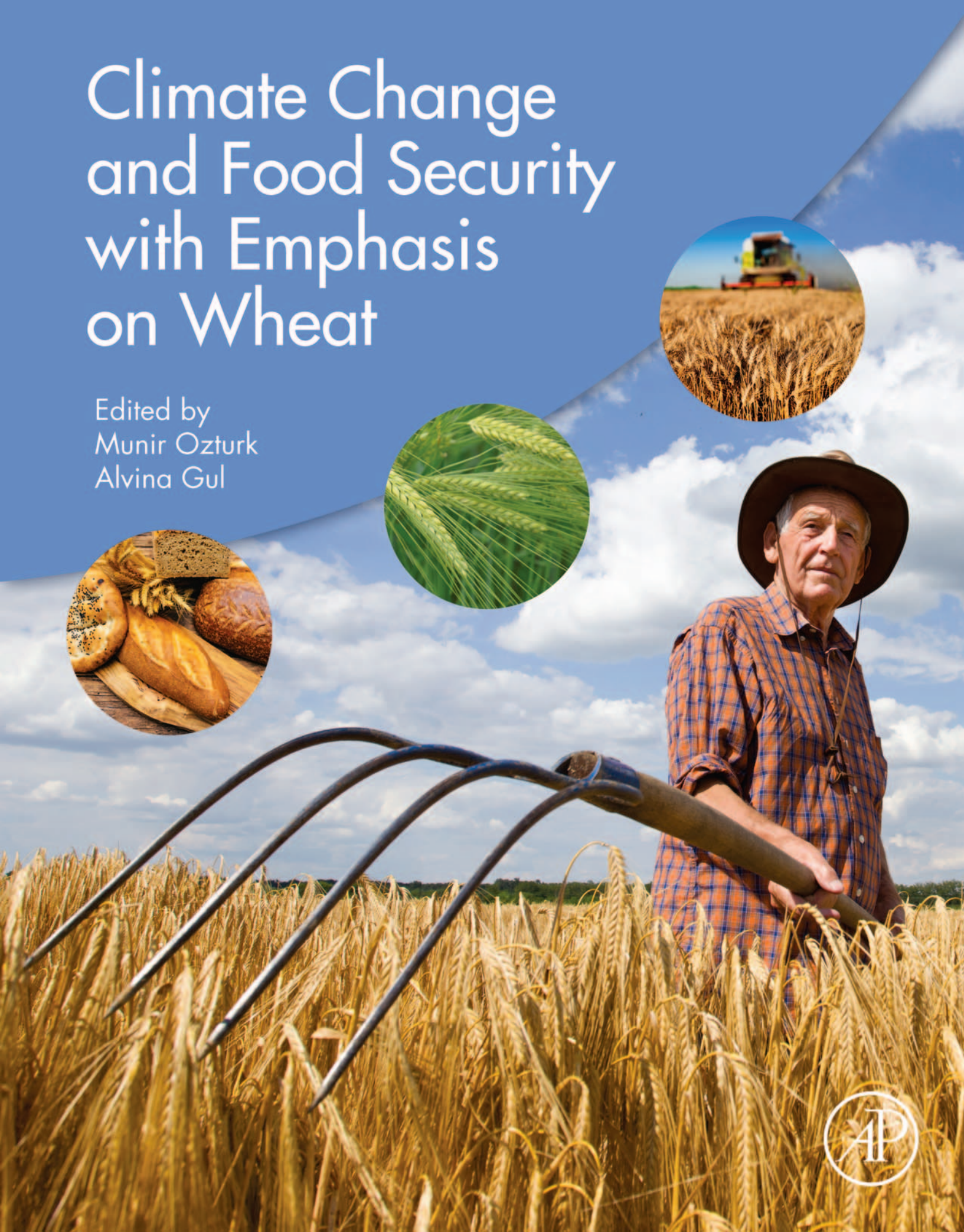
Climate Change and Food Security with Emphasis on Wheat

Edited by
Munir Ozturk
Alvina Gul



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ACADEMIC PRESS

An imprint of Elsevier

Academic Press is an imprint of Elsevier
125 London Wall, London EC2Y 5AS, United Kingdom
525 B Street, Suite 1650, San Diego, CA 92101, United States
50 Hampshire Street, 5th Floor, Cambridge, MA 02139, United States
The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, United Kingdom

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Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library

ISBN: 978-0-12-819527-7

Publisher: Charlotte Cockle
Acquisitions Editor: Nancy Maragioglio
Editorial Project Manager: Kelsey Connors
Production Project Manager: Prem Kumar Kaliamoorthi
Cover Designer: Victoria Pearson

Typeset by TNQ Technologies

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Foreword

"*Climate Change and Food Security with Emphasis on Wheat*" is a timely book providing a comprehensive review of a wide range of related topics. Climate change is defined as a significant long-term change in the average regional or global weather patterns. Primarily because of human activities, earth's climate is changing more rapidly than any time in the history of modern civilization. As a result, weather patterns are negatively affecting food security at a time when the world population growth is placing additional strain on the food supply. The world's population is projected to reach 9.7 billion in 2050 and 10 billion is believed to be the maximum carrying capacity of the earth based on food resources. The food crisis will be the mainstream concern for all of us. To meet the demand for food in 2050, production will need to double without increasing greenhouse gas emissions. These factors converge to generate the impetus for this volume.

The editors are eminently qualified to edit this interesting volume. Of special interest is the opening chapter by Mylonas et al. concerning farming practices to combat climate change. In this chapter, the authors point out the increasing prevalence of extreme weather and how it is affecting food security. They highlight the paramount importance of breeding new cultivars that can tolerate extreme weather conditions and propose that one approach to achieving stress tolerance would be to broaden the genetic base by using landraces, old cultivars, and crop wild relatives. They also emphasize the importance of optimizing agricultural practices, including planting date, fertilization rates, crop rotations, inoculation with arbuscular mycorrhizal fungi, and precision agriculture.

Drought is a major problem for wheat production in many regions, and this threat to wheat production is covered in five chapters that deal with mechanisms, gene expression, transcription factors, and Late Embryogenesis Abundant proteins (LEA proteins). LEA proteins protect other proteins from aggregation due to desiccation or osmotic stresses. Among the more serious issues facing wheat production in many parts of the world today is salinity. This topic is addressed in four of the chapters from various perspectives including cellular mechanisms, genetic control, transcription factors, and osmoprotectants. Wheat diseases are a major threat to wheat production worldwide, and this subject matter is discussed from the perspectives of specific diseases as well as breeding approaches to developing resistant varieties.

Previously many publications have been produced on the topic of climate change and food security, but lately very few reports are available highlighting the fact that climate has already imposed its negative impacts on the whole food system, particularly agriculture. The Food and Agriculture Organization (FAO) stated in a recent report, titled "The State of Agricultural Commodity Markets 2018," that by 2050, tropical regions will face major production losses due to the rise in earth's temperature which is eventually going to disrupt global trade, food consumption, and public health. It is expected that rising temperatures, extreme heat, drought, wildfire on rangelands, and heavy downpours will increasingly affect global agricultural productivity. Hence, challenges regarding crop yields and quality need to be addressed before it is too late.

Wheat as a major staple food in the world gains greater importance in satisfying hunger in both developed as well as developing countries. This volume will suggest remedies to meet the global food challenges caused by climatic change. It discusses both scientific measurements as well as resilience of rural people in order to help them cope with food safety threats. Adaptation to climate change should go hand in hand with mitigation in the agricultural sector, these two steps to climate change needs to be incorporated into the overall strategies. Effective adaptation strategies need to be built in order to combat the risk phenomenon to maintain and improve wheat grain production in the future. Development of cultivars resistant to harsh climatic conditions along with farmers' education is needed to build a balance between basic inputs such as fertilizer and irrigation.

It has been assembled and edited by Dr. Munir Ozturk a retired professor from Ege University, Izmir, Turkey. Dr. Ozturk has published more than 150 peer-reviewed papers in cited journals and 70 book chapters. He has published 43 books with Springer, Elsevier, and Cambridge Scholars. Dr. Alvina Gul is a widely published professor at the National University of Sciences and Technology (NUST), Islamabad, Pakistan. I have been in contact with Dr. Gul since 2016 when she came to Cornell as a visiting scientist. During her time at Cornell, she has worked on multiple projects mostly focusing on wheat regeneration in tissue culture and gene editing while continuing her research program at NUST and supervising graduate students there. She has published more than 80 peer-reviewed

publications and 94 book chapters. She has expanded her range of experiences as a visiting scientist at the University of Sydney, Kansas State University, and Cornell University.

Humans rely on cultivation of major food crops, wheat being the most important. All are being extensively cultivated to fulfill the demand for rapidly growing population. This volume assembles the fundamentals of existing knowledge pertaining to wheat production technologies. Also included are future perspectives covering the use of physiological and molecular enhancement. This book focuses on the strategies to cope with the increasing demand of food supply. It will be a valuable addition to the efforts for addressing food security issues. The authors' contributions as well as the efforts of editors are timely in the changing scenario of climate change–crop productivity interactions and food security. I am confident that the information presented here will be beneficial to those directly engaged in wheat production.

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Preface

Changes in climate with respect to food security are one of the hottest topics of the modern era. Increasing population with upcoming extreme climatic events including frequent heat waves and heavy rainfalls will pose a major threat to food security. Fruitful adaptations and strategies should be adopted in order to mitigate the adverse effects of climate change. As a major staple food in many parts of the world, wheat gains a lot of importance in remediating world's hunger. This book titled "*Climate Change and Food Security with Emphasis on Wheat*" offers an overview of latest information on assessing climate change impacts on production of wheat and also to describe practices to increase wheat production to combat climatic changes. This book is divided into 25 chapters and each chapter highlights useful ideas regarding wheat production and climatic changes.

