioxidant that detoxifies superoxide anion radical. It plays the role of the primary frontier against ROS (Alscher et al. 2002). This function of SOD is associated with the fact that, by eliminating superoxide radicals, this enzyme indirectly reduces the probability of formation of hydroxyl radicals, singlet oxygen, peroxynitrite, and other ROS, which, due to their high reactivity, cannot be removed by protein catalysts. SOD is represented by a significant number of molecular forms. In their active centers, there may be such metals as Cu, Zn, Mn, and Fe. The most common form of this enzyme in plant cells is Cu/Zn-SOD (Mr 30–33 kD). It is localized in cytosol, chloroplasts, mitochondria, peroxisomes, and apoplast. Less common are Mn-SOD and Fe-SOD (Alscher et al. 2002; Gill and Tuteja 2010).

There is evidence of the possibility of regulation of SOD by NO not only on a genetic level but also through posttranslational modifications. It is assumed that reversible nitrosylation can be one of the mechanisms of regulation of Cu/Zn-SOD activity (Marozkina and Gaston 2012; Arora et al. 2016).

At the treatment of intact wheat plants, as well as their isolated organs, with NO donors it noted both an increase in total activity of the enzyme and its decrease, as well as the absence of effects (Table 1). In response to the treatment of isolated wheat coleoptiles with 0.5 mM SNP, marked inhibition of enzyme activity was noted during the first 2 hours, but at 24 hours, it was significantly higher than the control value (Karpets et al. 2011). When wheat seedlings were incubated on medium with 0.1 mM SNP, the activity of SOD in roots was also inhibited in the first hours and then restored to its original values (Kaur et al. 2015). In some studies, the entry of SNP through the roots indicated an increase in enzyme activity in shoots and leaves (Tian and Lei 2006; Ali et al. 2017). In the roots of wheat seedlings, incubation on medium containing 2 mM SNP also showed an increase in SOD activity (Karpets et al. 2015b).

It is possible that the transient decrease in SOD activity under the influence of exogenous NO is associated with direct modifications of enzyme molecules, while the increase in enzyme activity is due to the transduction of the corresponding signal into genetic apparatus and enhancement of expression of the corresponding genes. It should be noted that the expression of SOD genes in most works on inducing resistance of wheat plants to stressors by exogenous NO has not been studied. At the same time, data on the inducing of SOD gene expression by NO have been obtained by the example of other plant species. Thus, in sweet potato cells, the increase of expression of the Cu/Zn-SOD gene was observed at SNP treatment (Lin et al. 2011).

With the use of isolated maize leaves, obtained data show the regulation of SOD activity by NO (Zhang et al. 2007). This phenomenon occurs to participation of many components of signaling network and the expression of corresponding genes, as evidenced by the removal of the effect of NO by mitogen-activated protein kinase (MAP kinase) inhibitors (Zhang et al. 2007). At the same time, the absence of the influence of antioxidant DMTU and inhibitor of NADPH oxidase diphenyleneiodonium on the manifestation of the effect of enzyme activation by the donor of NO was shown in this study. On the other hand, in experiments with wheat coleoptiles, the leveling of

Table 1 Effect of NO donors on the activity of antioxidant enzymes in wheat plants under stressors

Stressor	Organ	NO donor, concentration	Effect under normal conditions	Effect under the stressor's action	References
SOD					
PEG 6000 or PEG 8000, 15%	Shoots	SNP, 0.2 or 2 mM	Increased activity	Increased activity under the influence of 0.2 mM SNP	Tian and Lei (2006)
	Leaves	SNP, 0.3 mM	Not studied	Increased activity	Tan et al. (2008)
	Shoots	GSNO, 0.2 mM	Not studied	Increased activity	Khan et al. (2017)
Soil drought (25–30% FC)	Leaves	SNP, 0.5 or 2 mM	No effect	Increased activity under the influence of 0.5 mM SNP	Kolupaev et al. (2018)
NaCl, 150 mM	Leaves	SNP, 0.1 or 0.2 mM	Increased activity	Increased activity	Ali et al. (2017)
O_3, 160 ppb	Leaves	SNP, 0.2 mM	Not studied	Increased activity	Li et al. (2018)
43 °C, 10 min	Coleoptiles	SNP, 0.5 mM	Decrease with a subsequent increase	No effect	Karpets et al. (2011)
Pb, 50 or 250 μM	Roots	SNP, 0.1 mM	Decrease with subsequent recovery to original values	Decreased activity	Kaur et al. (2015)
Cd, 50 or 250 μM	Roots	SNP, 0.2 mM	No effect	Decreased activity	Singh et al. (2008)
Al, 200 μM	Leaves	SNP, 0.1 mM	No effect	Increased activity	Zhang et al. (2008)
Catalase					
PEG 6000 or PEG 8000, 15%	Shoots	SNP, 0.2 or 2 mM	Increased activity under the influence of 0.2 mM and decreased at the action of 2 mM SNP	No effect	Tian and Lei (2006)
	Leaves	SNP, 0.3 mM	Not studied	Increased activity	Tan et al. (2008)
	Shoots	SNP, 0.1 or 0.5 mM	Not studied	Increased activity	Zhang et al. (2003)
	Shoots	GSNO, 0.2 mM	Not studied	Increased activity	Khan et al. (2017)
Soil drought (25–30% FC)	Leaves	SNP, 0.5 or 2 mM	No effect	Increased activity under the influence of 0.5 mM SNP	Kolupaev et al. (2018)

(continued)

Table 1 (continued)

Stressor	Organ	NO donor, concentration	Effect under normal conditions	Effect under the stressor's action	References
38 °C, 2 days	Leaves	SNP, 0.25 mM	Decreased activity	Increased activity	Hasanuzzaman et al. (2012)
NaCl, 150 or 300 mM	Shoots	SNP, 1 mM	No effect	Increased activity	Hasanuzzaman et al. (2011)
NaCl, 150 mM	Leaves	SNP, 0.1 or 0.2 mM	Increased activity	Increased activity	Ali et al. (2017)
Pb, 50 or 250 μM	Roots	SNP, 0.1 mM	No effect	Decreased activity	Kaur et al. (2015)
Cd, 50 or 250 μM	Roots	SNP, 0.2 mM	No effect	No effect or decreased activity	Singh et al. (2008)
Al, 200 μM	Leaves	SNP, 0.1 mM	No effect	Increased activity	Zhang et al. (2008)
Non-specific peroxidase					
PEG 6000 or PEG 8000, 15%	Shoots	SNP, 0.2 or 2 mM	No effect	Increased activity	Tian and Lei (2006)
	Shoots	GSNO, 0,2 mM	Not studied	Increased activity	Khan et al. (2017)
PEG 6000, 25%	Shoots	SNP, 0.1 or 0.5 mM	Not studied	Increased activity	Zhang et al. (2003)
Soil drought (25–30% FC)	Leaves	SNP, 0.5 or 2 mM	Increased activity under the influence of 0.5 mM SNP	Increased activity under the influence of 0.5 mM SNP and decreased at the action of 2 mM SNP	Kolupaev et al. (2018)
38°C, 2 days	Leaves	SNP, 0.25 mM	Increased activity	Increased activity	Hasanuzzaman et al. (2012)
NaCl, 150 mM	Leaves	SNP, 0.1 or 0,2 mM	Increased activity	Increased activity	Ali et al. (2017)
NaCl, 150 or 300 mM	Shoots	SNP, 1 mM	No effect	Increased activity	Hasanuzzaman et al. (2011)
O_3, 160 ppb	Leaves	SNP, 0.2 mM	Not studied	Increased activity	Li et al. (2018)
Pb, 50 or 250 μM	Roots	SNP, 0.1 mM	No effect	Decreased activity	Kaur et al. (2015)
Ascorbate peroxidase					
PEG 8000, 15%	Shoots	GSNO, 0.2 mM	Not studied	Increased activity	Khan et al. (2017)

(continued)

Table 1 (continued)

Stressor	Organ	NO donor, concentration	Effect under normal conditions	Effect under the stressor's action	References
PEG 6000, 25%	Shoots	SNP, 0.1 or 0.5 mM	Not studied	Increased activity	Zhang et al. (2003)
NaCl, 150 or 300 mM	Shoots	SNP 1 mM	No effect	Increased activity	Hasanuzzaman et al. (2011)
Al, 200 μM	Leaves	SNP, 0.1 mM	No effect	Increased activity	Zhang et al. (2008)
Pb, 50 or 250 μM	Roots	SNP, 0.1 mM	No effect	Decreased activity	Kaur et al. (2015)
Glutathione *S*-transferase					
NaCl, 150 or 300 mM	Shoots	SNP, 1 mM	No effect	Increased activity	Hasanuzzaman et al. (2011)
38 °C, 2 days	Leaves	SNP, 0.25 mM	No effect	Increased activity	Hasanuzzaman et al. (2012)
Glutathione reductase					
PEG 8000, 15%	Shoots	GSNO, 0.2 mM	Not studied	Increased activity	Khan et al. (2017)
NaCl, 150 or 300 mM	Shoots	SNP, 1 mM	No effect	Increased activity	Hasanuzzaman et al. (2011)

NO-induced activation of the enzyme with butylhydroxytoluene (a scavenger of superoxide anion radicals) and imidazole (inhibitor of NADPH oxidase) was established (Karpets 2017). It is possible that the transduction of NO signal in cells of chlorophylliferous and non-photosynthetic tissues is different. In turn, the activation of NADPH oxidase, which was manifested in isolated coleoptiles of wheat under the influence of NO donor, was dependent on calcium. At the same time, calcium antagonists, preventing the NADPH oxidase-dependent ROS generation, inhibit the increase in SOD activity caused by exogenous NO (Karpets 2017).

Catalase (CAT) is a heme-containing enzyme that catalyzes the decomposition of H_2O_2 into the water and molecular oxygen and is localized predominantly in peroxisomes (Gill and Tuteja 2010). NO binds to iron in the heme and leads to the formation of ferric iron, which prevents binding of H_2O_2 to the metal ion, thereby inhibiting catalase activity (Arora et al. 2016).

Wheat seedlings showed an increase in CAT activity under the influence of 0.2 mM SNP and the inhibition of the enzyme by 2 mM NO donor (Tian and Lei 2006). At the same time, spraying of green wheat plants with 0.5 and 2 mM SNP did not affect the enzyme activity under normal conditions (Kolupaev et al. 2018). However, under drought conditions, the treatment of plants with 0.5 mM (but not

2 mM) SNP caused the increase in CAT activity. On the other hand, 2 mM SNP caused the increase in enzyme activity in roots of wheat seedlings and also promoted its preservation after damaging heating (Karpets et al. 2015b).

In general, in most studies under normal conditions, NO donors did not cause changes in CAT activity in organs of wheat plants (Table 1). At the same time, on the background of hyperthermia, salt stress, and aluminum ions, the increase in enzyme activity was observed in variants with NO donors. However, under the influence of heavy metals (cadmium and lead) and SNP, the activity of enzyme decreased (Singh et al. 2008; Kaur et al. 2015).

Ascorbate peroxidase (APX) and non-specific peroxidase (POX), like CAT, are heme-containing enzymes. They are localized in the cytoplasm and various cellular compartments (Gill and Tuteja 2010). In some studies, the ability of NO to bind to POX heme (Arora et al. 2016) was registered. For example, it has been shown that NO donors inhibit the activity of non-specific peroxidase in *Zinnia elegans*. Donor of peroxynitrite induced the tyrosine nitration of cytoplasmic ascorbate peroxidase in vivo in *Arabidopsis* plants (Lozano-Juste et al. 2011).

In wheat plants, a number of studies have shown the increase in activity of non-specific POX under the influence of NO donors at low concentrations (Table 1). Also, in variants with the action of exogenous NO, the higher activity of the enzyme in plant organs was registered under the action of stressors of various natures. The effects of nitric oxide donor registered under the action of lead were an exception. In this case, the treatment of plants with SNP caused the decrease in POX activity (Kaur et al. 2015).

The increase in activity of these enzymes in roots of wheat under the influence of antagonists of NO – 100 μM PTIO and 2 mM L-NAME (Karpets et al. 2015b) – indicates the dependence of activity of antioxidant enzymes (SOD, CAT, and non-specific POX) on plant NO status. Thus, the opposite actions – decrease in the content of NO (e.g., at treatment with PTIO or L-NAME) and increase in its amount (under the action of NO donors) – can lead to the phenomenologically similar effect, the increase in activity of antioxidant enzymes. In addition to the possibility of modifying the direct effect of NO on the activity of antioxidant enzymes, it cannot be excluded that overlapping the NO signal by PTIO or L-NAME can induce other signaling pathways leading to the activation of components of the antioxidant system. This seems likely in connection with the ability of NO to interact with ROS both on principle of synergism and antagonism (Baudouin 2011). In particular, it is possible that the decrease in NO content in plant tissues under the influence of PTIO or L-NAME resulted in the increase in ROS content, inducing antioxidant enzymes in them.

The effect of NO donors on APX activity in wheat has been studied to a lesser extent. Its increase in shoots and leaves was shown on the background of osmotic, salt stresses, and aluminum action (Table 1). However, under the influence of lead ions, the effect of exogenous NO was the opposite: the activity of enzyme decreased (Kaur et al. 2015).

On background of action of stressors of different natures, the activity of glutathione *S*-transferase and glutathione reductase under the influence of NO donors was also revealed (Table 1).

NO significantly affects the content of low-molecular antioxidants in plant cells. NO has a direct and indirect influence on the functioning of the ascorbate-glutathione cycle in plants (Arora et al. 2016). Thus, NO reacts with GSH to form GSNO, which has the ability to trans-nitrosylate proteins (Chaki et al. 2011). Also, *S*-nitrosoglutathione is considered as the transporter of NO molecules participating in signaling (Arora et al. 2016). GSNO is the powerful inducer of protective genes (del Rio et al. 2006).

NO has the ability to stimulate the synthesis of glutathione (Arora et al. 2016). On the other hand, NO can inhibit glutathione reductase by nitrosylating of sulfhydryl groups in its active site (Beltran et al. 2000). At the same time, the ability of NO to increase the activity of glutathione reductase in vivo (Zhang et al. 2007) was shown, which is probably related to the enhancement of expression of the corresponding gene by activation of the signaling network.

In wheat plants, the treatment with NO donor SNP promoted the increase in the content of ascorbate and GSH in leaves under the conditions of hyperthermia (Hasanuzzaman et al. 2012). The increase in salt tolerance of wheat under the influence of SNP was accompanied by the increase in the content of phenolic compounds, which also have high antioxidant activity (Kausar et al. 2013; Ali et al. 2017). The increase in activity of the key enzyme for synthesis of phenolic compounds – phenylalanine ammonia lyase – in wheat seedlings under the conditions of osmotic stress was also recorded (Lian and Lei 2006).

2.5.2 Proline Accumulation

In addition to the well-known function of inert, compatible osmolyte (Hare and Cress 1997), proline under the action of stressors performs a number of other interrelated functions, membrane-protective, chaperone, and antioxidant, and also participates in the regulation of expression of some genes. In the last decade, the intensive accumulation of results of studies of such proline functions (Szabados and Savoure 2009; Liang et al. 2013; Hossain et al. 2014) occurs. Proline has the ability to prevent the formation of aggregates of protein molecules and protect them from denaturing agents (Samuel et al. 2000; Hossain et al. 2014).

As a separate function, antioxidant effects of proline are currently being considered. Protective effect of proline on plants under the conditions of oxidative stress caused by paraquat (Radyukina et al. 2008) and H_2O_2 (Soshnikova et al. 2013) was shown. A number of studies have reported the reduction in the content of lipid peroxidation product malondialdehyde (MDA) in plant tissues under stress conditions at the influence of proline (Alia et al. 1997; Sairam and Srivastava 2000).

The most detailed changes in proline pool were studied when osmotic and salt stressors were exposed to plants. The proline content in plants under the action of such stressors can increase many times. It has been shown that the treatment of rice seedlings with the NO donor SNP increased their salt tolerance, and the expression of genes of enzymes of proline synthesis was enhanced (Uchida et al. 2002). The increase in salt tolerance of wheat under the influence of SNP was also accompanied by the rise in proline content (Kausar et al. 2013; Ali et al. 2017).

Ander the osmotic stress produced by PEG 6000, the proline content in leaves of young wheat plants increased at the treatment with SNP (Tan et al. 2008). Under the influence of 0.5 mM SNP, the proline content in wheat seedlings increased at germination of seeds on PEG 6000 solutions (Zhang et al. 2003). The proline content in wheat seedlings, exposed to the action of nonpenetrating osmotic (PEG 8000), was also increased under the influence of another NO donor GSNO (Khan et al. 2017).

At the same time, in experiments with green wheat plants subjected to drought in soil culture, it was shown that the influence of SNP on proline content in leaves was significantly dependent on the NO donor concentration: when spraying plants with 0.5 mM SNP, proline content decreased during drought, and under the influence of 2 mM SNP, on the contrary, it was increased (Kolupaev et al. 2018). However, when both concentrations of SNP (0.5 and 2 mM) were used, the inhibition of plant growth in drought conditions decreased. It is likely that an increase in drought resistance by spraying plants with SNP in the concentration of 0.5 mM, which did not cause an increase in proline content, was associated with the activation of other defense mechanisms, in particular, with the increase in activity of antioxidant enzymes (Kolupaev et al. 2018).

2.5.3 Other Protective Reactions

There is evidence of the involvement of NO in the induction of accumulation of stress proteins. Thus, in rice plants under the influence of NO donor SNP, expression of the gene encoding small HSP26 was enhanced (Uchida et al. 2002). NO influenced the DNA-binding activity of heat shock transcription factors, which in particularly caused accumulation of HSP18.2, which contributes to the development of heat resistance of *Arabidopsis* (Xuan et al. 2010). Also in experiments with tomato plants, the participation of NO in cooperation with ROS in the accumulation of HSP70 (Piterkova et al. 2013) was shown. Induction of accumulation of stress proteins by NO occurs with the participation of calcium ions and calmodulin (Khan et al. 2014). It is suggested that the NO signal, which induces accumulation of HSP70 in *Arabidopsis*, is transduced via AtCam3 (Xuan et al. 2010).

In wheat plants, the donor of NO caused the change in ion flows under salt stress: an increase in potassium concentration in cells and reduction in sodium were noted (Savvides et al. 2016).

3 Hydrogen Sulfide

To date, functions of H_2S as a signal mediator in mammalian cells have been sufficiently well studied; its involvement in the regulation of vascular tone, neuromodulation, cytoprotection, inflammation, and apoptosis has been established (Abe and Kimura 1996; Lowicka and Beltowski 2007; Gadalla and Snyder 2010; Zaichko et al. 2014). At the same time, ideas about a signal function of H_2S in plants were not completely formed (Hancock and Whiteman 2014).

Now it is shown that H_2S induces many plant protective systems (Wang et al. 2012; Li 2013; Li and Zhu 2014; Li et al. 2014). There are also evidences of changes in endogenous H_2S content in plant cells in response to external stimuli on plants (Jin et al. 2013; Lai et al. 2014). Nevertheless, these data are largely contradictory. There is still no clear consensus on whether H_2S is an “independent” signaling molecule in plants and what is its place in the complex signaling network, as already established for H_2O_2 and NO (Lisjak et al. 2013; Hancock and Whiteman 2014).

3.1 Hydrogen Sulfide Synthesis in Plants

Presently, L-cysteine desulfhydrase (EC 4.4.1.1) is considered as the key enzyme for synthesis of H_2S in plants, under the influence of which H_2S is formed from L-cysteine (Wang 2012; Li 2013). The formation of H_2S from D-cysteine under the action of, respectively, D-cysteine desulfhydrase (EC 4.4.1.15) is also possible. In addition, H_2S can be formed from sulfite under the action of sulfite reductase (EC 1.8.7.1) (Li 2013). In this case, reduced ferredoxin is used as a sulfur reducer (Fig. 4).

The intracellular localization of enzymatic systems that generate H_2S has not yet been studied sufficiently. It was shown that in *Arabidopsis* plants, L-cysteine desulfhydrase is localized mainly in plastids (L’eon et al. 2002), as well as in mitochondria (Riemenschneider et al. 2005). On the other hand, D-cysteine desulfhydrase is found mainly in the cytoplasm (Riemenschneider et al. 2005; Guo et al. 2016).

Synthesis of H_2S in wheat plants has not been enough studied. However, the inhibition of H_2S synthesis by pyruvate indicates the key role of L/D-cysteine desulfhydrases in H_2S synthesis in wheat (Shan et al. 2018).

Along with enzymes for synthesis of H_2S, the enzyme specializing in its degradation – O-acetylserine lyase – is found in plants (Lisjak et al. 2013) (Fig. 4). It is noteworthy that transformation of tobacco plants by the O-acetylserine lyase gene caused resistance to high concentrations of exogenous H_2S, which suggests that this enzyme is involved in regulation of endogenous and detoxifying of exogenous H_2S (Tai and Cook 2000).

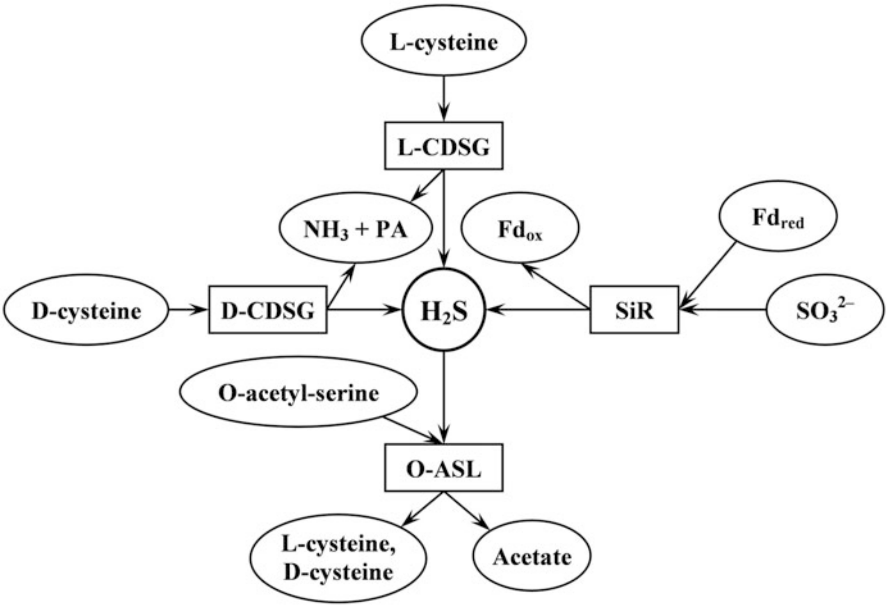


Fig. 4 Possible pathways of synthesis and scavenging of hydrogen sulfide in plants
Fd_{red} and Fd_{ox}, reduced and oxidized ferredoxin; L-CDSG and D-CDSG, L- and D-cysteine desulphhydrase; O-ALS, O-acetyl-L-serine liase; PA, piruvatic acid; SiR, sulfite reductase

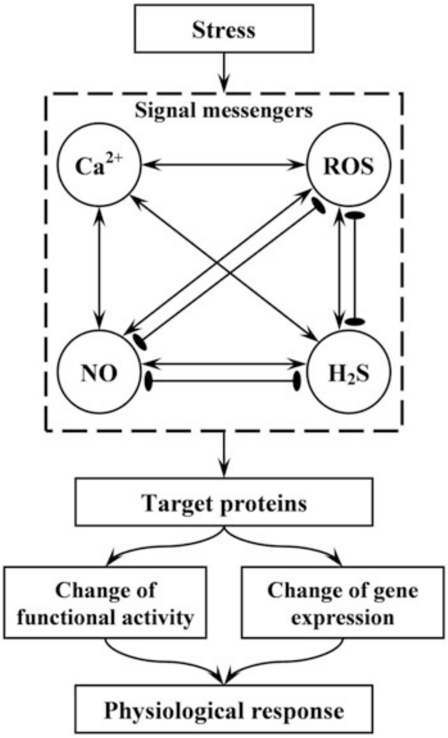
Presence in plant cells of specialized enzymatic systems for synthesis and degradation of H_2S, which allows delicately regulating its intracellular concentration, indirectly indicates the signal-regulatory role of H_2S.

3.2 *Transduction of Hydrogen Sulfide Signal*

Certain functions of H_2S in signal transduction and mechanism of its interaction with other signaling molecules are still poorly studied (Guo et al. 2016). So, specific sensors are not yet known, with the help of which cell finds out an increase in the concentration of H_2S (Li 2013). Also, mechanisms of direct induction of H_2S accumulation under action of stress factors are not clear (Fig. 5).

Hydrogen sulfide as a signal mediator, apparently, is most closely associated with NO. Thus, when inducing the heat resistance of maize seedlings by the action of NO donor SNP, the increase in the endogenous H_2S content was noted (Li et al. 2013). In this case, inhibitors of H_2S synthesis and its scavengers neutralized this effect; on the other hand, the H_2S donor GYY4137 enhanced the positive effect of SNP on heat resistance of seedlings. The authors concluded that H_2S as a signal mediator is located below NO (Li et al. 2013).

Fig. 5 Functional interaction of signal mediators at the moderate influence of stressors



At the same time, in experiments with alfalfa plants, the decrease positive effect of the donor of H_2S NaHS on salt tolerance of plants and expression of antioxidant enzyme genes by treatment with the NO scavenger PTIO was shown (Wang et al. 2012). Treatment of pea seedlings with sodium hydrosulfide increased their resistance to arsenic toxicity, with an increase in NO content (Singh et al. 2015). Thus, NO can mediate the transduction of H_2S signal into genetic apparatus of the plant cell.

The relationship between H_2S and NO can be not only positive but also negative (Hancock and Whiteman 2014, 2016). So, there are data about the inhibition of H_2S by the enzyme, similar to animal NO synthase, and preventing the NO signaling by H_2S. It is also assumed that direct interaction of NO and H_2S is possible (Lisjak et al. 2013).

In recent years, data have been obtained on the close relationship between ROS and NO signaling in plant cells (Tewari et al. 2008; Arora et al. 2016). Hydrogen sulfide, along with NO, can also participate in transduction and modulation of ROS signals. It was shown that the treatment of maize seedlings with H_2O_2, which induced heat resistance, affected the increase in the activity of L-cysteine desulfhydrase and H_2S content (Li et al. 2015a). This effect was eliminated by treatment of seedlings with PTIO, which may indicate the participation of NO in the H_2O_2-induced formation of H_2S.

Calcium is the key secondary mediator of plant cells (Kaur and Gupta 2005). In this connection, it is quite logical to accumulate information about its participation both in the formation of H_2S and in transduction of its signals into genetic apparatus. It was shown that the activation of L-cysteine desulfhydrase in cells of tobacco suspension culture under the conditions of heat stress took place with the participation of extracellular calcium since this effect was inhibited by pre-treatment with EGTA (Li et al. 2015b). Also, this enzyme was activated in the presence of calmodulin.

Calcium is also involved in the transduction of H_2S signals. Thus, treatment of *Setaria italica* with sodium hydrosulfide reduced the manifestation of the toxic effect of chromium (VI) (Fang et al. 2014). In this case, exogenous calcium caused the increase in effects of plants treatment with H_2S, and effect of EGTA, on the contrary, neutralized manifestation of the physiological effect of H_2S. At the same time, exogenous calcium enhanced chromium-induced production of H_2S in plants (Fang et al. 2014).

On the other hand, the *Arabidopsis* mutants on L-cysteine desulfhydrase gene were characterized by the weak calcium influx to the cytosol in response to drought (Jin et al. 2013). The authors concluded that H_2S affects the state of calcium channels. This assumption agrees with the data on leveling by the calcium antagonists of the influence of H_2S on heat resistance of wheat coleoptile cells, generation of ROS, and activity of antioxidant enzymes (Kolupaev et al. 2017a).

Between ROS and H_2S as physiologically active molecules, there also seem to be close bonds (Fig. 5). Thus, the drought-induced formation of H_2S in leaves of *Arabidopsis* was eliminated by treatment with the antioxidant ascorbic acid and inhibitors of enzymes that produce ROS–NADPH oxidase (diphenyleneiodonium) and extracellular peroxidase (salicylhydroxamic acid) (Wang 2012). In addition, mutants *atrbohD*, *atrbohF*, and *atrbohD/F* did not show increased H_2S production under drought conditions (Hancock and Whiteman 2014). It can be assumed that H_2O_2 is the mediator in the induction of formation of H_2S, which, in turn, causes the formation of adaptive reactions in response to drought. Experimental data have been obtained, indicating the presence of similar activation mechanisms for the synthesis of H_2S in wheat plants too. Thus, the increase in the formation of H_2S caused by the osmotic stress agent PEG was suppressed by NADPH oxidase inhibitor diphenyleneiodonium (Shan et al. 2017). However, there appear to be direct and inverse links between H_2S and H_2O_2 as signal mediators, since the inhibitor of H_2S synthesis pyruvate neutralized the drought-induced formation of a signal pool of H_2O_2 in wheat plants (Shan et al. 2017).

The increase in heat resistance of wheat coleoptile cells induced by H_2S donor was removed by the action of antioxidants, namely, butylhydroxytoluene and DMTU, as well as by inhibitor of NADPH oxidase imidazole, but not by extracellular peroxidase inhibitor salicylhydroxamic acid (Kolupaev et al. 2017a, b). At the same time, effects of increasing H_2O_2 content, activation of peroxidase and catalase, and increase in heat resistance were offset by inhibitor of Cu/Zn-SOD sodium diethyldithiocarbamate, which indicates the role of this enzyme in the formation of signal pool of H_2O_2 under the action of H_2S on wheat coleoptile cells (Kolupaev et al. 2017b). Apparently, H_2S, changing calcium homeostasis, activates NADPH oxidase; superoxide anion radical formed by this enzyme is converted by SOD into the signal form of ROS – H_2O_2.

On the other hand, there can be antagonistic relations between H_2S and ROS. In particular, many studies have shown the induction of an antioxidant system by exogenous H_2S (Shan et al. 2011; Hancock and Whiteman 2014). In this connection, it is suggested that the increase in the content of reduced glutathione, ascorbic acid, and activity of a number of antioxidant enzymes caused by H_2S should lead to the decrease in the content of ROS and modification of ROS signals (Hancock and Whiteman 2014). It is also reported on the direct interaction of H_2S with ROS, including superoxide and hydroxyl radicals, H_2O_2 (Li and Lancaster 2013). True, the importance of the direct contribution of H_2S to the regulation of ROS content remains disputed, since its concentration in cells is much lower than other antioxidants (Hancock and Whiteman 2014). In addition, a very low rate of H_2S interaction with oxidants is pointed.

Thus, H_2S as a signal mediator functions in close connection with calcium, ROS, and NO (Fig. 5). In this case, the increase in the concentration of intracellular calcium, ROS, or NO could be the stimulus for enhancing synthesis of H_2S (Jin and Pei 2015). On the other hand, it is likely that H_2S can open certain calcium channels and support the influx of calcium into the cytosol. The last one together with calmodulin can act as the mediator in the transduction of signal of H_2S into genetic apparatus. ROS and NO can also be the mediators in the realization of H_2S effects. However, H_2S, probably, depending on dose, as well as on the presence of other signal mediators, is able both to cause an effect of enhancing formation of ROS and NO in cells and to promote their neutralization.

Hydrogen sulfide can also have a direct effect on proteins involved in cellular signaling and maintenance of redox homeostasis. It is suggested that one of the direct mechanisms of H_2S influence on the state of proteins is *S*-sulfhydration of their thiol groups (Aroca et al. 2015). It was shown that *S*-sulfhydration affects the activity of a number of plant enzymes, in particular, APX. In *Arabidopsis* plants, there were identified 106 *S*-sulfhydrated proteins (Aroca et al. 2015). However, in other plant species, target proteins that undergo such modification remain practically unexplored. In addition to *S*-sulfhydration of proteins, the straight modification of some of them, especially enzymes, can be the direct interaction of H_2S with their iron-containing active sites (Li et al. 2017).

3.3 Change in Hydrogen Sulfide Content in Wheat Plants Under the Influence of Abiotic Stressors

Studies of the content of endogenous H_2S in plants under the action of stressors are not so numerous, but the effects of increasing in H_2S content in cells in response to the action of stressors are established in plants of many species. An increase in expression of L- and D-cysteine desulfhydrase genes in *Arabidopsis* plants in response to the action of drought has been shown. At the time, the production of H_2S in plants increased (Jin et al. 2011). The increase in the amount of transcripts of L-cysteine desulfhydrase and endogenous H_2S content in alfalfa has been demonstrated under the action of stress concentrations of sodium chloride (Lai et al. 2014). Increased expression of both L- and D-cysteine desulfhydrase genes and elevation of H_2S content was shown in seedlings of foxtail millet (*Setaria italica*) under the action of toxic concentrations of Cr^{6+} ions (Fang et al. 2014). The effect of increasing H_2S content was also revealed by the action of cadmium on plants of Bermuda grass (*Cynodon dactylon*) (Shi et al. 2014).

Effects of increase of H_2S content in tissues in wheat plants with moderate stressors are recorded too. As already noted, the H_2S content was increased in wheat seedlings in response to PEG treatment (Shan et al. 2017). The elevation of the content of H_2S in wheat seedlings was also shown under the action of stress phytohormone ABA (Shan et al. 2017). The content of H_2S in wheat under the influence of other factors is still unexplored.

3.4 Influence of Hydrogen Sulfide Donors on Resistance of Wheat Plants to Abiotic Stressors

At present, an increase in resistance of plants of different taxonomic groups, including wheat, to the action of stress factors of different nature under the influence of exogenous H_2S is shown. The donor of H_2S NaHS increased the heat resistance of intact seedlings (Yang et al. 2015) and isolated wheat coleoptiles (Kolupaev et al. 2017a). Treatment of wheat seeds with sodium hydrosulfide promoted their germination under osmotic stress created by PEG 6000 (Zhang et al. 2010).

In our experiments carried out in soil culture with wheat, it was shown that spraying of plants with NaHS solutions (0.1–0.5 mM) markedly softened the drought effect of growth inhibition and contributed to the preservation of chlorophyll pool (Kolupaev et al. 2019). The positive effect of sodium hydrosulfide on plants was eliminated by their treatment with scavenger of H_2S hydroxylamine. Pretreatment of plants with NaHS prevented the drought-induced elevation of contents of H_2O_2 and lipid peroxidation product MDA in leaves (Kolupaev et al. 2019).

Increased germination of wheat seeds under the conditions of salt stress at the influence of sodium hydrosulfide was shown (Ye et al. 2015). Treatment of wheat seedlings with NaHS reduced the effect of MDA accumulation induced by toxic concentrations of copper (Shan et al. 2012). Under the influence of a H_2S donor, the resistance of wheat plants to the action of chromium was increased (Li et al. 2016a, b). Also, when treated with NaHS, seed germination was enhanced under exposure to toxic concentrations of cadmium (Huang et al. 2016).

3.5 *Adaptive Reactions Induced by Hydrogen Sulfide*

3.5.1 Enzymatic Antioxidants

Hydrogen sulfide, like NO, has the ability to induce many components of plant antioxidant system. To date, many data on the influence of H_2S on an antioxidative system of plants of different species, including wheat, are accumulated. Treatment of wheat seeds, germinating under osmotic stress conditions, with H_2S donor sodium hydrosulfide, caused the increase in activity of CAT and APX (Zhang et al. 2010). Increased gene expression and increased activity of APX, glutathione reductase, and monodehydroascorbate reductase in H_2S-treated wheat plants, at followed exposure to PEG-induced osmotic stress, were also shown (Shan et al. 2018).

Treatment of green wheat plants with sodium hydrosulfide solution before soil drought promoted the increase in SOD activity and prevented the stress-induced decrease in catalase and guaiacol peroxidase activity in leaves (Kolupaev et al. 2019).

Activation of SOD, CAT, APX, and non-specific POX in wheat plants under salt stress was detected (Ye et al. 2015; Shan et al. 2017; da-Silva and Modolo 2018). In wheat seedlings treated with the H_2S donor, at heat stress the activity and expression of SOD, CAT, and APX were increased (Yang et al. 2015). Intensification of germination of wheat seeds on the background of cadmium toxic effects were accompanied by the increase in activity of non-specific POX, APX, and CAT (Huang et al. 2016).

3.5.2 Low-Molecular Antioxidants and Osmoprotectants

In a number of studies, the increase in the content of sugars, performing osmoprotective, membrane-protective, and antioxidant functions, under the influence of H_2S donors has been shown in wheat plants (Vagujfalvi et al. 1999). Thus, the rise in heat resistance of wheat seedlings induced by NaHS treatment was accompanied by an increase of sugar content (Yang et al. 2015). The rise in the content of sugars and starch in leaves of wheat under drought at the influence of treatment with sodium hydrosulfide was noted (Ding et al. 2018). At the germination of wheat seeds under conditions of salt stress, the content of sugars was increased under the influence of H_2S donor (Ye et al. 2015). The same effect was observed at germination of wheat seeds under the toxic action of cadmium (Huang et al. 2016). It should be noted that in some plant species, the treatment with H_2S donor increased the trehalose content. Thus, in corn plants, the inducing of heat resistance by the donor of H_2S was accompanied by the increase in the amount of trehalose (Li et al. 2014).

Under the influence of treatment with H_2S donors, changes in the content of other low-molecular protector proline in plant cells were also recorded (Lisjak et al. 2013). However, these effects are very ambiguous. Depending on the strength of stressor, as well as a donor of H_2S, both increase and decrease in the content of this amino acid are possible. Thus, the increase in proline content in millet plants under the influence of sodium hydrosulfide, as well as its combination with the stress influence of cadmium ions, was shown (Tian et al. 2016). This effect was accompanied by the increase in expression of Δ^1-pyrroline-5-carboxylate reductase gene and the decrease in expression of proline dehydrogenase gene. Similar effects were recorded in etiolated corn seedlings; the accumulation of proline was considered as one of the reasons for increasing their heat resistance (Li 2013). At the same time, it has been shown the decrease in proline content in cucumber plants under the conditions of salt stress at the influence of pre-treatment with the H_2S donor (Yu et al. 2013). Leveling the amount of proline under drought conditions after the influence of exogenous H_2S was also found in spinach sprouts (Chen et al. 2016). In wheat plants, spraying with sodium hydrosulfide (0.1 or 0.3 mM) in itself slightly increased proline content in leaves, but markedly increased accumulation under conditions of soil drought was shown (Kolupaev et al. 2019). In general, the effect of H_2S on the content of proline in wheat plants under the influence of stress factors remains insufficiently studied (Calderwood and Kopriva 2014).

Flavonoids belong to important low-molecular antioxidants (Khlestkina 2013). Particular mention should be made of the high antioxidant activity of anthocyanins, including their colorless tautomers, which can effectively deactivate superoxide anion radicals (Neill and Gould 2006). However, the effect of H_2S on their content is almost not studied. Recently, a slight increase in the content of colorless flavonoids (absorbing UV) and anthocyanins in barley plants has been revealed during induction of their resistance to UV-B by treatment with the H_2S donor (Li et al. 2016a, b). In our experiments, a significant (almost twofold) increase in the content of anthocyanins was observed after the influence of 0.3 mM NaHS in the leaves of wheat plants under the normal conditions and soil drought (Kolupaev et al. 2019). Also, under the influence of H_2S donor, there was the increase in the content of UV-B-absorbing flavonoids in leaves. It can be assumed that flavonoid compounds have the significant contribution to the protective action of the H_2S donor on wheat plants under drought conditions (Kolupaev et al. 2019).

It was shown that H_2S under the conditions of dehydration of wheat plants, created by PEG, influenced the expression of genes of 120 proteins, wherein under the influence of H_2S the expression of genes of 57 proteins enhanced and 63 – decreased (Ding et al. 2018). Hydrogen sulfide mostly influenced the expression of protein genes associated with carbohydrate metabolism, secondary metabolism, and synthesis of low-molecular antioxidants.

4 Conclusion and Future Perspective

NO and H_2S are powerful inducers of resistance of plants of many species to stress factors of different nature. Wheat is a species that is sufficiently responsive to treatment with NO and H_2S donors.

To study the NO-dependent physiological processes in plants, sodium nitroprusside is most often used as NO donor, more rarely *S*-nitrosoglutathione (GSNO) and *S*-nitroso-N-acetyl-penicillamine (Mur et al. 2013). At the same time, the possibility of inducing resistance of plants to stress factors by exogenous nitrate, L-arginine, and polyamines, which are natural substrates for enzymatic reactions of NO production, has been poorly investigated. However, in a number of studies, the increase in the endogenous content of NO in leaves and roots of wheat was observed during the treatment with these compounds (Rosales et al. 2011, 2012; Karpets et al. 2018). Moreover, the increase in the heat resistance of wheat by the influence of nitrate and L-arginine, which was dependent on the formation of NO from these compounds, was shown. In this connection, questions arise as to whether these compounds can be used to priming of plants as resistance inducers and how their properties as potential sources of NO correlate with other physiological effects, whether the normal nitrogen (in particular nitrate) plant nutrition affects NO signaling. The study of the effect of nitrogen nutrition on the manifestation of physiological effects of NO donors is only beginning (Baloti et al. 2018). The elucidation of questions of action of various sources of NO, including wheat physiology context, is complicated by the lack of clear ideas about the ways of formation of NO in higher plants in general.

The interaction of NO with other signal mediators, including during the formation of adaptive reactions of plants, does not have unambiguous representations too. In particular, calcium was detected both in the formation of NO signal and its transduction (Neill et al. 2008). In this case, the mechanism of increasing of calcium content in the cytosol under the influence of NO in higher plants remains a subject of discussion, primarily due to the lack of molecular genetic evidence for the presence of guanylate cyclase. The growth of its activity in animal cells causes the increase in cGMP concentration and the subsequent elevation of cADPR, which opens certain intracellular calcium channels.

The connection of NO with ROS also remains unclear. There are experimental data on both the location of NO after the ROS in signal chains and about their cooperative action (Karpets et al. 2015a). The relationship between NO and H_2S as signal mediators is even less studied, although there is a reason to believe that these mediators can have common action targets or activate common signal transduction pathways (Kharbech et al. 2017; He and He 2018).

Exogenous NO induces a wide range of protective reactions in wheat plants, activates antioxidant enzymes, in particular, SOD, and enzymes that remove H_2O_2 affects the functioning of the ascorbate-glutathione cycle. Apparently, NO is involved in the regulation of proline synthesis in wheat. However, its effects are ambiguous and, probably, depending on the state of redox homeostasis as a whole. Information on the effect of NO on the expression of genes encoding various HSPs has also been obtained. However, data on the effect of NO on the synthesis of HSP in wheat is not enough. There is information about the involvement of NO in the maintenance of ion homeostasis in wheat plants (Savvides et al. 2016).

Hydrogen sulfide, like NO, is capable of inducing many adaptive reactions in plants, which leads to the increase in their resistance to various stressors. Donors of

H_2S increased the resistance of wheat to damaging heating, drought, salinity, and action of heavy metals. However, the phenomenology of H_2S action has been studied much weaker in comparison with that for NO. A rather large amount of data was obtained only on the state of enzyme antioxidant system of plants under the action of H_2S donors (Zhang et al. 2010). Data on the ability of H_2S to significantly enhance synthesis of anthocyanins and other flavonoid compounds in wheat is of interest. Perhaps this is one of the leading mechanisms to increase of resistance of plants to stressors by the influence of H_2S (Yang et al. 2015; Shan et al. 2018; Kolupaev et al. 2019).

For the practical application of H_2S, the more detailed study of the phenomenology of its action on various components of protective systems is needed. It is also necessary to study the dependence of effects on dose, time, and frequency of plant treatment. Special comparative studies of the effect of signaling compounds on the plants of different species are worthwhile since the comparison of results obtained for different species under unequal experimental conditions is usually incorrect.

Signal mediators realize their effects in complex connection not only with each other but also with phytohormones. Hormonal status of plants has specific features. In this regard, it can be assumed that the effects of exogenous signal mediators as inducers of stress resistance will differ depending on specific features of the hormonal complex. However, for plants of *Triticum* genus, this question remains completely unexplored. Furthermore, it is tempting to study combined protective effects of stress phytohormones and signal mediators. In some cases, their combined use makes it possible to strengthen protective effects. Thus, when combined presowing treatment of wheat seeds with the foliar treatment of plants with NO donor SNP, their positive effect on drought resistance was significantly enhanced (Kolupaev et al. 2018). However, studies of such effects are still few in number.

Finally, the relationship between the induction of resistance of plants by exogenous compounds and their productivity understress and optimal conditions is largely unclear. Most of the results of the studies of the effect of exogenous compounds (including donors of NO and H_2S) on plant resistance were obtained in short-term laboratory experiments, which limits the possibility of extrapolating them to natural conditions (Hasanuzzaman et al. 2013). In this direction, the special investigations are also needed.

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Targeting Plant Hormones to Develop Abiotic Stress Resistance in Wheat

Ali Raza, Sundas Saher Mehmood, Javaria Tabassum, and Raufa Batool

Contents

Abstract Abiotic stresses comprising heat, drought, waterlogging, cold, salinity, and UV radiations are the main causes of many crop losses globally. Recently, avoiding these crop fatalities and production of more food to fulfill the requirement of increasing human need have extended extraordinary significance. Nevertheless, the proportion of agricultural land facing diverse abiotic stresses can be raised under a fluctuating global climate driven by anthropogenic activities. Identification of different mechanisms set up and used by plants to respond against abiotic stresses with their growth maintenance and survival under severe circumstances has great impact. Latest studies have revealed that plant hormones, e.g., auxins, ethylene, gibberellins, and cytokinins, with their innovative members that include brassinosteroids, strigolactones, and jasmonates may act as significant metabolic engineering objectives to induce abiotic stress tolerance in plants. This review condensed and analytically measured the functions of phytohormones in plant growth, development, and abiotic stress tolerance, in addition to the engineering of phytohormones to produce transgenic lines with abiotic stress tolerance. We have also discussed latest achievements for the identification of phytohormones involved under stressed conditions. Here we

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deduce the limitations and challenges for engineering phytohormones to produce transgenic lines having resistance against abiotic stresses by illustrating the recent research and progress to induce abiotic stress tolerance.

Keywords Abiotic stresses · Plant growth regulators · Phytohormones · Resistance · Wheat

1 Introduction

Common wheat (*Triticum aestivum* L.) is considered among one of the basic foods worldwide. Its cultivation had started about 8000 years ago from the Middle East and readily extended globally (Hao et al. 2017). Being considered as an important food crop, wheat is mainly targeted for agricultural improvements. Among all widely grown cereal grains, wheat provides the highest percentage of calories in the diet that constitute about 29% of overall cereal production in 2015 (Winfield et al. 2018). The production rate of wheat has been doubled over the past 60 years; its global production is 600 million tons produced from about 210 million hectares globally. National and regional breeders have produced the improved cultivars of wheat, which resulted in the increased production rate (Bramel 2017).

The increased population rate has raised the demand for wheat productivity globally. However, various biotic and abiotic stresses are the main cause of limitations in crop yield (Wani and Sah 2014). Its production rate must be increased to fulfill the food requirement of increasing population in the upcoming years (Tilman et al. 2011). Plants respond against different biotic and abiotic stresses with diverse and complex mechanisms than animals (Qin et al. 2011). Identification of such mechanisms by which plants induce tolerance against biotic and abiotic stresses is the crucial step for biotechnologists. Abiotic stresses like salinity, drought, and heat are the most common and substantial abiotic stresses among all (Hussain Wani et al. 2013). Most of the times, plants come across the biotic and abiotic stress stimuli from the surrounding environment. Being sessile in nature, plants only have the opportunity to adapt the growth and form to tolerate these stresses with the coordination of their physiological changes. There are many limitations in conventional breeding techniques to overcome these stresses because of the complexity of these traits involved in tolerance. Breeders require effective improvements to fulfill the growing food requirement globally. In this way, novel and persuasive methodologies have to be developed. Producing transgenic lines with phytohormone engineering can be a way of selection to harvest climate-irrepressible plants with greater yield.

Phytohormones regulate diverse cellular processes in plants even with their low concentration. These molecules act as chemical messengers for communication of a variety of cellular metabolic activities in vascular plants (Voß et al. 2014). Phytohormones have significant roles in plant growth and development and respond to biotic and abiotic stresses. These hormones regulate a variety of developmental processes along with signaling networks in plants under different biotic and abiotic stresses. Improvements in plant molecular biology have revolutionized the involvement of phytohormones in improving the damaging effects posed by abiotic stresses (Khan et al. 2013; Masood et al. 2012). Numerous phytohormones like abscisic acid (ABA), gibberellins (GAs), ethylene (ET), auxin (indole-3-acetic acid (IAA)), cytokinins (CKs), and brassinosteroids (BRs) that regulate plant development are also involved in controlling a variety of physiological and biological signaling and processes in the sessile plants. These cellular messengers may function as either adjacent or distant molecules from their positions of synthesis to respond against external stimuli or genetically automated progressive variations (Fahad et al. 2015a). Engineering phytohormones to produce transgenic varieties can help breeders and biotechnologists to harvest nutritionally and economically improved crops. Here we confer a summary of phytohormones along with their functions in plant growth and development, their response against abiotic stresses, and phytohormone engineering to produce transgenic lines with abiotic stress tolerance. We also confer latest researches and future aspects to increase the food quality and quantity by metabolic engineering to induce tolerance in plants.

1.1 Abiotic Stresses: Challenging the Changing World

As either biotic or abiotic stresses cause extensive crop loss worldwide, it is critical to investigate how these stresses disturb plant growth and development at molecular, biochemical, and physiological level and disrupt the overall yield of crops (Kazan 2015). Crop productivity is highly affected by various environmental factors, e.g., heat, drought, salinity, freezing, chilling, pathogens, ozone, and UV radiation. Stress responses may diversely be influenced by plants according to developmental stages of plant and biotic or abiotic stresses (Feller and Vaseva 2014). Some plants may be contrived at the early developmental stages but recover later and finally persist. Different species and genotypes of crops may markedly influence the susceptibility or resistance to various stresses.

Among all abiotic stresses, drought has been observed as the most severe stress that accounts for high decrement of agricultural production globally. Plant may undergo drought stress on any stage, and its function may be affected diversely thus requiring distinct mechanism for tolerance at different stages. While facing drought stress, various additional abiotic stresses generally occur such as high concentrations of salt, high temperatures, and additional toxic solutes with low availabilities of essential nutrients. Localization and time also have different effects upon stress conditions (Salekdeh et al. 2009; Fleury et al. 2010; Roy et al. 2011). These stresses affect crops by several means: plant growth and development, pigment components, membrane integrity, water associations, osmotic adjustments, and overall photosynthetic activity of plants (Pathak et al. 2014).

Heavy rains, excessive irrigations, and low infiltration rate of soils in the world cause flooding. Among most devastating natural occurrences, flooding and its prolonged appearances severely lower the crop yield in main agricultural lands

(Jackson et al. 2009). As many rivers are drying daily worldwide and even some have no water to eject to the sea so water is becoming the oil of the twenty-first century (Postel 2006). The second major stress is the salinity that reduces the crop yield heavily. Plants have diverse mechanisms and combinations of these mechanisms to produce tolerance against variety of stresses. Plant hormones are diverse in their function against each specific stress or combination of these stresses as some hormones exhibit multiple positive plant-protective functions against different stresses.

1.2 Combining Effect of Abiotic Stresses on Plants

Unluckily until now, there is poor understanding of mechanisms by which crops sustain their productivity under abiotic stresses. Climate fluctuations have complex effects on results of abiotic stresses that threaten the sustainability and agricultural yield. Recent agriculture faces various abiotic stresses, e.g., drought, heat, low temperature, and salinity, as the main elements disturbing crop productivity (Tardieu and Tuberosa 2010). New technologies are being developed day by day to enhance the crop yield and reduce the pre-harvest, and postharvest losses occurred due to devastating abiotic stresses (Gust et al. 2010). Complex and exclusive cellular and molecular responses, executed by the plants to minimize the loss and increase the survival rate, are occurred against different stresses. In response to abiotic stresses, plants adapt different strategies that boost their plant growth, development, and overall yield. These strategies cause changes in morphological and growth pattern as well as biochemical and physiological processes diversely against each stress.

Naturally, plants have to face different biotic or abiotic stresses in the environment. To conduct molecular studies under controlled conditions, researches on experimental plants are handled in the laboratory or greenhouse to avoid the actual conditions of stresses occurring in fields. To impose only one stress, different conditions can be controlled in the laboratories or greenhouses, which occur in the form of combinations of many environmental stresses naturally. Therefore, the trials conducted for estimating the impacts of combinations of stresses besides an individual stress may show advantageous consequences.

2 Phytohormones: Basic Intermediaries of Plant Responses Against Abiotic Stresses

Plants growth and development is regulated in response to several environmental stimuli (Wolters and Jürgens 2009). Plant hormones are biochemical molecules that are involved in controlling overall plant growth, development, germination up to

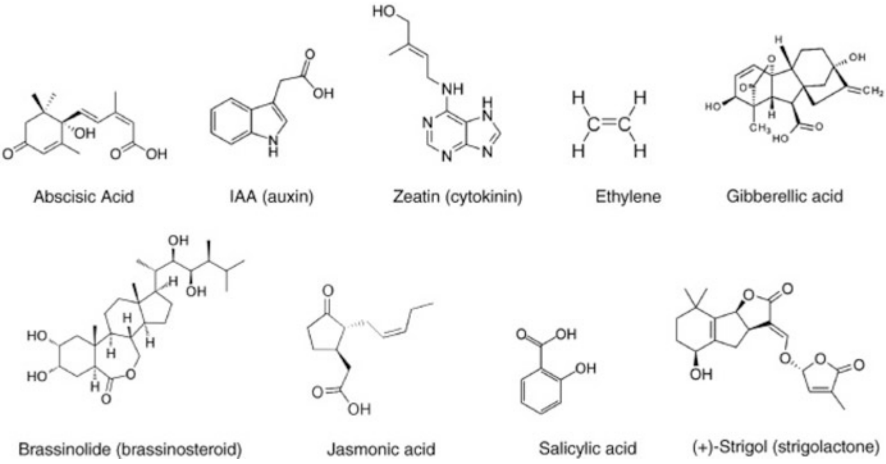

Fig. 1 Major classes of phytohormones involved in abiotic stress response and tolerance in plants (Wani et al. 2016)

fruit ripening, and seed distribution. Thus, these biochemical molecules lead the plant behavior in response to various environmental stresses (Fraire-Velázquez et al. 2011). This biomolecular control involves a complex signaling pathway from stimulus level to gene expression level (Azevedo et al. 2012). Phytohormone is a diverse class of signaling biomolecules, which are present in cells with small quantities to mediate responses against any internal or external stimuli. The fundamental roles of these biomolecules in stimulating plant acclimatization to the fluctuating situations by intervening growth, development, nutrient allocations, and source/sink alterations have been successfully recognized. Plant responses against abiotic stresses depend on several features; plant hormones are considered as significant endogenous constituents of cell's machinery to modulate molecular and physiological responses, a crucial prerequisite for plant existence and endurance as sessile entities (Fahad et al. 2015a). Phytohormones work either on the location of their synthesis or away following their transport within the plant body (Peleg and Blumwald 2011). These biomolecules are much important in plant growth and development at different stages. These biomolecules include IAA, CKs, ABA, ET, GAs, BRs, jasmonates (JAs), and salicylic acid (SA). Strigolactone (SL) is also a newly identified class of plant hormones (Fig. 1).

2.1 Abscisic Acid (ABA)

Plants are frequently disposed to a variety of abiotic stresses such as freezing, chilling, drought, salinity, high temperature, or heat stresses. ABA phytohormone has been identified as a vital biomolecule to respond against any abiotic stress

(Sharma et al. 2005). ABA is an essential isoprenoid plant hormone that is synthesized in the plastidal 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway. Unlike structurally related sesquiterpenes that are formed from the mevalonic acid-derived precursor farnesyl diphosphate, and after cleavage of C40 carotenoids in MEP, the C15 backbone of abscisic acid is produced. ABAs have a significant function at different stages of plant growth and life cycle, together with embryo morphogenesis, seed development and dormancy, stomatal opening, and accumulation of newly synthesized proteins and lipids mediating plant responses to different internal and external stimuli (Fahad et al. 2015a). ABA also acts as main internal signal that enables the plant to endure adverse environments (Keskin et al. 2010).

ABA is a crucial messenger in plant response to abiotic stresses, and its function against stress tolerance has attracted the researcher's attention. Endogenous ABA phytohormone level increases rapidly to respond to environmental stimuli by activating well-defined signaling pathways and in addition modifying the expression level of genes (O'Brien and Benková 2013). ABAs also upregulate up to 10% of protein-encoding genes (Nemhauser et al. 2006).

When plants face drought stress, ABA signals to the shoots experiencing stressful water-deficit conditions in the roots that eventually results in stomatal closure and reducing leaf expansion to promote water-saving antitranspirant action (Wilkinson et al. 2012). ABA promotes robust root growth and many structural modifications under water-deficit conditions and nitrogen deficiency (Giuliani et al. 2005; Zhang et al. 2007). ABA regulates many stress-responsive gene expression levels resulting in the production of dehydrins, LEA proteins, and other protective proteins (Sreenivasulu et al. 2012; Verslues et al. 2006). ABA maintains cell turgor by synthesized osmoprotectants and antioxidant enzymes that confer drought tolerance in the plant (Chaves et al. 2003). It was observed that a small proportion of ABA concentration also increases when plant faces salinity (Zhang et al. 2006).

2.2 Auxins (IAA)

After a long period of study, biosynthesis of auxins, its signaling pathways, and transportation of materials in cells are still a mystery (Ke et al. 2015). Auxin (AUX) is responsible for cell elongation in early growth stages and regulating genetic expression during developmental stages (Cohen and Gray 2008). Apart from this, researchers have found some interconnecting pathways for auxin synthesis in plants, four tryptophan (Trp)-dependent pathways and one Trp-independent pathway (Mano and Nemoto 2012). IAA (indole-3-acetic acid) is a phytohormone performing several functions. It is essential for plant nourishment as well as controlling the plant growth upon different stresses (Kazan 2013). It is very clear from the presence of auxin synthesis, signaling, and transportation system in single-celled green algae that auxin contributed a lot during the evolution of plant adaptation from seawater to land environments (De Smet et al. 2011). However, our understanding about the function of auxin regulation during plants growth and development has been improved, but its response against stress is still anonymous (Kazan 2013).

Remarkably, IAA evidences a fundamental role against salinity stress in plants (Fahad et al. 2015a; Iqbal et al. 2014). IAA is involved in boosting up growth rate of plant root and shoot under salinity or heavy metal stress (Egamberdieva 2009; Sheng and Xia 2006). Auxin has an important function in defending the body through expression of several genes in abiotic and abiotic stress responses (Fahad et al. 2015b). Primary auxin response genes, as indicated by the name, are transcribed by stimulation of auxin, and these genes have been found in numerous important plant species such as *Arabidopsis*, rice, and soybean (Javid et al. 2011). The main target is to identify the novel genes, which are responsible for producing tolerance against abiotic stress in major field crops.

2.3 Cytokinins (CKs)

CKs influence the plant growth rate and developmental processes such as chloroplast biogenesis, during cell division, leaf senescence, apical dominance, vascular differentiation nutrient mobilization, anthocyanin production, shoot differentiation, and photomorphogenic development, and hence proved to be the dominant among growth regulators (Davies 2010; Kang et al. 2012; Nishiyama et al. 2011). Endogenous levels of CKs being modified in response to stress are responsible for abiotic stresses like drought and salinity (Kang et al. 2012; Nishiyama et al. 2011; O'Brien and Benková 2013). Mutation and transgenic cells/tissues are responsible for the change in cytokinin metabolism enzymatic activity; moreover, this great technology is also involved in the production of increased stress tolerance for different crops (Zalabák et al. 2013).

Plant tolerance toward salinity can be enhanced by priming the seed with CKs (Iqbal et al. 2006). Plants respond toward CKs when applied externally, enhancing their endogenous levels and biosynthesis under stress conditions (Pospíšilová 2003a). Induction of ABA or water stress inhibits plant germination, also causing leaf and fruit deterioration. Application of CK can overcome this problem by germinating the dormant seed (Hadiarto and Tran 2011). Functions performed by CKs and ABA are contrary to each other (Pospíšilová 2003b). The inverse relation between CK contents and accumulation of ABA in water-stressed plants results in a higher amount of ABA/CK ratio. Enhancement in apical dominance with that of ABA regulation causing better adaptation toward drought stress is due to the reduction in CK levels (O'Brien and Benková 2013). However, CKs' role in plant development is very clear, but their reduction under stressful conditions is still mysterious and has to be discovered in the future.

2.4 Ethylene (ET)

Ethylene (ET), a gaseous phytohormone, is also essential for different plant growth stages including fruit ripening, flower senescence, and leaf and petal abscission; in addition, it also functions as a regulator of stress response (Groen and Whiteman 2014). The cyclic nonprotein amino acid ACC and methionine are a major source of producing ethylene via *S*-adenosyl-L-methionine (*AdoMet*) through biosynthesis. AdoMet is converted to ACC using ACC synthase; ACC is being catalyzed into ethylene via ACC oxidase (Kende 1993). Changes in endogenous ET levels in plants are the result of some abiotic stress. Higher concentrations of ET produced develop tolerance against heat stress by regulating defense mechanism (Larkindale et al. 2005). Chances of plant survival under unfavorable conditions become more when ET is accumulated under environmental stress (Ahmad and Prasad 2011). It is proposed to use ET function as regulating the gene expression where it is thought to be the effectors of ethylene signal (Klay et al. 2014). ET has a great collaboration with other phytohormones like jasmonic acid and salicylic acid. Plant defense mechanism against biotic stresses like pests and pathogens is regulated by these phytohormones (Kazan 2015). ET and ABA appear to affect the plant growth and development sometimes with a great interaction or in opposition (Yin et al. 2015). Hormone released under stress conditions is ethylene, but its production is ambiguous under salt stress. Higher salt tolerance is observed through ET signaling in *Arabidopsis* (Achard et al. 2006). An experiment performed by Cao et al. (2007) proposes that salt sensitivity is induced by the functioning of ethylene receptors; however, ACC can overcome this sensitivity. The positive or negative response of plants toward salt stress depends on the influence of receptor and ethylene on each other; ethylene signaling is essential for salt tolerance.

2.5 Gibberellins (GAs)

The gibberellins (GAs) belong to a large group of tetracyclic diterpenoid carboxylic acids, and some of them act as growth hormones in vascular plants with dominant GA1 and GA4 (Sponsel and Hedden 2010; Hedden and Thomas 2012). The GAs help in seed germination, stem elongation, leaf expansion, flower and trichome initiation and development, and fruit growth (Yamaguchi 2008).

GAs are induced under stress, and its signaling is responsible for plant growth against particular abiotic stress (Fig. 2). GAs leave a positive impact on the photosynthetic rate of plants, leaf expansion and elongation, light interception, and efficient nutrient use and is responsible for regulating various processes during plant development (Khan et al. 2007). They are needed to perform functions during growth for their whole life cycle. Rising evidence proved their dynamic roles toward abiotic stresses and adaptation of tolerance (Colebrook et al. 2014). The adverse effects due to

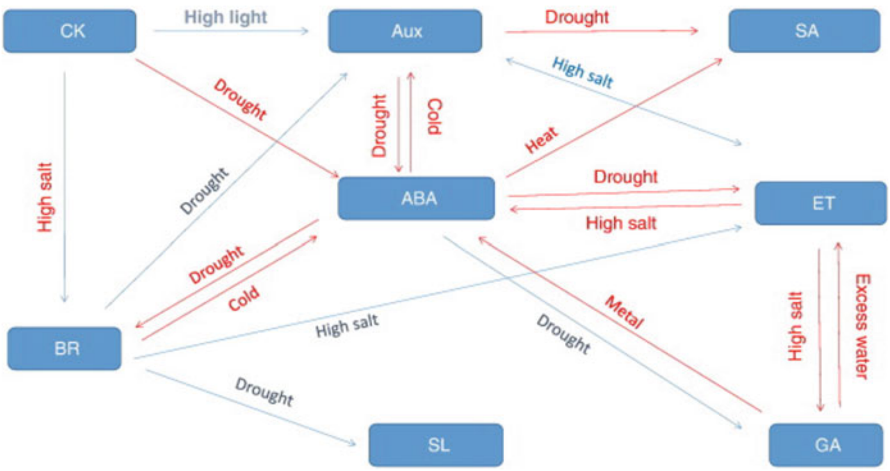

Fig. 2 The possible roles of phytohormones in abiotic stress tolerance and crosstalk between phytohormone signaling (Wani et al. 2016)

environmental stresses can be lessened by the production of gibberellins (Yamaguchi 2008). The role of GAs is studied in seedlings of *Arabidopsis thaliana* for their response toward osmotic stresses (Skirycz et al. 2011; Claeys et al. 2012). Tomato plant grown at low saline soils had better water use efficiency and low stomatal resistance under GA application which can lead toward a healthy and better yield of the crop (Maggio et al. 2010). GAs are known to have direct or indirect relations with all other phytohormones in frequent developmental stages and stimulus-response processes. Through this study, GA regulation is assumed as an outstanding method for protection against stress. Innovative crop protection approaches with some other global implications can be used as the basis for plant integration by using different regulating GA levels.

2.6 Brassinosteroids (BRs)

Brassinosteroids (BRs) include a comparatively latest group of polyhydroxy steroidal biomolecules having a strong potential for plant growth and better development. They were first found and studied in pollen grains of *Brassica napus*. Researchers have found more than 70 BRs in plants. Among these, three most bioactive BRs molecules, which are mostly studied in physiological and experimental investigations, include brassinolide, 24-epibrassinolide, and 28-homobrassinolide (Vardhini et al. 2006). BRs are involved in the regulation of ion uptake, (Khripach et al. 2000). Heavy metal and radioactive element accumulation that are hazardous for plant growth can be minimized by using BR application (Anuradha and Rao 2001). Their presence in different parts of plants, e.g., pollen, seeds, vascular cambium, flower buds, fruits, leaves, shoots, and roots, is responsible for several developmental stages, stem and root growth, floral initiation, and higher production of flowers and fruits (Bajguz and Hayat 2009). For abiotic stresses such as heat (Janeczko et al. 2011), chilling (Wang et al. 2014), soil salinity (Abbas et al. 2013), light (Kurepin et al. 2012), drought (Mahesh et al. 2013), flooding (Liang and Liang 2009), metals/metalloids (Bajguz 2010), and organic pollutants, BRs performed mitigating roles under impact of these stresses (Ahammed et al. 2012). A remarkable potential of BRs and related compounds for antioxidant defense system in response of overwhelming abiotic stress-induced oxidative burst is studied under recent research (Vardhini and Anjum 2015). There is still a huge scope to additionally explore the locations, mechanisms, enzymology of the biosynthesis of these molecules, source-sink relationships, developmental and stress physiology, microbe interactions, fungi, and animals and understand their influential uses (Fahad et al. 2015a).

2.7 Jasmonates (JAs)

The cyclopentanone phytohormones are a derivative of membrane fatty acids that include main methyl jasmonate (MeJA) and its free acid (jasmonic acids) produced from their metabolism and are characterized as jasmonates (JAs) extensively found in kingdom plantae. These versatile biomolecules are involved in critical plant developmental stages, flowering, senescence, fruiting, secondary metabolism, and negative or positive defense responses (Seo et al. 2001; Tani et al. 2008; Fahad et al. 2015c). JA is marked as the best characterized, ample, and well recognized among all the JAs. Apart from involvement in developing approaches of plants, JA responds quickly toward pathogenic attack as a plant defense response, as well as against environmental stresses including water-deficit, salinity, and low temperature (Pauwels et al. 2009; Seo et al. 2011). Numerous environmental stresses including salinity is a source of inducing JAs as a dynamic signaling molecules (Pauwels et al. 2009), drought (Seo et al. 2011; Du et al. 2013), and UV irradiation (Demkura et al. 2010). They can highly combat these detrimental environmental stimuli (Dar et al. 2015). Symptoms of efficient reduction in salinity stress are observed in soybean seedlings by the exogenous application of MeJA (Yoon et al. 2009). Pathogenesis-related genes are supposed to be switched on against stress by exogenous application of JA (Mei et al. 2006). Endogenous levels of JA improved in rice roots work efficiently against salinity stress and are stated to respond toward damages caused by salinity stress (Wang et al. 2001). Antioxidants are activated by JA applications thus lessening the heavy metal stress in plants (Yan et al. 2013). Accumulation of phytochelatins through MeJA produces tolerance in *A. thaliana* against heavy metal stresses like Cd and Cu (Maksymiec et al. 2007).

2.8 Salicylic Acid (SA)

Among numerous phenolic compounds synthesized by plants, SA has great importance. This is a plant hormone. The main function of this hormone is organic synthesis playing a key role in the pathogenesis-associated expression of proteins. Salicylic acid has been reported to be a key component responsible for growth and development of plants as well as their interaction with some other organisms (Senaratna et al. 2000; Miura and Tada 2014;). According to Khan et al. (2003), SA has been found to have a role in different plant functions like germination of seed, glycolysis, flowering, the yield of fruit, uptake of ions, and rate of photosynthesis, stomatal conductance, and transpiration. Two pathways are involved in the synthesis of SA. One pathway is IC pathway, and the other is the phenylalanine ammonia-lyase (PAL) pathway. In tomato and *Nicotiana benthamiana* iso-chorismate is the main pathway for SA production (Uppalapati et al. 2007; Catinot et al. 2008). SA treatment-responsive genes are mostly stress and signaling pathways related and leading to the ultimate death of cell (Jumali et al. 2011).

Most importantly, lower concentrations of SA are beneficial for plants, as low concentrations increase the antioxidant potential of plants. Higher SA concentrations are very harmful to the plants because it makes plants vulnerable to abiotic stresses and it also leads to cell death (Jumali et al. 2011).

SA is responsible for plant response to various abiotic stresses including water-deficit (Miura et al. 2013), salinity (Khodary 2004; Fahad and Bano 2012), freezing (Yang et al. 2012), and heat stress (Miura and Tada 2014). Together SA and ABA are involved in the regulation of drought stress responses (Miura and Tada 2014). The SA concentration was observed to increase twofold in barley roots by water deficit (Bandurska 2005). *PR1* and *PR2* are two SA-inducible genes (pathogenesis-related genes) inducing response against drought stress (Miura et al. 2013). Still, the comprehensive molecular mechanism of the role being played by SA in abiotic stress tolerance is unclear requiring more comprehensive investigations to un-reveal the underlying mechanisms.

2.9 Strigolactones (SL)

SLs belong to a small group of carotenoid-derived biomolecules. About 50 years ago, they were known to be seed germination stimulants in root parasitic plants, e.g., *Striga*, *Orobanche*, and *Phelipanche* (Ruyter-Spira et al. 2013). A single plant species can produce various types of SLs, whereas in case of intraspecific varieties, blends of different kinds and amounts of SL molecules can be observed (Yoneyama et al. 2013). Though SLs are synthesized and accumulated in small quantities in roots, other parts of the plants can also produce these biomolecules. The role of SLs in the development of root system architecture was proved by a comparative study of wild-type and mutant *Arabidopsis* plants (Koltai and Beveridge 2013). Applications of GR24, which is a synthetic and physically active SL (Gomez-Roldan et al. 2008), suppressed lateral root formation in the seedlings of wild-type and SL synthesis mutants (*max3* and *max4*) but not in the strigolactone-response mutant (*max2*), indicating *MAX2*-dependent negative impact of strigolactone on the development of lateral root (Kapulnik et al. 2011).

From the beginning of their evolution, SLs are thought to be involved in the response of plants to environmental stimuli. They are involved in the structure of root/shoot in higher plants in response to nutritional conditions (Kapulnik and Koltai 2014). They also act as signaling agents to interact with microbes. They also stimulate nodulation during legume-rhizobium interactions (Soto et al. 2010). Generally, SLs have a critical role in agriculture; they can be applied as inducers for the suicidal germination of parasitic plants (Vurro and Yoneyama 2012). It can be concluded that SLs are a class of molecules that help plants in signaling and they are a key regulators of plants adaptations in response to environmental conditions.

3 Cross Talk between Phytohormone Signaling

Plants need to identify and respond to environmental stresses in highly synchronized and specialized ways. Signaling pathways are responsible for the adaptation of plants to cope severe and harsh surroundings. Hormones act by triggering other messengers or phosphorylation cascades. Singh and Jwa (2013) have described insights on biosynthetic mechanisms and signaling components of ABA, IAA, BRs, GAs, JA, and ET. These are among the most important phytohormones. Hence the complexity continues because of all these factors (Pinheiro and Chaves 2010). Signal transduction cascade and fluctuations in phytohormones are considered as one of the earlier actions from plants in response to stresses.