Better farming practices such as cultivation of adaptable varieties (AVs), precision agriculture (PA), agronomic practices, and GPS-driven practices are extensively elaborated in Chapter 1. The Importance of genetic gain by exploiting wide hybridization as well as integration of a multidimensional framework is highlighted in Chapter 2. Various adaptation strategies to assess climate change impacts on wheat production in Turkey have been discussed in Chapter 3. Chapter 4 explains biochemical indicators that appear at the cellular level and physiological mechanisms to study salt tolerance at the genetic level in wheat. Stress-responsive genes and their potential role in conferring salt resistance, the intricate cross-talk mechanism between various signaling pathways that contribute to provide tolerance against salinity and the overexpression of salt-responsive genes with special reference to salinity-triggered enhanced synthesis of specific proteins, and enzymes has been elaborated in Chapter 5. Advanced bioengineering tools and an updated summary on the various osmoprotective mechanisms adapted by wheat for acclimatizing to salinity has been elaborated in Chapter 6. Chapter 7 is aimed to demonstrate detailed overview of transcription factor(s) (TF or TFs) that are promising source of attaining salinity tolerance in wheat. Chapter 8 provides an updated summary on the molecular mechanisms, i.e., abscisic acid (ABA)—dependent mechanism and ABA-independent mechanism adapted by wheat for acclimatizing drought. Chapter 9 reviews the possible threats to the wheat cultivars caused by drought stress around the world and the basis of tolerance and how it aids wheat to tolerate this stress. Also highlighted in this chapter are the cellular mechanisms adopted by wheat plant to overcome water stress, the improvements which can be brought in the existing varieties to increase yield and quality, and screening of drought-sensitive varieties from those which are drought susceptible. Drought-responsive expressed sequence tags (ESTs) have been reviewed in Chapter 10. Various drought adaptive mechanisms including osmoregulation, molecular markers, molecular techniques (molecular breeding, molecular-assisted selection, marker-assisted breeding, and molecular-assisted back processing) and mainly focusing the synthesis and mode of action of transcription factors (ZFPs, C2H2 zinc finger proteins; bZIP, basic leucine zipper; WRKY, worky; NAC; NF-Y, nuclear factor Y; MYB; ERB, ethylene response factor; and DREBs, dehydration responsive element binding factors) have been discussed in Chapter 11. Furthermore, different changes and molecular makeup in the plants during drought adaptive mechanisms such as detoxification, chaperone function, water transport, and lipid transfer proteins are also discussed in Chapter 11. The detailed mechanism of wheat LEA (Late Embryogenesis Abundant) proteins during the drought conditions or stress is discussed in Chapter 12. Chapter 13 provides a brief overview of osmoprotectants, the common types of osmoprotectants which are commercially available and mode of action of osmoprotectants with special reference to wheat. Losses caused by spot blotch as well as epidemiological insights and biochemical mechanisms of the pathogenesis are described in Chapter 14. Chapter 15 is about Karnal bunt (*Tilletia indica*) in wheat focusing climatic characteristics for the completion of the life cycle and the thresholds of inoculum of *Tilletia indica* and the potential economic impact on food security and effect of climate change by *Tilletia indica*. Chapter 16 focuses on diverse wheat-*Thinopyrum intermedium* breeding lines with potential to address wheat streak mosaic virus resistance in wheat. Chapter 17 summarizes the factors affecting postharvest life of wheat grains and analyzes the impact of climate change to postharvest losses of wheat production. The effects of climate changes in particular on wheat yield and on the sustainability of food security in Turkey are discussed in Chapters 18 and 20. Chapter 19 provides an understanding of the mechanisms of accumulation of trace elements in wheat, their phytotoxicity, and their effects on

wheat development and nutrition. Chapter 21 is an overview of the prospective strategies for conservation of genetic diversity in wheat landraces. Chapter 22 explains the current knowledge considering application of next-generation sequencing (NGS) in wheat research. In Chapter 23, the factors determining the accuracy of GS (genomic selection) are covered with an emphasis on three major prevalent approaches capable of improving the prediction accuracy: (1) GS models, (2) genotype $\times$ environment (G $\times$ E) interactions, and (3) high-throughput phenotyping (HTP) platforms. Approaches like zinc finger nucleases (ZFNs), transcription activator-like effector nuclease (TALENs), and clustered regularly interspaced short palindromic repeats (CRISPR) which are successfully used in editing wheat genome to get heritable variations for creating diversity and precision breeding are discussed in Chapter 24. Finally, Chapter 25 discusses climate risks, food insecurity, economic value of the global crisis, and economic impact of climate change with particular focus on food security with a few policy recommendations.

Editors

CHAPTER

1

Better farming practices to combat climate change

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OUTLINE

1. Introduction

Global wheat production faces significant challenges given the projected need to increase world wheat supply by about 70% until 2050 (CIMMYT, 2014), while there are restrictions for the expansion of crop-growing areas and limited available natural resources (Reynolds et al., 2011). Also, global warming is associated with increasing temperature and incidences of drought putting food security at risk (Lobell et al., 2013). An increased frequency of extreme weather events causing significant yield constraints is recorded (Semenov and Shewry, 2011), highlighting the future challenge to secure wheat productivity under the upcoming climatic and environmental variations (Porter and Semenov, 2005). It is imperative to provide solutions that can acclimatize wheat cultivation to the adverse effects

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https://doi.org/10.1016/B978-0-12-819527-7.00001-7

of environmental conditions displaying at the same time superior yield. Therefore, a holistic approach is necessary to bring together genetic improvement, crop management, capacity building, and knowledge (Ortiz et al., 2008). The current work aims to identify different farming practices that provide the potential to cope with these changes and provide low-cost and effective solutions to ensure sustainable wheat production under current and future climate change scenarios. This chapter analyzes adaptable varieties cultivation, precision agriculture (PA), agronomic practices for sustainable agriculture, diseases and pests forecasting systems, GPS-driven practices, and variable rate technologies.

2. Release of new varieties

New wheat cultivars are needed to adapt the crop to changing environments and meet the nutritional needs of people, particularly those in the developing world, where farmers increasingly adopt resource-conserving practices (Ortiz et al., 2008). Thus, genetic improvement is of paramount importance to ensure wheat productivity aiming at breed cultivars adapted to extreme environmental conditions displaying at the same time higher yield. Traditionally, the most important goal for wheat breeding, as one of the world's staple crops, is high and stable yield (Semenov et al., 2014). Wheat is a cool season crop, and thus, its productivity is sensitive to the increase of temperature and drought that causes major yield constraints (Ni et al., 2018). Currently, apart from the increase of yield potential, important priority for the wheat genetic improvement is the achievement of adaptability under adverse climatic conditions. Heat and drought stress are the major abiotic factors causing severe yield reductions, and it is expected that they will frequently occur in the future (Semenov et al., 2014).

In this framework, an essential aspect regarding the management of the available germplasm that should be taken into account is the concern for broadening the base of genetic resources and the use of alternative resources of genetic variability (landraces, old cultivars, crop wild relatives [CWRs]). During the previous decades, the intense selection pressure applied through genetic improvement to achieve varieties with high yielding potential caused erosion to the available genetic resources (Ren et al., 2013). The extensive use of modern high yielding varieties contributed in the gradual replacement of traditional varieties from cultivation and eventually, their genetic erosion (Akhalkatsi et al., 2010; Friis-Hansen, 1999).

A large number of local population-varieties of bread wheat, which are cultivated in the past and contributed decisively to the agricultural production and nutrition of the population, are lost (Lopes et al., 2015). As a consequence of this genetic narrowing, the allelic plasticity is reduced and has guide to a germplasm less adaptable to new environmental stresses, diseases, and pests and thus limited the genetic diversity that breeders may exploit and use (Makai et al., 2016; Tanksley and McCouch, 1997).

Therefore, studying and exploiting the genetic variability of landraces can be an alternative and viable solution for agriculture (Newton et al., 2010; Zeven, 1998). Landraces were long-term cultivated in low-input agricultural systems and were subjected to genetic change, selected for agronomic traits and their adaptability to environmental biotic and abiotic changes (Newton et al., 2010; Zeven, 1998).

Thus, they compose a valuable gene pool for adaptability to biotic and abiotic stresses, good productivity in low-input environments (Villa et al., 2005), and also high-quality local products (Koutsika-Sotiriou et al., 2010). Besides, traditional varieties are required to meet the needs of breeders to create new varieties suitable for low-input growth, which presupposes selection among populations that are adaptable to conditions of reduced (Koutis et al., 2012; Bladenopoulos et al., 2014). Several wheat landraces were assessed for their ability to absorb and save water, root surface density, water potential decline between the wettest and driest treatments, osmotic adjustment, and water loss (stomatal sensitivity and leaf senescence), showing a very good adaptation to drought (Karamanos et al., 2017).

In comparison with domesticated varieties, CWRs and primitive wheat sustained a much higher level of diversity since they have been developed in natural environments for thousands of years (Zhang et al., 2017). CWRs would be a valuable source of resistance to both abiotic and biotic stresses for the increased adaptability of the agricultural systems to adverse climatic conditions (Egan et al., 2018). Hence, a promising method to restore variability that could be useful to breeder would be interspecific hybridization between durum elite lines and wild relatives of the Gramineae family.

Wheat wild relatives that are members of the *Aegilops* (*Aegilops tauschii*, *Aegilops umbellulata*, *Aegilops speltoides*), *Triticum* (*Triticum dicoccum* and *Triticum dicoccoides*), and *Haynaldia* species have useful traits connected with adaptation to drought, cold, and salinity stresses (Trethowan, 2014; Trethowan and Mujeeb-Kazi, 2008).

Over the past few decades, the introduction of traits from wild species to cultivated crops proved to be a successful approach, mainly for overcoming biotic stresses, like stem rust resistance from the wild wheat *A. tauschii* Coss

(Assefa and Fehrmann, 2004). Regarding abiotic stress resistances, it is indicated that wheat wild relatives appear to have been exploited quite significantly. So, concerning wheat has sizable and well-established prebreeding programs that focus specifically on CWRs, leveraging advanced genomic tools, and diverse characterization and evaluation data (Hajjar and Hodgkin, 2007; Nemeth et al., 2015). The exploitation and use of wheat wild relatives could provide a solution to wheat breeders to increase wheat adaptability to marginal conditions; however, it must be taken into account the enhancement of the end-products quality (Mondal et al., 2016).

There are several environmental factors affecting crop production, where breeding could provide solutions. In this section, the potential for adaptation to high temperature and drought is presented as the most important, which are the most important abiotic factors causing yield constraints. Generally, the strategies for wheat adaptation to hotter and drier environments are more likely to involve "escape" rather than "tolerance" approaches (Semenov et al., 2014).

2.1 Adaptation for high temperature

Wheat is cultivated worldwide in temperate environments and in many tropical cropping systems (Reynolds et al., 2001) where terminal or continual heat stress affects its productivity. CIMMYT (1995) identified heat stress as one of their top research priorities, since high temperature is one of the most crucial environmental factors reducing crop yield. It is reported that the annual global temperature has been rising steadily and expected to reach an increase by 1.8−4.0°C until the end of the 21st century (Bita and Gerats, 2013). Since wheat is a cool season crop, its productivity is sensitive to heat stress, and it is expected that the increasing temperatures will negatively affect wheat yield in the upcoming years (Gouache et al., 2012). During the past years, the most important target for wheat breeding was high and stable yield. Today, the challenge is to ensure high and stable yield under environmental conditions where high temperatures might occur. Thus, the study of traits connected to tolerance to heat stress having high heritability is important because they would be useful as breeding tools for selection.

It is thoroughly studied that the impact of heat stress to physiological and molecular mechanisms is reflected mainly to membrane thermostability, photosynthesis, and starch synthesis inhibition (Reynolds et al., 2001; Mishra et al., 2017). The heat stress adaptability mechanisms mainly associated with final yield are the acceleration of the development (Midmore et al., 1984), evaporative cooling (Idso et al., 1984), the photosynthesis rate and the degradation rate of chlorophyll (Al-Khatib and Paulsen, 1990; Shpiler and Blum, 1990), and membrane thermostability on seedlings and flag leaves (Shanahan et al., 1990). Furthermore, it should be taken into consideration that the defense mechanisms against heat stress are complex and connected with genes associated to the regulation of photosynthesis, heat shock proteins, and antioxidants over different genetic backgrounds and connectivity of adaptive mechanisms (Mishra et al., 2017). Thus, several physiological mechanisms could contribute to heat tolerance in the field following different strategy approaches as stay-green, membrane thermostability, higher photosynthetic rate, higher membrane stability, slow chlorophyll degradation and increased accumulation of proline and secondary metabolites, and ingrained higher thermotolerance to several wheat cultivars, among others (Reynolds et al., 2001; Mishra et al., 2017). The recording of physicochemical and molecular indexes provides information for responses to stress that could give adaptability (Mishra et al., 2017). Physiological parameters measured such as canopy temperature depression and the measurement of electrolyte leakage to estimate membrane thermostability, leaf chlorophyll during grain filling, leaf conductance, and photosynthesis during heading was used to screen and evaluate different cultivars for thermotolerance (Reynolds et al., 1994). The screening of wheat germplasm on heat response ingrained thermotolerant and sensitive cultivars and may contribute to the identification of the different levels of thermotolerance among cultivars serving as a basis for gene mining (Mishra et al., 2017).