Numerous plant hormones work together to make a strong line of defense against any stress or undesirable environmental stimuli. It is believed that SA and ABA are the major phytohormones that control and regulate the signaling networks and pathways. In current years, interactions between phytohormones and their functions in response to abiotic stresses have increased their popularity. According to Kohli et al. (2013), interactions among phytohormones are not only helpful in attaining the defense goal against stress as well as growth and signaling.

For each hormone, the presence of various signaling intermediates indicates their apparent functions in such cross talks. To understand the cross talk among phytohormonal and defense signaling pathways is thus essential in a sense that it may disclose new prospective objectives for the host resistance mechanisms, development, and phytohormones (Grant and Jones 2009).

Now we have discussed the closing of stomata in the absence of subsequent amount of water and the role of phytohormones in this response. A complex signaling network primarily controls stomatal closing, and ABA acts as a trigger for this short-term response. According to Zhang et al. (2006), ABA also controls long-term responses related to growth such as root growth by optimizing the uptake of water by regulation of gene expression. ABA along with other signaling-related molecules and with other hormones like JA and NO in drought stress stimulates the closing of stomata. Interestingly, gene expression is regulated by the genes related to the response of ethylene, cytokinins, and auxins (Harrison 2012). It has been described previously by the scientists that production of JA in response to stress stimulates extracellular Ca^{2+} influx by interaction with a stomatal closure that is mediated by ABA. This interaction leads to the activation of H_2O_2/NO signaling (Harrison 2012).

According to Desikan et al. (2006), the closing of stomata due to ethylene is regulated by the signal transduction pathway. This pathway is also induced production as well as it is H_2O_2 dependent. Jasmonic acid is synthesized under stress conditions such as herbivory. Most of the signaling genes associated with jasmonic acid are being controlled by drought stress (Huang et al. 2008).

Interactions of JA and ABA increase Ca^{2+} influx, thus closing stomata. This interaction leads to the stimulation of CDKP synthesis, thus forming a signal cascade (Harrison 2012). Treating excised and turgid leaves of *Arabidopsis* for 10 min with ABA or MeJA causes reduction of stomatal aperture (Munemasa et al. 2007).

Scientists suggested that the formation of NO and ROS in guard cells is due to the interactions between ABA and MeJA; besides these, both are present in very low concentrations in plants that are MeJA insensitive. Under drought stress there was observed a 19-fold increase in MeJA, whereas ABA is increased by twofold due to poor seed set according to Kim et al. (2009) having an association with low productivity.

ABA-mediated gene regulation of transcription factors (TFs) triggered and influenced long-term biological and physiological responses to external abiotic stresses by binding to *ABREs* on ABA-regulated genes. Particularly, phosphorylation cascades lead to changes in ABA-regulated TFs as signaling stomatal closure do. For example, ABA-responsive *TFsABF1* and *ABF4* are activated when their phosphorylation is done by ABA-inducible kinases *CPK11* or *CPK4* (Zhu et al. 2007).

On the contrary, upon salinity stress, upregulation of JA pathway genes have been reported in barley (Walia et al. 2006). However, the comprehensive function of JA under water-deficit and salinity stresses remains unidentified; it could be linked as a biomolecule signaling cell death (Kohli et al. 2013). Nishiyama et al. (2011) in gene expression research discovered that exogenous ABA application downregulates iso-pentenyltransferase (*IPT*), a main cytokinin biosynthetic pathway gene, but upregulates cytokinin dehydrogenase- and oxidase-encoding genes. Moreover, in addition to its well-defined function in governing plant growth and development linked with auxins and BRs (Stamm and Kumar 2013), GA is also playing a significant role in cross talk of hormonal connections in signaling environmental stimuli (Depuydt and Hardtke 2011; Linkies and Leubner-Metzger 2012). Latest researches clarify the interaction between environmentally triggered ABA, GA, ET, and CK signals is vital in the determination of plant stress responses (Raza et al. 2019; Krouk et al. 2011; Iqbal et al. 2011; Qin et al. 2011).

Based on evidence it is said that phytohormones also counter harsh act conditions. For instance, in tomato a signal peptide system together with JA has been identified as a wound-induced salt stress adaptor (Capiati et al. 2006), which indicates cross-tolerance signaling. The potential functions of phytohormones in response to abiotic stresses and cross talk between phytohormone signaling are demonstrated in Fig. 2.

4 Conclusions and Upcoming Perspectives/Outlook

Agriculture-dependent economy of most countries is relying on fertile soils and suitable climatic conditions. However, environmental stresses are posing numerous challenges. For the last few years, the emphasis has been given to the underlying molecular mechanisms that are regulating hormone synthesis as well as their signaling and actions. Roles being played by the plant hormones in response to environmental stresses have also been focused.

Overall, phytohormones engineering is a significant area for abiotic stress tolerance, offering new prospects to conserve sustainable crop production globally to provide food under fluctuating environments. Phytohormones have main functions against abiotic stresses with the involvement of several stress-responsive genes to induce tolerance and adaptations in the plant against a variety of stresses. In recent years, with the improvement in genetic technology, many researches have been conducted to get better understanding of plant responses against abiotic stresses.

To overcome the harms being posed by the continuously changing environmental conditions and inducing abiotic stress tolerance in plants, phytohormone engineering is the most important approach. This can be helpful to overcome the hidden hunger worldwide. It involves multiple stress-responsive genes that is why it is more worthy. Due to the rapid advancement in technology during the last few years, scientists are researching with more focus on understanding the plant's responses to abiotic stresses.

Still, there remain many challenges to reveal and comprehend the complexity of stress-responsive pathways by signal transduction mechanism. For example, to get comprehensive understanding of plant responses against abiotic stresses in upcoming years, extensive work has to be performed at expression levels of genes involved in biosynthetic pathways of hormones, e.g., IAA. Recent researches indicate the initiation of phytohormone engineering. The functions of these biomolecules responding to fluctuating environmental conditions have been revealed, defining their main function in plant stress responses. This review describes the summary of phytohormone's role, cross-talk among these biomolecules, and the significance of studying combined internal and external stresses and phytohormone engineering techniques and approaches to develop stress-tolerant plants. These phytohormones function directly or indirectly in plant defense mechanisms as well as plant-environment interactions while facing a wide range of stresses.

Concluding the importance of phytohormone engineering as an appealing and interesting research field for the plant biologists, there is still a lot to be revealed, which can be done before the technology can reach its peak. Development of stable phytohormone-engineered crops is the most promising issue that needs to be focused for the production of some basic foods such as wheat, rice, and corn. To attain this objective, combinations of stresses have to be addressed in field trials.

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Plant Growth-Promoting Bacteria: Biotic Strategy to Cope with Abiotic Stresses in Wheat

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Contents

Abstract Plant growth-promoting bacteria (PGPB) are beneficial free-living soil, rhizospheric, epiphytic, and endophytic microorganisms capable to stimulate plant growth and increase host plant resistance and tolerance to a wide range of biotic and abiotic stresses. A number of PGPB associated with wheat and different cereals have

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been identified comprising bacterial strains belonging to such genera as *Bacillus*, *Azospirillum*, *Arthrobacter*, *Acinetobacter*, *Azotobacter*, *Citricoccus*, *Lysinibacillus*, *Burkholderia*, *Paenibacillus*, *Serratia*, *Pseudomonas*, etc. Several studies have confirmed that some species of bacteria associated with the rhizosphere of plants are useful for growth, development, and formation of yield and quality of agricultural crops. Furthermore, those bacteria which are capable to colonize internal plant tissues, namely, endophytes, may be more successful (compared to rhizospheric bacteria) in the promotion of plant growth and development under both normal and long-term stress conditions. PGPB-induced development of defense responses and the formation of tolerance under the exposure to various abiotic stresses have been demonstrated in numerous plants, including wheat. The mechanisms of such physiological effect of PGPB on host plants are believed to be varied, intertwined, and specific; PGPB positively affects on plants through biosynthesis of numerous biologically active compounds, for instance, substances with antibiotic and insecticidal activities, biosurfactants, siderophores, chelators, phytohormones, enzymes, and nitrogen fixation, regulating the level of ethylene in plants, and improving macro–/micronutrient bioavailability, development of systemic resistance to diseases, and tolerance to abiotic stresses with involving salicylate-dependent or jasmonate-dependent signaling pathways. In this review, the role of beneficial PGPB in ameliorating the many deleterious consequences during abiotic stresses has been considered. Besides, *B. subtilis*' efficiency on abiotic stress tolerance induction in wheat according to their ecological groups (ecotypes) is discussed as well.

Keywords PGPB · *B. subtilis* · Wheat · Abiotic stress tolerance · Systemic resistance

Abbreviations

ABA	abscisic acid
ACC	1-aminocyclopropane-1-carboxylate
APX	ascorbate peroxidase
ATP	energy supply
CAT	catalase
CKs	cytokinins
EC	electrical conductivity
EPS	exopolysaccharides
FDPs	flavodiiron proteins
GB	glycine betaine
GR	glutathione reductase
HL	high light
HM	heavy metal

HSFs	heat stress transcription factors
HT	high temperature
IAA	indole-3-acetic acid
ISR	induced systemic resistance
IST	induced systemic tolerance
JA	jasmonic acid
MDA	malondialdehyde
MSI	membrane stability index
NO	nitrogen oxide
NPQ	non-photochemical quenching
PA	peroxidase
PAL	phenylalanine ammonia lyase
PEG	polyethylene glycol
PSI	photosystem I
PSII	photosystem II
PGPB	plant growth-promoting bacteria
PGPR	plant growth-promoting rhizobacteria
ΔpH	pH gradient
ROS	reactive oxygen species
RuBisCO	ribulose-1,5-bisphosphate carboxylase/oxygenase
RWC	relative water content
SA	salicylic acid
SAR	systemic acquired resistance
SOD	superoxide dismutase
TDFs	transcript-derived fragments
TSS	total soluble sugar

1 Introduction

The rapid world's population growth, climate change, consumption of nature, and catastrophically high depletion rate of natural resources force agricultural production to a significant increase in food deficit. According to forecasts, the population of world by 2050 year will reach 9.1 billion people (FAO 2014). To ensure food security, the food production should increase by 70% mainly through the increase of major cereal crop productivity, including wheat plants (FAO 2014; Benedetto et al. 2017) which are commonly used for human consumption in many areas worldwide and supplying more than 50% of humanity's dietary energy (Ehrlich and Wilson 1991; Thrupp 2000; FAO 2014; Benedetto et al. 2017).

Abiotic stresses initiate major drawbacks which are significantly decreasing growth and productivity of agricultural crops like wheat plants (Kosova et al. 2015; Pereira 2016). Yield losses caused by abiotic stresses (temperature extremes, drought, salinity, pollutant toxicity, high light intensity, UV radiation, herbicides, various oxidative stresses, etc.) reached 50–82% and pose a serious danger to the agricultural industry and global food security (Benedetto et al. 2017). Several chemical approaches that have been successfully applied for the last decades to increase production and productivity have irreparably damaged the environment including land degradation; soil, water and air pollutions; as well as biodiversity losses. Therefore, there is a need to discover novel environmentally friendly and affordable coping strategies to reduce the global abiotic stresses threatening the agriculture. To decrease the detrimental impacts of different abiotic stresses on plant growth and development, several strategies have been developed, for example, genetic engineering of plants and application of beneficial strains of PGPB (Dimkpa et al. 2009; Glick 2014). Of particular interest is the last due to the activation of various physiological features of metabolism without causing adverse effects on host plants, humans, and the environment (Van Loon 2007; Van der Ent et al. 2009; Maksimov and Khairullin 2016).

PGPB are beneficial microorganisms stimulating plant growth and increasing their resistance to varied biotic (Beneduzi et al. 2012; Akram et al. 2013; Rahman et al. 2017) and abiotic stress conditions including drought, extreme temperatures, salinity, toxic metals, etc. (Rajkumar et al. 2008; Arzanesh et al. 2011; Upadhyay et al. 2012; Zarea et al. 2012; Asgari et al. 2012; Naveed et al. 2014; Han et al. 2015; Furlan et al. 2017; Barnawal et al. 2016; Furlan et al. 2017; Lastochkina et al. 2017a; Khan et al. 2017; Numan et al. 2018); therefore they lead to an increase in productivity and yield of plants. The growth-stimulating and protective effects of PGPB under different abiotic stresses have been discovered in varied plants, including wheat (Creus et al. 1997, 2004; Upadhyay et al. 2012; Turan et al. 2012; Lastochkina et al. 2017a; Çakmakçı et al. 2017), barley (Çakmakçı et al. 2007; Turan et al. 2012), maize (Cohen et al. 2009; Rojas-Tapias et al. 2012), cucumber (Egamberdieva et al. 2011), cabbage (Turan et al. 2014), strawberry (Esitken et al. 2010), lettuce (Yildirim et al. 2011), brahmi (Bharti et al. 2013), and sugar beet (Pusenkova et al. 2015, 2016) by several mechanisms. However the mechanisms by which PGPB enhance plant growth and stress resistance/tolerance are not completely understood; they supposed to include the production of a numerous bioactive compounds with antibiotic activity, biosurfactants, siderophores, chelators, phytohormones, enzymes, fixation of atmospheric nitrogen, and phosphate solubilization, improving macro−/micronutrient bioavailability in plants (Bottini et al. 2004; Grichko and Glick 2001; Berg 2009; Pérez-García et al. 2011; Sessitsch et al. 2012; Pandey et al. 2017), and induction of plant's systemic tolerance through pathways regulated by such signaling molecules as salicylic acid (SA) and jasmonic acid(JA)/ethylene (Van Loon 2007; Niu et al. 2011; Sayed et al. 2011; Garcia-Gutierrez et al. 2013). It was revealed that the liquid culture of *Bacillus subtilis* having a positive effect on plant growth and development contained such natural growth regulators as cytokinins (CKs), auxins, gibberellins (GB), and abscisic acid (ABA) (Sgroy et al. 2009). A number of studies suggested that those PGPB which are capable to produce 1-aminocyclopropane-1-carboxylate (ACC)-deaminase and auxins, particularly indole-3-acetic acid (IAA), protect plants most effectively against different stresses compared to non-producers (Egamberdieva and Kucharova

2009). The plants inoculated with PGPB and exposed to salt stress were characterized with elevated expression of genes and accumulation of osmoprotectants such as proline, glutamine, and betaine and activation of other multiple mechanisms, including the rapid upregulation of signaling pathways responsive to salt stress (Szabados and Savoure 2009; Lastochkina et al. 2017a). As revealed these changes are useful for efficient photosynthesis, growth, and integrity of the membrane, which ultimately provides a proper condition for plant growth. A number of recent studies reported that both growth-stimulating and anti-stress effects of PGPB are connected with their ability to produce such signaling molecules as SA and JA which play a pivotal role in launching systemic resistance and tolerance of plants to stresses by activating SA-dependent and JA-dependent defense signaling pathways (Fravel 2005; Forchetti et al. 2007; Chourdhary and Johri 2009; Sayed et al. 2011; Wenhao et al. 2012; Garcia-Gutierrez et al. 2013; Lastochkina et al. 2017a). With that, the whole chain of defense reactions on the way of PGPB-induced abiotic stress tolerance in plants is still far from clear. Moreover, the effectiveness of the same strain of PGPB can vary depending on many factors, for instance, plant species, their ecological and geographical origin, as well as varietal characteristics (Madry et al. 2013; Volis et al. 2015; Lastochkina et al. 2017b). Therefore, transparent understanding of the mechanisms used by the PGPB is extremely important for fully using the potential of these microbes as an important component of organic agriculture to increase crop productivity maintaining long-term soil fertility and sustainability in a clean environment.

In this chapter, recent progress in understanding the role of PGPB in the development of wheat plant defense responses and the formation of tolerance to different abiotic stresses are discussed. The current states of knowledge of the fundamental physiological and biochemical mechanisms about PGPB-induced abiotic stress tolerance in plants with the main focus on wheat have also been considered.

2 PGPB-Mediated Amelioration of the Damaging Effect of Abiotic Stresses on Wheat

Investigations of the mechanisms mediated by PGPB on plant stress resistance are of the most urgent problems in modern plant biology. Numerous data are available regarding the diversity of the physiological impact of beneficial PGPB on various plant organisms (Çakmakçı et al. 2007; Egamberdieva et al. 2011; Garcia-Gutierrez et al. 2013; Verma et al. 2016; Khan et al. 2017), which can be divided into (i) pronounced growth-stimulating and (ii) protective role against a wide range of adverse effects (Khalid et al. 2004; Sayed et al. 2011; Beneduzi et al. 2012; Pusenkova et al. 2015; Khan et al. 2017). In nature, plants are exposed to various abiotic stresses, for example, extreme temperatures, drought, salinity, heavy metals (HMs), UV radiations, and air pollution (Pareek et al. 2009; Pereira 2016), which result in reduced crop productivity. These stresses are often interrelated and induce general signaling pathways which regulate the cellular responses aimed at adaptation and therefore cause similar morphological, physiological, biochemical, and molecular genetic changes in plants (Munns and Tester 2008; Huang et al. 2008; Potters et al. 2009). Several studies have shown that various bacterial species of PGPB belonging to different genera contributes to the protection of host plants, including wheat, from diverse abiotic stresses and lead to plant growth promotion, nutrient uptake, and yield formation. These effects could be due to triggering varied defense responses which are diverse, intertwined, and often specific (Chakraborty et al. 2013; Meena et al. 2017; Numan et al. 2018).

2.1 Drought

Drought is one of the main abiotic stress factors of the environment in many regions of the world, leading to growth inhibition and reduced crop yields (Okuyama et al. 2004; Araus et al. 2008; Kosova et al. 2015; Khan et al. 2017). Numerous studies demonstrated that PGPB contributes to alleviating drought stress in wheat (Creus et al. 1997, 2004; Pereyra et al. 2012; Naveed et al. 2014; Timmusk et al. 2014; Çakmakçı et al. 2017; Barnawal et al. 2017). For example, wheat plants inoculated with *Azospirillum brasilense* strain Sp245 under exposure to drought were characterized with increased water content and apoplastic water function compared to non-inoculated control plants (Çakmakçı et al. 2017). Pereyra et al. (2012) demonstrated that application of *A. brasilense* Sp245 induced wider xylem vessels in wheat under osmotic stress that contribute to enhanced coleoptile hydraulic conductance and resulted in better water status in inoculated plants. In another study, wheat seedlings inoculated with *A. brasilense Sp245* under osmotic stress showed significant higher coleoptiles, better water status, and accumulation of fresh biomass (Alvarez et al. 1996). ABA-producing bacteria *Azospirillum* has been reported to promote tolerance of Arabidopsis, wheat, and maize to drought stress (Dodd et al. 2010). Application of *A. brasilense* strain INTA Az-39 positively impacts on wheat plants under dryland farming conditions due to increased plant growth, biomass accumulation, number of grains per spike, and yield (Díaz-Zorita and Fernández-Canigia 2009). Another finding also indicated that application of *Azospirillum* spp. in wheat resulted in alleviation of the damaging effect of drought stress on plant growth and yield formation due to regulating water characters (Arzanesh et al. 2011). Furlan et al. (2017) demonstrated that inoculation of wheat plants (Cv. CD-120 and Frontana) with *A. brasilense* and *H. seropedicae* contributes to maintaining a high relative water content (RWC), membrane stability, and increased tolerance of wheat to drought (Furlan et al. 2017).

PGPB-induced drought stress tolerance in plants is mediated by several mechanisms such as phytohormonal and ACC-deaminase activity, antioxidant defense, accumulation of osmolytes, volatile compounds, production of exopolysaccharides (EPS), and change in root morphology has been proposed (Timmusk et al. 2014; Barnawal et al. 2017). Phytohormones produced by plants such as IAA, ABA, CKs, GB, and ethylene are playing a major role in plant growth and development under both normal and abiotic stresses including drought (Frankenberger and Arshad 1995). The ability of PGPB to synthesize phytohormones including IAA, ABA, CKs, GBs, ethylene, SA, JA was demonstrated in a number of studies (Barnawal et al. 2017; Lastochkina et al. 2017a). Production of endogenous phytohormones plays a prominent role in the development of the anti-stress effect of PGPB. A wide range of plants, including wheat, inoculated with bacteria capable to produce IAA represent an increase in root initiation and growth which result in elevated water and nutrient uptake and plant tolerance under water deficiency stress (Dimkpa et al. 2009; Egamberdieva and Kucharova 2009). In another study, exposure of wheat (*Triticum aestivum*) plants inoculated by *A. brasilense* Sp245 under drought stress leads to formation of better grain yield with higher quality of minerals (K, Ca, and Mg), improved water potential, absolute and RWC, apoplastic water fraction, and lower cell wall elasticity which all critically affect drought tolerance in plants (Creus et al. 2004). Dual effects of *Azospirillum* on leaves by decreasing water potential and increasing water content that represent the capability of the bacteria to produce IAA and induce the formation and growth of lateral roots have been reported. These effects have been indirectly attributed to the increase in water absorption and nutrient uptake in wheat plants exposed to drought stress conditions (Arzanesh et al. 2011). *Rhizobium leguminosarum*, *R. phaseoli*, and *Mesorhizobium ciceri* demonstrated interaction with wheat plants under drought through improving growth of seedlings, their biomass, and tolerance to drought (Hussain et al. 2014). Besides, inoculation with *B. thuringiensis* AZP2 increased the biomass of wheat plants and resulted in fivefold higher survival under drought stress through considerable reduction of volatile emissions and increasing photosynthesis (Timmusk et al. 2014). Inoculation of wheat with *Burkholderia phytofirmans* PsJN significantly reduced the damaging impact of drought on RWC and assimilation rate of CO_2, thereby improving the rate of photosynthesis, chlorophyll content, and water-use efficiency compared to non-inoculated plants (Naveed et al. 2014). Similar results are reported in other studies as well (Chakraborty et al. 2013). However, drought leads to changes in the composition of phospholipids in wheat roots, increases phosphatidylcholine, and decreases phosphatidylethanolamine. Inoculation with *Azospirillum* inhibits these alterations in plants, although increased phosphatidylcholine and lower unsaturated phosphatidylethanolamine are observed (Pereyra et al. 2012). It has been suggested that inoculation of wheat by *Pseudomonas* sp. E2 and *Azotobacter chrocoocum* E1 mitigated drought stress due to improved anatomical changes, particularly the thickness of epidermis and mesophyll and phloem tissues, the diameter of xylem vessel, and the size of vascular bundles of the root system, whereas in non-inoculated plants, water deficit possibly decreases the anatomical values (El-Afry et al. 2012).

Plants' responses to stress condition cause the water regime disturbance including the enhancement of biosynthesis and accumulation of ABA. The regulatory pathways of ABA biosynthesis and accumulation in response to water deficit and the main stages of its signaling have been traced. Dehydration can (directly or indirectly) affect the enzyme activity of the calcium signaling system – associated with membrane-bound phospholipase C. When phospholipase C is hydrolyzed with membrane phospholipids, 1,4,5-trisphosphate is formed, which causes the opening of the calcium channels. Enhanced cytosolic calcium concentration causes an increase in protein kinases activity, which phosphorylates transcription regulation factors. This, in particular, activates the expression of the genes and enzymes involved in the synthesis of ABA. ABA effect on the level of ABA-sensitive genes transcription can be explained by the involvement of the secondary messengers such as hydrogen peroxide. Hydrogen peroxide accumulation is associated with the ability of ABA to increase the activity of NADPH oxidase, reactive oxygen species (ROS), phospholipids, calcium ions, and nitrogen oxide (NO) (Kwak et al. 2006). Nearly 2/3 of the 2000 drought-induced genes are regulated by ABA (Huang et al. 2008), which underlies the plant's adaptation to various stresses resulted in water regime disturbance. Some strains of PGPB have been revealed to increase plant secreted levels of ABA following the imposition of water stress. However, it is hard to explain whether ABA is produced by bacterium or plant. Furthermore, it was reported that the wheat aquaporin gene TaAQP7 (encoding water transport) was activated following exposure to drought stress and blocked by inhibiting the biosynthesis of ABA, which is consistent with the participation of ABA in the upregulation of TaAQP7 as a modulator of plants' drought tolerance. It has been revealed *Arthrobacter protophormiae* SA3 and *B. subtilis* LDR2 inoculations counteract with the increase of ABA and ACC under both drought and salt stresses, while *Dietzia natronolimnaea* STR1 did not have a significant impact on the content of ABA and ACC. Inoculations of wheat plants with plant growth-promoting rhizobacteria (PGPR) strains STR1, SA3, and LDR2 enhanced the *TaCTR1* gene expression levels in treated plants in comparison to non-treated control ones under salt and drought stresses. Application of PGPR improved the expression of *TaDREB2* gene encoding a transcription factor playing an important role in improving plants' tolerance under abiotic stresses (Barnawal et al. 2017).

Water deficit like other stressors causes oxidative stress in plants, which is associated with increased ROS production including superoxide anion radicals ($O_2^{\bullet -}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), alkoxy radicals, and hydroxyl radicals ($OH^{\bullet}$) which potentially force negative impact on the integrity of plant cell membrane structures. One notable role in neutralizing the impact of oxidative stress belongs to the antioxidant defenses involving both enzymatic (peroxidase (PA), catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR)) and non-enzymatic (ascorbic acid, cysteine, glutathione) components serving to prevent accumulation of ROS and mitigate the oxidative damage caused by drought (Kaushal and Wani 2015). Current evidence indicates the effect of PGPB on the activity of PA, CAT, SOD, and APX involved in the utilization of ROS (Ullah and Bano 2015). The decrease in the harmful impact of oxidative stress by PGPB has been shown in many plants, including wheat (Kasim et al. 2013; Kang et al. 2014). A study conducted on wheat demonstrated that bacterial inoculation increased the activities of PA and CAT in plants under water stress condition in comparison with non-inoculated ones (Khalafallah and Abo-Ghalia 2008). Kasim et al. (2013) revealed that priming of wheat with *A. brasilense* NO40 and *B. amyloliquefaciens* 5113 prevented the drought-induced decrease in fresh and dry weights of plants and improved homeostatic mechanisms resulted in drought tolerance by reducing the adverse effect of drought stress in wheat (Kasim et al. 2013).

Adaptation of plants to drought stress is related with the cumulation of compatible solutes and osmolytes such as proline, betaines, polyamines, sugars, amino acids, as well as water-deficit-related proteins, particularly dehydrins (Yancey et al. 1982; Close 1996). Increased level of osmolytes maintains water status in plant cells and protects proteins and membranes from stress-induced damages (Sandhya et al. 2010). Various studies revealed that in response to drought stress, PGPB are capable to secrete osmolytes, which function synergistically with plants-produced osmolytes and stimulate growth due to increasing root cells' osmotic potential (Paul et al. 2008; Dimkpa et al. 2009). A key role in plant protection from stresses is given to the crucial osmoprotectant proline, which possesses the properties of chaperones and involved in osmoprotection system of plants, reducing the degree of damage caused by dehydration of cellular structures (Shakirova et al. 2012). The involvement of proline in the spectrum of the protective action of PGPB in wheat and other different plant species has been shown frequently (Paul et al. 2008; Dimkpa et al. 2009; Gusain et al. 2015; Shintu and Jayaram 2015; Lastochkina et al. 2017a). For example, the use of PGPB increased biomass and the RWC of the leaves by accumulating Pro in maize under drought stress (Sandhya et al. 2010). Moreover, PGPB can protect plants from drought stress damages by synthesizing the osmoprotectant trehalose. Trehalose is a highly stable glucoside because of including two molecules of α-glucose that forms a gel phase (replacing water) as cells dehydrate. Therefore it is capable of reducing the damage to cells from drought (Suarez et al. 2008).

2.1.1 Effect of PGPB on Wheat Ecotypes with Different Drought Tolerance Strategies

Wheat is a crop with great adaptive potential which allows it to widely spread over the globe. Significant areas of wheat cultivation are in Russia where the crop is classified into several ecological groups or ecotypes. Depending on the time of drought onset, two of them comprising the forest-steppe West Siberian and the steppe Volga ecotypes pose different drought adaptation strategies (Zhukovsky 1957). Plants of the forest-steppe West Siberian ecotype are characterized by a gradual germination rate and a long phase of tillering; however, at the same time, a rapid development of the root system can be observed among them. Contrariwise the steppe Volga ecotype varieties are characterized by intensive growth at the beginning of the vegetation period by using of reserved moisture from spring period in the soil, and therefore, in the drought raised from summer, these ecotype varieties are characterized by a well-branched network of the root system, which contributes to the formation of a good yield in these conditions.

It is known that the effectiveness of the same strain of PGPB can vary based on several factors like plant species, their ecological and geographical origin, and varietal characteristics (Madry et al. 2013; Volis et al. 2015; Lastochkina et al. 2017b). Therefore, the ecotypic-dependent efficacy of *B. subtilis* 26D bacteria on the drought tolerance of wheat plants is detected in the early stages of ontogenesis. It was shown that wheat varieties belonging to different ecological groups demonstrate different drought tolerance when inoculated by *B. subtilis* in the same growth conditions (Lastochkina et al. 2017b). It was revealed that under the stress condition caused by moisture deficiency, the influence of *B. subtilis* bacteria on the drought tolerance of wheat varieties in different ecotypes was observed at the initial stages of ontogenesis, which, apparently, is associated with different adaptation strategies used against drought stress by plants. Thus, the pretreatment of *B. subtilis* promoted better germination of the seeds of the variety (Saratovskaya-55) of the steppe Volga ecotype under the conditions of the simulated drought and, in opposite scenario, had an inhibitory effect on the germination of seeds of the variety (Omskaya-35) which is representative of the forest-steppe West Siberian ecotype (Lastochkina et al. 2017b).

In this regard, the study of the specific features of the implementation of protective mechanisms for drought under the influence of *B. subtilis* in different ecotypes of wheat with different strategies for adaptation to drought stress is of great relevance. This will make it possible to reveal the mechanisms by which drought tolerance is elevated in the certain ecotypes by PGPB inoculation, in particular *B. subtilis*. This will help to reveal the genetic potential in PGPB and increase the productivity of wheat, grown in different ecological and geographical regions worldwide.

2.2 High Temperature

High temperature (HT) stress is another major problem limiting wheat yield and quality in most of growing areas worldwide (Mohammadi 2011; Hasanuzzaman et al. 2013). Heat affects wheat at different developmental stages reducing germination of seeds, plant growth, photosynthesis rate, respiration, decreasing the grain number per spike and leading to formation of shriveled grains with poor quality (Mohammadi 2011; Hasanuzzaman et al. 2013; Iqbal et al. 2017; Kang et al. 2017). Even short time exposure to elevated temperatures can cause serious damage of cellular homeostasis and cell death due to protein denaturation and aggregation, enzyme inactivation both in mitochondria and chloroplasts, protein synthesis inhibition, membrane lipid fluidity, as well as membrane integrity losses (Howarth 2005). To cope with the damaging effect of HT stress, plants develop a whole spectrum of physiological, biochemical, and molecular responses such as enhancement of heat shocks and related protein expression; changes in level of phytohormones; ROS scavenging; accumulation of antioxidants, compatible solutes, and osmolytes; activation of the mechanisms contributing to the maintaining of the stability of cell membrane structures; as well as calcium-dependent protein kinase and mitogen-activated protein kinase cascades. More detailed information about the impact of HT on different species of plants and their specific strategies for thermotolerance has been summarized and well described (Howarth 2005; Kotak et al. 2007; Hasanuzzaman et al. 2013).

In literature, there are not so many studies devoted to an investigation of the effect of PGPB on wheat tolerance under HT stress in comparison with other types of abiotic and biotic stresses. Nevertheless, available information indicates about the positive effect of PGPB on heat stress tolerance of wheat plants (Ali et al. 2011; Abd El-Daim et al. 2014, 2017; Kang et al. 2017; Sarkar et al. 2017). For example, Abd El-Daim et al. (2014) revealed that wheat pretreatment with *B. amyloliquefaciens* 5113 and *A. brasilense* NO40 improved plant survival under heat stress demonstrating a protective effect of these bacteria. Inoculation of wheat plants with *Pseudomonas putida* AKMP7 improved their survival and growth under heat stress significantly increasing the length of plants (roots and shoots), their biomass accumulation, and grain formation in comparison with non-inoculated control plants under the same conditions (Ali et al. 2011). Application of *B. safensis* strain NCBIJX660689 and *Ochrobactrum pseudogrignonense* strain NCBIJX660688 maintained a fresh weight of wheat seedlings and RWC status of seeds in comparison to non-inoculated ones even in the maximum stressed conditions (Sarkar et al. 2017).

The positive impact of bacterial priming can be reflected both on growth parameters of plant and on the survival of cells as well. Application of PGPB can improve cell viability and acquired thermotolerance of plants under HT stress. Sarkar et al. (2017) reported that the percentage of cell viability in wheat plants priming with *B. safensis* was significantly high even after exposure to 40 °C for 12 h. The findings indicate that plant growth-promoting rhizobacteria mitigate HT stress-induced damaging effects on wheat through activating antioxidant system; reducing the production of ROS, the level of membrane, and chloroplast injury; as well as increasing the content of chlorophyll and production of redox enzymes and osmolytes maintaining the structure, thereby resulting in improved thermotolerance (Sarkar et al. 2017). Likewise, it was revealed that the redox status of the bacterial-inoculated plants is improved during HT stress, and only minor changes in metabolism are necessary in order to provide increased heat tolerance. In particular, *B. amyloliquefaciens* and *A. brasilense* reduced regeneration of ROS and changes in the metabolome of *Triticum aestivum* plants (Abd El-Daim et al. 2014). Other findings also demonstrated that PGPB could protect wheat plants under HT stress by producing antioxidant factors or modulate photosynthesis decreasing ROS (Yang et al. 2009). It was revealed that PGPR strains *B. safensis* NCBIJX660689 and *O. pseudogrignonense* NCBIJX660688 contribute to decreasing HT-induced raised level of ROS such as H_2O_2 and $O_2^{\bullet-}$ in wheat after exposure under heat stress during 12 h (Sarkar et al. 2017). Furthermore, *B. safensis* inoculation reduced MDA accumulation and electrolyte leakage, whereas *O. pseudogrignonense* did not show such effectiveness as *B. safensis*. Interestingly, *B. safensis* was also more effective in minimizing HT stress reducing chlorophyll content and ultrastructural damages of chloroplasts that may be responsible for restoring the systems PSI and PSII. Moreover, it was observed that activities of PA and CAT and accumulation of ascorbic acid, GR, and GB in leaves were significantly higher in wheat plants inoculated with *B. safensis* than *O. pseudogrignonense* (Sarkar et al. 2017). According to other findings, after HT stress in PGPR-inoculated plants, the APX, SOD, and GR activities and overexpression of these redox enzymes notably enhanced (Singh and Grover 2008). The rapid increase in the activity APX and SOD in PGPR-inoculated plants at the first hours of HT stress indicated that these redox enzymes act as the first defense line against heat stress which probably facilitates thermotolerance (Sarkar et al. 2017). Other researchers also reported that during HT stress, wheat plants inoculated with *B. amyloliquefaciens* strain 5113 and *A. brasilense* strain NO40 overexpressed APX1 transcripts along with MDHAR, DHAR, and GR (Abd El-Daim et al. 2014). Inoculation with *P. putida* AKMP7 reduced membrane damage as well as APX, CAT, and SOD antioxidant enzyme activities under HT stress. Moreover, AKMP7-inoculated wheat plants were characterized by an improved content of cellular metabolites including proline, sugars, amino acids, proteins, chlorophyll, and starch in comparison with non-treated control plants (Ali et al. 2011).

According to Abd El-Daim et al. (2014), inoculation with such PGPR as *B. amyloliquefaciens* strain 5113 and *A. brasilense* strain NO40 resulted in enhanced heat tolerance of wheat due to the elevating level of some heat shock proteins which are controlled by heat stress transcription factors (Hsfs) (Abd El-Daim et al. 2014) and plays a pivotal role in response to heat stress and acquiring plant thermotolerance (Kotak et al. 2007). The heat shock factor 3 (HsfA3), necessary for control of many heat shock genes, was strongly upregulated by heat stress, while PGPB-inoculated non-stressed and stressed plants showed a lower response. The heat-inducible transcription factor (HsfB1) controlling a later phase transcription of many heat shock genes as a co-activator was upregulated during HT stress both in PGPB-inoculated and stressed wheat plants, while bacterial inoculation alone caused a small increase in transcript levels. Bacterial-treated plants under stress conditions showed about 50% lower HT stress-induced expression of the multiprotein bridging factor 1c (MBF1C) playing an important role as a crucial thermotolerance regulator (Suzuki et al. 2008).

Other findings allow suggesting that PGPB improve wheat thermotolerance due to their ability to affect central metabolic events of the host plants due to decreasing stress-induced accumulation of such metabolites as glucose, sucrose, stachyose, γ-aminobutyric acid, galactinol, methionine, alanine, *S*-methylmethionine, choline, and threonine in leaves (Abd El-Daim et al. 2014, 2017). For example, analysis of trehalose phosphate synthase 5 (TPS5) transcript levels in wheat plants showed that *Bacillus* treatment reduced heat stress-induced TPS5 expression by 50% (Abd El-Daim et al. 2014). It was observed that HSP17.8 up-regulated in HT-stressed wheat plants and response varied depending on cultivars and strains of bacteria. However, inoculation with PGPB strains in most cases led to a decrease in the transcription levels of HSP17.8 under heat stress. Increased HSP17.8 levels were detected in bacterial-inoculated non-stressed plants as well, which indicates that *Bacillus* activates some tolerance mechanisms at normal conditions (Abd El-Daim et al. 2014) and exerts a preadaptation effect on wheat plants to subsequent possible stress conditions. Recently, Abd El-Daim et al. (2017) studied the expression of 31 transcript-derived fragments (TDFs) involved in *B. amyloliquefaciens* 5113-mediated tolerance to heat, cold, and drought in wheat. It was found that 21% of the TDFs were upregulated only in heat-stressed plants. These data indicate there are unique mechanisms for plant tolerance to heat stress.

Thus, PGPB seems to be a beneficial approach to alleviate the negative impacts of HT stress on wheat, although further researches are needed for fully understanding the underlying mechanisms which will allow uncovering the potential of these beneficial bacteria to cope with damaging effects of heat stresses on yield and quality of wheat.

2.3 Salinity

Salinity is one of the most common abiotic stress factors in the world decreasing plant growth, development, and yield formation (Munns and Tester 2008; Cambrolle et al. 2011). The total amount of soils which is adversely affected by salinization is around 20% (62 million ha) and 40% in arid/semiarid regions and irrigated lands, respectively (Zahran 1997; Khan et al. 2015). The soils can be attributed as saline when soil extract's electrical conductivity (EC) is 4 dS/m (equivalent to 40 mM NaCl and 0.2 MPa osmotic pressure) or more (Munns and Tester 2008). In saline soils, NaCl is the most common soluble salt, but a number of other dissolved salts such as $MgSO_4$, Na_2SO_4, $CaSO_4$, KCl, Na_2CO_3, and $MgCl_2$ may contribute to salt stress as well (Munns and Tester 2008). In plants, salinity induces both osmotic and oxidative stresses as well as leads to stomata closure and reduction of leaf expansion (Hasegawa et al. 2000). Furthermore, salt stress causes essential nutrient deficiency (such as K^+) and toxicity effect of Na^+ ions inside the plants, which as a result inhibit photosynthesis, lipid metabolism, protein synthesis, and biomass accumulation (Munns and Tester 2008; Asgari et al. 2012).

PGPB can be successfully used to protect many plants from damaging impacts of salt stress. A number of studies showed the capability of PGPB to develop varied defense responses aimed to reduce the harmful salinity effects on different plants, including wheat (Bacilio et al. 2004; Ali et al. 2014; Han et al. 2015; Barnawal et al. 2016, 2017; Lastochkina et al. 2017a; Khan et al. 2017; Numan et al. 2018). For instance, inoculation with *D. natronolimnaea* STR1 increased the root and shoot length in the wheat plant through increasing the content of photosynthetic pigments, the enzymatic activity of CAT and APX, and the expression of antioxidant genes in comparison with non-inoculated control plants (Bharti et al. 2016). *D. natronolimnaea* STR1 and *A. protophormiae* SA3 facilitated plants' tolerance to salinity by increasing photosynthetic activity under both salinity and drought (Barnawal et al. 2017). Treatment of wheat with *B. aquimaris* contributes to higher P accumulation in plants under salt stress (Upadhyay et al. 2011). Ashraf et al. (2004) demonstrated that PGPB-producing EPS resulted in sodium uptake restriction and plant growth stimulation under salinity (Ashraf et al. 2004). Different authors revealed that application of *A. brasilense* reduced the damaging impacts of NaCl defense responses on wheat (Creus et al. 1997). It has been revealed that protective effect of endophytic *B. subtilis* 10-4 on wheat plant growth under salinity (NaCl) was associated with the ability of bacteria to increase seed germination, length of shoots and roots, biomass accumulation, and water holding capacity of leaf and decrease the level of statolitic starch hydrolysis in roots caused by salinity (Lastochkina et al. 2016). It has been assumed that positive effect of *B. subtilis* 10-4 on wheat under salt stress is also associated with the ability of bacterial strain to provide rigid lignin deposition in the root cell walls of wheat under both normal and salinity conditions. This indicates an increase of the barrier properties in wheat plants that interfere with the penetration of toxic sodium ions under the influence of *B. subtilis* 10-4 (Lastochkina et al. 2016). PGPR strains *P. putida* 108, *P. putida* 4, *P. fluorescens* 153, and *P. fluorescens* 169 alleviate salinity stress on wheat as well (Abbaspoor et al. 2009). Investigation of the two salt-tolerant PGPR *Arthrobacter* sp. and *B. subtilis* effects on wheat under different salinity regimes demonstrated reduction of the salinity stress effects on plants inoculated with bacteria (Upadhyay et al. 2012). Similarly, it was reported that rhizosphere bacterium *Azospirillum* strains (*A. brasilense* NH, *A. lipoferum*) support wheat plants to cope with salinity (Bacilio et al. 2004; Nabti et al. 2010; Nia et al. 2012). *Azospirillum* strain isolated from saline soil promotes the growth of wheat plants under salinity by increasing N concentrations without affecting P, Na, and Cl level. Therefore, it could be concluded that the mechanisms underlying *Azospirillum*-inoculated plant growth-promoting bacteria in wheat irrigated with saline water are associated with photosynthetic pigments and accumulation of high solute N concentrations. Moreover, it can be suggested that *Azospirillum* strains which are adapted to higher salinity environments may have a greater ability to improve wheat growth (Nia et al. 2012). It was shown that *Bacillus* sp. EN1 and EN6, *Thalassobacillus* sp. ID, *Halomonas* sp. IA, *Zhihengliuella* sp. EN3, *S. succinus* EN4, and *Oceanobacillus* sp. EN8 ameliorated the harmful effect of salt stress on wheat (Orhan 2016). Although growth reduction with 200 mM NaCl was estimated up to 58.4%, *Bacillus* sp. EN1 improved growth reduction in wheat plants to 15.58%. Similarly, the amelioration rates of the other strains were 10.27%, 6.50%, 30.65%, 20.89%, 25.85%, and 33.73% for EN3, EN4, EN6, EN8, IA, and ID, respectively. Only the non-plant growth-promoting bacterial strain IE represented the null effect on wheat growth under salinity. Among the investigated bacterial strains, EN1 (*Bacillus* sp.), EN3 (*Z. halotolerans*), EN4 (*S. succinus*), EN6 (*B. gibsonii*), EN8 (*O. oncorhynchi*), IA (*Halomonas* sp.), and ID (*Thalassobacillus* sp.) had the highest plant growth-promoting potential under NaCl (200 mM). In most of the other studies, PGPB strains promoted plant growth under both 200 mM NaCl and other different salt concentration as well (Karlidag et al. 2011; Yildirim et al. 2011; Nia et al. 2012; Lastochkina et al. 2017a). Treatment of wheat with *Klebsiell*a sp. SBP-8 under exposure on salinity (150–200 mM) and high temperature (30–40 °C) stress led to an improvement of the stress conditions by increasing chlorophyll content and biomass accumulation and decreasing stress-induced inhibition of plant growth

(10–100%). Furthermore, *strain* SBP-8 caused efflux of Na^+ (65%) and increased uptake of K^+ (84.21%) in wheat plants. Thus, SBP-8 improves wheat growth and protects it from salt stress by more than one mechanism including ACC-deaminase activity effect and K^+/Na^+ ratio modulation in plants (Singh et al. 2015).

It is indicated that rhizosphere microbial populations may be categorized by their ability to impact on plant growth as beneficial, neutral, and harmful. For example, from 25 bacterial isolates, only 28% showed plant growth-stimulating activity, 44% represent neutral effect, and 28% pose a negative impact on plant growth. Simultaneously, plant growth can be associated with the capacity of microorganisms to synthesize auxin-dependent ACC-deaminase enzyme regulating biosynthesis of ethylene in plants (Glick 2014). Sadeghi et al. (2012) revealed that *Streptomyces* produces IAA and auxin in the presence of salt and increases wheat growth under salinity (Sadeghi et al. 2012). In a different study, IAA and siderophores producing *B. subtilis* strain 10-4 significantly increased the growth of wheat and accumulation of plants biomass under normal and salinity (Lastochkina et al. 2017a). The auxin synthesis by the bacterium *B. subtilis* FZB24 promotes root system development by which improves plant ability to absorb more water and nutrients. It has been shown that IAA produced by *Sinorhizobium* sp., *Pseudomonas* sp., *Pantoea* sp., *Rhizobium* sp., *Enterobacter* sp., *Marinobacterium* sp., and *Acinetobacter* sp. positively influences germination of seeds and growth of wheat plants under salt stress (Sorty et al. 2016). Moreover, it has been shown that application of PGPB, for example, *B. subtilis* LDR2, *A. protophormiae* SA3, and *D. natronolimnaea* STR1, contributes to the increase of endogenous IAA level in the wheat under salt stress and leads to enhanced plant tolerance (Barnawal et al. 2017). In another study has been shown that treatment of wheat with salt-tolerant *Halomonas* sp. having the ability to produce IAA - led to an increase of IAA level in wheat rhizosphere, as a result, enhancing plant growth in compare to non-treated controls (Tiwari et al. 2011). These studies revealed that regulation of IAA biosynthesis in plants by PGPB both endophytic and rhizospheric could be considered as important salt tolerance strategy. Sustainable growth in wheat plants under salt stress has been supported when inoculated by ACC-deaminase containing PGPR from the genus *Pseudomonas* (Zahir et al. 2009). Other researchers also reported that plant growth can be improved by rhizobacteria producing ACC-deaminase, particularly under stress conditions. However, some findings indicated that rhizobacteria can exert negative effect on wheat growth which could be attributed to their ability to produce phytotoxic metabolites. Interestingly, the salt-tolerant rhizobacterial isolate Y22 producing the highest level of ACC-deaminase (about 399 nmol mg^{-1} h^{-1}) and IAA in both presence (12.32 μg mL^{-1}) and absence of L-tryptophan (34.76 μg mL^{-1}) demonstrated a negative impact on the growth of wheat plants. It was assumed that such negative impact of Y22 on the growth of wheat may be related with high IAA production (Spaepen et al. 2007) and/or significantly enhanced activity of ACC-deaminase. In confirmation of this assumption, other researchers also demonstrated that bacteria capable of higher (300–400 nmol mg^{-1} h^{-1}) ACC-deaminase production did not significantly improve plant growth (Penrose and Glick 2003).

Therefore, it can be suggested that bacteria varied in activity of ACC-deaminase may differentially regulate wheat growth under salt stress condition (Khan et al. 2017).

CKs production is considered as a common PGPB trait which is participated in the formation of plant tolerance to abiotic stresses (Dodd et al. 2010). PGPB can affect the concentration of exogenous CK in plant either with the biosynthesis of CK or shifting its homeostasis in plants. Plants inoculated by CK-producing *B. subtilis* showed the increased level of chlorophyll and endogenous CK, which as a result led to the excessed plant biomass (shoots and roots) (Arkhipova et al. 2007).

ABA is one of the main stress phytohormones accumulating in plants under abiotic stress conditions including salinity. Stress-induced increased level of ABA resulted in activation of varied defense mechanisms; in particular, it begins to express genes responsible for plant stress tolerance (Shakirova et al. 2012; Sah et al. 2016). The capacity of PGPB (*Bacillus*, *Brevibacterium*, *Azospirillum*, *Lysinibacillus*, and *Pseudomonas*) to affect ABA level in plants, particularly under stressful conditions including salinity, was detected (Dodd et al. 2010; Belimov et al. 2014). It was shown that many PGPB (e.g., *B. licheniformis*, *A. brasilense*, *P. fluorescens*, *Novosphingobium* sp., *Variovorax paradoxus*, *Rhodococcus* sp., etc.) produce ABA in in vitro condition (Dodd et al. 2010; Belimov et al. 2014). Naz with colleagues (2009) demonstrated that PGPB could synthesize ABA under salt stress and improve plant growth exposed to salinity. The stomata closure is one of the fastest reactions in response to stress induced by ABA which increase Ca^{2+} concentration in the cytosol and ultimately led to the activation of the ion channels in plasmalemma, the turgor loss, and the closure of the stomatal slit. This can be associated with ABA-induced enhancement of H_2O_2 level, serving as the signal intermediary of ABA stomata closure initiation (Jiang and Zhang 2002). Stomata closure resulted in a reduction of photosynthetic activity and inhibition of plant growth both in leaf and roots (Nilson and Assmann 2007). This finding indicates that the ability of PGPB to produce ABA plays a pivotal role in interactions of PGPB and plants under stresses (Dodd 2003). According to Barnawal et al. (2017), PGPR are capable to confer abiotic stress tolerance in wheat through increasing endogenous IAA content, decreasing ABA/ACC concentration and expression of such regulatory component as CTR1, and negatively regulating ethylene signaling pathway and transcription factor DREB2 (Barnawal et al. 2017).

Discovering the capacity of PGPB exerts anti-stress effect on wheat exposed to salinity provided an insight that these bacteria may mitigate the damaging impact of salinity-induced oxidative stress in plants. Recently, it has been revealed that inoculation of wheat (*Triticum aestivum* L.) seeds by endophytic bacteria *B. subtilis* strain 10-4 helps to decrease salinity-induced ROS accumulation including O_2 and H_2O_2 in plants as well as SOD and PA activities, which indicates an obvious protective role of *B. subtilis* on wheat plants growing under NaCl stress (Lastochkina et al. 2017a). Furthermore, strain 10-4 reduced MDA accumulation under salinity which indicates the hampered oxidative stress in inoculated plants. Hence, these bacteria are capable to regulate H_2O_2 level as well (Lastochkina et al. 2017a). Bharti et al. (2016) revealed that PGPR-inoculated plants increased the expression of genes related to such antioxidant enzymes as CAT, SOD, APX, GR, GPX, and POD as well as increased proline accumulation; all these may explain improved salt tolerance of plants (Bharti et al. 2016).

To alleviate the harmful impacts of salt stress and support water status, plants actively synthesize multifunctional proteins such as chaperones, proteases, its inhibitors, and low-molecular organic compounds including amino acids, betaines, and sugars (Szabados and Savoure 2009; Shakirova et al. 2012). PGPB can counteract osmotic stress and enhance wheat salinity stress tolerance through overproduction of various osmoprotectants or compatible solutes (Serraj and Sinclair 2002; Zarea et al. 2012). To date, numerous studies have demonstrated the ability of PGPB to mitigate damaging impact of salt stress on wheat and increase plants' tolerance through biosynthesis of osmolytes which play a major role in plant adaptation to stresses leading to dehydration (Casanovas et al. 2003; Zarea et al. 2012; Lastochkina et al. 2017a). For example, increased accumulation of osmoprotectant Pro in wheat plants grown under saline conditions upon endophytic *B. subtilis* 10-4 inoculation alleviates salinity stress and improves wheat growth (Lastochkina et al. 2017a). Application of strain 10-4 resulted in proline accumulation also in wheat grown under normal (non-saline) conditions, which possibly plays a significant role in maintaining better water status in plant tissues and exerts a positive effect on protein turnover, structure of membranes, biomolecules, as well as acting as ROS scavengers protecting DNA from damages (Lastochkina et al. 2017). It is well known that Pro stabilizes subcellular structures (membranes, proteins), scavenges ROS, and manages cellular redox buffers under salinity, thereby alleviating damaging impacts of salinity on plants (Kohler et al. 2009). Accumulation of proline is a sensitive physiological indicator of plants' response to stresses, i.e., salinity contributing to maintain water balance and mitigate damaging effects of salinity-induced oxidative stress (Peng et al. 2008). Zarea et al. (2012) reported enhanced proline accumulation in wheat when their roots are colonized by PGPR. Similarly, *Azospirillum* accumulates Pro in plants as an osmoprotectant (Casanovas et al. 2003). Different studies allowed to report that Pro protects plants against salinity and osmotic stresses by adjusting osmotic pressure and stabilizing various functional performance including electron transport complex II and crucial enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) (Makela et al. 2000). Upadhyay et al. (2012) demonstrated PGPR significantly contributed to wheat osmotolerance under salinity through increased Pro and total soluble sugar (TSS) level in inoculated plants. These findings indicate that increased TSS concentration in plants is the substantial alternative defense mechanism of PGPB to cope with damaging impacts of salt stress on plants (Upadhyay et al. 2012). Inoculation with *B. subtilis* 10-4 causes a significant increase in the level of SA in wheat plants under non-stressed (normal) conditions and decreases the salinity-induced increase in SA level, which may indicate the preadaptive function of bacteria on wheat to stresses leading to dehydration via activation of salicylate-dependent signaling pathways (Lastochkina et al. 2017a). In favor of this assumption is data about *B. subtilis* 10-4 possesses substantial induction of the transcriptional activity of the *PR-1* gene which is a reliable marker for the development of salicylate-dependent signaling pathway, while the *PR-9* gene, which is introduced as a marker for jasmonate signaling pathway, was not expressed under both normal and salinity conditions (Lastochkina et al. 2017a). Different findings demonstrated that plant salinity tolerance mediated by PGPB is a complicated phenomenon including activation of ROS scavenging, ABA and SA signaling, and other various compounds inducing defense response mechanisms to protecting plants from salinity-caused oxidative and osmotic stresses (Serraj and Sinclair 2002; Casanovas et al. 2003; Zarea et al. 2012; Upadhyay et al. 2012; Bharti et al. 2016; Lastochkina et al. 2017a). However, despite numerous studies, the knowledge regarding PGPB-host plant interaction and underlying physiological responses leading to the formation of wheat tolerance to various modes of salinity are still in the initial stage.

2.4 Toxic Metals

Global industrial activities along with excessive anthropogenic contaminants contribute toward the massive environmental pollutions. In general, contaminants led to the deterioration of agricultural soil quality; however, deposited pollutant such as HMs (HM) cause a variety of disorders in a different organism. Soil contamination with HM has become a common phenomenon throughout the world due to the increase in the scale of anthropogenic activities. Plants are growing on HM-contaminated soils, characterized by small growth rates and yields (Ma et al. 2016). Moreover, accumulated HM in plants enter the food chain and result in further detrimental effects in humans and animals. Some of the direct toxic effects in plants caused by high concentrations of HM include a decrease in the activities of cytoplasmic enzymes and damage to the structures of cells owing to oxidative stress development (Jadia and Fulekar 2009). An example of the indirect toxic effect is the replacement of cations by HM in the functional groups existing in various bioorganic compounds (Sytar et al. 2016). This may affect fundamental reactions and alter downstream pathways. Moreover, the negative influence of HM on the activity of soil microorganisms can indirectly affect plant's growth as well. HMs can influence plant-associated microorganisms' diversity, thus influencing beneficial plant-bacteria interactions. Besides, a high concentration of HMs can directly decrease the number of beneficial soil microorganisms, hence leading to a decrease in the organic matter decomposition, which can reduce the content of certain nutrients in the soil. However, in the opposite scenario, some rhizospheric microorganisms like PGPB significantly alter the bioavailability of HMs in soil (Kong and Glick 2017). PGPB can grow in the environment that is contaminated with HM and protect plants growing in polluted soils from the toxic impacts of HM (Hao et al. 2015; Chaudhary and Khan 2018). Various strains of PGPB possess different mechanisms to reduce HM toxicity and tolerance induction by mobilization, immobilization, and transformation. Such mechanisms include exclusion, extrusion, active removal, biotransformation, biosorption, precipitation, and bioaccumulation of metals in both external and intracellular spaces of plant cells. These processes can influence the solubility and bioavailability of the introduced metal to the plant which subsequently can alter relative toxic effects (Rajkumar et al. 2008). Although to some extent, existing bacteria in the HM-contaminated soils possibly will become more resistant to the certain toxicants. Such metal-resistant PGPB are practically important for both stimulating plant growth and remediation of HM-contaminated environments (Pal et al. 2005). It was observed that when *Triticum aestivum* L. plants are inoculated by *Pseudomonas* sp., they represent better growth under chromium (Cr) stress condition in comparison with non-inoculated plants. This can be attributed to (i) reduced toxic Cr ion uptake and (ii) increased endogenous auxin concentration in plants (Hasnain and Sabri 1997). The last can be supported by IAA-producing bacteria, through induction of auxin-producing related genes in plants or regulated auxin translocation by bacteria within plants. Although the direct effect of auxin in PGPB-regulated HM phytoremediation is still unknown, numerous studies have suggested an indirect role of auxin by alteration of root structure (Kong and Glick 2017), modulation of plant development (Gravel et al. 2007), and expression of the plant growth-related proteins (Rajkumar et al. 2012) under stress condition. Likewise, ACC-deaminase-producing bacteria such as *P. fluorescens* Q14 and *B. thuringiensis* KAP5 have been reported to increase root and shoot length and biomass under Cr stress conditions in wheat in comparison with non-treated controls (Shahzadi et al. 2013). Implying the pivotal role of ACC-deaminase-producing PGPB in wheat growth improvement under exposure to HM-stress along with enhancement the process of bioremediation in an environment contaminated with Cr. Likewise, bacterial mobilization of Cr in soil associated with total accumulation of Cr has been investigated in different varieties of wheat plants (Jamali et al. 2009). Singh and co-worker showed that PGPR (*Pseudomonas* spp.) capable of ACC-deaminase activities were tolerant to Cr, cadmium (Cd), cuprum (Cu), and lead (Pb) toxicity as well as are able to increase growth of wheat (Singh et al. 2013). A different study by Govindasamy and colleagues revealed that growth-stimulating capacity of ACC-deaminase-producing PGPR in wheat plants under Cd stress significantly enhances root elongation and minimizes ethylene level in seedlings which is possibly due to the modulation of stress-related ethylene biosynthesis (Govindasamy et al. 2015). Naseem et al. (2016) demonstrated bacterial treatment of wheat (*Triticum aestivum* var. Inqilab 97) with *Bacillus* sp. AMP2, *Kushneria avicenniae* AHT, *A. mysorens* AHA, *Halomonas* sp. AST, and *Halomonas venusta* APA caused a reduction in the Cr uptake by seedlings at both 10 and 20 μg mL^{-1} concentrations in different chromium salt exposures ($CrCl_3$, K_2CrO_4, and $K_2Cr_2O_7$) when compared with non-inoculated plants. Moreover, increased level of acid phosphatase and PA was recorded in bacterial-inoculated plants compared to the controls (Naseem et al. 2016). Elevated growth rate in the presence of Pb has also been reported in wheat plants when inoculated by *B. subtilis* QM3 (Chaudhary and Khan 2018) which could be attributed to increased activity of antioxidants including CAT, PA, SOD, and APX and decreased metal content in inoculated root tissues (Hao et al. 2015). Likewise, a reduction in detrimental effects of Cd pollution on wheat plants by PGPR inoculation has been shown and indicated that PGPR increase the wheat plant growth by chelating of Cd and modulating its bioavailability in the rhizosphere (Hassan et al. 2016).

PGPB have been potentially suggested to produce metal-specific ligands, namely, siderophores, capable of metal and mineral mobilization in the rhizosphere which ultimately result in enhanced level of nutrients and HM uptake. Siderophores' effect on metal accumulation in plants has been well documented implying the contribution of PGPB in the modulation of plant metal toxicity (Sinha and Mukherjee 2008; Braud et al. 2009; Rajkumar et al. 2010; Rajkumar et al. 2012).

Besides the effects on growth promotion by PGPB under the HM availability, PGPB may function as a microbial remediator by regulating of the toxicants pool through induction of chelate-assisted remediators (Lucy et al. 2004; Bashan et al. 2008). The combination of PGPB with the properties of the hyperaccumulator/hyperstabilizer is recognized as an effective system in limiting the toxicity of HM in soil (Ma et al. 2011; Marques et al. 2013; Qiu et al. 2014). Experiments conducted by a number of researchers showed that bacteria are capable of metal accumulation at an early stage of growth. It has been suggested that *Bacillus* sp. 14 cells grown in the rhizosphere culture are able to absorb Cd ions from the lag phase stretched to the early exponential growth phase, and probably in further stages, the metal migrates to the surface of the bacterial cells (Sungurtseva et al. 2015). Similarly, a significant accumulation of Cd has been reported in the rhizobacterium *Bacillus* sp. 13 and *B. thuringiensis* DM55 cells starting from lag phase to the early stage of exponential growth when inoculated in the liquid culture (El-Helow et al. 2000).

However, PGPG-assisted phytoremediation is considered as a successful strategy for plant growing in HM-contaminated soils. Their function in natural condition is affected by various environmental stressors (Gerhardt et al. 2009). Moreover, metals are not distributed uniformly in the field which makes it challengeable for any investigation in the field trials; therefore data obtained from variable condition would be difficult to interpret. Hence, the practical effect of PGPB treatment on HM in natural condition is yet under debate. Nevertheless, PGPB are still a highlight alternative for HM removal in polluted soils. Therefore in order to improve the capability of PGPB in phytoremediation assistance, intensive future researches are required. The primary attention could be on discovering/developing the strains with the capacity to absorb greater amount of HMs than normal bacteria. PGPB with the ability to absorb various metals would alternatively be suitable for multiple metal-contaminated fields. Besides, PGPB capable of sticking to the plants which move toward the plant root growth will provide an opportunity to remove HM in the contaminated soil in deeper layers. In this regard, biotechnological approaches to make transgenic bacteria with wide-angle capacity can be used as an effective strategy for soil reclamation.

2.5 *High Lights*

Light is a source of energy that ensures plant growth through photosynthesis and serves as a signal involved in the regulation of growth and developmental processes (Chen et al. 2004). Various light characteristics including intensity, wavelengths, and duration can influence gas exchange responses of plants. Light also drives opening or closure of the stomata; in fact stomata close when plants are exposed to darkness and they open by exposure to light.

At the same time, the reaction of plants to light depends on various factors such as plant species, growing season, methods of cultivation, and intensity of environmental light as well (Kozai 2016). Excessively absorbed light can act as a stress factor which adversely impact on photosynthetic apparatus and other physiological processes of plants. High light (HL) intensities decrease photosynthetic activity, stimulate the formation of ROS, cause oxidative damages of cells, and result in plant growth inhibition (Dat et al. 2000; Vranová et al. 2002; Miyake et al. 2009; Gu et al. 2017). Under HL stress conditions, excessively absorbed light energy cannot be used in photochemical reactions of plants and occur photo-inhibition. The process exerts damaging effect on photosystem II (PSII) and was accompanied by photooxidation of pigments, destruction of carotenoids, bleaching of chlorophylls, and destruction of chloroplast structures (Vass 2012; Roach and Krieger-Liszkay 2014). In response to HL stress, plants induce a range of defense mechanisms, particularly aimed to cope with photo-inhibition process (Müller et al. 2001; Zhao et al. 2017).

Photosystem I (PSI) is sensitive to stress-induced ROS. When ferredoxin (an electron carrier in PSI) is in the highly reduced state, it can reduce molecular oxygen to $O_2^{\bullet -}$ in a process called Mehler reaction. Generation of $O_2^{\bullet -}$ competes with electron transfer to NADP+ $O_2^{\bullet -}$ is a ROS species that can reduce metal ions resulted in the formation of hydroxyl radicals ($^{\bullet}OH$) following reaction with H_2O_2. $^{\bullet}OH$ radical is a very aggressive molecule which can easily lead to damage to membranes and proteins. There are no enzymes to directly eliminate $^{\bullet}OH$ radical. Therefore, it is vital for plants to inhibit reduction of the metal ions through the prompt elimination of $O_2^{\bullet -}$ radicals. $O_2^{\bullet -}$ formed in this way is eliminated by the action of a series of enzymes that scavenge ROS, in particular APX and SOD. In this process, $O_2^{\bullet -}$ converts to H_2O_2 and O_2 through the action of SOD. Thereafter, APX converts H_2O_2 to water. This process called the water-water cycle because it starts with water and ends with the production of water. Water-water cycle creates a pH gradient (ΔpH) across the thylakoid membranes in PSI. NPQ energy dissipation increases due to ΔpH across the membranes and lack of production of NADPH in PSI (Makino et al. 2002).

Flavodiiron proteins (FDPs) constitute a large family of soluble enzymes in some bacteria and archaea (Vicente et al. 2008). They prevent generation of ROS during electron transport through transferring electrons to oxygen or nitric oxide. Using global gene expression profiling of unicellular cyanobacterium *Synechocystis*, it was shown that the transcription of some genes related to the FDPs is induced by HL stress (Hihara et al. 2001) and UV-B radiation (Huang et al. 2002). Some studies suggest that cyanobacterial FDPs take part in preventing ROS production due to photooxidation and photo-inhibition processes during electron transport. In accordance, it has been reported that FDPs FLV1/FLV3 carry out a Mehler-like reaction that regenerates NADP+ and, as a result, prevents photooxidation (Allahverdiyeva et al. 2013) and function of FLV2/FLV4 in alternative electron transfer and alleviate PSII excitation pressure, as a result preventing photo-inhibition (Zhang et al. 2009).

Due to this function of flavodiiron proteins, cyanobacterium *Synechocystis* does not need ΔpH to prevent over-reduction of ferredoxin during high light exposure (Allahverdiyeva et al. 2013). However, higher plants lack the flavodiiron proteins, and they use non-photochemical quenching (NPQ) to safeguard their photosystems. Introducing flavodiiron proteins into plant electron transport chain can be an efficient approach to prevent photooxidation and photo-inhibition damages. Apart from high light stress, the CO_2 limitation can also induce the transcription of genes related to the flavodiiron proteins (Wang et al. 2004). It was revealed that treatment of wheat root with *B. subtilis* from harsh environments increases survival of drought-stressed wheat plants and causes greater photosynthesis activity and biomass accumulation (Timmusk et al. 2014). However, the mechanism of photosynthesis improvements by PGPB is not known so far.

3 PGPB-Mediated Induced Systemic Tolerance to Abiotic Stresses in Wheat

PGPB-induced physio-biochemical defense responses leading to host plants' tolerance to adverse environmental abiotic stresses including drought, salinity, and many others are described as induced systemic tolerance (IST) (Yang et al. 2009; Arya et al. 2018). It is believed that the main pathways in which the activation of protective mechanisms occurs throughout the whole plant are induced system resistance (ISR) and system-acquired resistance (SAR) (Pieterse et al. 2012). The bacterial determinants of ISR, as well as its activation pathways in plants, have been significantly appreciated over the past decade. It has been revealed that PGPB triggered both SAR and ISR of host plants (De Meyer et al. 1999; Van Loon 2007). The role of PGPB in the launch of IST in plants exposed under abiotic stress factors has only been revealed and investigated very recently (Sarma et al. 2018). The whole influence of PGPB-mediated conditioned responses in plants, whether on a physical, biochemical, or molecular level, can lead to protection of plants against disease stress factors of biotic and abiotic nature. Several reports have suggested that PGPB acts as elicitors for improving the tolerance of plants to unfavorable abiotic stress factors including salinity, drought, and deficiency/excess of nutrients (Lastochkina et al. 2017a; Sarma et al. 2018; Arya et al. 2018). PGPB-host plant interaction resulted in local and systemic defense response activation, which is controlling such signaling molecules as SA, JA, and ethylene (Koornneef and Pieterse 2008). Some researchers reported the key target affected by the PGPB is the plant signaling pathways, regulated by SA and JA, leading to the development of protective responses to stresses (Van Loon 2007; Chourdhary and Johri 2009; Niu et al. 2011; Garcia-Gutierrez et al. 2013; Veselova et al. 2015). However, it is not yet quite clear how exactly PGPB regulates the protective system of host plants and how PGPB-induced plant protective signal system interacts with classical signaling pathways, in particular, induced by SA and JA. On the one hand, it is considered that the influence of PGPB is similar to the action of "weak" pathogens on plants, and on the other hand, they produce metabolites with hormonal and signaling functions (auxins, CKs, ethylene, gibberellins, ABA, SA, and JA) (Dodd et al. 2010; Veselova et al. 2015).

Since SA and JA protective responses are the dominant primary signals of local and systemic-induced defense response of plants under different stress factors (Shakirova et al. 2012), the anti-stress effect of PGPB on plants might be explained by its capacity to synthesize these molecules (Fravel 2005; Chourdhary and Johri 2009; Sayed et al. 2011; Wenhao et al. 2012; Garcia-Gutierrez et al. 2013; Veselova et al. 2015; Lastochkina et al. 2017a). In support of this proposal, it was revealed that PGPB produces SA in the rhizosphere and thereby triggers SA-dependent defense signaling pathways in plants. It was demonstrated that under normal growth conditions in plants inoculated with *Promicromonospora* sp., *A. calcoaceticus*, and *B. cepacia*, the content of endogenous SA was much higher (around 1.5-fold) than in control. The same tendency was observed when plants were grown under stress condition, but in contrast to normal growth conditions, the level of SA accumulation was more pronounced. Herewith, during drought and salinity stresses in PGPB-inoculated plants, the increase of SA was 0.7–1.4-fold over in comparison with control (Kang et al. 2014). The findings demonstrated that SA biosynthesis pathway is upregulated in response to PGPB and stresses. Different studies also revealed that PGPB, particularly endophytic *B. pumilus* and *Achromobacter xylosoxidans*, improve growth and development of plants exposed to water stress through the overproduction of endogenous SA (Forchetti et al. 2007; Garcia-Gutierrez et al. 2013). Similarly, in wheat seedlings inoculated with endophytic bacteria *B. subtilis* increased the level of endogenous SA under both normal and salinity (2% NaCl) conditions (Lastochkina et al. 2017a). It was suggested that *B. subtilis* exerts a preadaptation effect on plants to the subsequent possible impact of salt stress due to increasing SA level under normal conditions, thereby activating SA-dependent defense signaling pathways (Lastochkina et al. 2016; Lastochkina et al. 2017a). The findings about accumulation of *PR-1* gene transcripts in inoculated wheat seedlings indicate the formation of *B. subtilis*-induced plant tolerance to salinity may be related to the activation of SA signaling defense pathway as well (unpublished data). It is known that SA signal transduction required NPR1 regulatory protein (Vlot et al. 2009). NPR1 interaction with transcriptional factors of TGA family leads to the expression of SA-sensitive PR proteins, particularly, *PR-1* genes serve as the most studied marker of SAR (Vlot et al. 2009). It was revealed *B. cereus* AR156 induced the systemic resistance of plants via NPR-1- and the SA-dependent signaling pathway, without affecting the JA–/ethylene-dependent pathways (Niu et al. 2015). It should be noted that overproduction of SA in plants along with participating in SAR makes an important contribution in plant growth and development under non-stress (normal) growth conditions as well (Shakirova et al. 2012). It favor of the likelihood that PGPB-induced SA accumulation plays a pivotal role in plant's growth and developmental processes under stressful conditions suggests such well known facts that SA both endogenous and exogenous regulate plant defense response mechanisms under a wide range of stresses including drought, salinity, low/high temperatures, toxic metals, UV radiation and other (Shakirova and Bezrukova 1997; Shakirova et al. 2003; Horvath et al. 2007; Nazar et al. 2011; Shakirova et al. 2012). Thereby, there is no doubt that SA plays a pivotal role in the non-specific regulation of plant tolerance through numerous defense responses (An and Mou 2011; Shakirova et al. 2012). Obviously, PGPB-induced accumulation of endogenous SA can make a significant contribution in PGPB-mediated amelioration of abiotic stress damaging effect on plants. With that, a particular attention is another phytohormone JA, which also plays a major role in the launch of ISR mechanisms in response to diseases and various abiotic stresses, thereby increasing plant stress resistance and tolerance. For example, it has been reported that some PGPB activate ISR through JA−/ethylene-dependent pathways and independent from SA involvement (Pieterse et al. 1998; Pettersson and Baath 2004). JA is essential for regulation of various physiological processes at different developmental phases (e.g., germination of seeds, formation of generative organs, flowering, ripening, assimilation transport, storage of nutrients, and others) as well as stress responses (Creelman and Mullet 1995; Wasternack 2007; Balbi and Devoto 2008; Shimizu et al. 2011). It was discovered that JA in cooperation with ethylene plays a pivotal role in the launching of ISR of plants in response to different injuries, for instance, attack of pathogens and pests, accompanied by the expression of protective proteins, particularly PR genes (Wasternack 2007; Van der Ent et al. 2009; Bari and Jones 2009; Ballare 2011). Along with this, numerous evidences reported that JA plays a major role in increasing different plants' tolerance to various abiotic stresses (drought, low/high temperatures, salinity, HM, and UV radiation) through increasing JA biosynthesis and thereby launching different defense responses laying on the basis of plant's abiotic stress development (Bandurska et al. 2003; Kang et al. 2005; Clarke et al. 2009; Shakirova et al. 2010, 2012).