The impact of heat stress on wheat growth is differentiated according to the stage of development (Reynolds et al., 1994). Although agronomic traits are affected at every developmental stage, the preflowering and anthesis stages are relatively more sensitive to high temperatures compared with postflowering stages (Cossani and Reynolds, 2012; Yang et al., 2013). Mainly, during preflowering and flowering stages, short periods of high temperature can reduce grain number per spike and yield (Yang et al., 2013).

Anthesis is considered the most sensitive period of wheat growth where high temperatures have the most significant negative impact on crop production and quality that is critical for the determination of the final cereal grain yield (Ortiz-Monasterio et al., 1994). Moreover, Ortiz-Monasterio et al. (1994) reported that a period around 20 days before and 10 days after anthesis is a timing where high-temperature events (>30°C) lead to reduced grain numbers with the interval immediately close to anthesis (5 days before to days after) being particularly sensitive (Wheeler et al., 1996).

An accepted upper limit to the increase of temperature near flowering for wheat without reductions in grain number is around 31°C (Porter and Gawith, 1999), with the sensitivity depends on the development stage (Dias and Lidon, 2010) and the genotype (Langer et al., 2014). This recorded sensitivity of wheat to high temperatures has been connected with accelerated development (Blum et al., 2001) and photosynthesis reduction (Salvucci and Crafts-Brandner, 2004). Many experimental results support the view that the high temperatures around flowering caused a directly significant decrease to the number of grains and eventually to the final grain yield (Barnabás et al., 2008; Ortiz-Monasterio et al., 1994). The reduction of wheat grain number due to the exposure to high temperature during anthesis is primarily associated with effects on pollen fertility (Calderini et al., 1999).

During grain filling, the increase of temperature above an upper limit causes a reduction in photosynthesis and eventually a significant decline of grain weight. The inhibition of photosynthesis due to heat stress reduced the available photosynthetic assimilates and dramatically impaired grain filling (Blum et al., 1994). Grain filling in wheat is affected by the level of available photosynthetic assimilates produced in leaves and stems (Blum et al., 1994). The duration and the rate of grain filling determine the final grain yield in wheat (Barnabás et al., 2008). This is connected and defined by the availability of the current assimilate production via photosynthesis in leaves and stems (Blum et al., 1994). The increase of temperature above 34°C results in the reduction of final grain weight via shortening the duration of grain filling and decreasing photosynthetic rates (Blum, 1986).

Genetic diversity in wheat is well documented since wheat cultivars showed variability in heat stress responses where the different reaction was recorded in the morphophysiological, biochemical, and molecular analyses (Reynolds et al., 1994). The membrane stability and increased accumulation of osmolytes and secondary metabolites are connected with comparatively thermotolerant cultivars. This shows evidence that, under heat stress, some cultivars could adapt the agrophysiological traits and exhibit amplified expression of genes related to heat tolerance defense (Mishra et al., 2017). Conclusively, the main traits that can be applied for selection for heat tolerance and used as breeding tools are canopy temperature depression, leaf stomatal conductance, and membrane thermostability that may be used as indirect selection criterion (Richards et al., 2001).

In the above context, plant breeders and crop scientists face significant challenges since they have limited time and available resources to select effectively the most suitable traits for improvement (Foulkes et al., 2011; Semenov and Halford, 2009). The development and release of new wheat cultivars better adapted to the upcoming climatic conditions is an effective, low-cost agricultural practice to ensure wheat productivity under abiotic or biotic stresses (Ortiz et al., 2008). The evaluation of available wheat germplasm, broadening the base of genetic resources and breeding, is one of the promising approaches to address the expected effects of climate change in wheat productivity and yield stability (Rajaram and Hettel, 1994; Barnabás et al., 2008).

Traditionally, breeders were mainly focused on crop productivity rather than adaptation under diverse and marginal conditions (Barnabás et al., 2008; Tokatlidis, 2013). Currently, it is widely recognized that the necessity to identify, develop, and deploy germplasm that can remain unaffected by extreme weather events ensures stable yield production in both “good” and “bad” years (Chapman et al., 2012; Fischer and Edmeades, 2010; Keating et al., 2010).

2.2 Adaptation for drought

According to the global warming forecast, wheat yield may decrease in lower latitudes due to upcoming water scarcity or drought (Ortiz et al., 2008). As a result, global weather change poses significant challenges to agriculture to be sufficiently productive under dry environments (Richards et al., 2001). The wheat germplasm improvement is considered an approach to deal with these yield constraints to achieve higher tolerance to stresses. Consequently, the maintenance of wheat yield under these adverse conditions should be a priority for plant breeders (Ortiz et al., 2008).

The development of drought-tolerant wheat varieties and eventually water-use efficient crops is an optimum mean to defense the crop against adverse effects of drought. Worldwide, significant efforts to mitigate drought through breeding resilient varieties are underway. However, it must be taken into account that drought tolerance is a complex trait that is controlled by numerous genes, (Bernardo, 2008), and its full expression is affected by the environment (Mwadzingeni et al., 2016). Thus, progress in genetic gain for high productivity under dry conditions is prevented, showing that the achievement of genetic gains in terms of yield under drought conditions is not an easy task (Richards et al., 2014).

The estimation of the existing genetic diversity within and between wheat populations is the basis to gain a clear view of the genetic structure and to achieve the improvement of quantitative traits regarding tolerance to marginal environmental conditions (Mwadzingeni et al., 2016). The gene expression analyses aspire to enlighten molecular processes during seed growth and development, constituting valuable resources to better understand the impact

of the growth environment on gene expression. This will provide breeders with new tools to develop cultivars showing better adaptability to upcoming global climate change (Altenbach, 2012). Therefore, it is important to focus on ideotypes having characteristics connected with tolerance to drought that will be useful for breeding. Traits such as the delay of leaf senescence and/or an increased floral survival rate in wheat cultivars enable to lead to an increased number of grains at maturity. Also, a significant challenge is breeding for improved stress tolerance especially during meiosis and anthesis (Semenov et al., 2014).

Direct selection for yield in drought-prone environments is crucial for wheat improvement since there are many integrating factors affecting final grain weight, and a holistic evaluation is needed (Richards et al., 2014). Screening methods would use several techniques to identify germplasm tolerant to drought. In this framework, the use of phenotypic characteristics for the selection of wheat germplasm for drought tolerance is widely recognized. The utilization of phenotyping technologies with automated systems for recording and statistical analysis of big data connected to plant growth permits fast and accurate quantification and monitoring of various phenotypic traits on large scale (Araus and Cairns, 2013). The use of several digital sensors using near- or far-infrared reflectance, thermometers, and cameras enables the detail measurements of critical phenotypic traits (Araus and Cairns, 2013). Another screening method for breeding cereals for drought is based on carbon isotope discrimination (Δ). Δ technique would be useful for screening cereal genotypes for the adaptability under environmental constraints although high cost could be a limiting factor for their extensive use in breeding program; alternatively, a cheaper method could be the use of grain ash content that is relevant to grain yield (Tsialtas and Tokatlidis, 2008).

The management of the genetic diversity to improve drought tolerance will be achieved through modification and selection for adaptive mechanisms including, drought escape, dehydration avoidance, and dehydration tolerance. Escape strategies of genotypes are based on successful reproduction before the onset of severe stress, having short life cycle, a higher rate of growth or the efficient storage, and use of reserves for seed production (Blum et al., 2001). Dehydration avoidance includes strategies aiming at the maintenance of a high (favorable) plant water status during stress, as the result of minimized water loss due to stomatal closure, reduced leaf area and senescence of older leaves, or the increased water uptake (e.g., by increased root growth) (Blum, 2011). A significant component of drought resistance of wheat cultivars could be dehydration avoidance, as reported for a released Australian wheat cultivar (Munns and Richards, 2007). Blum (2011) indicates that traits associated with dehydration avoidance conserve plant water status and turgor through the effective use of water.

Relatively simple heritable constitutive plant morphological and developmental traits can have a decisive effect on crop performance and productivity under drought stress (Blum, 2011), that operates mainly through dehydration avoidance and effective use of water like root depth, plant leaf area as determined by leaf size or tillering, early flowering, leaf surface properties, or morphological features of the reproductive system, which influences fertility under stress (Blum, 2011).

Finally, the maintenance of plant function under limited water availability and/or the recovery of plant water status and plant function after drought may involve osmotic adjustments (Ashraf, 2010). Osmotic adjustment in wheat is regulated by one major and a few minor genes having high heritability (Moinuddin, 2005). The tolerance to drought may also be attributed to the efficient scavenging of reactive oxygen species formed as a result of disturbed metabolism (Yang et al., 2010). A unique and efficient component of dehydration tolerance, to cope with drought stress, in most grain crops is stem assimilates utilization for grain filling (Blum, 2011). Although the mechanism of mobilization of the stem assimilates to the grain is not fully explained, it is accepted that the mobilization of stem reserve to the seed should be maximized to achieve its postflowering drought resistance (Yang and Zhang, 2006).

Another approach is the improvement of water use efficiency (WUE) aspires to achieve a reduction in the necessary water for production of the current level of crop production (crop output per water input), which is considered an approach to meet the future food need under an environment where water will be increasingly limited factor (Mei et al., 2013). Deng et al. (2006) underline the need to develop new varieties for high WUE; this approach has a great potential for the future since less effort was devoted to breed new crop varieties with a high yield and WUE; this needs less investment and higher sustainable efficiency for the growers in comparison with the agronomic water-saving methods (Zhang et al., 2011).

The adequately productive agriculture under diverse and adverse conditions is a prerequisite to ensure the sustainable food production in a highly variable environment (Tokatlidis, 2013). Drought is a critical factor associated with climate change that limits wheat productivity. Although significant investment and breeding efforts were made to achieve drought tolerance improvement, still a lot of work is required for tangible results. Significant progress will be possible if breeders will cooperate with other interdisciplinary experts aiming at developing drought-tolerant and high-yielding wheat cultivars.

Many times, drought stress is associated with heat stress (Jha et al., 2014). So to succeed improved grain yield and quality of wheat under water limited conditions, simultaneously breeding for both stresses should be done in the near future.

3. Agronomic practices

Humanity will have to meet the challenge of increasing food production. However, climate change will result in variability of production and crop losses, which may threaten food security (Wheeler and Braun, 2013). Except for the release of new varieties with tolerance to abiotic stresses, applying the optimum agronomic practices plays an essential role in combating climate change. Study of agricultural practices will contribute to the design of sustainable cropping systems and will result to more stable crop production (Van Eerd et al., 2014).