The main difference between ISR and SAR is often associated with the dependence of SAR from endogenous SA accumulation. It is known that some PGPB are capable to launch SA-dependent signaling defense pathways even by producing a small amount (nanograms) of SA in plant's rhizosphere. However, different findings indicated that most PGPB can activate ISR through defense pathways independent from SA, probably due to involving JA−/ethylene-dependent signaling pathways. It is also believed that the development of ISR could be associated not only with increasing the level of these phytohormones but with increasing the sensitivity to them, which, in turn, may lead to the expression of another set of protective genes (Arya et al. 2018). At the same time it is well known that in response to biotic/abiotic stresses in plants increases the biosynthesis "stress phytohormone" ethylene, which plays a major role in accelerating senescence, abscission and as a role leading to growth retardation and death of tissues (Stearns and Glick 2003; Lim and Kim 2013). To date, numerous findings are reported that those PGPB which are capable to produce ACC-deaminase could effectively control ethylene level in plants, thereby preventing the damaging action of stresses and leading to increasing of host plant resistance and tolerance (Hao et al. 2007; Ali et al. 2014; Glick 2014). Thus, a number of findings indicated about the possible participation of SA- and JA−/ethylene-depending defense signaling pathways in the realization of anti-stress effects of PGPB on host plants under abiotic stresses, however, the mechanisms underlying in PGPB-induced systemic tolerance in plants, including wheat, is still far from clear.

4 Conclusion

PGPB application is an eco-friendly approach which leads to improved plant growth, soil health, nutrient absorption, and plant tolerance to unfavorable environmental stresses. Thus, PGPB application is a very attractive strategy to cope with abiotic stresses to provide effective and environmentally friendly solutions for increased different crop productivities including wheat. PGPB serve as a substantial component of organic farming and play a pivotal role in long-term sustainability maintaining soil fertility and will become a viable alternative to farmers to improve ultimate yield per unit area in organic farming and food production. However, despite the fact that PGPB-mediated positive effects on plant growth and development under both normal and stressful conditions are reported frequently, the underlying mechanisms by which PGPB affect plants are not fully understood. Understanding the interactions between PGPB and host plants under normal and stressful conditions will open prospects and challenges for the future to unravel PGPB potentials that increase crop productivity, including wheat, by developing sustainable agriculture and support future food security. *This work was partially supported by RFBR grant* №*19-016-00035A*.

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Progress and Challenges of Wheat Production in the Era of Climate Change: A Bangladesh Perspective

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Contents

Abstract In Bangladesh after rice, wheat is considered the second most important staple cereal. Although Bangladesh is one of the principal rice-consuming countries with per capita consumption of rice 171 kg year^{-1}, the consumption of wheat in Bangladesh has intensely increased over the years. From the year 1961 to 2013, the annual per capita wheat intake in Bangladesh has increased by 102% from 8.62 to 17.47 kg. Currently, Bangladesh mostly relies on import to meet surging demand. During 2011–2013, triennium average, Bangladesh imported 2.86 million tons of

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wheat worth of USD 957.4 million. During 2018 only, about 7.0 million tons of wheat has been imported, which is nearly 80% of the total wheat supplied in the country consisting of domestic production and import. It is anticipated that wheat intake will be further increased in Bangladesh in the future, due to the changes in lifestyle which stems from an increase in income and speedy urbanization. It is therefore imperative to supply more wheat in Bangladesh in the future to ensure food demand of growing population in Bangladesh. At the same time, sustainable wheat production in Bangladesh is threatened by several stresses (biotic and abiotic) in addition to the competition of wheat with other winter crops. The chapter has highlighted the major constraints and prospects of wheat cultivation in relation to possible improved technologies under changing climate and provided an up-to-date and comprehensive information on the wheat research of Bangladesh in relation to global warming. This chapter will thus allow wheat researchers to make a comprehensive new breeding and management programs in Bangladesh to mitigate future global warming, especially for recently emerged wheat blast disease in Bangladesh including South Asia.

Keywords Abiotic stress · Biotic stress · Bangladesh · Changing climate · Wheat

1 Introduction

The three major staple crops, wheat (*Triticum aestivum* L.), maize (*Zea mays*), and rice (*Oryza sativa*), are the fundamental blocks of food security in the world. These three major bowls of cereal supply 50% of the dietary energy to humanity (FAO 2018a). Among the three major staple crops, wheat is the most cultivated crop in the world and was domesticated around 10,000 years before (Eckardt 2010). For example, in 2016, wheat was cultivated at least in 124 countries on 220.1 million ha of land (FAO 2018b). In contrast, maize and rice were cultivated in 169 and 119 countries and on 187.9 and 159.8 million ha of land, respectively (FAO 2018b). In 2016, with an average wheat yield 3.4 t ha^{-1}, total wheat production in the globe was 749.5 million metric ton (MMT) (FAO 2018b). In the same year, rice and maize yields were 4.63 t ha^{-1} and 5.64 t ha^{-1}, respectively, and total rice and maize production were 740.9 MMT and 1060.1MMT, respectively.

Globally, wheat is cultivated in various agroclimatic zones ranging from the hot and humid area in Bangladesh in South Asia to extreme cold areas such as Kazakhstan and Canada. Based on biotic and abiotic stresses, rainfall, humidity, temperature, and major requirements for crop establishment, the global wheat area has been divided into 12 mega-environments (ME) (Fig. 1, Wheat Atlas 2016). Bangladesh, in South Asia, along with Paraguay in South America and parts of Nigeria and Sudan in Africa is located in ME 5 (Fig. 1). The ME 5 is characterized by high tropical rainfall; high humidity and the minimum temperature range between 11 °C and 16 °C, and wheat are sown in autumn. The major stresses in ME 5 are heat stress, spot blotch, and leaf and stem rust (Wheat Atlas 2016). Although wheat blast was

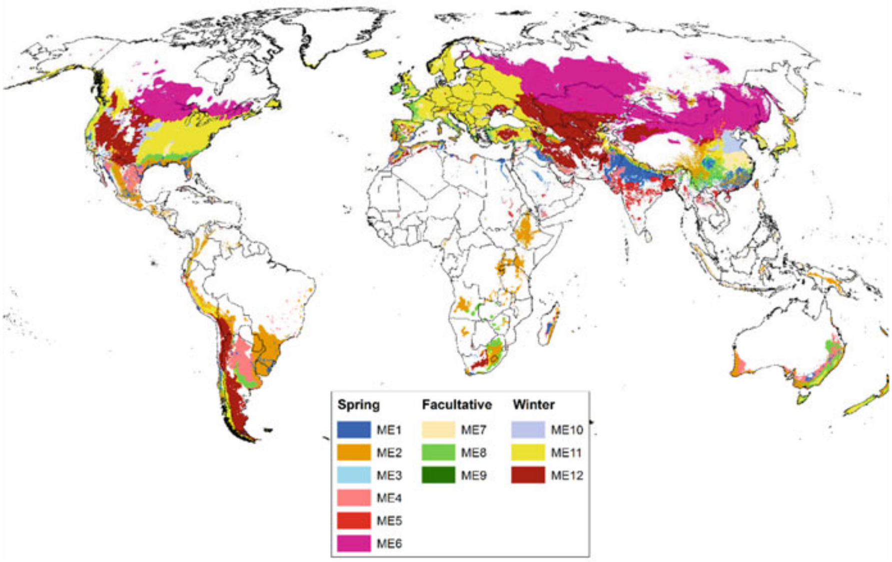

Fig. 1 Global map of wheat mega-environments based on Braun et al. (2010). Curtsey: Dr. Kai Sonder, Head, GIS, International Maize and Wheat Improvement Center (CIMMYT), Mexico

originally confined in Latin America (Malaker et al. 2016; Islam et al. 2016), in the year 2016, for the first time in the history, wheat blast has emerged in Bangladesh (ME 5). Wheat blast-induced yield loss in Bangladesh was recorded at 5% in the affected field of Bhola District to 51% in the affected field of Jhenaidah District (Islam et al. 2016).

Globally, wheat consumption ranges between yearly per capita 1.89 kg in Laos and 222.4 kg in Azerbaijan with per capita yearly average consumption 70.9 kg in 175 countries in the world (FAO 2018b). However, globally the average yearly per capita wheat consumption has increased by more than 19% from 54.9 kg to 65.4 kg from 1961 to 2013 (FAO 2018b). Interestingly, the rate of increase in wheat consumption is much higher in the poverty-stricken sub-Saharan African countries (Mason et al. 2015) and in the traditional rice-growing countries of South and Southeast Asia (Mottaleb et al. 2018a). For example, in Kenya, during 1961 to 2013, the yearly per capita wheat consumption increased by 356% from 7.6 kg to 34.7 kg, in Zambia increased by 38.6% from 7.4 kg to 12.1 kg, and in Zimbabwe by 49.3% from nearly 21 kg to 31.3 kg in the same period (FAO 2018b). In Asia, the yearly per capita wheat consumption has also been increasing in the traditional rice-producing and rice-consuming countries, such as in India and Indonesia. For example, in India from 1961 to 2013, the yearly per capita wheat consumption has increased by 117%, and at the same time in Indonesia, the yearly per capita wheat consumption had increased by 1442% (FAO 2018b).

With yearly per capita rice consumption of 171.7 kg, Bangladesh is one of the largest rice- producing and rice-consuming countries in the world (FAO 2018b). However, like many other sub-Saharan African and East and South Asian countries, wheat consumption in Bangladesh has been increasing significantly over the years (Mottaleb et al. 2018a, b). In 1963, the yearly per capita wheat consumption in Bangladesh was less than 11 kg that supplied daily 94 kcal per person (FAO 2018b). However, in 2013, the yearly per capita wheat consumption has increased at 17.5 kg, which is 59.4% more than the consumption level in 1963, and, currently, wheat supplies daily 150 kcal per capita (FAO 2018b).

With nearly 160 million population, Bangladesh is a rapidly emerging economy in South Asia. Since 2000, the GDP of Bangladesh, on average, has increased by 3.8–7.1% per annum (World Bank 2018a, b). As a result, the per capita nominal GDP of Bangladesh has increased from $363 in 2000 to $1516 in 2017 (World Bank 2018a, b). The US Department of Agriculture (2015) projected that the GDP of Bangladesh would increase by more than 6% per annum during 2018–2030. The urbanization process in Bangladesh is also rapid. In 2001, nearly 20% of the total 134 million population of Bangladesh was living in urban areas, whereas in 2018 nearly 36% of more than 160 million population of Bangladesh is currently living in urban areas (World Bank 2017a). Considering the medium fertility rate, it is projected that by 2050, the total population of Bangladesh will be 202 million (UN 2015), 56% of which is projected to reside in the urban areas (World Bank 2017b). The rapid economic growth, speedy urbanization, and the allied changes in lifestyle are responsible for the increased consumption of wheat in Bangladesh (e.g., Barker et al. 1985; Hossain 1998; Pingali 2007; Mottaleb et al. 2018b). It is expected that the faster economic growth and speedy urbanization process may further increase the wheat demand in Bangladesh in the future.

Worryingly, due to the population pressure, resources such as the per capita internally renewable freshwater (cubic meters) and the arable land (per capita/ha) in Bangladesh have been declining over the years. For example, the renewable internal freshwater per capita in 1971 was 1553.3 cubic meters, and the arable land was 0.1 ha per capita. In contrast, in 2014, the renewable internal freshwater per capita was reduced at 658.7 cubic meters, and the per capita arable land reduced at 0.05 ha (World Bank 2018a, b). It indicates additional wheat has to be produced from less land and water to meet the ever-growing demand; Bangladesh will rely more on import. In addition to declining resources, the change in global climate can also play significantly negative impacts on wheat and other cereal production in Bangladesh (IPCC 2007).

In Bangladesh, despite the yield growth, the total domestic wheat production remains more or less static due to the gradual decrease in wheat area (BBS 2018). Currently, the domestic production can only meet around 20% of the total wheat consumption of the country (USDA 2018; Barma 2018), and the demand-supply gap is met by import. In 1972, wheat was grown in only 0.13 million ha with a production of 0.11 million metric ton (MMT) (Hossain and Teixeira da Silva 2013). With the strong initiative of the government, wheat area gradually rose to its highest pick of 0.85 million ha with record production of 1.9 MMT. The wheat area in Bangladesh, however, started declining due to competition with other *rabi* crops, such as hybrid maize, and the area currently reduced to 0.42 million ha in

2017 with a production of 1.3 MMT with record wheat productivity of 3.13 t ha^{-1} (BBS 2018). However, out of total wheat consumption of 7.1 MMT in 2016–2017 in Bangladesh, wheat import contributed more than 80% (BBS 2018). Considering market volatility and the growing importance of wheat in Bangladesh's diet, a complete dependency on import cannot be a sustainable option.

This chapter examines the progress and challenges of wheat production in Bangladesh considering the increasing demand for wheat in light of the changing climate. This chapter is organized as follows. Section 2 elaborates the importance of wheat as a food grain in the world as well as Bangladesh. Section 3 presents scenario of wheat production at the global scale under changing climate. Section 4 presents historical background with purposes and objectives for wheat production in Bangladesh. Section 5 includes current trends of areas and production of wheat in Bangladesh. Section 6 presents the development of wheat varieties under changing climate. Section 7 presents constraints of wheat production in Bangladesh focusing on abiotic and biotic stresses and social constraints. Section 8 presents breeding and biotechnological approaches to improve stress tolerance wheat in Bangladesh. Section 9 presents research advances through agronomic practices for enhancing sustainable wheat production. Section 10 includes research progress on grain quality of wheat. Section 11 presents international linkages, collaboration, and policy issues for wheat production in Bangladesh; and finally Sect. 12 includes conclusion and policy implications.

2 Importance of Wheat as a Food Grain in the World as Well as Bangladesh

In human history, the domestication of wheat was a major landmark as it contributed to the transformation of the hunter-gatherer and nomadic primitive society to a more established agrarian society (Eckardt 2010). Since its domestication around 10,000 years ago, the crop became a major source of food grain in the world. With the increase in population, wheat cultivation was expanded dramatically across countries. In 1961, wheat was cultivated on 204.2 million ha of land in at least 94 countries, whereas in 2016, wheat was cultivated at least in 124 countries on 220.1 million ha of land (FAO 2018b). With yearly per capita current consumption of wheat 65.4 kg globally, wheat supplies on average per capita daily 527 kcal dietary energy, 15.9 grams protein and 2.43 grams fat (Table 1). Interestingly, over the years the yearly per capita wheat consumption in Europe and Oceania has been declining, whereas the yearly per capita wheat consumption in Africa, Americas and South America, Asia, and South Asia and Bangladesh has been increasing. In particular, the rate of increase in wheat consumption in Africa, Asia, and South Asia is higher compared to other regions (Table 1).

Table 1 Wheat as food in the world and selected regions of the world and Bangladesh

Region	World	Africa	Americas	South America	Europe	Oceania	Asia	South Asia	Bangladesh
Food supply quantity: kg/capita/year									
1963	55.4	29.6	57.0	52.0	131.3	96.9	30.2	36.0	11.0
1973	59.0	36.2	57.2	53.6	120.6	81.5	43.2	54.0	32.4
1983	67.5	45.8	61.1	58.8	114.4	77.3	59.6	59.9	27.2
1993	69.9	47.5	62.5	53.6	106.8	70.6	67.7	66.7	17.6
2003	66.8	46.7	63.2	57.2	108.7	71.6	63.7	65.7	21.3
2013	65.4	47.7	61.4	57.1	109.0	70.8	62.9	67.6	17.5
Food supply: kcal/capita/day									
1963	420	234	414	388	952	759	248	304	94
1973	458	285	418	399	875	635	360	457	276
1983	537	361	443	430	842	599	504	506	232
1993	562	374	456	397	806	552	567	558	150
2003	540	369	469	440	820	577	537	550	182
2013	527	376	459	429	827	579	524	566	150

Adapted from FAO (2018b)

Among the South Asian countries, the wheat consumption has dramatically increased in India (Rao 2000; Gandhi et al. 2004; Pingali 2007; Kumar et al. 2007; Mittal 2007; Deaton and Dreze 2009) and Bangladesh (Timsina et al. 2018; Mottaleb et al. 2018a, b, c). Using Bangladesh Household Income and Expenditure Survey data, Mottaleb et al. (2018a, b) demonstrate that the increased wheat consumption in Bangladesh is positively linked with the urbanization and the level of education and economic affluence of the households. It means economically affluent and urban households and households headed by educated heads and spouses consume more wheat than others. The increasing wheat consumption phenomenon in Asia and India, in particular, is termed as the westernization of Asian diets (Pingali 2007). Bangladesh and other South Asian countries, such as India and Nepal are economically emerging, and wheat is going to play a more important role in the South Asian diet in the future.

Even though with per capita rice consumption yearly 171 kg Bangladesh is the largest rice-consuming country in the world, the consumption of wheat has increased by 102% from 8.62 to 17.47 kg during 1961 to 2013 (Index Mundi 2018). Currently, Bangladesh mostly relies on import to meet surging demand due to the increasing consumer demand and also decreasing production (Index Mundi 2018; Figs. 2 and 3). During 2011–2013, triennium average, Bangladesh imported 2.86 million tons of wheat worth of USD 957.4 million (FAO 2018a). During 2018 only, about 7.0 million metric tons of grain has been imported (Index Mundi 2018) which is nearly 80% of the total wheat supplied in the country consisting of domestic production and import. With the changes in lifestyle which stems from an increase in income and speedy urbanization, it is projected that wheat consumption will further increase in Bangladesh in the future.

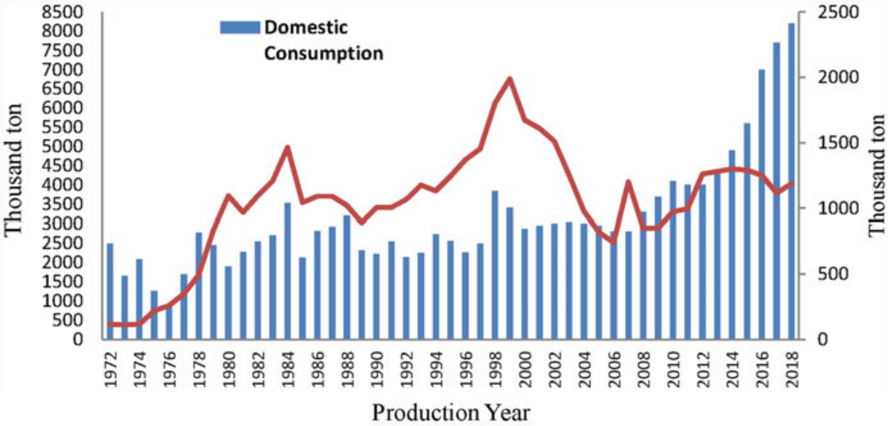

Fig. 2 Domestic consumption and production of wheat in 1000 ton, 1972–1918. (Data source: Index Mundi 2018; Barma 2018)

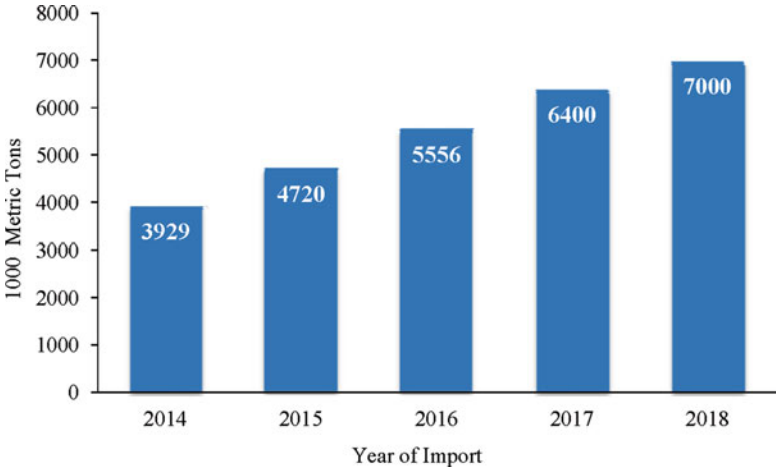

Fig. 3 Last 5-year import of wheat grain, 2014–2018 (1000′ MT). (Data source: Index Mundi 2018; Barma 2018)

3 Historical Background with Purposes and Objectives for Wheat Production in Bangladesh

Compared to rice, the major staple crop of Bangladesh, wheat is relatively a new crop in this country. The first initiative of wheat research in Bengal province was documented in 1936 (Ahmed and Meisner 1996). The notorious famine in 1943 in Bengal province that killed more than 3 million poor people from starvation and malnutrition (e.g., Sen 1981) forced the British Raj to strengthen wheat production in Bangladesh (the Bengal province) as an additional winter crop to ensure food security. Until 1955, *Gangajali* and *Jamali* were two local wheat varieties farmers produced sporadically (Ahmed and Meisner 1996).

During Pakistan period (1947–1971), government adopted some efforts to introduce wheat as an alternative winter crop realizing that rice alone could not meet food requirement of the ever-growing population of the country (Sarker et al. 2011). During 1955–1960, IP-52 and IP-125 wheat varieties developed by the Imperial Institute of Agricultural Research, New Delhi, were released in Bangladesh (Ahmed and Meisner 1996). The breakthrough, in research, however, came in 1965, when two Mexican high-yielding wheat varieties Sonora 64 and Penjamo 62 were tested in the northern part of Bangladesh and found promising (Ahmed and Meisner 1996; Hossain and Teixeira da Silva 2012). However, despite the spectacular performance of "Sonora 64" and "Penjamo 62" varieties, wheat was continuously treated as a nontraditional crop until the 1980s (Sarker et al. 2011). This was mainly because of the rapid expansion of the dry season irrigated *boro* rice, which emerged as the major competing crop of wheat. As rice is the staple food, the expansion of irrigated high-yielding modern *boro* rice in the dry season significantly outweighs wheat production in Bangladesh by increasing the net profitability of producing *boro* rice than any other winter crops including wheat (Morris et al. 1997). Consequently, wheat production in Bangladesh did not expand until recently. The nonavailability of the good-quality wheat seeds was another prominent problem on the expansion of wheat cultivation in Bangladesh during that time (e.g., Ahmed and Meisner 1996).

In 1965 and 1968, the head wheat breeder of CIMMYT visited Pakistan and convinced the national government that even without disturbing major crop production such as rice, it is possible to produce wheat on more than 1.5 million hectares of land in East Pakistan (Bangladesh) (Borlaug 1970; Byerlee and Siddiq 1994). During the same period, a massive program for producing high-yielding wheat in West Pakistan was already underway under active government support. After independence in 1971, the government emphasized the expansion of rice cultivation to ensure food security in the country while giving less importance to wheat at the beginning (Ahmed and Meisner 1996). Attitude toward wheat production, however, changed by a visit of the chief breeder and top scientists of CIMMYT in Bangladesh in 1974. The CIMMYT scientists successfully convinced Bangladesh government the country needs to diversify crop production to reduce climate-related risks in food production. As seed availability was the major problem, in 1975, the government imported 4000 tons of Sonalika and Kalyansona wheat seed from India and Mexico (Hossain and Teixeira da Silva 2013). The national government also trained the agriculture extension officers ahead of the wheat season. Ahmed and Meisner (1996) explained that this was the first major, well-organized, and successful government intervention to expand wheat production in Bangladesh.

4 Trend Areas, Production, and National Average Yield of Wheat in Bangladesh

Wheat is the important cereal next to rice in Bangladesh, which plays an important role in attaining food and nutritional security. In Bangladesh, the area of wheat in the year 1998–1999 was 0.85 million hectares (ha), and the production in the same year was 1.9 million ton (BBS 2011; WRC 2018), which was about 18 times more over the production of 1970–1971 and double the production of 1980–1981. The remarkable success in wheat production in the country was due to development of high-yielding and stress-tolerant wheat varieties with improved production technologies and also dissemination of these technologies to the farmers' field within a short period (Ahmed and Meisner 1996; Hossain and Teixeira da Silva 2013). However, in the previous year (in 1999), both area and production of wheat started to decrease mostly (area and production were 0.350 million ha and 1.30 m ton, respectively which is almost half of 1999) (BBS 2011), due to crop competition with maize, potato, *boro* rice, and vegetables and also lack of adaptation of good varieties as well as dissemination of improved management practices. However, the productivity has been increased significantly from 2.0 t ha^{-1} (1900) to 3.13 t ha^{-1} in 2016–2017 due to the introduction of heat-tolerant high-yielding wheat varieties and adoption of

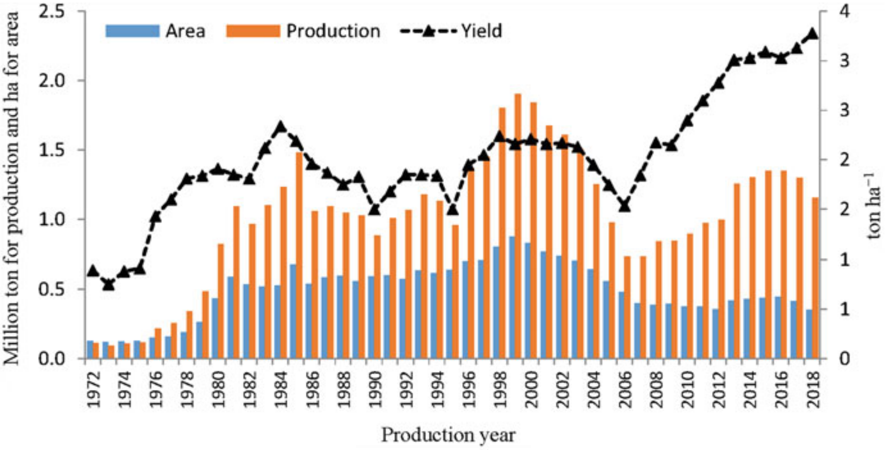

Fig. 4 Trend of area, production, and national average yield of wheat from 1972 to 2018. (Data source: Index Mundi 2018; Barma 2018)

wheat production technologies and dissemination of those to the farmers' field (Fig. 4). While, with an increase in disposable income, households tend to consume more high value-added food (Mottaleb et al. 2018a, b), wheat consumption in Bangladesh has been increasing every year, due to rapid dietary changes which are evident from the increase of import from 33.54 million metric ton in 2013 to 70.0 million metric ton in 2018 (Index Mundi 2018). During 2017–2018, 1.153 million tons of wheat was produced from 0.350 million ha that can meet only 20% of the national requirement (WRC 2018). On the other hand, the demand of wheat has been increasing every year at the rate of 13% due to rapid changes in dietary habit, socioeconomic upliftment, enhancement of per capita income, the rapid growth of fast food restaurant, the establishment of branded bakery and biscuit industries, etc. Due to the decrease in wheat area by 15% than the previous year, wheat production also reduced to about 12%. However, there is a significant increase in wheat productivity of 3.28 t ha^{-1} which was possible through the dissemination of high-yielding, disease-resistant, and stress-tolerant varieties and improved management practices to the farmers (Barma 2018; WRC 2018).

5 Development of Wheat Varieties Under Changing Climate

Wheat Research Centre (WRC) of BARI is entrusted to the research works for the improvement of wheat in Bangladesh and already released 33 high-yielding stress-tolerant varieties for commercial cultivation (Table 2). The recently released varieties are moderately tolerant to abiotic stresses such as terminal heat stress, drought, and salinity and also resistant/tolerant to major foliar diseases. Varieties released

Table 2 Cross and pedigree of released wheat varieties in Bangladesh

SL.	Variety name	Pedigree	Year of release	Average yield (t ha^{-1})
1	Sonora 64	YT 54/N10B//2*Y 54	1968	3.1
		II 8469-2Y-6C-6Y-4C-2Y-1C-0 MEX		
2	Kalyansona	PJ/GB 55, II 8156	1968	3.1
3	Inia 66	LR 64/SON 64	1972	3.2
		II 19008-83 M-100Y-100 M-100Y-100C		
4	Norteno 67	LR 64/SON 64	1972	3.5
		II 19008-52 M-4Y-3 M-2Y-OBGD (CIMMYT, Mexico)		
5	Sonalika	1154–388/AN/3/YT54/N1OB/LR64	1973	2.9
		II 18427-4R-1 M		
6	Tanori 71	SON 64/CNOREC//INIA 66	1974	3.7
		II 25717-4Y-3 M-1Y-0 M-0 MEX		
7	Nuri	Not available	1974	3.1
8	Jupateco 73	II 12300//LR 64/8156/3/NOR	1974	3.7
		II 30842-31R-2 M-2Y-0 M-0 MEX		
9	Balaka	PI'S′/HD 845	1979	3.3
		HD 1981-100JA-0I		
10	Doel	SON 64/KL REND//23,584	1979	3.0
		II 26592-8Y-2 M-2Y-0 M-0I		
11	Pavon 76	VCM//CNO/7C/3/KAL/BB	1979	3.7
		CM 8399-D-4 M-3Y-1 M-IY-IM-0Y-0BGD		
12	Ananda	KAL/BB	1983	2.8
		CM 26992-30 M-300Y-300 M-500 M-OY-OJA		
13	Kanchan	UP301/C306	1983	3.6
		1187–1-1P-5P-5JO-0JO		
14	Akbar	RON/TOB 'S'	1983	3.4
		CM 7705-3 M-1Y-2 M-2Y-OY-OJO		
15	Barkat	JUN'S′	1983	3.0
		CM 33483-C-7 M		
16	Aghrani	INIA/3/SON 64/P416OE//SON 64	1987	3.1
		PK 6841-2A-1A-OA		
17	Sawgat	IAS58/3/KAL/BB/2/ALD 'S'/4/OLN/TRM//ALD 'S'	1993	3.2
		CM 69201-B-1Y-3 M-7Y-1 M-OY		
18	Protiva	KU Head Selection	1993	3.3
19	BARI Gom 19 (Sourav)	NAC/VEE (NL 560)	1998	4.0
		CM 64224-5Y-1 M-1Y-2 M-0Y		
20	BARI Gom 20 (Gourab)	TURACO/CHIL	1998	4.1
		CM 92354-33 M-0Y-0 M-6Y-0B		
21	BARI Gom 21 (Shatabdi)	MRNG/BVC//BLO/PVN/3/PJB-81	2000	4.3
		CM98472-1JO-0JO-0JO-1JO-0JO-0R2DI		

(continued)

Table 2 (continued)

SL.	Variety name	Pedigree	Year of release	Average yield (t ha^{-1})
22	BARI Gom 22 (Sufi)	KAN/6/COQ/F61.70//CNDR/3/OLN/4/PHO/5/MRNG/ALDAN//CNO BD (JE) 349-X-0JE-9DI-10HR	2005	4.3
23	BARI Gom 23 (Bijoy)	NL297*2/LR25	2005	4.7
24	BARI Gom 24 (Prodip)	G. 162/BL 1316//NL 297	2005	4.7
25	BARI Gom 25	ZSH 12/HLB 19//2*NL297	2010	4.3
26	BARI Gom 26	ICTAL 123/3/RAWAL 87//VEE/HD 2285 BD(JO)9585-0JO-3JE-0JE-0JE-HRDI-RC5DI	2010	4.3
27	BARI Gom 27	WAXWING*2/VIVISTI CGSS01BOOO56T-099Y-099 M-099 M-099Y-099 M-14Y-0B	2012	4.6
28	BARI Gom 28	CHIL/2*STAR/4/BOW/CROW//BUC/PVN/3/2*VEE#10 CMSS95Y00624S-0100Y-0200 M-17Y-010 M-5Y-0 M	2012	4.8
29	BARI Gom 29	SOURAV/7/KLAT/SOREN//PSN/3/BOW/4/VEE#5. 10/5/CNO 67/MFD//MON/3/SERI/6/NL297 BD(DI)112S-0DI-030DI-030DI-030DI-9DI	2014	4.8
30	BARI Gom 30	BAW 677 (PASTOR/3/VEE#5//DOVE/BUC)/Bijoy BD(JA)1365S-0DI-15DI-3DI-HR12R3DI	2014	4.8
31	BARI Gom 31	KAL/BB/YD/3/PASTOR CMSS99M00981S-0P0M-040SY-040 M-040SY-16 M-0ZTY-0 M	2017	4.8
32	BARI Gom 32	SHATABDI/GOURAB BD(DI)1686S-0DI-1DI-0DI-0DI-3DI	2017	4.8
33	BARI Gom 33	KACHU/SOLALA CMSS09Y00580S-099Y-38 M-0WGY-4B-0Y	2017	4.8

Data source: Barma (2018)

since 2000 are high yielding and are mostly grown in the field, and percent coverage of released wheat varieties in the field is given in Fig. 5. Most of the released varieties are also early in maturity with their average yield of 3.1 to 4.8 t ha^{-1}. Year-wise released varieties and their yield ranges are also presented in Table 3. Among the latest popular 12 elite wheat varieties developed since 2000, 11 were found resistant against leaf rust (except “BARI Gom 24” (“Prodip”), and 3 varieties such as “BARI Gom 26,” “BARI Gom 27,” and “BARI Gom 29” were found resistant to stem rust (Ug99 race). “BARI Gom 21” (“Shatabdi”), “BARI Gom 30,” and “BARI Gom 32” were found tolerant against wheat blast (WB), whereas

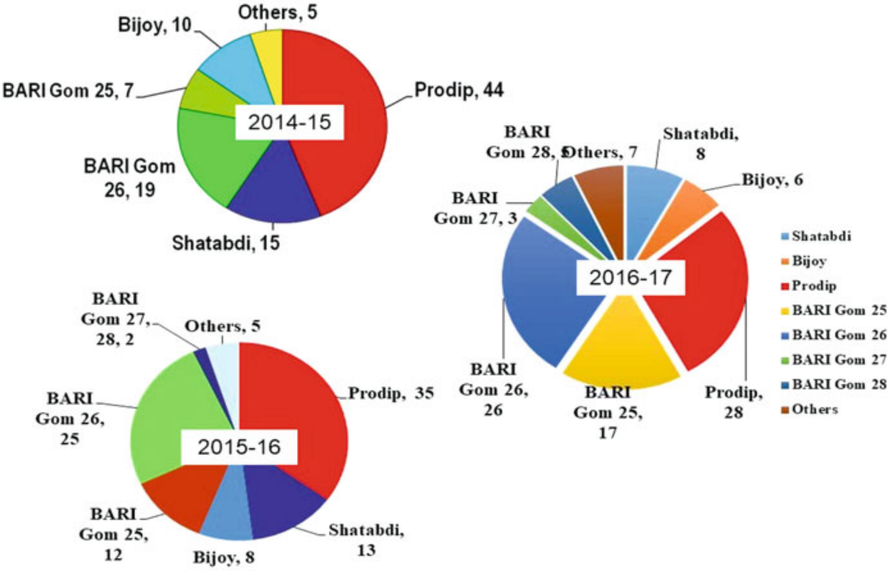

Fig. 5 Varietal coverage (%) in all over the country in the last 3 years (2014 to 2017). (Data source: Barma 2018)

Table 3 List of wheat varieties so far released by WRC, BARI since independent (1970)

SL#	Year of release	Number of varieties released	Yield range (t ha^{-1})
1	1970–1979	11	2.6–3.6
2	1980–1989	5	3.3–4.0
3	1990–1999	4	3.3–4.8
4	2000–2009	4	3.6–5.1
5	2010–2014	6	4.0–5.5
6	2015–2017	3	4.5–5.5

Data source: Barma (2018)

"BARI Gom 33" was found resistant against WB. Another two varieties such as "BARI Gom 28" and "BARI Gom 29" were found moderately susceptible against wheat blast (WB) (Table 4).

6 Constraints of Wheat Production in Bangladesh

6.1 Abiotic Stresses

Based on biotic and abiotic stresses, rainfall, humidity, temperature, and major requirements for crop establishment, the global wheat area has been divided into

Table 4 Percent coverage of existing elite wheat varieties and reaction to rust diseases

SL no.	Name of major varieties	Year of release	Coverage (%)	Reaction to diseases LR	 SR Ug99 race)	 WB
1	BARI Gom 21 (Shatabdi)	2000	8	R	–	TOL
2	BARI Gom 23 (Bijoy)	2005	6	R	–	S
3	BARI Gom 24 (Prodip)	2005	28	S	–	S
4	BARI Gom 25	2010	17	R	–	S
5	BARI Gom 26	2010	26	R	R	S
6	BARI Gom 27	2012	3	R	R	S
7	BARI Gom 28	2012	5	R	–	MS
8	BARI Gom 29	2014	0.4	R	R	MS
9	BARI Gom 30	2014	0.6	R	–	TOL
10	BARI Gom 31	2017	–	R	–	S
11	BARI Gom 32	2017	–	R	–	TOL
12	BARI Gom 33	2017	–	R	–	R

Data source: Barma (2018)
LR leaf rust; *SR* (Ug99 race), stem rust, *WB* wheat blast, *R* resistance, *S* susceptible, *MS* moderately susceptible, *TOL* tolerance

12 mega-environments (ME) (Fig. 1, Wheat Atlas 2016). Bangladesh, in South Asia, along with Paraguay in South America and parts of Nigeria and Sudan in Africa is located in ME 5 (Fig. 1). The ME 5 is characterized by high tropical rainfall, high humidity, and the minimum temperature range between 11 and 16 °C, and wheat is sown in autumn (Wheat Atlas 2016). Bangladesh is located between the Himalayas and the Bay of Bengal; the country is very prone to natural disasters (World Bank 2009). Due to one of the most climate-vulnerable countries in the world, climate change accelerates the intensity and frequency of salinity, drought, high-temperature stress, flash floods, etc.

There are two ways to mitigate stresses in wheat, either by developing and practicing improved heat stress management practices or by developing and using tolerant cultivars against specific stress (Farooq et al. 2011). Modern wheat varieties are not sufficiently tolerant against stress and are susceptible to extreme abiotic stresses (Hussain et al. 2016). Therefore, developing cultivars tolerant to heat stress and other abiotic stresses is challenging for wheat breeders in Bangladesh (Hossain and Teixeira da Silva 2013). Considering the burning issues, scientists in WRC of BARI are trying to develop wheat varieties which are suitable to cultivate under abiotic stress conditions to meet the food security of increasing population.

A detailed description for the development of wheat varieties against abiotic stresses under changing climate is presented in Sect. 7.1.

6.2 Biotic Constraints Especially Diseases

Bangladesh, in South Asia, along with Paraguay in South America and parts of Nigeria and Sudan in Africa is located in ME 5 (Fig. 1), which is characterized by high tropical rainfall, high humidity, and the minimum temperature range between 11 °C and 16 °C. As a result, the area is highly vulnerable to major diseases such as spot blotch and leaf and stem rust (Wheat Atlas 2016).

Among them, *Bipolaris* leaf blight (spot blotch) caused by *Bipolaris sorokiniana* (Sacc.) Shoemaker is most important. The disease occurs every year in all wheat-growing areas of the country with varying degrees of severity depending on cultivar, sowing time, and location.

The second most important disease is leaf rust caused by *Puccinia triticina* Eriks. The disease usually appears in mid-February under the agroclimatic condition of Bangladesh. It may cause severe yield losses if a susceptible variety is late sown and infection occurs early in the crop season. The popular variety "Prodip" has become susceptible to leaf rust and may be seriously affected under late-sown condition. Stem rust caused by *P. graminis* Pers. f. sp. *tritici* Eriks. & Henn. was observed in 2014 and 2015 in the rust trap nurseries after three decades, but no Ug99 detected. Yellow rust caused by *P. striiformis* West. f. sp. *tritici* Eriks. & Henn. occurs occasionally with low to moderate severity. So far none of the rusts have reached an epidemic level in Bangladesh, but damaging epidemics may occur, particularly if a new virulent race develops or is introduced. Other diseases of regular occurrence are seedling blight caused by *B. sorokiniana*, foot and root rot caused by *Sclerotium rolfsii* Sacc., head blight caused by *B. sorokiniana*, and black point incited mainly by *B. sorokiniana* and *Alternaria alternata* (Fr.) Keiss. However, head blight and black point were quite frequent in 2017–2018. Powdery mildew caused by *Erysiphe graminis* f. sp. *tritici* has been observed since 2012 in late February with sporadic infection, though the disease was also noticed as sporadic in the 2017–2018 crop cycle.

A detailed description for the development of wheat varieties against different diseases under changing climate is presented in Sect. 7.2.

6.2.1 Wheat Blast: A New Threat on Food Security of Increasing Population

Although wheat blast (WB) caused by the fungus *Magnaporthe oryzae* pathotype *Triticum* (MoT) was most confined in Latin America (Malaker et al. 2016; Callaway 2016; Islam et al. 2016), in the year 2016, for the first time in the history, WB disease has been reported in Bangladesh (ME 5), which affected nearly 15,000 ha (3.5% of the total 0.43 million ha of wheat area in Bangladesh), with wheat yields in the affected fields reduced by 5–51% (Islam et al. 2016).

The disease also reappeared in 2017 and 2018 with comparatively low disease severity, and about 5–10% and 1–5% yield loss occurred, respectively (Malaker et al. 2016; Callaway 2016; Islam et al. 2016; Chowdhury et al. 2017). Presently the disease is under monitoring and surveillance, and short-, medium-, and long-term research strategies are underway to mitigate the threat of wheat blast (Table 5). *Fusarium* head blight (FHB) is a major concern of many wheat-growing countries wherever it occurred. During the last cropping season (in the year 2018), the disease with high prevalence was observed in a trial of HarvestPlus at WRC-Dinajpur (Reza et al. 2018). Though till now its occurrence in farmer's field in a negligible level. So, if the disease reappeared to the coming year likewise, it might be an issue to pave research priority. Major research thrust was given on screening and evaluation for disease resistance, testing the fungicidal efficacy, and disease monitoring in national and international nurseries and farmers' fields.

Although the invasion of wheat blast is first time reported in Bangladesh in 2016 (Callaway 2016; Islam et al. 2016; Malaker et al. 2016), there is a possibility to spread into South Asia including India, Pakistan, Nepal, and China (Government of India 2016; Press Trust of India 2017). As a result WB incidence in Bangladesh has brought an attention to the governments of different countries in South Asia and the international community of plant pathologists, to expose an urgent need to develop strategies to limit the spread of this destructive pathogen (McDonald and Stukenbrock 2016; Sadat and Choi 2017; Saharan et al. 2016; Sharma 2017; Singh et al. 2016; Ceresini et al. 2018). Mottaleb et al. (2018d) warned that more than 17.1% (nearly 7 million ha) of the total 40.85 million ha of wheat area in Bangladesh, India, and Pakistan is vulnerable to wheat blast, and only a 5% reduction in the wheat production only in the blast vulnerable area can reduce wheat production by 886,000 metric ton worth of US$132 million.

Table 5 Comparative status of blast incidence in 2016, 2017, and 2018

Events	2016	2017	2018
Infection time	Mid-February	Mid-January	Early February
Weather situation	Rain at flowering time (35 mm in Feb) with warm temperature (Min. 18-23 °C, Max. 21-28 °C)	High humidity due to fog at flowering and warm temperature (min. 16–18 °C and max. 24–26 °C)	Fluctuation of day-night temperature (min. 10–12 °C and max. 26–28 °C) with high humidity/fog
Area affected	15,000 ha (DAE)	22 ha (DAE)	–
Yield losses	25–30%	5–10%	1–5%
Districts affected	Meherpur, Jhenaidah, Chuadanga, Jessore, Magura, Kushtia, Barisal, Bhola	Previous districts + some additional districts: Faridpur, Rajshahi, Pabna	Meherpur, Jhenaidah, Chuadanga, Jessore, Kushtia, Bhola, Faridpur, Rajshahi, Rajbari, Natore, Tangail, Jamalpur, Cumilla

Data source: Reza et al. (2018)

Since wheat blast is a threat to wheat production in Bangladesh and South Asia, short-, medium-, and long-term strategies have been formulated to mitigate the threat to sustaining wheat production in this region in collaboration with CIMMYT, ACIAR, and USDA to develop blast-resistant wheat variety.

6.3 Crop Competition in Wheat-Growing Season

One of the major challenges of expanding wheat in Bangladesh is crop competition in the winter. In a study, Mottaleb et al. (2018b) showed that the incidence of wheat cultivation in Bangladesh is mostly limited among the medium and large farm holders in Bangladesh, who have some luxury to allocate land for wheat cultivation after allocating land for *boro* rice. Although Bangladesh achieved self-sufficiency in rice production, excessive extraction of groundwater for rice cultivation especially for irrigating of *boro* rice is a major concern as its cultivation associated with negative impacts on the agroecology and environment (Alauddin and Quiggin 2008). Due to the reliance on groundwater irrigation mainly for *boro* rice, the groundwater levels in Bangladesh have been reportedly declining between 0.01 and 0.05 meter yearly (Shamsudduha et al. 2009; Dey et al. 2013). Other major crops competing with wheat are maize, potato, vegetable crops, etc. The present policy of the government is to promote *aus* rice (upland rice) replacing *boro* rice in high and medium land to save underground water and give more space for winter crops like wheat.

6.3.1 Constraints in Productivity Enhancement and Emerging Challenges

Major production constraints of wheat under Bangladesh context are global warming, short winter, inadequate crop management, less availability of quality seed, slow adoption of new varieties, and the threat of new diseases due to climate change. Depletion of organic matter is another constraint common for all crops that come from high cropping intensity. However, wheat cultivation is less costly, resource-conserving, environmentally friendly, and economically viable. The national average yield during 2001–2008 was around 2.00 t ha^{-1}. However, wheat productivity has started increasing systematically from 2009 and rose to 3.13 t ha^{-1} in 2017 (Index Mundi 2018; Barma 2018). Still, the demonstration average yield of new varieties is about 3.6 t ha^{-1}. At research stations with optimum management, the mean yield of new existing wheat varieties so far recorded is 4.5–6.5 t ha^{-1} (Barma 2018). So, still, there is a yield gap of about 1.4 ton per ha between research station yield and farmers' yield.

6.3.2 High Production Cost and Low Wheat Grain Price

In addition, the per hectare irrigation costs for *boro* rice cultivation are estimated at USD178, whereas it is only USD76 for wheat (Lagos and Hossain 2016). Consequently, the overall production costs of *boro* rice are relatively high compared to wheat. For example, the per hectare production cost of *boro* rice is reported as US$ 913–1319, while for wheat it is US$ 663 (Lagos and Hossain 2016; Sujan et al. 2017; CIMMYT 2015). Consequently, the benefit-cost ratio for *boro* rice in Bangladesh is 0.82, whereas for wheat it is calculated as 1.24 (Lagos and Hossain 2016). It means the return from boro rice after USD100 will be USD 82, but it will be US$ 124 in the case of wheat. As wheat consumption in Bangladesh has been increasing rapidly, and as marginal return from wheat is higher than *boro* rice, there is a large potential for wheat cultivation expansion in Bangladesh.

7 Breeding and Biotechnological Approaches to Improve Stress Tolerance Wheat in Bangladesh

The yield potentiality and disease resistance of the upcoming varieties are to be increased to enhance wheat production in the country, which can be achieved through good agronomic management. Yield potential can be increased through strategic crosses based on pyramiding yield potential traits, disease resistance, physiological traits conferring tolerance to abiotic stresses, etc. in the agronomically superior adapted genotypes. Thus, the main objective of hybridization is to create variability by combining and recombining desirable genes in the background of different adapted genotypes followed by a selection of desirable plants in subsequent generations to develop improved varieties for the target environment. Major focus has been given to developing high-yielding, disease-resistant, and stress-tolerant variety with a wide range of adaptability.

Development of abiotic stresses such as heat drought and salinity tolerant and also wheat blast-resistant variety has been given the highest research priority under the context of global climate change. Marker-assisted selection has been introduced to develop multiple stress-tolerant varieties. Development of varieties with the improved nutritional quality especially Zn content has been addressed in the program. The performance of newly developed wheat lines from national and international sources especially CIMMYT is being evaluated under different growing environments across the country.

7.1 Development of Abiotic Stress Resistance Varieties/Lines Under Changing Climate

7.1.1 Development of Wheat Varieties Tolerant to Early- and Late-Sown Heat Stress

Every crop has an optimal temperature range for growth and development, and temperature below or exceeding the upper limit hampers the life cycle of affected crops that leads to decrease in the final yield. A decrease in the production of *aman* (monsoon rice) rice by 2.94, 53.06, and 17.28 tons, respectively, was due to a 10 °C increase in maximum temperature at vegetative, reproductive, and ripening stage (Islam 2008). An increase in winter temperature by 2–4 °C may exceed the loss by 60% of the achievable yields of wheat and potato (Karim 1993; Islam 2008). Subsequently, the temperature sensitivity also affects the soil respiration and soil organic matter decomposition (Leite and Madari 2011).

In Bangladesh, some areas of lands become vacant in late October to early November due to the expansion of short duration rice varieties which is suitable for growing wheat. But seeding of wheat during this period is not yet recommended. Temperature remains comparatively high during this period which has a detrimental effect during germination and crop establishment stages causing considerable yield loss. Heat stress during early crop growth is called "juvenile heat stress" which causes less biomass, less tillering, i.e., poor crop stand, shortened vegetative period, i.e., early heading with less number of grains per spike, and reduced spike length. Sometimes optimum sown wheat also suffers from early heat stress. Usually, farmers don't like to hold their land empty for a long time to avoid loss of residual soil moisture. Development of early heat-tolerant wheat line/variety has great potential to increase the area and productivity of wheat. The research program has been initiated to evaluate and select promising wheat genotypes with early heat tolerance and high-yield potential suitable for early seeding.

On the other hand, one of the major constraints for wheat production in Bangladesh is late planting, due to the late harvest of T. *aman* rice. Late-planted wheat is facing high-temperature stress during grain filling which shortens the grain filling period, resulting in shriveled grain that leads to low yields. So, top research priority has been given for the development of heat-tolerant variety suitable for the late-sown environment. Therefore, all the genotypes developed from national and international sources are screened under heat stress condition manipulating sowing dates. Morphophysiological traits related to heat tolerance traits are being incorporated in the adapted genotypes through hybridization to develop high-yielding heat-tolerant wheat varieties. WRC has already released 33 high-yielding, abiotic and biotic stress-tolerant varieties for commercial cultivation (Table 2).

7.1.2 Technologies for Enhancing Wheat Areas in Dry Land

Wheat in Bangladesh is subjected to multiple simultaneous stresses like heat and drought. Bangladesh is at higher risk from moisture stress, 3.5 million ha land is affected by drought, and wheat is one of the major cereal crops under this threat which affected about 47% area of the country and 53% of the population (Alam 2015). However, due to changing climate, the incidence and intensity of drought are increasing. Due to global warming, in the last 25 years, already four major droughts have occurred mostly in northwestern Bangladesh (Selvaraju et al. 2006) during *rabi* (dry/winter) season (Huq 2006). The devastating and regular droughts occurred due to the lack of late rainfall. In the years 1973, 1978–1979, 1981–1982, 1989, 1992, and 1994–1995, Bangladesh already has faced major droughts. In the year 1978–1979, due to drought 50 to 100%, more food grain production was loosed, which the greater than that of the flood in 1974 (Selvaraju et al. 2006). According to IPCC awareness report, rice yield potentiality will be reduced by 8% and wheat yield by 32% within 2050 in Bangladesh (Hossain and Teixeira da Silva 2013).

Drought-tolerant genotypes provide a comprehensive approach for mitigating production-related risk that influences wheat production in Bangladesh. Screening of wheat genotypes under drought stress environment has been initiated at Rajshahi to identify drought-tolerant varieties. Incorporation of drought tolerance characters into adapted varieties is also under progress. Emphasis has also been given to collect and evaluate germplasm from national and international sources to screen against drought stress environment especially in Barind area of Rajshahi. Besides, resource-conserving technologies like a raised bed, strip tillage, etc. along with crop residue incorporation are suggested for drought-prone areas to manage drought stress. Considering the importance of the issue, researchers in WRC of BARI studied 35 genotypes under drought and well-watered condition in 2 consecutive years. Based on the changes in growth phenomena, dry matter production and partitioning, changes in physiological activities, remobilization of pre-anthesis assimilates to the reproductive organ, and grain yield under drought condition, the genotypes "BARI Gom 26" and "BAW 1169" were recommended for drought-prone region of Bangladesh (unpublished data, Table 6).

Table 6 Three wheat genotypes and their pedigree evaluated under water-deficit condition

		Grain yield (t ha^{-1})		
Genotypes	Cross/pedigree	Well-watered	Drought	% Reduction
BARI Gom 26	ICTAL123/3/RAWAL87//VEE/HD2285 BD (JOY) 86-0JO-3JE-010JE-010JE-HRDI-RC5DI	5.59	4.04	27.67
BAW 1169	SHATABDI/BAW 923 BD(DI) 1134S-0DI-4DI-010DI-010DI-1DI-DIRC3	5.41	2.95	45.53
BAW 1167	BL 3877 = KAUZ/STAR/CMH 81.749//BL 2224 NC 02B3616-5B-020 M-020B-3B-0B	5.18	3.44	33.56
LSD (5%)		0.60		
CV (%)		7.04		

7.1.3 Development of Varieties/Lines for Coastal Salt Regions of Bangladesh

Similar to heat stress and drought, salinity is one of the major limitations to wheat production worldwide including the southern part of Bangladesh (Parida and Das 2005; Fahad et al. 2015). Most of the coastal areas are located in the southern part of Bangladesh under the medium high land category (Rahman and Ahsan 2001). Out of 2.85 million hectares of coastal areas of Bangladesh, nearly 0.84 million hectares are affected by varying intensities of salinity (Karim et al. 1990).

Introduction of salinity-tolerant crop varieties for overcoming the salinity problem has been considered the most feasible and economic, and it has recently received much attention (Ashraf and Wu 1994). So far only one saline-tolerant variety “BARI Gom 25” has been developed by WRC. Screening is the most important procedures to find out the salt-tolerant genotypes of crops from available germplasm. Characters such as germination, survival, and seedling growth or biomass accumulation have been the most commonly used criteria for identifying salinity tolerance in plants (Khan et al. 2007; Akram et al. 2010). Salt tolerance, however, is usually assayed in terms of absolute or relative growth or yield (accumulation of biomass or grain yield) (Khan et al. 2007). Because biomass production under saline conditions is one of the important traits for high yield. Therefore, screening a large number of genotypes for seedling growth under high salinity has been initiated saline-tolerant cultivar or introducing the screened material for cultivation on salt-affected soils. Moreover, a collaborative research program in collaboration with CSIRO, Australia, with ACIAR support has been undertaken to incorporate saline tolerance in adapted genotypes.

Nowadays, the scope of expanding wheat in the traditional area is very limited due to completion with other crops in *rabi* season (Rawson et al. 2007; Rawson 2011). So, wheat may be expanded to the southern coastal region of Bangladesh where such huge area remains fallow in *rabi* dry season with varying levels of salinity (Karim et al. 1990). The research program is underway to develop wheat varieties which are suitable to cultivate in coastal saline regions of Bangladesh (Khan et al. 2018; Table 7). During 2017–2018, a total of 24 wheat genotypes were tested in four saline-tolerant locations to select the saline-tolerant wheat genotypes under ACIAR that supported the project. On the basis of field performance and yield data, genotypes “BARI Gom 25,” “BARI Gom 29,” “BARI Gom 30,” “BARI Gom 33,” “BAW 1147,” “BAW 1208,” “BAW 1272,” “BAW 1290,” “BAW 1293,” and “KRL-210” were found salt tolerant in coastal four selected districts of Bangladesh (Table 7).

7.1.4 Accelerating Variety Release Through Doubled Haploid Breeding

The conventional breeding method requires several generations for getting homozygous lines to develop wheat varieties which is a time-consuming process. The

Table 7 Yield performance of 24 wheat genotypes under varying levels of salinity (2.56–4.29 dS m^{-1}) in four coastal districts of southern Bangladesh

	Yield (kg ha^{-1})							
Genotype	Barishal 1	Barishal 2	Patuakhali 1	Patuakhali 2	Khulna 1	Khulna 2	Satkhira 1	Satkhira 2
BARI Gom 21	2650	3670	2040	2460	2940	3420	1520	1380
BARI Gom 23	2200	3270	2100	2780	2900	3060	2760	1590
BARI Gom 24	3070	3840	2090	2860	2910	3400	2300	1460
BARI Gom 25	2590	2780	2060	2640	3450	3790	2580	1530
BARI Gom 26	2690	3500	2030	2720	3480	3210	2320	1300
BARI Gom 27	2260	3540	2160	2830	3510	3530	2750	2050
BARI Gom 28	2920	4250	2050	2560	4180	3810	2400	1660
BARI Gom 29	3600	3310	1990	2590	3480	3840	2250	2120
BARI Gom 30	2310	3160	1960	2390	3910	3850	2380	1800
BARI Gom 31	3350	3670	2220	2830	3790	3770	2720	580
BARI Gom 32	2520	2930	2170	2560	3060	3300	2140	1670
BARI Gom 33	2980	3580	2020	2590	2880	3110	2080	1540
KRL 1–4	1910	2310	2100	2850	2960	3060	2300	750
KRL 19	2820	2720	2030	2720	3090	3180	3070	2140
KRL 210	2650	3570	1910	2220	3290	3450	2480	1370
BAW 1147	3060	3340	2510	2990	2890	3220	2780	1490
BAW 1194	2990	3810	1960	2080	3560	3790	2490	1550
BAW 1208	2720	3020	2280	2900	3360	3350	2570	2380
BAW 1272	2340	3100	2130	2790	3700	3840	2440	1270
BAW 1280	3330	3210	2110	2690	3170	3400	2460	1680
BAW 1286	2710	3620	1880	2490	2870	3100	2470	1180
BAW 1290	2860	4230	2020	2140	3360	3450	2750	1830
BAW 1293	3910	4250	2140	2930	2810	3300	2140	1440
BAW 1295	2420	2640	1810	2200	3140	3430	1010	670
Min.	1910	2310	1810	2080	2810	3060	1010	580
Max.	3910	4250	2510	2990	4180	3850	3070	2380
Mean	2780	3390	2070	2620	3280	3440	2380	1520

Adapted from Khan et al. (2018)

production of doubled haploid (DH) facilitated development of homozygous lines from a crop plant instantly. The selection efficiency depends on uniform homozygous line production which facilitates better discrimination among genotypes within only one generation in breeding nurseries, building it a valuable technique for both wheat breeding and genetic studies.

Within a relatively short time, anther culture is one of the most important plant breeding techniques to produce new homozygous genotypes (Flavell 1981). However, this technique may cause undesirable genetic alterations due to gametoclonal variation (Huang 1996; Raina 1997). The means and genetic variances can be affected by these factors in a breeding population, thus hampering selection of population (Ma et al. 1999). Furthermore, DHs of wheat can be made by interspecific crosses. In DH method, the selective elimination occurs during embryogenesis of alien chromosomes; as a result haploid embryo appears.

Firstly, barley (*Hordeum bulbosum*) was used as the pollen parent for DH (Barclay 1975). Though most of the wheat genotypes show disability of cross with *Hordeum bulbosum* due to the presence of dominant allele *Kr1* on chromosome 5B and/or allele *Kr2* on chromosome 5A (Snape et al. 1979), these two dominant alleles *Kr1* and *Kr2* are responsible for the limited crossability.

In contrast, haploid wheat plants produced through wheat x maize cross and recalcitrant genotypes have not been seen because the chromosomes of maize are eliminated at early embryonic stages (Laurie and Bennett 1988), and *Kr* genes cannot affect the efficiency of haploid production (Laurie and Bennett 1988). Several studies have been proven that different species such as sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) are also possible pollinators for wheat haploid production (Ahmad and Comeau 1990; Inagaki and Mujeeb-Kazi 1995). WRC already adopted the protocol of doubled haploid through wheat x maize cross-pollination. Two young scientists have been trained, and by this time good progress was made in producing doubled haploid plants of targeted crosses.

In addition to this, a project has been undertaken to develop speed breeding facilities to advance the generation quickly and to shorten the variety release time.

7.1.5 Genetic Gain of Wheat Varieties in Bangladesh

Wheat Research Center (Barma 2018) has so far developed 33 wheat varieties until 2017. The rapid adoption of new varieties and other improved production technologies causes a substantial yield increase in recent years and the ever highest national average yield of 3.13 t ha^{-1}. The recognition of increased yield will be realized by significant use of the genetic values of varieties, amended agronomy, irrigation, and proper fertilization. It is necessary to document the genetic gains in grain yield of recently released varieties under fungicide spray and unsprayed with irrigated timely sown (ITS) conditions to support in the future wheat breeding program.

The mean performance of all varieties over both sprayed and unsprayed condition is presented in Table 8. The mean effect for all traits was statistically significant. Among the varieties, “BARI Gom 32” was the earliest maturing and dwarf in stature,

Table 8 Interaction effect of variety and fungicide sprayed condition on grain spike^{-1}, TGW, spikelet spike^{-1}, and yield

	Grain spike^{-1}		TGW (gm)		Spikelet spike^{-1}		Yield (kg ha^{-1})		
Variety	Sprayed	Unsprayed	Sprayed	Unsprayed	Sprayed	Unsprayed	Sprayed	Unsprayed	% Of yield lose for unsprayed wheat
Sonalika	50	49	43.6	43.3	17	16	4923	4200	15
Kanchan	50	44	48.9	41.6	20	18	6160	5436	12
Shatabdi	53	51	47.3	47.7	17	17	6137	4611	25
Prodip	52	47	58.4	57.1	20	18	5733	5690	1
BARI Gom 26	54	54	49.8	49.3	17	17	6460	6308	2
BARI Gom 28	53	43	48.5	50.4	17	15	6314	5910	6
BARI Gom 30	43	44	53.6	48.4	14	15	6023	5619	7
BARI Gom 32	35	37	57.5	54.2	15	15	5450	5589	-3
F-test	ns		**		ns		ns		
LSD (0.05)	–		2.34		–		–		
CV (%)	10.8		2.8		8.9		4.5		

Adapted from Alam et al. (2018

** 5% level of significance; ns non significance) which can escape terminal heat stress and also lodging. "Kanchan" released in 1983 still produced the highest number of spikes m^{-2} (492) followed by "BARI Gom 28" and "Shatabdi." The highest grain spike^{-1} was found in Shatabdi followed by "BARI Gom 26" and Prodip. The highest TGW was recorded in "Prodip" (57.8 g) followed by "BARI Gom 32" (55.9 g) and "BARI Gom 30" (51 g). The highest number of spikelet spike^{-1} is also recorded in Prodip. Under the sprayed condition, "BARI Gom 26" produced the highest yield (6384 kg ha^{-1}) followed by "BARI Gom 28" (6112 kg ha^{-1}) and "BARI Gom 30" (6023 kg ha^{-1}) (Alam et al. 2018; Table 8).

The highest yield loss (25%) was recorded in Shatabdi released in 2000 in comparison to unsprayed condition (Fig. 6). The yield of "BARI Gom 32" was higher under an unsprayed condition which might be due to better resistance to foliar diseases. However, the wheat varieties of newly released ("Prodip," "BARI Gom 26," "BARI Gom 28," and "BARI Gom 30") showed very insignificant yield loss in comparison to unsprayed than previously released wheat varieties ("Sonalika," "Kanchan," "Shatabdi"). The average yield of sprayed wheat is slightly higher ($y = 0.1838x - 315.16$) than unsprayed wheat ($y = 0.3123x - 576.75$). In this year, the temperature was favorable during the wheat-growing period. Therefore, the BpLB and leaf rust were lower compared with other years. So, the yield loss for unsprayed was low in Dinajpur.

7.2 Development of Biotic Stress-Tolerant Variety/Genotype Under Changing the Climate

7.2.1 Development of Wheat Variety/Genotype Tolerant to *Bipolaris* Leaf Blight

Considering the nature of the damage and wide occurrence throughout the country, *Bipolaris* leaf blight (BpLB) caused by *Bipolaris sorokiniana* (teleomorph, *Cochliobolus sativus*) is the most important disease of wheat in Bangladesh. Not only leaf blight but the pathogen also causes seedling blight, head blight, and black point disease of wheat (Goswami et al. 2004). High degree of resistance to BpLB almost lacks in the cultivated varieties. Seed-borne nature, wide genetic and environmental variability, and wide host range (Duveiller and Gilchrist 1994) of the pathogen are the main problems toward developing resistant varieties. The severity of the disease increases with plant age, and disease development becomes faster during grain filling period when high temperature accompanied by high relative humidity prevails (Alam et al. 1994). Evaluation of varieties or lines against different diseases under the inoculated condition is an essential prerequisite toward the development of resistant varieties. In the context, researchers of WRC are working hard to develop varieties that are resistant against BpLB.

An effort was made by researchers of Reza et al. (2018) to evaluate the reactions of 56 wheat genotypes consisting of advanced lines and check varieties against

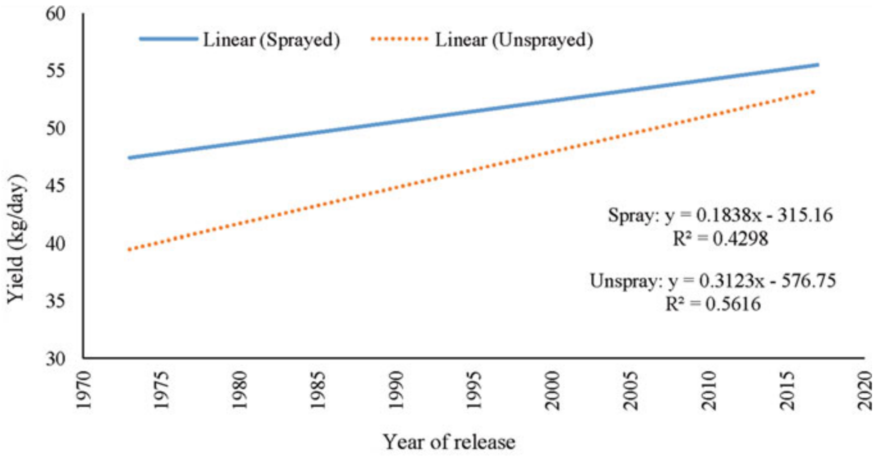

Fig. 6 Comparison of genetic gain in grain yield (kg day^{-1}) of spray and un-spray of eight popular wheat varieties in Bangladesh. (Adapted from Alam et al. 2018)

Bipolaris leaf blight under inoculated condition. The tested varieties and lines showed different levels of resistance and susceptibility against the disease. Among the tested 56 genotypes, 2 were found as resistant, 8 were moderately resistant, 19 were each moderately susceptible, 19 were susceptible, and the rest 8 were as highly susceptible (Table 9).

7.2.2 Development of Wheat Genotypes Tolerant to Leaf and Stem Rust

Among the three wheat rust diseases in Bangladesh, leaf or brown rust caused by *Puccinia triticina* Eriks. is the second most important disease after *BpLB*. Depending on genotypes, sowing times, and locations, the disease occurs all over the country with varying levels of severity. Yield losses due to leaf rust are usually less than 10% but can be increased 30% or more depending on the level of susceptibility, environmental conditions, and the stage of the crop (Singh et al. 2002). In Bangladesh, the disease generally appears in mid-February, and severity is increasing between mid and late March. However, severity is high in late-planted wheat than those planted in optimum times. But losses would be significantly higher if a susceptible variety is grown under late-sown condition.

Use of resistant variety is the most dependable and economic approach for the control of the rust diseases. Therefore, major emphasis has been given to screen breeding lines against leaf rust under field and inoculated condition toward the development of resistant varieties. A group of leaf rust-resistant varieties/lines with the existence of different *Lr* genes is being maintained in a crossing block. Hybridization program has been going on to incorporate different *Lr* genes to the adapted genotypes for developing varieties with durable resistance. Based on

Table 9 Grading of wheat genotypes against BpLB under inoculated condition

Variety/line	% DLA on F leaf	Reaction
Chirya 7 and Milan/Sha 7 = 2	≤ 10	Resistant
BAW1254, BAW1295, BAW1316, BAW1317, Shatabdi, BARI Gom 29, BARI Gom 30, and BAW1300 = 8	11–30	Moderately Resistant
BAW1203, BAW1208, BAW1243, BAW1272, BAW1280, BAW1303, BAW1318, BAW1322, BAW1325, BAW1326, BAW1328, BAW1331, BAW1334, BAW1337, WBSN75, WBSN92, BARI Gom 31, BARI Gom 32, BARI Gom 33 = 19	31–50	Moderately Susceptible
BAW1194, BAW1286, BAW1293, BAW1296, BAW1297, BAW1299, BAW1304, BAW1324, BAW1327, BAW1329, BAW1332, BAW1333, BAW1335, BAW1338, WBSN81, Prodip, BARI Gom 25, BARI Gom 26, and BARI Gom 28 = 19	51–70	Susceptible
BAW1290, BAW1321, BAW1323, BAW1330, BAW1336, Sonalika, Kanchan, and CIANO 79 = 8	>70	Highly Susceptible

Adapted from Reza et al. (2018)

Scale used for grading lines into resistance category: % disease severity, resistant (0–10), moderately resistant (20–30), moderately susceptible (40–50), susceptible (60–10)

Table 10 Grading wheat genotypes into resistance category

Variety/line	Leaf rust score	Resistance category
BAW1203, BAW1286, BAW1338, BARI Gom 27, BARI Gom 28, BARI Gom 29, BARI Gom 30, BARI Gom 31, BARI Gom 32, BARI Gom 33, Shatabdi, Sourav, Bijoy, CIANO 79, BAW1194, BAW1208, BAW1243, BAW1254, BAW1272, BAW1280, BAW1290, BAW1293, BAW1295, BAW1296, BAW1297, BAW1299, BAW1304, BAW1316, BAW1317, BAW1321, BAW1322, BAW1323, BAW1324, BAW1325, BAW1326, BAW1327, BAW1329, BAW1330, BAW1331, BAW1334, BAW1335, BAW1336, BAW1337, BAW1300 = 44	0-10MSS	Resistant
Sonora 64, Kalyansona, Sonalika, Prodip, BARI Gom 25, BARI Gom 26, BAW1303, BAW1318, BAW1328, BAW1332, and BAW 1333 = 11	20–30S	Moderately resistant
Dirk	40–50S	Moderately susceptible
Morocco	60–100S	Susceptible

Adapted from Alam et al. (2018)

Resistance category: resistant (R) = 0–10%, moderately resistant (MR) = 20–30%, moderately susceptible (MS) = 40–50%, susceptible (S) = 60–100% severity

disease severity, most of the newly released varieties are resistant/moderately resistant to leaf rust, and among those "BARI Gom 27" and "BARI Gom 30" were found completely free from leaf rust. Based on disease severity, most numbers of advanced lines have been identified as resistant to leaf rust (Alam et al. 2018; Table 10).