Drought and salinity are significant stresses for plants, affect the productivity negatively, and are associated with climate change. In South Mediterranean countries, water availability is the main limiting factor of cereals production and follows the nitrogen (N) availability (Garabet et al., 1998). Drought management strategies could reduce the effects of drought stress. A good way to handle drought stress is to avoid it by the proper selection of early mature cultivars by which grain filling is completed or is in the end when the drought or the heat stress starts to be severe (Tewolde et al., 2006; Mondal et al., 2015). Tewolde et al. (2006) concluded that early heading is an important and useful single trait for adaptation to areas prone to high-temperature stress during the postheading period. It is important the proper selection of sowing time, in order to avoid heat and drought stresses during grain filling period, in areas with such abiotic stresses.

Early sowing (end of October and beginning of November in South Europe) results in the development of a good root system before winter. So the wheat plants are more tolerant to low winter temperature and succeed good tillering and early growth. Studies about the effect of delayed seeding showed significant effect on yield and interactions between sowing date, genotype, and weather conditions (Baloch et al., 2010; Dai et al., 2017). In another study, optimum sowing date resulted in 25% higher grain yield in durum wheat in comparison with late sowing date (Ehdaie and Waines, 2001). Similar results found Forster et al. (2017) in a 2-year experiment by using three commercial cultivars in wheat.

In crop rotation, two or more crops are grown one after the other, while intercropping two or more crops growing simultaneously on the same land. The use of legumes in a wheat agrosystem both in rotation and in intercropping increases crop diversity, reduces external inputs, improves soil N availability through N-fixing process, increases soil moisture, and breaks diseases and weeds cycle (Ryan et al., 2008a,b). On the other hand, durum wheat needs large amounts of N for good production and quality (Garrido-Lestache et al., 2005; Grant et al., 2001). Wheat in a crop rotation system produces on average 16% more grains than wheat in monoculture (de Cárcer et al., 2019). Similar results in wheat yield succeeded when the rotation includes cereal−grain legume intercropping system (Monti et al., 2019). So crop rotation with legumes or intercropping included a legume, resulting in reduction of N fertilizer that will be applied in wheat culture that follows and also increases wheat yield. The combination of increased N-use efficiency and increased yield that succeeded fulfills the term “eco-efficient” agriculture, which aimed in sustainable and efficient use of resources in agriculture and land management (Keating et al., 2010). Sustainable crop production is a main target in agriculture, because it lowers the risk created by climate change and results in food security.

Arbuscular mycorrhizal fungi (AMF) can result in sustainability of wheat agrosystems in favor and adverse environments (Al-Karaki et al., 2004; Bernardo et al., 2017; Mathur et al., 2018). AMF have a beneficial symbiosis with several crop species (Martín-Robles et al., 2018), providing phosphorus (P) and nitrogen (N) from the soil to plants in exchange with photosynthetic products (Hawkins et al., 2000; Martín-Robles et al., 2018). Mathur et al. (2018) studied the effect of AMF inoculation on wheat crop under drought stress and found that drought stress−induced damage to the structure and function of photosystem (PSII and PSI) was reduced by AMF colonization. Al-Karaki et al. (2004) studied the effects of AMF inoculation on growth, grain yield, and mineral acquisition of two winter wheat cultivars grown in the field under well-watered and water-stressed conditions. It was found that biomass, grain yields, and shoot P and Fe concentration are higher in mycorrhizal than nonmycorrhizal plots irrespective of soil moisture, demonstrating the potential of AMF inoculation to reduce the effects of drought stress on wheat grown in semiarid areas of the world (Al-Karaki et al., 2004). Mycorrhizal fungus *Glomus mosseae* enhances the growth, yield, and nutrients (P, Mg) uptake of the durum wheat (Karagiannidis and Hadjisavva-Zinoviadi, 1998). Fileccia et al. (2017) found that AMF symbiosis did not increase the durum wheat tolerance to salt stress but, instead through a plurality of mechanisms, host plant is subject to a level of salt stress lower than that of nonmycorrhizal plants.

3.1 Fertilization

The main target of a soil fertility program is a good wheat production retaining soil fertility and resulting in sustainable agriculture. Soil test is necessary for the proper planning of a fertility program but has some cost. Other important factors are the fertilizer rates of application, placement, and timing. The last two decades has increased the use of visible near-infrared reflectance (vis-NIR) spectroscopy which is a low cost, non-destructive, and fast technique that requires a minimum of sample preparation. Vis-NIR can estimate several soil properties (mainly clay minerals, organic matter, and soil water) in situ or in the laboratory and can help in the fertilization program (Wetterlind et al., 2013). Proper fertilization of wheat can help respond to abiotic stresses (drought stress, salinity stress). Drought stress is a major threat to reducing wheat production especially in low rainfall areas such as semiarid areas where wheat is most cultivated (Abad et al., 2004; Garrido-Lestache et al., 2005; Ottman et al., 2000).

3.1.1 Nitrogen

Nitrogen (N) is a very important factor that limits yield in nonfertilized agriculture. N is the most important element for plant growth and essential yield-limiting nutrient in wheat production. N is taken up from the soil in ammonium (NH_4^+) and nitrate (NO_3^-) forms. Adequate N is necessary for good wheat production, since a shortage of N causes reduced tillering, plant growth, grain filling, and protein content (Garrido-Lestache et al., 2005; Ottman et al., 2000). In dry condition, N efficiency at harvest is low, and many researchers had worked with the influence of the source, rate, timing, splitting, and placement of nitrogen on grain yield and quality (Abad et al., 2004; Garrido-Lestache et al., 2005; Grant et al., 2001). Grant et al. (2001) conducted a 4-year experiment at two locations in the center of Canada to investigate the effect of source, timing, and placement of N on grain yield and N recovery of durum wheat under reduced tillage (RT) and conventional tillage (CT) management. Spring application of N reduced the differences among fertilizer sources and tillage systems in comparison with foliar application. On the clay loam soil, spring-balanced N results in higher yield, while in drier soils, foliar application resulted in similar or higher yield (Grant et al., 2001). Selection of a suitable source timing and placement combination may be more critical in RT management in comparison with CT management (Grant et al., 2001).

A part of nitrogen fertilization applied during sowing for good tillering and the other part with spring topdress application targeting to provide sufficient N to support the growth. Abad et al. (2004) in a 2-year experiment in Spain tested seven nitrogen treatments with different rated and timing in two irrigated fields in low winter rainfall areas. The experimentation showed that foliar application of urea at the flag leaf stage had no effects on grain yield and almost negligible effects on grain quality in these Mediterranean conditions. Moreover, they found that it is essential for the determination of N fertilization to measure the initial nitrate content of the soil in low winter rainfall areas (Abad et al., 2004). An application of 100 kg N ha^{-1} could result in better grain yields with good quality (protein contents, gluten strength, vitreousness, and carotenoids). For highest quality, this rate could be doubled. Timing and N source should be planned to fit to the soil type, tillage system, and climatic conditions. Split topdressing N application could result in higher yield and quality, e.g., ~1/4 to 1/3 of total spring N application during ~end of February (Feekes 3) (Large, 1954) to help tillering and the rest N from ~end of March to beginning of April (Feekes 5). However, the success of the topdressing N application is depended from soil moisture.

The use of slow-release fertilizers is a way to minimize N leaching in sandy soils (Wang and Alva, 1996). Also, low volatilization losses could be achieved by the use of nutritional activators regulating soil microorganisms, which are responsible for the transformation of N into a form useable by the plant (Giovannini et al., 2009). However, experiments with slow-release N fertilizers did not lead to any advantage in terms of yield or grain quality in field experiments in Spain (Diez et al., 1997) and Italy and seemed to be affected by rainfall during the growing season and soil texture and moisture (Marinaccio et al., 2016).

The measurement of chlorophyll (SPAD) is a technique to estimate the wheat N status and to regulate the spring N fertilization (Follett et al., 1992). Debaeke et al. (2006) found similar results only in wheat field with inadequate N, while in overfertilized wheat, SPAD index could not be used to predict grain yield and protein content with accuracy. In overfertilized wheat, the nitrogen nutrition index (NNI), which is calculated from the crop biomass and the total plant N content by using an N-dilution curve, could be a solution (Debaeke et al., 2006).

3.1.2 Phosphorus

Phosphorus (P) is a major plant nutrient that affects all biological processes and is generally involved in plant growth. P is crusial for growth of roots and had been found that low levels of P (10 μM P) caused more reduction on growth of roots than salinity (100 mM NaCl), in both salt-tolerant and salt-sensitive wheat cultivars (Abbas et al., 2018). Harvest removes every year a large amount of soil P that needs to return with the application of P

fertilizer for sustainable durum wheat production. The amount of P applied to durum wheat could base on a soil test, and phosphorus fertilizer should be applied during sowing. P is influenced by alkaline (pH > 7) soil conditions and $CaCO_3$ content; as a result, nearly 80% of P applied by fertilizers could be fixed in the soil (Barrow, 1980). Naima et al. (2015) tried to specify the proper P dose to succeed good production and after a 3-year experiment in arid climate and sandy soils concluded that the selection of proper cultivar, appropriate use of fertilizer, and the optimal dose are the solutions for sustainable agriculture. In sandy alkaline calcareous soil, the optimal P dose was 60 kg ha^{-1} (Naima et al., 2015). Also, they found that increased P uptake resulted in increasing P content, grain yield, number of spikes/m^2, and N uptake regardless of year. The type of fertilizer did not affect the yield and yield components significantly, making the selection of the fertilizer depending on price (Naima et al., 2015). Also, application of P at high rate (120 kg ha^{-1}) could compensate the drastic effect of water stress to yield and yield components in wheat (Mumtaz et al., 2014).

3.1.3 Potassium

For many years, the fertilization of durum wheat included excessive N and inadequate potassium (K), leading to continual depletion of soil K. K is an essential element for plants since it increases enzyme activity, affects respiration, enhances photosynthesis, and regulates stomata opening, resulting in reduced transpiration. So the fertilization program of durum wheat should design in such a way to provide adequate K to durum wheat plants. Pettigrew (2008) proposed increased potassium supply or the development of cultivars, which use more efficiently the K, to succeed increased wheat productivity and improved quality. Adequate K supply improved tolerance against different stress conditions by activating antioxidant defense systems (Hasanuzzaman et al., 2018). Nutrition with K can increase tolerance to drought and heat stresses and to diseases while it could reduce the harmful effects of salinity and result in better yield (Dias and Lidon, 2010; Mann et al., 2004; Wei et al., 2013). Many researchers reported the role of potassium in the increase of productivity and the improvement of quality of wheat under drought and heat (Dias and Lidon, 2010; Hasanuzzaman et al., 2018; Mesbah, 2009; Wei et al., 2013). Mesbah (2009) found that foliar spray with K in sandy soils that contain small amounts of K and inorganic matter could increase yield, yield components (number of tillers/plant, number of spikelet's/spike, grain weight), and WUE of wheat. Wei et al. (2013) found that adequate external K supply could increase wheat tolerance to drought stress and suggested that a promising strategy for better production to arid and semiarid areas could be the combination of adequate external K and drought-tolerant cultivars. Regarding the heat stress, the foliar spraying of potassium increased the heat tolerance of wheat by increasing photosynthesis, translocation, and accumulation of photosynthates as well as the dry matter, factors that are related to stress resistance and subsequently resulted in increased plant yields (Dias and Lidon, 2010; Mesbah, 2009).

Adequate K supply levels in combination with changes in NH_4^+/NO_3^- ration could result in reducing waterlogging, which causes significant yield losses of ~15%——20% (Guo et al., 2019; Herzog et al., 2016). K fertilization can reduce stalk lodging (Sweeney et al., 2011), improve synthesis of protein (Mengel et al., 1981), increase photosynthesis during the grain filling stage (Raza et al., 2012), increase the spike length and the number of spikelets per spike (Raza et al., 2014), and increase the grain number (Raza et al., 2012) and the yield (Duan et al., 2014; Raza et al., 2014).

3.1.4 Microelements

Elements in solution cultures that are required in large quantities are called macronutrients (N, P, K, Ca, Mg, or S), while those needed in small amounts (Mn, Cu, Zn, Mo, B, C1) are classified as micronutrients. Both macronutrients and micronutrients are essential for plants. The usual wheat fertilization does not include micronutrients. However, some of them are not available to the durum because they are inadequate quantities in some soils or are fixed in the soil or for other reasons.

Zinc (Zn) application enhanced reactive biosynthesis and improved the effects caused by drought stress, so it may be used in arid and semiarid environments to increase grain yield (Ma et al., 2017). Moreover, foliar application of boron (B) and manganese Mn) at a late growth stage can increase grain yield and WUE of water-stressed wheat plants (Karim et al., 2012). In wheat plants with copper (Cu) deficiency, the number and size of pollen grains is severely restricted, while pollen grains lack fertility (Graham, 1975).

3.2 Conservation agriculture

Conservation agriculture is a concept based on minimum soil distribution, residue retention for permanent soil cover, and crop diversification that provides the potential to improve soil resilience and contributes to sustainable crop production (Hobbs et al., 2008). It aspires to achieve sustainable land management, protection of the

environment, and adaptation to climate change (FAO, 2017) and includes several types of soil cultivation and tillage. In this framework, conservation tillage is the practice that promotes continuous soil cover in the form of live crops or crop residues; it involves any method of soil cultivation that leaves the crop residues of the previous year on the field before and after planting the preceding crop to diminish soil erosion and runoff and assure that at least 30% of the soil surface is covered with crop residue/organic residue following planting (Dinnes, 2004). Then, reduced tillage is the tillage application within a crop rotation that is reduced in intensity (use of shallow disk harrowing instead of plowing) and/or the number of tillage events and zero tillage as the most extreme form of minimum soil movement that, in combination with crop residue retention, it improves top soil structure and eventually affects soil flora and fauna and subsequently disease pressure (Verhulst et al., 2011). These alternative tillage techniques aspire to address the negative effects of intensive tillage that contributes to soil sensitivity to erosion and water losses and drought, both of which may increase under climate change. Also, it is reported that tillage affected crop growth and the number of grains per square meter in several wheat types (Honsdorf et al., 2018).

In general, the reduced tillage systems are of low cost in comparison with the conventional tillage systems because they require less machinery repair and maintenance cost and also less labor time due to fewer tillage treatments for the preparation of the seedbed (Kimble et al., 2007). Zero tillage technology reduces the costs of field preparation, and it also saves time and labor cost per hectare. Also, the reduced fuel consumption results in diminish fuel cost and reduced carbon emitted to the atmosphere. Zero tillage could reduce greenhouse gas (GHG) emissions and increase crop yields in dry climates, thus contributing to the decrease of climate change and the potential for global warming (Huang et al., 2018).

4. Diseases, insect pests, and weeds concerning to climate change and crop management practices

Wheat occupies about 220 million hectares around the world, the most significant area by any other plant, and is the basis of human nutrition in many regions of the earth. The main crop area is the temperate areas of the earth. However, wheat is cultivated in many tropical and subtropical countries. Throughout the world, wheat occupies about 15% of cultivated land (FAO, 2019).

Although the wheat yield is determined by the cultivars (genetic potential), the final yield of the crop is significantly affected by the diseases, the animal pests, the weeds, and other factors. Estimates of potential losses of wheat yield due to weeds, animal pests (arthropods, nematodes, rodents, birds, etc.), pathogens, and viruses amounted to 23%, 8.7%, 15.6%, and 2.5%, respectively. Crop protection practices have reduced overall 49.8% potential losses to 28.2% actual losses, consisting of 7.7% of weeds, 7.9% of animal pests, 10.2% of pathogens, and 2.4% of viruses (Oerke, 2006). The distribution in space and time, as well as the proliferation of plant diseases, insects, weeds, etc., are primarily determined by climate, as temperature, light, and water are significant factors in controlling their growth (Rosenzweig et al., 2001). However, the estimation on overall potential wheat crop losses due to climate change is not possible because of the unpredictable adaptation of certain pests to new climatic conditions (Lamichhane et al., 2015).

According to Oerke (2006), diseases and weeds are responsible for the highest losses in wheat production worldwide. The incidence of diseases, especially rusts, powdery mildew, and blotch diseases increases with the intensity of crop productivity. In areas with low productivity and without seed dressing, soil-borne pathogens appear more important. Animal pests cause significant losses in some areas, while virus-related losses are of minor global importance.

The major biotic factors that are responsible for wheat yield losses with their predicted development due to climate change and how to mitigate their impact on wheat are described.

4.1 Pathogen and wheat diseases

A major factor affecting the crop yield is diseases. According to Strange and Scott (2005), at least 10% of global food production is lost due to plant diseases. For the development of a plant disease, a pathogen and a host must come in contact and must interact in the appropriate environmental conditions. The interactions of these three components of disease have often been visualized as a triangle known as the "plant disease triangle." Each side of the triangle represents one of the three components. The length of each side of the triangle is proportional to the contribution of each component to the disease. If any of the three components is zero, there can be no disease (Agrios, 2005).

Climate change undoubtedly affects environmental conditions. Climatic factors that change and affect plant diseases are temperature, precipitation, drought, carbon dioxide (CO_2), and other "GHGs" such as nitrous oxide and methane, precipitation, ozone, and "extreme events" (Newton et al., 2012). These factors are expected to affect directly and in a variety of ways the epidemiology of wheat diseases, including the primary inoculum, the progression of disease during the wheat growing season, the duration of the epidemics, and also the physiology, growth, resistance, or susceptibility of the wheat (host) to diseases and the pathogens—wheat relationship. They will also affect the management of wheat diseases, which will control their dispersal. The possible occurrence of extreme and unexpected weather events will cause severe conditions for any spraying. However, while climate change is likely to affect the infection, aggressiveness, or virulence of pathogens, it could be offset by a concurrent increase in the resistance of the host (wheat) without eventually changing the impact of the disease (Garrett et al., 2006).

Generally, rising temperatures and CO_2 levels increase some diseases and reduce others. A change in temperature due to climate change is likely to affect both the host plant (wheat) and the pathogen (Petzoldt and Seaman, 2006). Also, it will have potential impacts on the spread of infectious diseases and their survival between seasons (Gautam et al., 2013). Many plant diseases are more severe after mild winters or during warmer conditions (Harvell et al., 2002). Boland et al. (2004), while considering that the primary inoculum, the establishment, and the progress of wheat diseases will present various enhancing and mitigating changes in Canada, consider that the duration of the epidemics will not be affected.

Increased environmental CO_2 can affect both wheat and pathogens in many ways. High concentrations of CO_2 are likely to increase C:N ratios of residuals, which will reduce the decomposition of plant debris in the field (Ball, 1997), where the pathogens overwinter, resulting in higher levels of primary inoculum at the beginning of the growing season and, finally, earlier and faster epidemics (Manning and von Tiedemann, 1995). McElrone et al. (2005) suggested that there is a potential reduction in the incidence and severity of diseases where the pathogens target the stomata due to reduced stomatal opening and altered leaf chemistry. It is expected to favor the production of wheat biomass (Gautam et al., 2013; Manning and von Tiedemann, 1995; Kimball et al., 1993), grain yield, photosynthesis, and WUE and to reduce the damage from ozone, while new races of pathogens may rapidly evolve at high temperature and CO_2, in a favorable microclimate within enlarged canopy (Debela and Tola, 2018). The increase in ozone levels has had opposite effects to those caused by CO_2. According to Juroszek and von Tiedemann (2013), pathogens are rarely directly affected by elevated CO_2 and O_3, but these are more often indirectly affected through host plant (wheat) responses to elevated CO_2 and O_3. Ozone has rather indirect effects on pathogens through negative effects on a number of plant processes, e.g., photosynthesis (Krupa et al., 2001). Elevated O_3 decreased wheat grain yield (29%), aboveground biomass (18%), photosynthetic rates (20%), Rubisco activity (19%), stomatal conductance (22%), and chlorophyll content (40%) (Feng et al., 2008). These negative effects of ozone on wheat can be equalized by the increase of CO_2, but CO_2 is not capable of compensating the effects of fungal infection (Tiedemann and Firsching, 2000). Concentrations of air pollutants (ozone, SO_2, nitrogen oxides, etc.) increased during the 20th century, and these affect photosynthesis, respiration, carbon allocation, and stomatal function and (Darrall, 1989) and may impair disease resistance mechanisms (Bearchell et al., 2005). Changes in GHG concentration, e.g., methane (CH_4) and sulfur dioxide (SO_2), and UV-B radiation will have different effects on pathogens and pathogen—wheat interactions, with varying incidence and disease severity (Gautam et al., 2013; Chakraborty et al., 2000). Rainfall may affect the infection in particular, and CO_2 changes could affect the entry of the pathogens from the leaves' stomata (Newton et al., 2012). More frequent and extreme rainfalls will create favorable environments for the pathogens for more and longer periods (Petzoldt and Seaman, 2006). Precipitation will increase the humidity, and wet wheat canopies will result in a favorable environment for development of diseases.

4.1.1 The wheat rusts

There are three different rust diseases of wheat: leaf rust (brown rust), stripe rust (yellow rust), and stem rust (black rust). The fungus that causes leaf rust is *Puccinia triticina* Eriks (formerly known as *Puccinia recondita*) and mainly attacks the leaves; the one that causes stripe rust is *Puccinia striiformis* f. sp. *tritici* and mainly attacks the leaves and the glume; and the stem rust is caused by the *Puccinia graminis* f. sp. *tritici* that attacks mostly the leaves, the stems, and the spikes. All rust fungi are obligate parasites and only survive on living plants.

Each rust has a different regional significance. Stripe rust appears to be more important in west Asia, southern Africa, the Far East (China), South America, and northern Europe; leaf rust in South Asia, northern Africa, South East Asia, and South America; and stem rust in North America, Australasia, northern Africa, South Africa, and, to some extent, Europe (Mclntosh et al., 1995).

The rusts spread rapidly and reduce the yield and quality of the wheat. Significant factors for the infection are the susceptibility of the cultivar, the race of the pathogen, the timing of the infection, and the weather. Damage to wheat

depends on the stage of plant development at the time of infection and the severity of the disease. High levels of disease before or during heading usually have the greatest effect on yield. The main methods of wheat rust control are breeding-resistant cultivars and chemical control. However, due to the low yield or low price of wheat, the use of fungicides is not amortized; the best solution is the use of resistant cultivars, which in fact have significantly reduced the losses from by rusts for years.