7.2.3 Development of Wheat Genotypes Resistant to Stem Rust

Stem rust caused by *Puccinia graminis* f. sp. *tritici* is an important disease of wheat, particularly in Africa. In Bangladesh, the disease was not observed in the last three decades, but recently in 2014, it was detected in some entries of the rust trap nurseries. So, this is not unlikely that the disease will appear on a large scale in the future and cause damage to wheat. A virulent race of stem rust called *Ug99* was identified in Uganda in 1999 (Pretorius et al. 2000) and subsequently found in epidemic proportions in Kenya and Ethiopia. Sudan, Yemen, Iran, and Tanzania are also affected, and some variants of the race have been confirmed in those countries including South Africa, Mozambique, and Zimbabwe (Singh et al. 2011). The experts of Borlaug Global Rust Initiative (BGRI) have predicted the further movement of *Ug99* and other virulent strains to the important wheat production areas of the Indian subcontinent and beyond (Singh et al. 2008). CIMMYT has developed some wheat germplasms with a good level of stem rust resistance and high-yield potential. The materials were distributed worldwide through Stem Rust Resistance Screening Nursery (SRRSN) for direct release or use in breeding programmers to mitigate the threat of stem rust. Scientists in WRC of BARI are trying to develop wheat genotypes which are resistant against stem rust of wheat. Every year advances lines, and selected segregating generations are sent to KALRO, Kenya, to screen the germplasm against *Ug99* in collaboration with CIMMYT. Among the recent commercial varieties, “BARI Gom 26,” “BARI Gom 27,” and “BARI Gom 29” were found resistant to stem rust (*Ug99* race) (Table 4).

7.2.4 Development of Wheat Genotypes Resistant to Wheat Blast

Wheat blast is a devastating disease and appeared as a new threat to wheat production in Bangladesh and South Asia. As a short-term solution, appropriate fungicides at an affordable price have been suggested to the farmers to control the disease, especially in the blast-conducive environments. However, a long-term and sustainable solution development of blast-resistant wheat varieties is the most important. Therefore, there is a critical need for identification of new sources of resistance to WB and development of blast-resistant wheat variety. A comprehensive breeding program has been undertaken to identify sources of resistance to WB, and their deployment adapted wheat genotypes in collaboration with CIMMYT/ACIAR. A precision phenotyping platform (PPP) has been established at Jessore for large-scale screening against WB with the support from CIMMYT and ACIAR (Fig. 7). During the 2017–2018 wheat season, about 5000 germplasms were received from CIMMYT and have been screened against WB, and some resistant genotypes have been identified.

In the meantime one blast-resistant variety “BARI Gom 33” has been released in the year 2017, which possesses 2NS translocation and is enriched with zinc (50–55 ppm). Three other varieties such as “BARI Gom 21” (Shatabdi), “BARI Gom 30,” and

Fig. 7 Precision phenotyping platform (PPP) at RARS, Jessore for wheat blast (WB). In 2017–2018 about 5000 germplasm including elite and advance lines have been screened against WB through the help of CIMMYT-ACIAR. (Adapted from Reza et al. 2018)

"BARI Gom 32" showed a moderate level of tolerance to WB, where most popular variety "BARI Gom 26" was found the most susceptible to WB (Table 4).

7.2.4.1 Genomic DNA Extraction

For each wheat genotype, to amplify 2NS translocation, genomic DNA was extracted from wheat seedlings of 10-day-old using CTAB (cetyl trimethylammonium bromide) method discovered by Stein et al. (2001).

It is well known that 2NS translocation-based blast resistance is working well in many backgrounds and is being utilized for developing blast-resistant varieties. This translocation occurred from *Aegilops ventricosa* of 2NS chromosome arm, a segment of 25–38 cM to the 2AS distal region in the wheat chromosome. Kohli et al. (2011) reported that wheat genotype Milan derived from the CIMMYT line showed high levels of resistance against wheat blast under field conditions, though the genetic basis of resistance has not yet been discovered in Milan (Kohli et al. 2011). Now, the blast resistance source of other genotypes is widely deployed, but it should be effective for long duration (Kohli et al. 2011). Scientists of the Bangladesh Wheat and Maize Research Institute have initiated screening of blast-resistant wheat genotypes using 2NS markers. Moreover, a number of crosses have been made between genotypes having 2NS translocation and non-2NS translocation to develop 2NS-based blast-resistant varieties.

In the year 2017–2018, 80 wheat genotypes (58 advance lines from different nurseries/trials and 22 wheat varieties) were evaluated for blast resistance using a 2NS marker (adapted from Alam et al. 2018; Table 11). The genomic DNA extraction and PCR amplification and gel electrophoresis methods were followed to run the marker. Details describing these screening methods are as follows:

7.2.4.2 PCR Amplification and Gel Electrophoresis

The specific primer of 2NS VENTRIUP (5′-AGG GGC TAC TGA CCA AGG CT-3′), LN2 (5′-TGC AGC TAC AGC AGT ATG TAC ACA AAA-3′) (Cruz et al. 2016) was used for screening wheat blast-resistant genes in a 2NS segment of wheat germplasms. The reaction volume of PCR was 10 μL and performed using a Veriti Thermal Cycler (Applied Biosystems, USA). The reaction product contained 40–100 ng of genomic DNA, 2× PCR master mix, and 10 μM each primer and ddH$_2$O. The amplification program of VENTRUIP-F/LN2-R was as follows: 94 °C for 3 min (enzyme activation); 30 cycles of 94 °C for 45 s (melting), 65 °C for 30 s (annealing), and 72 °C for 60 s (extension); and 7 min for final extension at 72 °C. After PCR, the products (10 μl each) were stained with ethidium bromide (EtBr) and run on 1.5% agarose gel.

After observation primer (VENTRUIP-F/LN2-R) was confirmed that one commercial variety (“BARI Gom 33”), two advanced lines (“BAW 1300” and “BAW

Table 11 Pedigree of wheat genotypes having 2NS translocation

SL. no.	Nursery	Variety/ BAW	Pedigree/selection history
1	Variety	BARI Gom 33	KACHU/SOLALA CMSS09Y00580S-099Y-38 M-0WGY-4B-0Y
2	CVD	BAW 1280	BAJ #1*2/TECUE #1 CMSS07Y01100T-099TOPM-099Y-099 M-099Y-1 M-0WGY
3	CVD	BAW 1300	ROELFS-F-007/4/BOBWHITE/NEELKANT//CATBIRD/3/ CATBIRD/5/FRET-2/TUKURU//FRET-2 CMSS-06-Y00605T-099TOPM-099Y-099ZTM-099Y-099 M-11WGY-0B
4	BWSN-2	E-21	PRODIP/BAW 1075 BD11JA1823S-099JA-50JA-50JA-30JA-5JA
5	BWSN-2	E-46	T.DICOCCONCI9309/AE.SQUARROSA(409)//MUTUS/3/ 2*MUTUS CMSS12B01381T-099TOPY-099 M-099Y-39 M-0WGY
6	BWSN-2	E-73	KVZ/PPR47.89C//FRANCOLIN#1/3/2*PAURAQ/4/UP2338*2/ KKTS*2//YANACMSS11Y00500S-099Y-099 M-3WGY-0B
7	BWSN-2	E-74	MELON//FILIN/MILAN/3/FILIN/5/CROC_1/AE. SQUARROSA 4)/3/T.DICOCCONPI94625/AE.SQUARROSA (CMSS10B00690T-099TOPY-099 M-099Y-20 M-0WGY

Adapted from Alam et al. (2018)

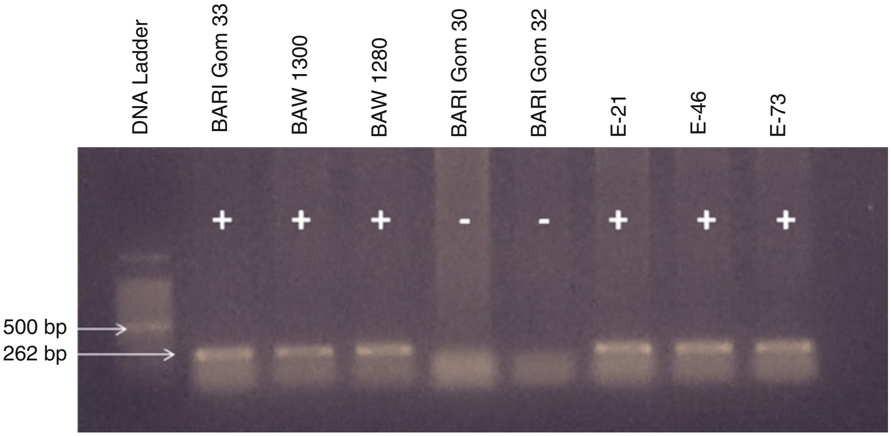

Fig. 8 PCR amplification with 2NS specific primers VENTRUIP-F/LN2-R. (Adapted from Alam et al. 2018)

1280”), and four genotypes from BWSN-II (Bangladesh Wheat Screening Nursery-II) (“E-21,” “E-46,” “E-73,” and “E-74”) contain blast resistance genes in 2NS segment (Alam et al. 2018; Fig. 8). The pedigree and blast reaction under field condition in irrigated late sown (ILS) at Jessore location of 2NS translocated genotypes are presented in Table 11. All of 2NS translocated wheat genotypes showed “0” reaction where susceptible check showed 75% wheat blast severity. Research findings of this experiment will be helpful for detecting 2NS translocated wheat genotypes for developing high-yielding blast-resistant wheat varieties through marker-assisted selection.

Therefore it is concluded that this used primer was found to be very useful. For detecting blast-resistant genes in 2NS translocation in wheat and can be used for screening blast-resistant wheat genotypes. This diagnostic marker can also be used in a different filial generation (F_1 to F_6) through MAS method in the national wheat breeding program.

Screening by applying high disease pressure would be helpful in selecting the best varieties among a lot which have the potential to be served as genetic stock for the subsequent use of breeders. In the context, a total of 25 elite wheat genotypes were evaluated against wheat blast and collected from different sources including check varieties under an artificially inoculated condition at RARS Jessore during 2017–2018 (Reza et al. 2018).

As the location was found favorable for wheat blast according to previous 2-year disease data, the tested varieties/lines showed varying levels of resistance and susceptible reaction against the disease. Seven genotypes were scored as resistant, six moderately resistant, seven moderately susceptible, and the rest five as highly susceptible. Disease scoring was done based on the standard scale of 0–100. Among the genotypes, seven genotypes were found resistant based on % disease severity (blast). Percentage of disease severity of those resistant lines ranged from 0% to 10%. The

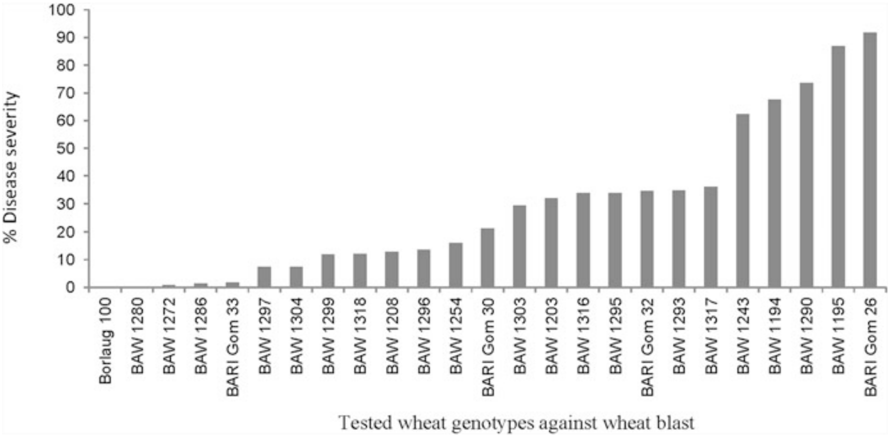

Fig. 9 Elite germplasm screening against WB under artificially inoculated condition. (Adapted from Reza et al. 2018)

resistant variety “BARI Gom 33” was found with 1.8% disease severity, while the most susceptible variety “BARI Gom 26” observed about 91.7%. Genotypes “BAW 1300,” “BAW 1272,” “BAW 1280,” and “BAW 1286” were found as most promising for further evaluation in the next season to release as varieties (Fig. 9).

7.2.5 Technologies for Enhancing Wheat Blast Management

7.2.5.1 Integrated Approaches to Mitigate the Threat of Wheat Blast at a Glance

WB is a devastating disease and established in the southwestern region of Bangladesh, and complete eradication is not possible. Moreover, any single approach will not be worthwhile to control the disease. Therefore, the adoption of integrated approaches is very important to manage the disease at a lower level. Few of the integrated approaches adopted in Bangladesh are shown below:

- Awareness creation among wheat growers and all stakeholders is highly important in the short term.
- Collection of seed from the disease-free area.
- Seed treatment with proper fungicide to reduce the initial load of inoculum.
- Optimum sowing of the crop to avoid disease infection.
- Use of resistant (“BARI Gom 33”) and tolerant varieties (“BARI Gom 30,” “BARI Gom 32”).
- Development and deployment of appropriate fungicides as a preventive spray.
- Collaborative breeding approach to developing blast-resistant variety through national and international support.

- Disease surveillance and monitoring.
- Disease forecasting.
- Quick dissemination of the seed of resistant varieties.
- Human resource and capacity development for wheat blast management.

7.2.5.2 Efficacy of Seed Treating Fungicides in Reducing the Prevalence of Seed-Borne *P. oryzae* and Their Subsequent Effect on Wheat

The WB disease usually occurs on all aerial plant parts, but the most conspicuous symptom is observed on a spike. Severe WB epidemics have coincided with the wet season, warm temperatures, and high humidity. Breakdown of resistance due to the evolution of new pathotype/race may develop epidemic of WB under favorable environmental conditions. In the absence of resistance, seed treatment with fungicides has been considered as an alternative option to reduce the inoculum density at a minimum level (Reis 1991). The use of healthy seeds provides a means of reducing primary inoculum and, in turn, reduces foliage infection and seedling blight. Seed-borne infection can be reduced by treating seeds with different chemicals/fungicides. Management of seed-borne diseases through seed treatment is most economical, durable, and an effective control measure. Nghiep and Gaur (2005) reported that results of vitavax, thiram, and mancozeb were the best to reduce the seed-borne infection as compared to the other chemicals. Several fungicides have been employed in the control of fungal diseases of rice. Among them, carboxin, thiram, mancozeb, and iprodione were reported to be very effective against the disease.

Scientists in WRC of BARI are trying to find out fungicides which are suitable for sustainable wheat production in Bangladesh. In the context, an experiment was conducted in two environmental conditions of Bangladesh: at WRC, Dinajpur (Lab.), and RARS, Jessore (Field), during 2017–2018 crop growing season. Four fungicides of different groups were tested for their efficacy against WB disease and its causal organism. The fungicides, namely, Provax-200 WP (carboxin 37.5% + thiram 37.5%), Vita Flo 200 FF (carboxin 17.5% + thiram 17.5%), Rovral 50 WP (iprodione 50%), and Goldman 80 WP (mancozeb 80%) were tested. An untreated control was also maintained for comparison. The seeds of susceptible variety “BARI Gom 26” were examined with an initial 72% inoculum prevalence on seeds. In the blotter method, 400 seeds were treated separately for each fungicide. All the fungicides were found very effective against *P. oryzae* control (100% control) in laboratory condition in blotter method. Seed treatment with these fungicides also significantly increased plant population over control treatment in field condition, but none of them was found effective in reducing disease incidence. Seeds treated with fungicides not only reduce/control initial inoculums of *P. oryzae* but also control other seed-borne fungi (*B. sorokiniana*, *Alternaria*, *Curvularia*, *Fusarium* sp. etc.) (Reza et al. 2018; Table 12). Seeds treated with these fungicides were found very effective in reducing *P. oryzae* incidence from seeds. Although there was no significant effect on disease control, it keeps initial inoculums to a minimal level.

Table 12 Efficacy of seed treating fungicides in controlling wheat blast/*P. oryzae* at RARS, Jessore 2017–2018

Fungicide	Dose	% disease severity	TGW (g)	Yieldplot^{-1} (g)	Yield increased (%)	Disease/*P. oryzae* controlled (%)	
						Field	Laboratory
Provax 200 WP	3 g kg-^{1} seed	12.3	29.50	548	15	15	100
Vita Flo 200 FF	3 ml kg^{-1} seed	12.6	29.75	533	12	13	100
Rovral 50 WP	3 ml kg^{-1} seed	13.1	32.75	589	24	10	100
Goldman 80 WP	3 ml kg^{-1} seed	11.9	30.50	540	14	18	100
Control (unsprayed)		14.5	29.75	476	0	–	–
LSD $_{(0.05)}$		8.69	3.80	54.57	–	–	–
Level of significance		NS	NS	*	–	–	–

Source: Reza et al. (2018)
* 1% level of significance

Seed treated with fungicides not only reduce/control P. oryzae but also controls other seedborne fungi (*B. sorokinia, Alternaria, Curvularia, Fusarium* sp. etc).

7.2.5.3 Efficacy of Foliar Fungicides in Controlling Wheat Blast

In the absence of resistance, foliar sprays with fungicides have been considered as an interim measure to reduce the disease to a certain level. Among many fungicides, tebuconazole, trifloxystrobin, and tricyclazole were reported to be very effective against the disease.

A study was undertaken to evaluate the efficacy of foliar fungicides in controlling WB under field condition. Six fungicides of different groups were tested for their efficacy against WB. The fungicides, namely, Nativo 75 WG (tebunaconazole 50% + trifloxystrobin 25%), Amistar Top 325 SC (azoxystrobin 20% + difenoconazole 12.5%), Folicur 250 EW (tebuconazole 25%), Opponent 75 WG (tebuconazole 50% + trifloxystrobin 25%), Filia 525 SE (propiconazole 12.5% + tricyclazole 40%), and Trooper 75 WP (tricyclazole 75%) were tested. The fungicides were sprayed twice, once at the heading stage and another at 12–15 days after the first spray. An unsprayed control was maintained for comparison. The susceptible variety "BARI Gom 26" was tested for this study. All of these fungicides were found effective in controlling the disease as compared to control plots. Among them, Opponent 75 WG was found very effective in controlling wheat blast with least disease severity (2%) followed by Filia 525 SE and Trooper 75 WP. The highest yield increase of 38% was obtained from spraying with Nativo 75 WG, which was followed by Amistar Top 325 SC and Folicur 250 EW. The highest net profit was also obtained from spraying with Nativo 75 WG, while the lowest with treatment Folicur 250 EW (Reza et al. 2018; Table 13). The unsprayed plots showed

Table 13 Efficacy of foliar fungicides in controlling wheat blast

Fungicides	Dose	% disease controlled	Yield (kg ha^{-1})	% yield increased	Yield increased (kg ha^{-1})	Fungicide + spraying cost (Tk ha^{-1})	Profit (Tk ha^{-1})
Nativo 75 WG	0.6 g L^{-1}	94	3230	38	897	6575	18,532
Folicur 250 EW	1 ml L^{-1}	93	3063	31	730	4250	12,440
Amistar Top 325 SC	1 ml L^{-1}	94	3060	31	727	5400	14,539
Trooper 75 WP	0.8 g L^{-1}	97	3000	29	667	5808	14,417
Opponent 75 WG	0.6 g L^{-1}	98	3039	30	706	8000	12,956
Filia 525 SE	2 ml L^{-1}	97	2973	27	640	6800	12,520
Unsprayed		–	2333	0	0	–	–
LSD (0.05)		–	95.80	–	–	–	–
Level of significance		–	***	–	–	–	–

Reza et al. (2018)
***means 1% level of significance

with the least disease control. The highest grain yield and net profit were found higher with fungicide Nativo 75 WG sprayed plot, followed by Amistar Top 325 SC and Folicur 250 EW, and the lowest profit and yield were recorded with fungicide Filia 525 SE applied plot (Reza et al. 2018; Table 13).

7.2.5.4 Efficacy of Fungicides in Controlling *Bipolaris* Leaf Blight and Leaf Rust of Wheat

Expression of resistance to *Bipolaris* leaf blight is less sustained under favorable conditions of disease development in the rice-wheat cropping systems of South Asia. In the absence of the good level of resistance, foliar sprays with fungicides have been considered as an alternative option to reduce the disease under field condition (Duveiller et al. 2005). Leaf rust of wheat caused by *Puccinia triticina* Eriks. can also be controlled with the foliar application of fungicides. Among many fungicides, propiconazole and tebuconazole were reported to be effective against both the diseases.

Scientists of WRC are trying to find out suitable fungicides as an alternative of resistant wheat for controlling BpLB and leaf rust under field condition. Seven fungicides were evaluated under field condition for controlling BpLB and leaf rust of wheat. Among the fungicides, four fungicides such as Tilt 250 EC (propiconazole), Folicur 250 EC (tebuconazole), Awal 72 WP (zineb + hexaconazole), and Master Zeb 80 WP (mancozeb) were used as standard check, while the other three, i.e., Amistar Top 325 SC (azoxystrobin 20% + difenoconazole 12.5%), Score 250 EC (difenoconazole 25%), and Nativo 75 WG (tebuconazole 50% + trifloxystrobin 25%), were tested as new fungicides. The fungicides were sprayed twice, once at heading stage and another at 15 days after first spraying. An unsprayed control was maintained for comparison. The susceptible variety Kanchan was used for BpLB and Morocco for leaf rust. All the seven selected fungicides, viz., Nativo 75 WG, Tilt 250 EC, Folicur 250 EC, Master Zeb 80 WP, Awal 72 WP, Amistar Top 325 SC, and Score 250 EC, were found very effective in controlling *Bipolaris* leaf blight and also leaf rust of wheat. These fungicides reduced *Bipolaris* leaf blight by 93–97% with 20–31% increase in grain yield and leaf rust by 98–100% with 151–179% yield increase (Reza et al. 2018; Tables 14 and 15).

8 Improved Agronomic Practices for Enhancing Sustainable Wheat Production Under Changing Climate

8.1 Adjustment of Seeding Time

The optimum time for sowing of wheat is measured to be an important management strategy, because it is under the control of farmers (Laghari et al. 2010).

Table 14 Effect of fungicides on *Bipolaris* leaf blight and yield of wheat cv. Kanchan

Fungicides	Dose	% DLA	TGW	Yield	Yield increase	Disease control
		(F leaf)	(g)	Plot^{-1} (g)	(%)	(%)
Tilt 250 EC	0.5 ml L^{-1}	5.9	41.22	1075	23	94
Folicur 250 EW	0.5 ml L^{-1}	2.6	41.25	1093	25	97
Score 325 EC	0.5 ml L^{-1}	3.4	41.22	1073	22	96
Amistar Top 325 SC	1 ml L^{-1}	5.8	42.03	1102	26	94
Master Zeb 80 WP	2 g L^{-1}	6.9	40.48	1053	20	93
Awal 72 WP	2 g L^{-1}	3.5	41.10	1131	29	96
Nativo 75 WG	0.6 g L^{-1}	2.5	42.65	1151	31	97
Control (unsprayed)		96.0	37.30	876	0	0
LSD (0.05)		4.35	1.52	102.66	–	–
Level of significance		***	***	**	–	–

Data source: Reza et al. (2018)
DLA diseased leaf area, *** = significant at 0.1%
** 5% level of significance

Table 15 Effect of fungicides on leaf rust and grain yield of wheat cv. Morocco

Fungicides	Dose	% DLA	TGW	Yield	Yield increase	Disease control
		(F leaf)	(g)	Plot^{-1} (g)	(%)	(%)
Tilt 250 EC	0.5 ml L^{-1}	0.0	31.27	784	170	100
Folicur 250 EC	0.5 ml L^{-1}	0.0	30.12	783	170	100
Score 325 EC	0.5 ml L^{-1}	0.0	31.77	760	162	100
Amistar Top 325 SC	1 ml L^{-1}	0.0	31.87	773	166	100
Master Zeb 80 WP	2 g L^{-1}	1.5	25.37	730	151	98
Awal 72 WP	2 g L^{-1}	1.3	29.30	752	159	98
Nativo 75 WG	0.6 g L^{-1}	0.0	31.67	809	179	100
Control (unsprayed)		87.0	22.87	290	0	0
LSD (0.05)		2.42	2.88	125.67	–	–
Level of significance		***	***	***	–	–

Data source: Reza et al. (2018)
DLA diseased leaf area, *** 1% level of significance

Mid-November to first week of December is considered as an optimum sowing time of wheat in Bangladesh (Hossain and Teixeira da Silva 2012; Hossain et al. 2013). Temperature above or below optimum limits the growth and development of plant through altering the physiological process of plant (Hakim et al. 2012; Hossain et al. 2012; Hossain et al. 2013). A delay in sowing suppressed yield, caused by a reduction in the yield contributing characters such as tillers, grains spike^{-1}, and grain yield (Ahmed 1986; Tahir et al. 2009; Jahan et al. 2018a, b).

To find out optimum sowing time for specific varieties/genotypes and to identify the heat-tolerant wheat lines for future breeding program to develop heat-tolerant wheat varieties, 50 wheat genotypes were evaluated in the year 2016–2017 under irrigated timely sown (ITS) and irrigated late-sown heat stress conditions of Dinajpur, Joydebpur, and Jessore locations through semiarid wheat yield trial nursery. Among the genotypes, 16 genotypes (i.e., "Gen.-7," "Gen.-9," "Gen.-11," "Gen.-13," "Gen.-14," "Gen.-16," "Gen.-19," "Gen.-22," "Gen.-30," "Gen.-31," "Gen.-33," "Gen.-36," "Gen.-38," "Gen.-40," "Gen.-42," and "Gen.-48") performed better under ILS condition and selected for future breeding program to develop heat-tolerant varieties (Hossain et al. 2018a; Table 16).

Similarly, Jahan et al. (2018a; Fig. 10) conducted a field experiment in 2 consecutive years with three existing wheat varieties ("BARI Gom 26," "BARI Gom 27," "BARI Gom 28") and three advance lines ("BAW 1130," "BAW 1138," "BAW 1140"). These genotypes were evaluated under six sowing conditions of four agroecological zones (AEZs) of Bangladesh to identify wheat genotypes suitable for a heat stress environment by using stress susceptibility index (SSI). Among the genotypes, two existing varieties (i.e., "BARI Gom 28" and "BARI Gom 26") were recorded tolerant against early sowing heat stress, late sowing heat stress, slightly late sowing heat stress, very late sowing heat stress, and extremely late heat stress conditions in four AEZs of Bangladesh, whereas variety "BARI Gom 27" was susceptible to all levels of heat stress conditions. Correlation analysis between GY and SSI also confirmed that two exiting varieties "BARI Gom 28" and "BARI Gom 26" and advance line "BAW 1140" were tolerant against all levels of heat stress conditions; variety "BARI Gom 27" and advance line "BAW 1130" were susceptible against all levels of heat stress conditions.

To confirm the previous recommended sowing times, recently six elite wheat varieties were evaluated under different sowing conditions of Dinajpur, Rajshahi, and Jessore to assess the yield potentiality of recently developed elite wheat varieties in diverse sowing condition, to identify the best seeding condition for a variety, and to find out the heat-tolerant and heat-susceptible variety. After observation, it was noted that under the environmental condition of Dinajpur, it was observed that all of the wheat varieties sown at optimum sowing condition (25 Nov.) produced the maximum yield, while the yield of all varieties was decreased significantly ($P \leq 0.05$) when sown at late, while in the environmental condition of Rajshahi and Jessore, wheat sown on the first week of December (05 Dec.) to mid-December (15 Dec.) performed the best than sown on 25 Nov. Considering the varieties, "BARI Gom 30" (4091.80 kg ha^{-1}) performed the best in all sowing conditions as well as late-sown heat stress condition of Dinajpur, which was significantly alike to "BARI Gom 32" (4021.86) and "BARI Gom 33" (4060.53 kg ha^{-1}), whereas in the environmental condition of Rajshahi, the variety "BARI Gom 33" was recorded with the maximum grain yield (3538.00 kg ha^{-1}) under the sowing condition of Dec. 15 sowing, followed by "BARI Gom 31" (3354.67 kg ha^{-1}) and "BARI Gom 28" at same sowing condition. If we consider the yield performance of all varieties under all

Table 16 Interaction effect of genotype, location and seeding time on TGW, and yield (kg ha^{-1}) of selected wheat genotypes

	TGW (g)						Yield (kg ha^{-1})					
	Dinajpur (AEZ-1)		Joydebpur (AEZ-28)		Jessore (AEZ-11)		Dinajpur (AEZ-1)		Joydebpur (AEZ-28)		Jessore (AEZ-11)	
Genotypes	ITS	ILS	ITS	ILS	ITS	ILS	ITS	ILS	ITS	ILS	ITS	ILS
BARI Gom 21	47.3	36.8	51.0	37.4	46.5	34.5	5919	3218	3610	2442	5488	2223
BARI Gom 26	47.1	36.4	50.3	41.8	44.0	32.5	6336	3915	3179	2417	4508	2655
Gen.-7	52.1	39.8	57.9	43.0	52.5	33.0	5719	4610	3570	2020	4313	2403
Gen.-9	52.4	44.3	47.2	40.3	51.0	36.5	5525	5229	3367	2147	4965	3533
Gen.-11	52.8	44.4	46.0	45.0	50.0	35.5	5169	3624	2450	2588	4635	3403
Gen.-13	55.6	45.0	54.2	47.4	50.0	30.5	6280	5491	3640	2355	4555	2630
Gen.-14	52.1	47.4	54.9	47.7	49.5	34.5	5770	5018	3428	2097	4748	2563
Gen.-16	60.0	47.2	56.4	45.3	53.0	38.5	6408	4100	3220	1600	5235	2608
Gen.-19	47.4	39.9	40.9	43.4	45.5	33.0	4408	4398	2377	1789	4283	2845
Gen.-22	56.1	44.3	44.5	41.5	50.5	40.0	6011	5369	2795	2279	4998	2365
Gen.-30	48.6	38.4	46.7	42.0	48.5	31.5	6542	4790	4610	3043	4635	2998
Gen.-31	49.3	39.9	52.3	42.7	46.5	29.0	5240	4095	4610	2770	3940	2270
Gen.-33	56.6	47.3	56.0	48.3	56.5	37.5	4640	4507	3618	2192	4468	2715
Gen.-36	51.0	45.1	51.0	45.1	47.5	39.5	5085	4274	3575	1873	4738	3385
Gen.-38	55.9	47.2	53.4	45.3	51.0	36.5	5721	4447	3842	2340	5050	2510
Gen.-40	59.6	49.3	57.0	48.8	55.0	36.0	6061	4709	3279	2337	4905	3220
Gen.-42	56.4	45.2	54.9	43.9	50.0	32.5	5909	4232	3835	1995	5013	2490
Gen.-48	57.1	47.4	59.9	51.6	57.5	34.0	5100	4506	4432	1875	4150	2188
F-test	**						**					
LSD (0.05)	4.22						827.04					
CV (%)	4.8						11					

Adapted from Hossain et al. (2018a)
ITS irrigated time sowing, *ILS* irrigated late sowing
** 1% level of significance

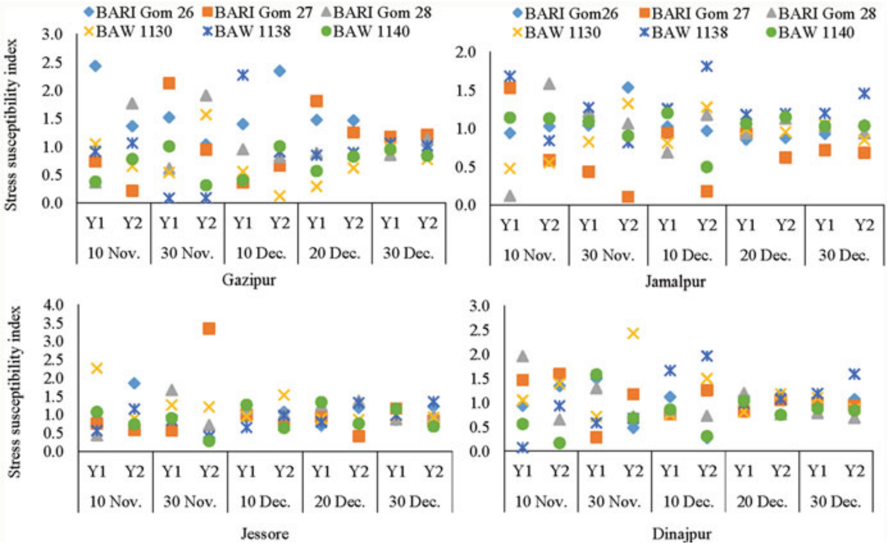

Fig. 10 Stress susceptibility index of six wheat genotypes, experienced as early and late heat stress, when grown under six sowing dates in 2012–2013 (Y1) and 2013–2014 (Y2) in four locations of Bangladesh. (Adapted from Jahan et al. 2018a)

sowing conditions of Jessore, “BARI Gom 32” and “BARI Gom 30” produced the statistically similar and the maximum grain yield in all sowing conditions, followed by “BARI Gom 31.” While in Dec. 05, “BARI Gom 32” also produced the maximum yield, this variety also produced the second highest and third highest yield under the sowing condition of Dec. 15 and Dec. 25 in the environmental condition of Jessore. After observation, it was also noticed that location-specific environmental/sowing condition is very important to explore the potentiality of a specific variety (Hossain et al. 2018b; Fig. 11).

8.2 *Optimizing Seeding Rate*

The optimal seeding rate is measured as the best management approach for enhancing the grain yield (GY) of wheat (Sarker et al. 2007; Sarker et al. 2009; Laghari et al. 2010). This is particularly important because it is controlled by farmers (Laghari et al. 2010). However, seeds are a costly input for farmers (Sarker et al. 2009; Farooq et al. 2016). Optimum plant density, which can be achieved by maintaining optimum seeding rate, may vary greatly with the area, climatic conditions, soils, sowing time, variety, and management (Li et al. 2016). Iqbal et al. (2010) and Chauhdary et al. (2016) noticed that if optimum seeding rate is exceeded, GY of wheat may be reduced by stunting the development of tillers and effective tillers; but this can be favored for genotypes which have less tillering habits (Chauhdary et al.

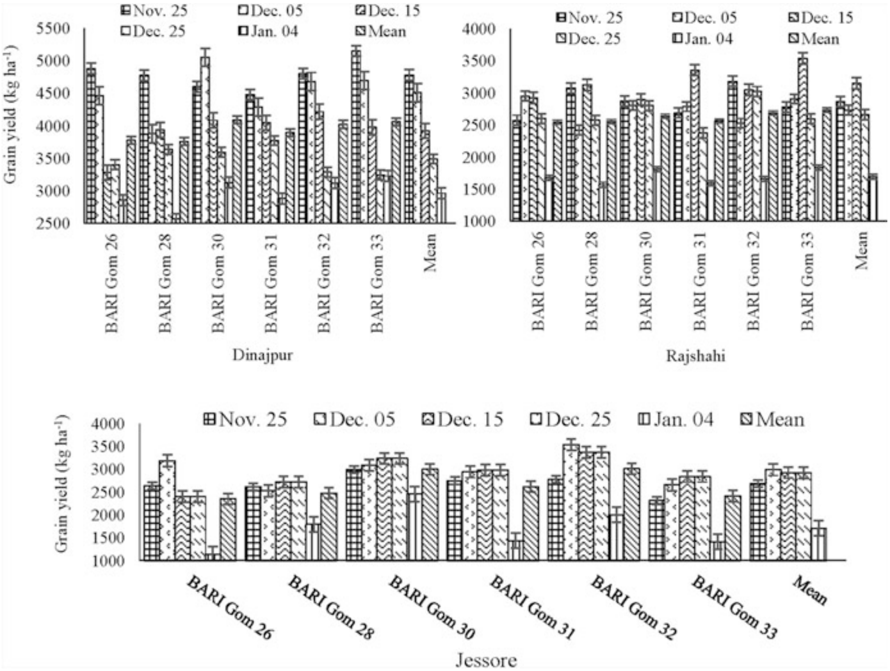

Fig. 11 Yield of wheat varieties is affected by sowing dates in Dinajpur, Rajshshi, and Jessore locations. Bars for yield of different wheat varieties are significantly different at $P \leq 0.05$ (LSD test). Mean ± SE in each bar was calculated from three replications for each treatment. (Adapted from Hossain et al. 2018b)

2016; Xie et al. 2016). However, farmers in Bangladesh are using a much higher seeding rate, sometimes even double the recommended rate, with the aim of controlling weeds, repelling birds, and achieving higher GY (Sarker et al. 2007). At the same time, wheat seeds are also considered to be an expensive input, and farmers often use low-quality and recycled seeds due to the high cost of seed from new and improved varieties (Sarker et al. 2009; Farooq et al. 2016). Considering the important issue, a seeding rate of 120 kg ha^{-1} was recommended by the Wheat Research Centre (WRC) in Bangladesh, irrespective of the variety, from the very initial stage of wheat introduction and expansion in Bangladesh (Razzaque et al. 2000; Islam et al. 2004), while Sarker et al. (2007) and Sarker et al. (2009) recommended that varieties with medium- to large-sized seed rate should 120 kg ha^{-1} and varieties with small seed rate should 100 kg ha^{-1}.