Mboup et al. (2012) studied the behavior of the fungal pathogen *P. striiformis* f. sp. *tritici* and considered temperature as an important determinant of yellow rust epidemics and found strong temperature effects as well as genotype×temperature interactions in pathogen fitness traits. Increasing winter temperatures will result in faster development of leaf rust. However, since the increase in the average daily maximum yield during the development of the grain reduces the yield losses (Murray et al., 1994), the yield of wheat grain does not appear to be affected (Chakraborty et al., 1998). Wheat leaf rust resistance genes are temperature sensitive (Das et al., 2017; Dyck and Johnson, 1983) and responded differently at different temperatures (Browder and Eversmeyer, 1986). However, while Tiedemann and Firsching (2000) reported that leaf rust was strongly inhibited by ozone, Pfleeger et al. (1999) found that there was no interaction between ozone and wheat leaf rust.

It is not known the effect of climate change on the three rusts and especially on the ability of pathogens to overcome the resistance of wheat cultivars. However, increased CO_2 concentrations and higher temperatures will probably lead to an increase of the biomass and the canopy of the wheat crop to a larger area available for pathogen attack (Das et al., 2017). Climate change is likely to lead to a diversification of the life cycle of pathogens, and if new climatic conditions are favorable for the development of rusts, there will be a corresponding increase in the rate of evolution of new pathotypes and hence epidemics.

Recently, new, dangerous strains of fungi appear due to climate change. A new strain of stem rust destroyed tens of thousands of hectares of crops in Italy, in 2016. Two new strains of yellow rust have been spotted, one in Europe and North Africa and the other in East Africa and central Asia (Bhattacharya, 2017).

4.1.2 Wheat powdery mildew

It is caused by the obligate, biotrophic ascomycetous fungus *Blumeria graminis* (DC) Speer f. sp. *tritici* Em Marchal (Bgt) (syn. *Erysiphe graminis* (DC) f. sp. *tritici*), which attacks all aboveground wheat parts, including stems, leaves, and spikes. The optimal temperature for infection is around 15−20°C, but infection can take place in a range of 5−30°C. High relative humidity (>95%) also favors spore germination, but free water inhibits spore germination (Agrios, 2005; Cowger et al., 2012; Basandrai and Basandrai, 2017). Till today, 54 powdery mildew-resistant genes have been identified, cataloged, and designated as *Pm1* to *Pm54* with multiple alleles at some loci (Basandrai and Basandrai, 2017).

The importance of powdery mildew for the wheat is expected to be increased in the northern countries due to the milder climate (Roos et al., 2011), but it is expected to be limited its growth in the Mediterranean area, unless the pathogen will adapt to higher temperatures (Matić et al., 2018). High levels of O_3 will increase the wheat susceptibility to powdery mildew (Tiedemann et al., 1991; Tiedemann, 1992; Mina et al., 2016), but high levels of CO_2 are expected to reduce significantly the growth of the disease (Thompson et al., 1993; Matić et al., 2018). However, the combination of increased concentrations of CO_2 and higher temperatures will probably lead to the wheat-dense canopy, which favors the powdery mildew (Das et al., 2017).

4.1.3 The blotch diseases

The blotch diseases are Septoria tritici blotch, Septoria nodorum blotch, and Tan spot and are caused by the Ascomycete fungi *Zymoseptoria tritici* (formerly known as *Mycosphaerella graminicola* or *Septoria tritici)*, *Parastagonospora nodorum* (synonym: anamorph *Stagonospora;* teleomorph *Phaeosphaeria nodorum*), and *Pyrenophora tritici-repentis* (anamorph *Drechslera tritici-repentis*), respectively.

The higher temperatures, especially the nighttime temperatures in March, were positively correlated with an overall increase in spot blotch severity and reductions in wheat yield (Sharma et al., 2007). Increasing summer rainfall will result in more host emergence (volunteers, weeds) and result in more available rust inoculum to infect early sown wheat. The increase of precipitation before and after heading would also increase the severity of Septoria tritici blotch (Chakraborty et al., 1998). Bearchell et al. (2005) and Shaw et al. (2008) suggest that the ratio of the pathogens *P. nodorum*: *M. graminicola* that cause two septoria blotch diseases in the United Kingdom and the dynamic of pathogens are linked to changes in sulfur air pollution (SO_2) and affected by meteorological, host, and agronomic factors. High levels of O_3 will increase the wheat susceptibility to leaf spot disease and spot blotch (Tiedemann et al., 1991; Tiedemann, 1992; Mina et al., 2016).

4.1.4 Fusarium head blight

Fusarium head blight (FHB), also known as scab, is caused by species of fungi in the genus *Fusarium*, of which *Fusarium graminearum*, *Fusarium culmorum*, and *Fusarium avenaceum* are the most common and most virulent, and their geographical distribution appears to be related to temperature and moisture (Wegulo et al., 2015).

Vaughan et al. (2016) suggest that wheat may be more susceptible to *Fusarium* infection under future climate conditions. The compositions of *Fusarium* species responsible for FHB and mycotoxins produced by them will change due to global warming and other human activities (Yli-Mattila, 2010). Also, wheat anthesis will be earlier, and FHB epidemics will be more severe (Madwick et al., 2011).

4.1.5 Wheat bunt

Tilletia caries (synonym: *Tilletia tritici*) and *Tilletia laevis* (synonym: *Tilletia foetida*) cause the common bunt, whereas *Tilletia controversa* causes dwarf bunt and *Tilletia indica* causes Karnal bunt (Agrios, 2005).

Baker et al. (2000), by studying a humid thermal index resulting from relative humidity and maximum daily temperature predict for 2050 the spread of Karnal bunt, in much of Europe. Because *T. indica* has the potential to enter, establish, and cause unacceptable impacts in the wheat-growing areas of Europe, Sansford et al. (2008) justify the necessity of maintenance of the minimal phytosanitary requirements that are in place in European countries and that are aimed at preventing entry.

4.1.6 Insect pests

Climate change is expected to change the geographical distribution of insect pests, impacting significantly on the temperature range, but also the food availability for the pests and their natural enemies. The insect populations may be unstable, resulting in outbreaks in some regions with higher losses in wheat production, while losses may be reduced in others.

Climate conditions (e.g., temperature range, day length, etc.) are the most important abiotic factors affecting the distribution, overwintering and over summering, growth, number of generations, interspecific interactions, and dynamics of the insect populations when host plants are available. Phenology, reproduction, and growth of insects are significantly affected by their exposure to different climatic values (Lamichhane et al., 2015).

Temperature is the main factor that affects insect herbivores directly. Rising temperatures increase the rate at which insects can digest food, thus causing damage to crops at a faster rate, while in temperate areas, the increase in temperature could make the insects more active and reproductive (Deutsch et al., 2018). Tian et al. (2019) found that elevated temperature decreased AMF colonization rates on wheat roots and increased the aphid population, which may negatively impact wheat grain yield and quality (decreased wet gluten, Zeleny, protein, total soluble sugar, and starch and increased fiber).

Precipitation changes could impact insect pests in different ways. Some insects are removed from crops by heavy rains, and others are sensitive to drought (Petzoldt and Seaman, 2006).

Thus, some insect species may disappear, especially the most specialized, and spread other secondary less harmful today. The way of impact of changing climatic conditions on insects will vary between species depending on the environment, life history, and their ability to adapt (War et al., 2016).

4.1.7 Weeds

Climate change could effect on expanding the geographical range of weeds (migration of weeds or introduction of them into new areas), changing species life cycles, and population dynamics. Subsequently, weed migration will lead to a differential structure and composition of weed communities within natural and managed ecosystems (Ramesh et al., 2017).

Weeds compete with wheat for space, light, water, and nutrient availability. Climate change will lead to complex wheat−weed interactions and affect the competitiveness between wheat and weeds to exploit environmental resources. Weeds with different photosynthetic pathways C3 and C4 may exhibit different responses to increased CO_2 and temperatures, which may affect the dynamics of wheat−weed competition (Varanasi et al., 2016). When weeds are C4 plants with a different photosynthetic pathway from wheat (C3), weeds probably will respond differently at stressful levels of environmental factors (temperature, light, water, nutrients). Changes in concentrations of CO_2 and other GHG could exert direct physiological and indirect climatic effects on weed/wheat interactions and influence weed management strategies (Patterson, 1995).

The wind helps seed dispersal of weeds. Any increase in wind is likely to increase the dispersion of weed species seeds, including invaders. Changes in time and amount of precipitation are likely to alter germination, plant size,

seed production, and other biological aspects of weeds. Extreme rainfall will favor competition between invasive weeds and wheat with negative impacts on the wheat yield. Rising temperatures are likely to allow the spread of invasive weeds from lower to higher latitudes (Ziska et al., 2011).

Because weeds seem to respond more positively than wheat to the increased CO_2, the potential for increased competition and increased losses is created. Wheat crops could be reduced in yields where control of weeds is absent or insufficient. Although weeds, like all plants, depend on moisture for seed germination and final plant size, moisture is a key factor for overwintering and seed production. Both the quantity and the rainfall time can also be significant (Hatfield et al., 2011).

Environmental factors such as light, CO_2, temperature, soil moisture, relative humidity, precipitation, and wind can directly affect the effectiveness of the herbicide by altering the penetration and translocation of herbicides within the plant or indirectly by changing the growth and physiological traits of plants. The herbicides applied to the soil are mainly affected by moisture and soil temperature, whereas those applied to the leaves are affected by many environmental factors (Varanasi et al., 2016).

The herbicide efficacy appears to be negatively affected by elevated CO_2. The absorption of foliar herbicides decreases due to a decrease in the number or aperture of the stomata, or a change in the thickness or size of the leaves. The intake of soil-applied herbicides is limited by changes in CO_2-induced transpiration (Hatfield et al., 2011).

4.2 Management practices for pathogen and wheat diseases to mitigate climate change

4.2.1 Diseases

Climate change will certainly have a major impact on wheat pests with potential impact on researchers (breeders, plant pathologists, agronomists, climatologists, etc.), farmers, and policymakers.

Strategies will be required to develop methods for diseases' control (reduction of the primary inoculum, conditions to reduce the spread of diseases). New resistant or tolerant cultivars should be bred which, combined with effective plant protection products, will maintain healthy wheat crops. Further research is needed to ensure those warning systems that predict the establishment and development of wheat diseases (directly based on the initial contamination and indirectly based on climatic conditions) are accurate to guide plant protection product applications for disease control over high-risk periods and/or locations and avoid unnecessary fungicide applications in low-risk situations.

For integrated management of the wheat diseases in the future, it is necessary to be established monitoring and early warning systems for the prediction of epidemics. Also, the phytosanitary requirements for the incoming genetic material in the countries, which are aimed at preventing the entry of new pathogens, should be maintained.

Farmers have to sow healthy seeds. To reduce inoculum sources, they have to follow the proper crop rotation, fertilization, and cultural practices, and they have to spray with the appropriate fungicides or to apply alternative biological measures to control the diseases. Moreover, they have to control the weeds and the volunteer plants (hosts) where pathogens overwintering. The use of fungicides is suggested when they are needed as part of integrated pest management.

But the best long-term strategy to mitigate the threat of the diseases is to use resistant cultivars, that are released through the breeding programs. A breeding program strategy must continuously monitor the variability of the pathogens, searching for and exploiting effective sources of resistance and breeding, and releasing and monitoring the new resistant cultivars. The newly released cultivars must have levels of resistance adequate not only to prevent crop loss but also to significantly reduce the pathogen population. Management of disease resistance in cultivars after they are released in agriculture is perhaps more important than achieving resistance in the first instance (Mclntosh et al., 1995).

In addition to new resistant cultivars, management practices based on modern technologies, such as PA, remote sense and control, information technology, and nanotechnology, will facilitate effective disease control and reduce yield losses.

4.2.2 Insect pests

Existing insect pest management systems should be improved to monitor, detect, and inform farmers about possible changes in insect pest distribution, population ecology, damage assessment, losses of yield, and impact assessment (War et al., 2016).

Due to the ban of many insecticides over human and environmental health concerns, new strategies should be adopted. A key factor for successful insect pest management will probably be the biological control of their

populations. So, it will be very useful to release and establish natural enemies, which require further research (Aguilar-Fenollosa and Jacas, 2014). A significant factor is intercropping, which is a viable practice to reduce insecticide use in wheat production systems (Lopes et al., 2016). Also, a well-designed rotation system can provide habitat and food to insect pests' natural enemies, such as parasitoids and predators. Another critical factor is the crop sowing date. Karadjova and Krusteva (2016) found that the abundance of aphid *Sitobion avenae* significantly reduced with late sowing. However, farmers could forecast the presence of the aphids using the percentage of attacked stems.

4.2.3 Weeds

It is necessary to determine the vulnerability of wheat crop to invasive weeds in an uncertain climate. So, predicted models have to be developed that approach local environmental conditions with the main local weeds and the most likely invaders interacting with the wheat crop. Stratonovitch et al. (2012) have developed a simulation model for winter wheat and the competitive weed *Alopecurus myosuroides* in the United Kingdom.

The weeds show greater elasticity in response to increasing CO_2 compared with the crops, due to the narrower genetic background of the cultivated plants. However, the recognition of specific genetic, morphological, or phenotypic characteristics either in relative weeds or in the less bred cultivated relatives and their transfer by appropriate techniques to wheat could be the focus of future work to improve wheat in response to increased atmospheric CO_2 or to climatic extremes (Hatfield et al., 2011; Ziska and McClung, 2008).

Weed management is an important factor for high yield. Farmers and weed scientists around the world have several options for weed control, including cultural, mechanical, chemical, and biological methods. Chemical weed management through the use of herbicides is the most economical and widely used alternative for the most developed countries, including the United States (Varanasi et al., 2016).

If climate change affects negatively weed control with herbicides, there is an overall assumption that weed control can continue to be effective with additional spraying or increasing herbicide concentrations. However, this would alter the environmental and financial costs of using pesticides (Hatfield et al., 2011).

The traditional way of controlling weeds before herbicides could help in cases the efficacy of herbicides will reduce due to climatic changes. It would base on a combination of several management practices and the choice of crop rotation. Farmers could insert in the crop rotation systems, except competitive wheat cultivars, pasture, or other annual competitive species.

5. Precision agriculture

Cereal grains have been a primary source of nourishment for humans, while wheat and rice are, respectively, the first and second most cultivated cereal crops in the world (FAOSTAT, 2019). "Green Revolution" led scientists to breed highly demanding wheat varieties that would flourish in the new agricultural normal: monoculture, dense planting, fertilizer intensive, machine harvestable, and water intensive (Flachs, 2016). The high yield potential of these wheat and rice varieties is attributed to their short stature, high responsiveness to fertilizers, and disease resistance (Borlaug, 1971).

Anthropogenic GHG emissions have increased in the last decades, driven greatly by the population and economic growth. GHG emissions per utilized agricultural area have increased due to the intensification of agricultural activities as a result of the continuous demand for more food. For instance, European Union's agricultural sector accounted for 10% of the European Union's total GHG emissions in 2015, producing 426,473 kilotons of CO_2 equivalent of non-CO_2 GHGs (EUROSTAT, 2017). In the United States, GHGs from agriculture are reported at levels of 9% in 2017, and they are contributed mainly by livestock, agricultural soils, and rice production (US EPA, 2015). Since 2010, China has become the largest GHG emitter in the world, accounting for approximately 11% of the global GHG emissions, a fact that has drawn widespread attention both domestically and internationally (Wang et al., 2014; Zou et al., 2015). Finally, agriculture is currently the fourth largest source of GHG emissions in Australia, responsible for 13% of Australia's emissions (Bourne et al., 2018). Consequently, GHGs inducing climate change cause less resilient agricultural production systems increasing the degradation of earth's natural resources.

PA practices have the potential of reducing GHGs through a significant mitigation of agricultural inputs by using remote sensing methods combined with high-tech equipment following spatial driven applications based on the real needs of the cultivated fields. Therefore, more efficient and effective crop management toward sustainable agriculture production models can drive innovative farming practices, which can assist in accurate decision-making and scheduling.

5.1 Precision agriculture in cereals

The use of nitrogen (N) fertilizer has changed global N cycle markedly and has been causing various negative environmental consequences such as eutrophication of surface water, global warming, and ozone layer depletion (Gruber and Galloway, 2008; Liu et al., 2016; Seitzinger, 2008). Modern production agriculture requires efficient, sustainable, and environmentally sound management practices. N is a critical factor in achieving optimum grain yields in cereal crops (Aulakh and Malhi, 2005; Fageria and Baligar, 2001), but its assimilation by the plant is governed by the complex rules of the plant–soil–water system. For example, N is the nutrient input typically required in large quantities for achieving high yields in lowland rice, but soils under these conditions are saturated, flooded, and anaerobic and, therefore, N use efficiency is low (Buresh et al., 1993). However, more than 50% of the applied N is not assimilated by the rice plant, and it is lost through different mechanisms including ammonia volatilization, surface runoff, nitrification–denitrification, and leaching (Dong et al., 2012; Rochette et al., 2013; Savant and Stangel, 1990).

Nitrous oxide (N_2O) is the primarly GHG related to agricultural soil emissions, essentially due to microbial transformation of nitrogen in the soil. This concerns N mineral fertilizers, manure spreading, and N from crop residues incorporated into the soil or lixiviation of surplus nitrogen. N_2O has high global warming potential (298 times higher than CO_2), and it should be minimized to reduce agricultural GHG emissions in total. The application of mineral N in the form of chemical fertilizers can also increase the N_2O emissions (Balafoutis et al., 2017). Therefore, N fertilizer management strategies that increase crop productivity and N use efficiency, while reducing negative environmental consequences, have to focus on parameters such as optimum time, rate, and spatial distribution methods that synchronize plant N requirements with N supply, to reduce N losses and maximize uptake of applied N in the crop (Islam et al., 2016). Legislative measures in the European Union, adopted to comply with the Directive 91/676/EEC concerning the "Protection of Waters against Pollution caused by Nitrates from Agricultural Sources," in some cases did not obtain the expected results and are not always accepted (or complied with) by farmers (Macgregor and Warren, 2006; Mouratiadou et al., 2010).

PA—also known as precision farming— is a site-specific form of agriculture that aims to optimize farm inputs, improve efficiency, and reduce environmental footprints by focusing on the right management practice at the right rate at the right time in the right place (Gebbers and Adamchuk, 2010). It employs information technology, specialized machinery, and remotely sensed or proximal data, to reduce the inputs but secure production at the same time. In the broadest sense, PA is the application of management decisions in space and time based on identifying, quantifying, and responding to variability (Leonard, 2015). Although the optimization of fertilizer application—and especially of N fertilization—has always been the primary focus of PA management practices due to its importance in achieving optimal yield in cereal crops, PA is now employed to optimally manage all agricultural inputs, from herbicides and water to seeding and fuel consumption.

5.2 Precision N fertilization

A major challenge in N management through PA techniques is the accurate prediction and mapping of plant agronomic traits related to plant nutrient status and—most importantly—to N content. Traditionally, soil-based testing methods have been widely used for providing N recommendation for upland crops (Filippi et al., 2019). Although accurate, this is a resource-inefficient approach, since it requires measurements from a dense sampling grid for the spatial interpolation to be representative of the soil properties of each portion of the field. Automated systems with wireless sensors have been proposed as a remedy (Li et al., 2014a,b), but such systems have not found widespread use. Remote or proximal sensing technologies offer a viable alternative for deriving precise N recommendations through the dynamic nondestructive estimation of plant N status throughout the growing season, along with predictions of other agronomic traits of interest (e.g., yield). Coupled with the rapidly advancing technology of unmanned aerial vehicle (UAV) platforms, they are nowadays starting to offer cost-effective solutions to various aspects of crop monitoring and sustainable crop management (Gago et al., 2015; Hunt and Daughtry, 2017; Khanal et al., 2017; Yang et al., 2018).

A number of active canopy sensors for estimating yield-related agronomic traits in cereal crops have been proposed for supporting precision N management. Sensors such as GreenSeeker (Trimble Navigation Limited, Sunnyvale, CA, USA) (Yao et al., 2014; Zhang et al., 2019; Zheng et al., 2016), Crop Cicle (Holland Scientific, Lincoln, NE, USA) (Cao et al., 2017, 2015), RapidSCAN (Holland Scientific, Lincoln, NE, USA) (Aranguren et al., 2018; Lu et al., 2017), and fluorescence meters (Yang et al., 2016; Zecha et al., 2017) have been utilized. For active field applications, these sensors are installed on the machinery for real-time sensing (Schwalbert et al., 2019), although this

approach can become cost-inefficient (time and energy consuming) if the tractor must enter the field just for monitoring the N status, at growth stages other than the appropriate for fertilizer application or weed and pest management.

A substantial number of studies have investigated the relationship between narrow-band vegetation indices (VIs) and various agronomic traits of cereal crops. The VIs are calculated from the spectral signatures obtained from handheld spectrometers, which are portable nonimaging hyperspectral sensors acquiring single spectral signatures from a small (typically circular) surface over the canopy. Monitoring whole plant or leaf N status has been the primary focus (Dunn et al., 2016; Inoue et al., 2012; Li et al., 2014a,b; Mahajan et al., 2017; Moharana and Dutta, 2016; Prey et al., 2018; Prey and Schmidhalter, 2019; Shi et al., 2015; Tan et al., 2018; Tian et al., 2014; Wang et al., 2012; Zhao et al., 2012a,b), but other agronomic traits such as aboveground biomass (Cheng et al., 2017; Gnyp et al., 2014, p. 2014; Huang et al., 2004; Zheng et al., 2015), leaf area index (LAI) (Din et al., 2017; Inoue et al., 2016; Kimura et al., 2004; Wang et al., 2011; Xie et al., 2016), chlorophyll content (Kasim et al., 2018; Lee et al., 2011; Swain et al., 2007), yield (Kanke et al., 2016; Kawamura et al., 2018), or even variations in nitrogen status between varieties have been studied (Moharana et al., 2018). These approaches typically construct empirical models through linear regression for each possible pair of agronomic traits versus VIs, thus identifying the individual VIs that are highly correlated with each agronomic trait. Other studies have used the whole hyperspectral signatures as input to multivariable N status prediction models, using modeling techniques such as partial least squares combined with multiple linear regression (Dunn et al., 2016) or nonlinear models such as support vector regression (Tan et al., 2018).