Recently, a field research was conducted in 2 consecutive years with five newly released wheat varieties ("BARI Gom 24," "BARI Gom 25," "BARI Gom 26," "BARI Gom 27," and "BARI Gom 28") to find out the optimum seeding rate for recently developed wheat varieties for reducing the production cost. Considerably maximum GY ($p \leq 0.05$) was obtained with a seeding rate of 140 kg ha^{-1} for all varieties, compared to other rates. A seeding rate less than the recommended rate

(120 kg ha^{-1}) for all varieties failed to produce comparable GY in both years. Among all varieties, “BARI Gom 26” had the highest GY, while “BARI Gom 25” had the lowest GY in both years. Since the combine effect of variety and seeding rate on GY did not vary significantly ($p \leq 0.05$) in both years, surplus GY was 467 and 233 kg ha^{-1}, respectively, for “BARI Gom 24,” 63 and 75 kg ha^{-1} for “BARI Gom 25,” 81 and 93 kg ha^{-1} for “BARI Gom 26,” 23 and 66 kg ha^{-1} for “BARI Gom 27,” and 152 and 220 kg ha^{-1} for “BARI Gom 28” in the first and second year when seeded at 140 kg ha^{-1}. For the same seed rate, the GY of “BARI Gom 24” increased by 5.3 to 9.6% and that of “BARI Gom 28” increased from 2.8 to 5% over the 2 years. Therefore, a seeding rate of 140 kg seed ha^{-1} is recommended for “BARI Gom 24” and “BARI Gom 28,” while the current recommended rate (120 kg ha^{-1}) should be continued for the other three varieties when grown under irrigation on the Old Himalayan Piedmont Plain of Bangladesh (Akhter et al. 2018; Table 17). Another 2-year research result also recommended

Table 17 Increase/decrease in yield (%) at 100 and 140 kg seed ha^{-1} compared to present recommended seeding rate (120 kg ha^{-1})

		Seed yield (kg ha^{-1})	% Increase/decrease in yield (kg ha^{-1})	Seed yield (kg ha^{-1})	% Increase/decrease in yield (kg ha^{-1})
Treatments		2013–14		2014–15	
Seeding rate (kg ha^{-1})					
100		5085	−147 (2.8%)	4279	−182 (4.1%)
120		5232	–	4461	–
140		5389	157 (3.0%)	4598	137 (3.07%)
F-test		**		**	
Variety x seeding rate interaction					
BARI Gom 24	100	4702	−170 (3.5%)	4180	−220 (5.0%)
	120	4872	–	4398	–
	140	5339	467 (9.6%)	4630	233 (5.3%)
BARI Gom 25	100	4688	−140 (2.9%)	4022	−110 (5.3%)
	120	4828	–	4128	–
	140	4891	63 (1.3%)	4203	75 (1.8%)
BARI Gom 26	100	5579	−80 (1.4%)	4450	−280 (4.7%)
	120	5656	–	4728	–
	140	5737	81 (1.4)	4820	93 (2.0%)
BARI Gom 27	100	5184	−260 (4.8%)	4427	−360 (4.8%)
	120	5436	–	4590	–
	140	5459	23 (0.2%)	4656	66 (1.4%)
BARI Gom 28	100	5270	−100 (1.9%)	4318	−140 (4.9%)
	120	5368	–	4460	–
	140	5520	152 (2.8%)	4680	220 (5.0%)
F-test		NS		NS	
CV (%)		3.10		3.52	

Adapted from Akhter et al. (2018)

seed rate at 140 kg ha^{-1} for newly released Zn-enriched blast-tolerant variety BARI Gom 33 (Jahan et al. 2018b).

8.3 Seeding with the Appropriate Machine for Reducing Production Cost

Agricultural mechanization has a significant contribution to agricultural development, and its purposes are increasing land and labor efficiency by reducing the difficulty in farming operation, bringing more lands under cultivation, and saving energy and resources. Since tillage is the basic operation in farming, in Bangladesh, traditionally land is highly fragmented; as a result, walking tractors are the major sources for field operations as these are much more productive than animal traction and become an economic alternative to small farming (Bill 1999; Hossain et al. 2002; Solomon 2017).

Wheat sowing period is very limited in Bangladesh due to a short period of winter. Late sowing is considered as a one of the key constraints for reducing the GY of wheat (Hossain et al. 2018b). On the other hand, tillage and sowing are costly, laborious, and time-consuming for wheat cultivation as after harvesting of T. *aman* (summer rice), farmers do not have enough time for land preparation with traditional bullock-driven plow. On the other hand, the availability of animal draft power is decreasing day by day. Normally, for conventional tillage, 10–22 days are required,

Fig. 12 Uniform seeding through power tiller operated seeder (PTOS)

because in conventional tillage take in 4–5 passes plow and then 10–12 times of laddering (Meisner et al. 1997). In case of power tiller seeder, tillage, seeding in line, laddering, and proper placement and delivery of seed and fertilizers into the soil could be done simultaneously (Ganesh 1999; Hossain et al. 2002; Rawson et al. 2007; Fig. 12). Hence, the farmers are becoming more dependent on mechanical power (Hossain et al. 2002). Nowadays, power tillers are existing in all over the country, and the most of the wheat farmers are using power tillers for wheat cultivation (Saunders 1991; Meisner 1996; Hossain et al. 2012).

The planter could get the power for a ground wheel for picking and delivering the wheat seeds. It could maintain the seed uniformly between rows to rows as well as seed to seed with similar depth. A uniform distribution of seed with 20 cm spacing along the row planting is desirable. The cup metering mechanism required to hold the seed in each cup should be between 12 and 15 seeds based on the physical property carried out to maintain the seed rate of 100 to 120 kg ha^{-1}, and the required plant population should be 350–380 plants m^{-2}, and it could place the seed 3–5 cm below the ground surface (Hossain et al. 2002; Solomon 2017). The planter (Fig. 13) consists of a cup feed metering mechanism, seed hopper, furrow opener, wheel, and shafts. The planter was designed to perform the following functions: (a) to carry the seeds, (b) to open furrow to the uniform depth, (c) to meter the seeds, (d) to place the seed in furrows in an acceptable pattern, and (e) to cover the seeds and compact the soil around the seed. A detailed description of a

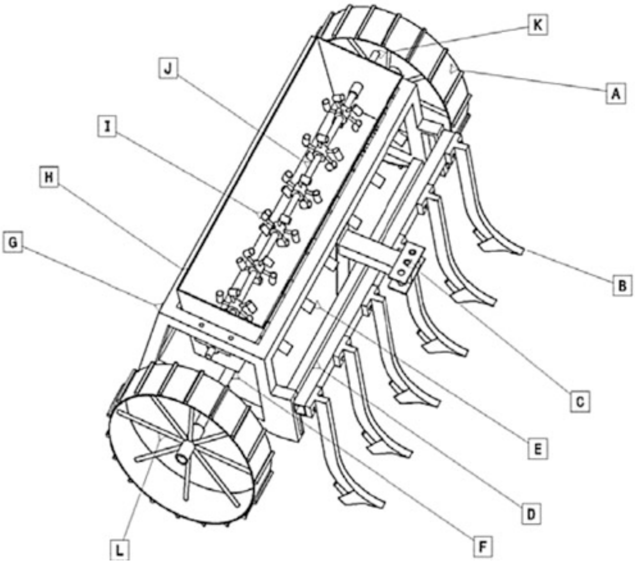

Fig. 13 Different parts of power tiller operated seeder: (**a**) ground drive wheel, (**b**) furrow openers and boot, (**c**) drawbar, (**d**) furrow opener frame, (**e**) seed outlet orifice, (**f**) wheel shaft, (**g**) frame, (**h**) hopper, (**i**) cup-type metering mechanism, (**j**) seed metering shaft, (**k**) chain and sprocket, and (**l**) spoke. (Adapted from Solomon 2017)

PTOS is as follows: (A) ground drive wheel, (B) furrow openers and boot, (C) drawbar, (D) furrow opener frame, (E) seed outlet orifice, (F) wheel shaft, (G) frame, (H) hopper, (I) cup-type metering mechanism, (J) seed metering shaft, (K) chain and sprocket, and (L) spoke (Solomon 2017; Fig. 13).

8.4 Seeding at Optimum Depth

The depth of seed sowing is an important management strategy that influences the development and stand establishment of plants that lead to influence the final grain yield of wheat (Taiz and Zeiger 2002; Akman and Topal 2013). Optimum sowing depth is thus the desired goal for seedling emergence and establishment of all crops. Optimum root systems can access greater soil profiles to absorb and accumulate more water and nutrients (Garnett et al. 2009). If seeds are sown at too shallow a depth, then sowing results in poor germination due to inadequate soil moisture in the top soil layer (Desbiolles 2002), while seeds sown at excessively deeper depths result in significantly reduced seedling emergence, crop establishment, and yield (Desbiolles 2002; Mohan et al. 2013).

Similar to a root system, coleoptile length in wheat is also positively correlated with growth and yield, and when seeds are sown too deep (9 cm), this can result in seedlings with a shorter coleoptile and a marked decline in yield (Yagmur and Kaydan 2009). Mohan et al. (2013) and Odeleye et al. (2007) noted that if seeds are placed deeper than the length of coleoptiles, then the shoot has to displace

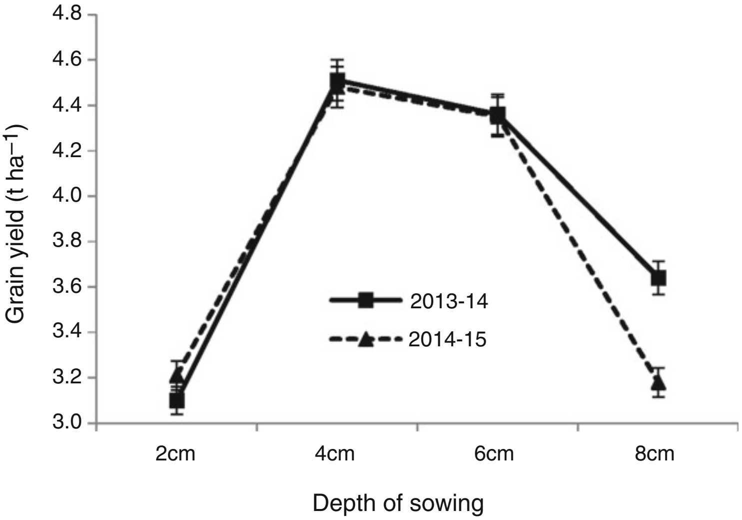

Fig. 14 Grain yield of wheat as affected by sowing depth. Mean (±SD) was calculated from three replicates for each treatment and significantly different at $P \leq 0.05$ (LSD test). (Adapted from Bazzaz et al. 2018)

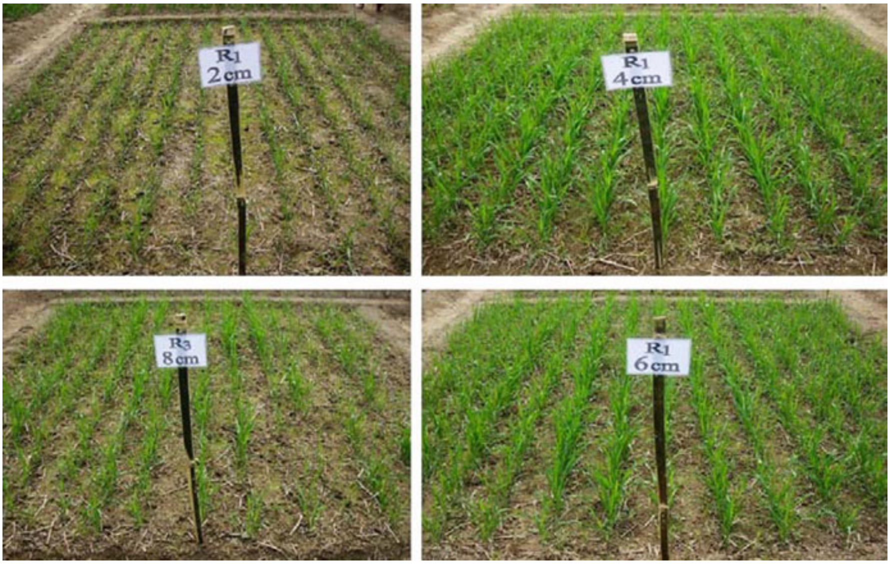

Fig. 15 Wheat seedling at different depths of sowing recorded at 25 DAS. (Adapted from Bazzaz et al. 2018)

superficial mechanical obstacles. The sowing depth for wheat has a continuous impact on spikes m^{-2} and finally on grain yield. Thus, a suitable depth of sowing is essential for emergence and successful crop production (Joshi et al. 2007; Rebetzke et al. 2007). Bazzaz et al. (2018; Figs. 14 and 15) revealed that optimum sowing depth for sandy and silty loam soils should be 4–6 cm for wheat seeding in Bangladesh.

8.5 Balance Fertilizer and Irrigation Management

Natural or synthetic origin of any material that supplies one or several essential nutrients for the growth and development of plants is called a fertilizer. Chemical fertilizers should include more than three essential elements; for example, NPK are considered the most significant plant nutrition. Secondary important chemical fertilizers should include the elements boron, sulfur, zinc, iron, magnesium, calcium, etc. (Mengel and Kirkby 1978). While manure and composts are known as organic fertilizers. It is estimated that 40–60% of all crop production fully depends on fertilizer application (Johnston and Bruulsema 2014). Hence, to secure future food demand under future changing climate, fertilizers could play a substantial role for the increasing population in the world. Environmentally friendly and to increase the fertilizer use efficiency, fertilizers should be used in a right source, right rate, right time, and right place (Mikkelsen 2011; Johnston and Bruulsema 2014; IPNI 2012, 2018).

In Bangladesh, 3000–4000 kg acre^{-1} (30–40 kg decimal^{-1}) cow dung is suggested to be applied before land preparation, whereas chemical fertilizers such as 100–27–40-20-1 kg ha^{-1} of N, P, K, S, and B are recommended to be applied for sustainable wheat production. To increase the fertilizers' use efficiency, 2/3 of nitrogen in combination with full quantity of other fertilizers should be applied as a basal during final land preparation. The remaining 1/3 N fertilizer should be applied immediately after the first irrigation (Bazzaz et al. 2018; Hossain et al. 2018a). First irrigation must be at 17–21 days after sowing (DAS); second and third irrigations must at booting (50–55 DAS) and grain filling (70–75 DAS) stages. Soils in the northern part of Bangladesh are acidic. Therefore it is recommended that if soil pH is 4.0 to 5.0, 800 kg acre^{-1} dolochun ($CaCO_3$) should be applied in moist soils at 7–10 days before sowing. If soil pH is 5.0 to 6.0, 400 kg acre^{-1} dolochun ($CaCO_3$) should be applied to reduce the soil acidity (Hossain et al. 2011).

8.6 Seed Treatment for Maximum Yield Through Accelerating Better Germination

The Bangladesh Wheat and Maize Research Institute (BWMRI) (earlier name, Wheat Research Center of Bangladesh Agricultural Research Institute) suggests to farmers for seeds treated with Provax-200 WP at 3 g fungicide kg^{-1} seed before sowing. This fungicide contains carboxin and thiram. For achieving excellent seed germination and for protecting fungal diseases in the soil of Bangladesh during the seedling stage, Provax-200 WP is an excellent fungicide (Hossain and Teixeira da Silva 2012). Germination of seed treating seeds were increased 20–22%, and ultimately increased the grain yield at 10–12% (Hossain and Teixeira da Silva 2012).

8.7 Weed Management

In Eastern Gangetic Plains (EGP) including Bangladesh, wheat area and production intensify day by day with high speed because of increasing demand for human consumption and food industries in the region. Presently wheat is grown more than 80% by manual sowing after intensive five to six tillage operations which delayed the wheat sowing at least 1–2 weeks. Late planting of wheat was identified as a higher weed infestation than optimum sowing. Therefore optimum time of sowing is important to overcome the weed infestation.

We can also overcome the problem through direct seeding immediately after rice harvest into the unbroken soil. A number of repetitive tillage operations increase the cost of cultivation and fuel consumption and delay planting in two ways: by repetitive tillage operations and by manual sowing. The traditional weed management in wheat after 30–35 days after seeding is that generally farmers cut the weeds with hand weeding which further consumed more labor. On the other hand, after seeding wheat growers face major challenges for weed management due to lack of pre- and postemergence herbicides in the wheat-growing areas of Bangladesh. Therefore, conservation agricultural (CA)-based new agronomic management practices are advocating to overcome these challenges. The zero−/strip-tilled wheat/permanent beds or till the soil with fresh beds is an alternate option through mechanized precision planting in a single pass. The CA-based crop management techniques face major concern of weed management initially.

Scientists of BWMRI are trying to find out appropriate weed management practices under CA-based system to overcome the weed infestation in a wheat field. In the context, a field research was carried out to assess the economic efficacy of different herbicides to control weed in wheat under zero-till and conventional tillage systems. Treatments were eight herbicides, one each weedy check and weed-free treatment (Table 18, Fig. 16). Considering the weed control efficiency, grain yield, and economic point of view, affinity and pinoxaden + metsulfuron were the best under strip tillage and conventional tillage system in Dinajpur location. In Rajshahi, it was pinoxaden + cartrazone both under the strip and conventional tillage system (Hossain et al. 2018c; Table 18 and Fig. 16).

8.8 Conservation Agricultural Practices

Nearly 85% of the area in the Indo-Gangetic Plain (IGP) of South Asia (including India, Pakistan, Nepal, and Bangladesh) followed intensive rice-wheat sequential irrigated cropping systems (Timsina and Connor 2001). As a result, productivity and fertility in the area are declining. To meet the food demand of increasing population, scientists are trying to introduce resource-conserving technologies (RCT) among the farmers. The farmers are also showing interest to grow a crop with RCT because it reduces cultivation cost, protects degrading soil, and saves water without any yield sacrifice. Also, RCT offers the opportunity to plant wheat timely. Delayed wheat planting reduces yield at 1.3% per day after Nov. 30. Due to scarcity and the high cost of labor and for reducing cultivation cost, RCT are essential for farming. Zero-till, bed planting strip tillage, and PTOS tillage options are known as RCT. However, for getting expected crop yields with RCT, a full package of production technologies especially fertilizer management should be provided. Broadcasting fertilizer enhances losses of fertilizer and reduces fertilizer use efficiency in RCT tillage options especially in zero-till and bed planting practices. On the other hand, there are many pieces of evidence that residue retention has a significant contribution to crop productivity and soil fertility with the sustainable way (Limon-Ortega et al. 2000; Singh et al. 2009a, b; Naresh et al. 2012). The work on residue management

Table 18 Weed control efficiency of different herbicides under two tillage system in both the locations

	Dinajpur		Rajshahi		Dinajpur		Rajshahi		Dinajpur		Rajshahi	
	Strip	Con.	Strip	Con.	Strip	Con.	Strip	Con.	Strip	Con.	Strip	Con.
Herbicides	% WCE of grass				% WCE of broadleaf				% WCE of sedge			
T1	20	25	53	48	57	43	45	21	5	46	33	19
T2	17	42	49	48	66	14	38	32	42	44	46	21
T3	44	44	39	49	31	20	46	9	26	43	44	24
T4	40	64	49	48	74	81	34	17	−7	36	51	20
T5	−14	39	55	50	64	49	36	26	3	37	44	10
T6	46	49	53	45	44	76	35	15	−25	42	41	21
T7	2	22	53	43	56	36	36	18	77	73	44	27
T8	1	37	56	38	64	3	35	17	81	78	49	34
T9	0	0	0	0	0	0	0	0	0	0	0	0
T10	62	54	55	47	63	43	28	18	73	54	52	17

Adapted from Hossain et al. (2018c)

WCE weed control efficiency, *Con.* conventional, *T1* ready-mix formulation (sulfosulfuron + metsulfuron) (trade name, Satasat), *T2* ready-mix formulation (mesosulfuron + idosulfuron) (trade name, Atlantis), *T3* pinoxaden (trade name, Axial), *T4* ready-mix formulation (carfentrazone + isoproturon) (Affinity, Bangladeshi), *T5* pinoxaden (Axial) + metsulfuron (Convo), *T6* pinoxaden (Axial) + carfentrazone (Affinity, Indian), *T7* halosulfuron (Sempra), *T8* halosulfuron (Sempra) + pinoxaden (Axial), *T9* weedy check, *T10* weed-free

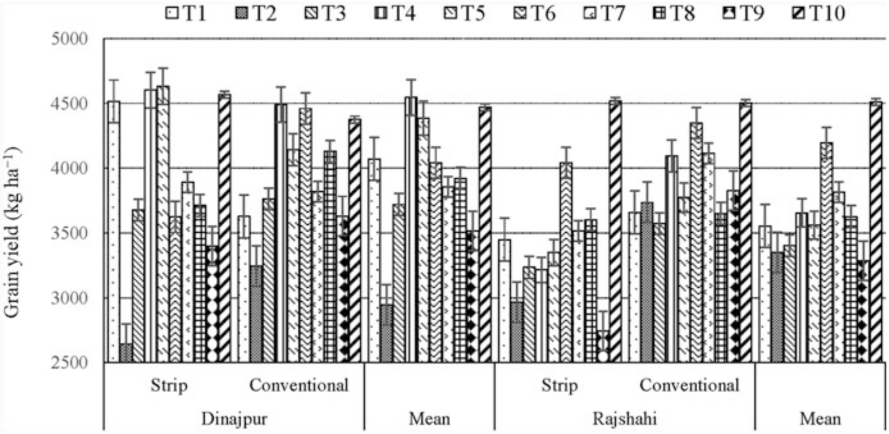

Fig. 16 Yield of wheat is influenced by herbicidal weed control methods under strip and conventional tillage system in two agroecological zones of Bangladesh. (Adapted from Hossain et al. (2018c)). *T1* ready-mix formulation (sulfosulfuron + metsulfuron) (trade name, Satasat), *T2* ready-mix formulation (mesosulfuron + idosulfuron) (trade name, Atlantis), *T3* pinoxaden (trade name: Axial), *T4* ready-mix formulation (carfentrazone + isoproturon) (Affinity, Bangladeshi), *T5* pinoxaden (Axial) + metsulfuron (Convo), *T6* pinoxaden (Axial) + carfentrazone (Affinity, Indian), *T7* halosulfuron (Sempra), *T8* halosulfuron (Sempra) + pinoxaden (Axial), *T9* weedy check; T10, weed-free

with RCT is rare in this country. So, scientists in the IGP are trying to find out the sustainable yield from the pattern and improve soil fertility and productivity.

8.9 Appropriate Wheat-Based Pattern

In Bangladesh, most of the wheat-growing farmers particularly in the northwestern part of Bangladesh are growing wheat in wheat-fallow-T. *aman* rice cropping pattern in the light soil for decades. Some farmers are growing wheat in wheat-jute-T. *aman* rice cropping pattern (Kabir and Islam 2012). There is the scope of introducing mung bean in the fallow period after wheat, and some farmers already started growing mung bean in *Kharif-I* after wheat. In some places of the northwestern part of Bangladesh, farmers are growing early potato before wheat sowing to earn more from the potato of the higher market price. For growing early potato, most of the lands remain fallow during Kharif II season due to lack of knowledge or short duration *aman* rice varieties (Kabir and Islam 2012). After wheat, farmers are growing maize or mung bean and then transplanted (T.) *aman* rice (Kabir and Islam 2012). Considering the important issue under changing climate, BWMRI of Bangladesh recommended some wheat-based cropping pattern after 4-year observation which is economically viable and environmentally friendly (Sarker et al. 2014).

Table 19 Wheat-based cropping pattern suitable for the light soil of northwestern part of Bangladesh

Cropping pattern 1																
Crops	**Potato**				**Maize**				***T. aman* rice**							
	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012				
Variety	Granola	Granola	Diamant	Cardinal	Pacific 984	Pacific 984	Pacific 984	Pacific 984	BRRI 31	BRRI 49	BRRI 49	BRRI 49				
Yield (kg ha^{-1})	7037 (±510)	20,494 (±592)	36,794 (±962)	28,278 (±181)	8155 (±530)	8582 (±234)	12,332 (±261)	8776 (±202)	2960 (±145)	4373 (±181)	4741 (±340)	4953 (±223)				
Cropping pattern 2																
Crops	**Potato**				**Wheat**				**Mung bean**				**T. aman rice**			
	2008	2009	2010	2011	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012
Variety	Granola	Granola	Granola	Granola	BARI 24	BARI 24	BARI 25	BARI 25	BARI 6	BARI 6	BARI 6	BARI 6	Bina 7	Bina 7	Bina 7	Bina 7
Yield (kg ha^{-1})	9660 (±479)	7631 (±208)	8393 (±576)	16,652 (±540)	3460 (±49)	3284 (±253)	4591 (±198)	3114 (±63)	552 (±97)	1454 (±261)	1323 (±38)	1152 (±119)	4175 (±56)	4362 (±372)	5214 (±209)	5387 (±97)
Cropping pattern 3																
Crops	**Wheat**				**Mung bean**				**T. aman rice**							
	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012				
Variety	BARI 24	BARI 24	BARI 26	BARI 26	BARI 6	BARI 6	BARI 6	BARI 6	BRRI 31	BRRI 49	BRRI 49	BRRI 49				
Yield (kg ha^{-1})	4289 (±650)	4649 (±204)	4726 (±237)	5551 (±33)	615 (±110)	1506 (±152)	1411 (±147)	996 (±23)	4147 (±367)	4571 (±23)	5383 (±290)	5189 (±105)				
Cropping pattern 4																
Crops	**Wheat**				**T. aus rice**				**T. aman rice**							
	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012				
Variety	BARI 24	BARI 24	BARI 26	BARI 26	BR 26	BR 26	BR 26	BR 26	BRRI 31	BRRI 49	BRRI 49	BRRI 49				
Yield (kg ha^{-1})	4247 (±116)	4780 (±227)	4383 (±45)	5737 (±78)	3149 (±96)	3229 (±26)	2941 (±214)	3041 (±93)	3260 (±133)	4369 (±256)	4793 (±301)	4740 (±115)				

(continued)

Table 19 (continued)

Cropping pattern 5																
Crops	**Wheat**				**Jute**				**T. aman rice**							
	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012				
Variety	BARI 24	BARI 24	BARI 26	BARI 26	O 9897	O 9897	O 9897	O 9897	BRRI 31	BRRI 49	BRRI 49	BRRI 49				
Yield (kg ha^{-1})	3986 (±2)	4883 (±400)	4557 (±184)	5318 (±236)	2333 (±33)	2950 (±297)	2892 (±189)	3242 (±128)	3767 (±154)	4341 (±94)	4691 (±312)	4897 (±158)				
Cropping pattern 6																
Crops	**Potato**				**Wheat**				**Maize**				**T. Aman Rice**			
	2008	2009	2010	2011	2008–2009	2009–2010	2010–2011	2011–2012	2009	2010	2011	2012	2009	2010	2011	2012
Variety	Granola	Granola	Granola	Granola	BARI 24	BARI 24	BARI 25	BARI 25	Pacific 984	Pacific 984	Pacific 984	Pacific 984	Bina 7	Bina 7	Bina 7	Bina 7
Yield (kg ha^{-1})	10,525 (±638)	7701 (±449)	9494 (±275)	17,522 (±852)	3740 (±105)	3685 (±82)	4617 (±210)	3094 (±93)	5813 (±361)	9794 (±166)	9186 (±152)	7303 (±183)	3708 (±376)	4282 (±306)	4382 (±88)	5335 (±194)

Adapted from Sarker et al. (2014)

Figure in the parentheses indicates the standard error (±SE) of the mean

Among the wheat-based cropping pattern, early planted potato produced a lower yield, but it can accommodate a total of four crops in a cropping pattern with the higher gross return and gross margin. It was observed that a cropping pattern where potato was included gave the maximum benefit. Two four-crop-based cropping patterns, viz., potato-wheat-maize-T. *aman* rice and potato-wheat-mung bean-T. aman rice, with a three-crop cropping pattern (potato-maize-T. aman rice) are suitable for the light soil of the northwestern part of Bangladesh. Additionally, other two three-crop cropping patterns, viz., wheat-jute-T. aman rice and wheat-mung bean-T. aman rice, can be recommended for the region, especially for the marginal farmers (Sarker et al. 2014; Table 19).

8.10 Research Progress on Grain Quality of Wheat

Wheat area and its average production in Bangladesh are decreasing day by day, while demand is increasing due to increasing population. Food security is our first goal. Food security means sufficient food availability for the end user along with proper nutrition particularly fifth essential element zinc (Zn) for a human being. It is a vital micronutrient for the human body that takes part in many biological processes (Frassinetti et al. 2006). It is estimated that around 17% of the population across the globe are at risk of inadequate Zn intake and around 100,000 children who are younger than 5 years die every year due to Zn insufficiency (Bouis 2003; Lassi et al. 2016). WHO reported that Zn and Fe inadequacy is a serious health problem worldwide, and more than 3 billion people are faced in their deficiency (Graham et al. 2012).

Bio-fortification approach for proliferation of micronutrient concentration of staple foods through plant breeding can provide a rural-based, sustainable, and cost-effective intervention in combating micronutrient deficiency. Therefore, researchers are paying their attention to grow more food along with good nutrition especially bio-fortified or enrichment of Zn element. CIMMYT is working with national and international partners to invent and distribute bio-fortified wheat cultivars with vital yield and essential core traits. The first proof of concept results from the CIMMYT-derived high Zn lines tested in target environments which identified high Zn candidate varieties with durable resistance to rusts (Velu et al. 2012; Hao et al. 2014). There was hardly any correlation between grain Zn and grain yield, suggesting that enriched grain Zn can be combined in elite genetic backgrounds with no yield penalty (Velu et al. 2012). Identification of major QTLs attributing to high Zn would accelerate breeding efficiency. The objective of the study is to evaluate 50 Zn-enriched elite wheat lines developed by CIMMYT and to select suitable high-yielding genotypes along with the good agronomic background.

Considering the burning issue, the Bangladesh Wheat and Maize Research Institute (previous name, Wheat Research Centre of Bangladesh Agricultural Research Institute (BARI)) is working closely with CIMMYT to develop and deploy bio-fortified wheat varieties since 2013. As an output of the collaborative research, Bangladesh has released a bio-fortified wheat variety, namely, "BARI Gom 33" (before releasing, namely. "BAW 1260"), in 2017. It also possesses 2NS translocation which indicates a good level of tolerance against WB and is enriched with 50–55 ppm Zn.

8.11 Participatory Variety Selection (PVS)

BWMRI has released 33 varieties established by using conventional plant breeding tool, and many of these varieties have high-yield potential and tolerance against biotic and abiotic stresses. For quick dissemination of new varieties, every year BWMRI has been conducting more than 100s of demonstrations using new varieties through the Department of Agricultural Extension (DAE), NGOs, and scientists of BARI, providing different types of training (including the whole family) to thousands of wheat farmers, conducting farmers' rallies, field days, workshops, etc. But this type of adoption is not good enough, although the technology transfer activities of BWMRI are quite good. This slow adoption was probably due to insufficient skill of the farmers about existing elite wheat varieties, lack of exactly improved varieties, selection of genotypes in the situations (research station trials) that does not suit well with the farmers' field situation, etc.

By this time, participatory variety selection (PVS) has been found to be very effective in addressing many of these problems in many crops and countries of the world. PVS could be very useful to categorize farmers' suitable new wheat cultivars, and thus farmers could overcome the constraints that cause by using old or outdated or stress-susceptible varieties (Joshi and Witcombe 1996; Pandit et al. 2011). In addition, production increases when farmers adopt new varieties through identification in PVS research (Witcombe 1999). Furthermore, PVS also increases the efficiency of the scientists (Bellon 2001) as well as farmers' knowledge (Grisley and Shamambo 1993; Spearling and Loevinsohn 1993) for development of new wheat varieties. In the dissemination system, farmers directly participated during variety testing and selection process; as a result, adoption rates can be increased (Joshi et al. 1995). Keeping these in view, PVS research program has been undertaken, and all the varieties released since 1998 passed through participatory variety selection and so becoming popular among the farmers.

8.12 Variety Maintenance and Breeder Seed Production

Breeders take a small quantity of very pure seed stock upon release of a new variety. This stock represents a new variety as parental materials and also for future maintenance and seed multiplication (Laverack 1994). BWMRI maintenance breeding program is always trying extremely to maintain the purity of varieties and cultivars. A seed program capable of providing farmers with good-quality seed is essential to a nation's agricultural development (Johnson 1980), and seed is not just something planted by the farmers or companies; it is the carrier of the genetic potential for higher crop production (Dolouche and Potts 1971). Pure line theory is still one of the best conceptions for maintaining varietal purity of cereal crops. BWMRI maintenance breeding program had also been developed on the basis of the conception of pure line theory to preserve transparency as well as to produce the best quality of breeder seed in order to supply a handful amount to Bangladesh Agricultural Development Corporation (BADC) and some NGOs. Every year BWMRI produces about 60 ton breeders' seed of the commercial varieties and supplies to the registered seed growers.

9 International Linkages, Collaboration, and Policy Issues for Wheat Production in Bangladesh

CIMMYT has worked closely with BWMRI for promoting wheat cultivation in Bangladesh since the initial stage. It provided exclusive wheat germplasm to select genotypes, which are suitable to the environmental condition of Bangladesh. Many wheat scientists participated in training programmes at CIMMYT, Mexico, for wheat improvement, agronomic management, appropriate machinery, wheat seed quality, and conservation agriculture (Pandit et al. 2011) and also trained some BADC, DAE (Department of Agricultural Extension), NARS, and NGO personnel to improve the wheat seed production for the farmers of Bangladesh. It started from 1969 and continued.

In addition, BWMRI collaborates with CIMMYT, CIDA, AusAID, CSIRO and ACIAR, Australia, and USAID for improving the facility and development of manpower of the BWMRI in Bangladesh (Pandit et al. 2011). Recently, BWMRI has been researching in collaboration with CIMMYT, KSU, ACIAR, and USAID to develop blast-resistant wheat variety. Precision phenotyping platform (PPP) has been established at RARS Jessore with CIMMYT/ACIAR funding for large-scale screening of wheat blast. Few blast-resistant genotypes are also identified for further evaluation. A large number of germplasm received from CIMMYT have enriched our wheat genetic stock for proper evaluation and screening. This provides us the opportunity to select exotic genotypes against wheat blast and also adapted to our environmental conditions.

10 Future Strategies to Meet the Challenges of Changing Climate

- Harnessing genetic resources to accelerate breeding gains to address climate change issues.

- Development of high-yield potential and biotic and abiotic stress-resistant wheat varieties and having good end-use quality.
- Develop high-throughput phenotyping and genomic selection to identify useful alleles/traits for stress tolerance.
- Strategic deployment of traits/alleles into adapted genotypes with good agronomic background through MAS.
- Double haploid breeding and introduce speed breeding technology, bio-fortification, and nutritional improvement.
- Rapid multiplication of seeds of new wheat varieties.
- Short-, medium-, and long-term breeding plan to develop wheat blast-resistant variety.
- Improved crop management such as time of seeding, appropriate seed rate, sowing methods and sowing depth, balanced fertilizers, and irrigation management.
- Using resource conservation technology for improving fertility and productivity of soils in changing climate.
- Strengthen international collaboration and capacity development.

11 Conclusion and Outlook

In Bangladesh after rice, wheat is the second most important food grain. However, Bangladesh mostly depends on import to encounter the demand of wheat for the growing population. Its demand is increasing day by day, due to change in lifestyle and also increase in income and speedy urbanization. Therefore, it is imperative to increase the wheat production to ensure food security in the future of growing population. Wheat production in Bangladesh is facing many constraints such as terminal heat stress, drought, salinity, soil acidity, and many diseases. In addition, wheat also competes with different *rabi* crops during the wheat season. In the study, we tried to provide updated information on wheat research in Bangladesh in contracts with changing climate. This evidence and predictions from the study will provide wheat researchers to plan new breeding and other improved programs to mitigate food security in future under changing climate. The present chapter also tried to highlight what are the indicators for food security in the wider circumstance of South Asia, especially for a new emerging threat like wheat blast.

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