The aforementioned studies based on nonimaging spectrometers are important in that they identify the spectral wavelengths and/or VIs that could prove useful for predicting N status or other traits in cereal crops. For example, it has been reported that wavelengths in the green- and red-edge portion of the electromagnetic spectrum and relevant VIs exhibit high correlation with N status and biomass (Cheng et al., 2017; Inoue et al., 2012; Kanke et al., 2016; Prey and Schmidhalter, 2019), along with the typical VIs incorporating the NIR channel. However, canopy-level spectral data from spectrometers become inappropriate for fine-scale precision farming, since that would require an extremely time-consuming and cost-inefficient dense sampling. In addition, the calculation of optimized VIs requires the sensor to incorporate bands at very specific wavelengths, which are typically not available in most multispectral sensors. Recently, compact hyperspectral sensors that can be mounted onboard UAVs (or movable structures above the canopy) have been developed and successfully employed for estimating agronomic traits of cereal crops (Elsayed et al., 2018; Onoyama et al., 2017, 2015; Zheng et al., 2016a,b; Zhou et al., 2017). Nowadays, the use of these systems is still limited in PA applications, because their cost is relatively high, and processing such large volumes of data is quite challenging. However, they have great potential for being operationally employed in the future. Very recently, the potential use of a hyperspectral light detection and ranging system that can also provide vertical information within the canopy has been showcased (Du et al., 2017; Du et al., 2016a,b), but this is still an experimental platform.

Multispectral imaging sensor is probably the most widely employed system for PA applications in cereals cultivation. Traditionally, satellite imagery has been employed for monitoring plant growth and agronomic traits. Medium- to high-resolution satellite imagery (spatial resolution of 10−30 m) has been employed for providing estimations of plant crop stages (De Bernardis et al., 2016), LAI (Campos-Taberner et al., 2016; Semeraro et al., 2019), relative within-field variability (Barbanti et al., 2018; Maestrini and Basso, 2018), nutrient status (Delloye et al., 2018; Nutini et al., 2018), and yield (Busetto et al., 2017; Lai et al., 2018; Lyle et al., 2013; Noureldin et al., 2013; Silvestro et al., 2017) or has been incorporated within growth simulation models (Hank et al., 2015; Pagani et al., 2019; Yang et al., 2017). High-resolution synthetic aperture radar data have been employed for estimating morphological traits (most notably height) (Yuzugullu et al., 2016, 2015). Finally, a few studies have used commercial high-resolution (spatial resolution less than 10 m) satellite imagery to estimate N status (Castaldi et al., 2016; Huang et al., 2017; Magney et al., 2017; Zhao et al., 2015) or within-field variability (Busetto et al., 2017; Shang et al., 2015). An important drawback of this approach is the high cost of high-resolution satellite images, as almost all vendors enforce a large minimum area that can be ordered for a single image. Nevertheless, this is expected to change in the near future with the infiltration in the PA market of microsatellite image providers.

With the rapid development of UAV platforms (load capacity and flying autonomy), compact and lightweight multispectral sensors onboard UAVs provide a cost-efficient approach to PA in cereal crops today. The ultrahigh resolution of low-altitude flights allows the estimation of features such as plant height, LAI, agronomic stage, or within-field variability even with low-cost typical RGB cameras (Du and Noguchi, 2017; Marino and Alvino, 2019, 2018; Song and Wang, 2019; Zhu et al., 2016). Good correlation of certain VIs calculated from multispectral sensors

(RGB plus NIR channel), and measurements from chlorophyll meters have been reported (Saberioon and Gholizadeh, 2016; Swain et al., 2007), which could be used for estimating leaf N uptake (Zhang et al., 2016).

The actual application of spatially differentiated N doses is performed using variable rate technology (VRT) machineries, which are specialized systems that can adapt locally the rate of the fertilizer application based on preloaded spatially variable fertilization maps. The latter are derived through empirical models exploiting the results of the aforementioned agronomic trait estimations methods (Feng et al., 2018; Stamatiadis et al., 2018). The systems are driven by high-precision GNSS (global navigation satellite system) services that can achieve positional accuracy at centimeter level (Dabove and Manzino, 2014; Vázquez et al., 2018). Moreover, special sensors that are mounted on the combine and can accurately measure yield for each point within a single field during harvesting (Choi et al., 2014; Fravel et al., 2013; Long and McCallum, 2015), which can be exploited for making informed decisions the following growing season. The whole process is assisted by specialized software applications, even open-source ones (Leroux et al., 2018). There is also an ongoing initiative among prominent PA machinery manufacturers to define manufacturer-independent data exchange protocols, so that different machinery can communicate seemingly (Blank et al., 2013).

5.3 Biotic and abiotic stress monitoring and management

Monitoring biotic and abiotic stress in cereal crops is another prominent PA application field, which attains increasing interest. Photographs from simple RGB cameras (either handheld or onboard UAV) can be analyzed with state-of-the-art machine-learning algorithms to identify weed infestation (Berge et al., 2012; Jurado-Expósito et al., 2019; Lambert et al., 2018; Pahikkala et al., 2015; Tenhunen et al., 2019). Early identification of fungal diseases (especially yellow rust in wheat) is also of primary importance, and methodologies based on the analysis of data from various sources have been proposed, such as hyperspectral data (Huang et al., 2014; Lin et al., 2018), UAV images (Su et al., 2018), proximal RGB images (Du et al., 2016a,b), thermal images (Antonucci et al., 2013), fluorescence spectra (Römer et al., 2011), and even simple smartphone photos (Picon et al., 2019). Pest identification and monitoring methods have also been proposed, either using remote sensing data (Zhao et al., 2012a,b) or empirical models based on spatial prediction of dispersion methods (Merrill et al., 2015). After identification, the treatment can be applied locally using VRT systems similar to those used for PA N fertilization or even specialized autonomous robotic systems (Berge et al., 2012; Pérez-Ruiz et al., 2015). Finally, methodologies for predicting or identifying abiotic stresses such as frost risk (Yue et al., 2016) or heavy metal risk (Lv et al., 2014) can be applied for optimal crop protection and yield sustainability.

5.4 Smart irrigation

The efficient use of water in agriculture is one of the major agricultural challenges and modern technologies could contribute to this. To accomplish the efficient use of water, experts rely on data collected by soil, plant, and atmosphere to manage properly the irrigation requirements of the crops (Puerto et al., 2013). These data can be measured using special sensors. Although meteorological variables are representative of a large area and can be easily measured by a single sensor for a vast land extension, soil and plant variables have a large spatial variability. More recent trends led to the development of low-cost sensing systems to measure temperature and soil moisture, using sensors that can be placed on suitable sites of the fields for monitoring maize, wheat, sorghum, etc. The sensing system is based on a feedback control mechanism, which regulates the water flow in the real-time based on the instantaneous temperature and moisture data (Tyagi et al., 2011). Climate is a major factor in estimating the water requirements of the crops, while weather stations installed in different regions can provide data of key variables such as evapotranspiration that are of great importance to estimate the water requirements of the crops. The most common approach of using weather variables is to develop crop water requirement models for decision-making support (Navarro-Hellín et al., 2016). Soil variables, such as soil moisture content or soil matric potential, are considered by many authors as a crucial part of scheduling tools for managing irrigation (Cardenas-Lailhacar and Dukes, 2010; Soulis et al., 2015). Human expertise has been proved effective in assisting irrigation management, but it is not scalable and available to every field, farm, and crop. It is slow in the analysis of the data and real-time processing. Instead, applying machine learning techniques to replace the manual models and to assist experts creates automatic irrigation decision support systems. Giusti and Marsili-Libelli (2015) presented decision systems capable of predicting the volumetric water content of the soil based on local climate data.

6. Future perspectives

It is challenging to create a simple model of approaches for high and stable wheat productivity under water-limited/high temperature conditions and generally under climate change conditions.

Plant breeding should focus both on overall plant development and on flowering time and grain development stages since the last two stages are significantly affected by the climate change conditions and significantly affect the yield. Therefore, a better understanding of those developmental stages and in combination with the exploitation of more tolerant to abiotic and biotic stress genetic resources will result in the release of new varieties more adaptable to climate change conditions.

Finally, the combination of the use of more adaptable to abiotic and biotic stress varieties and of the application of PA and agronomic practices, which reduce stress effects, will result in higher and stable wheat production contributing to food security.

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CHAPTER

2

Ensuring sustainable food security: exploiting alien genetic diversity in wheat breeding for adaptation to emerging stresses

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OUTLINE

1. Ensuring food security: the challenge of zero hunger

Poverty alleviation is a global challenge and shared responsibility. The past three decades of global poverty reduction efforts are attributed to have lifted more than a billion people out of extreme poverty (World Bank, 2017). Furthermore, the rate of worldwide poverty today is lower than it has ever been in the recorded history of mankind. Nonetheless, meeting the target of reducing extreme poverty still requires substantially greater efforts. In spite of the tremendous global progress in tackling poverty, the number of vulnerable people still remains unacceptably high (Liu et al., 2018). Likewise, there remain significant challenges, and the rate of poverty decline has decelerated more recently, raising concerns about achieving the goal of ending poverty by 2030 (Mundial, 2018).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00002-9

Looking into the global population trends and food security targets set for 2050, production of high-quality food must be doubled in ways that are environmentally and socially sustainable (Ramírez-González et al., 2018; Mujeeb-Kazi et al., 2019). This seems an enormous task as many of these production constraints are associated with "climate change" (Mujeeb-Kazi et al., 2017). Nonetheless, feeding the ever-growing population entails farmers to produce additional food from limited land and water resources. The current practices of crop improvements are insufficient to uphold the demands of future populace numbers or the increasing scale of potential climate change impacts (Ali et al., 2016; Tariq et al., 2018). Therefore, approaches that integrate food security and climate change concerns hold immense promise in addressing both biotic and abiotic stresses in wheat (Borrill et al., 2019).

It is anticipated that the global climate variations are likely to make it tough to achieve the set targets for yield increases in many parts of the world. Major constraints of yield losses will include extreme weather events and the incidence of such events, which are expected to intensify with climate change (Abberton et al., 2016). Environmental hazards and urban expansions of arable land are limiting our potential to address food security concerns, and by 2050, this may result in shrinkage of the globally harvested area by 8%−20%. Similarly, major cereal production areas in the subcontinent may get interfered if there are climate changes, melting of Himalayan glaciers altering the monsoon spectra, and flooding and drought patterns in Asia (Young, 1999; Nellemann et al., 2009; Chakraborty and Newton, 2011).

With no exaggeration, climate change will have a marked impact on the geographical distribution of plant species in both natural and managed ecosystems with varying magnitudes. Endemic/natural vegetation will face challenges like competition with species; thereby, new combinations of species are likely to arise, whereas, in agriculturally managed ecosystems, climate change will have severe socioeconomic implications and will largely shape the society's ability to use available resources (Coakley et al., 1999). Preparing agricultural systems for climate change−related impacts would require more resilient agricultural system and investments in relevant infrastructure (Abberton et al., 2016; Rasheed et al., 2017). Therefore, addressing food security and zero hunger challenge, the need to recognize cohesive efforts for transforming and reorienting agricultural systems demands support of food security and stringent focus on climatic resilience (Borrill et al., 2019; Mujeeb-Kazi et al., 2019).

2. Bread wheat as a conduit toward food security

With over 749 million tons of annual production, bread wheat (*Triticum aestivum* L., AABBDD 2n = 6x = 42) has become a universal cereal crop with potential of addressing the growing demands of world's food supply (Masood et al., 2016; FAO, 2018; Borrill et al., 2019). Currently, wheat is a staple food providing some 35% of the human calories (Peng et al., 2004; Rasheed et al., 2017). Furthermore, wheat is adapted to varied environmental conditions and is cultivated on an extensive area that is more than assigned to any other crop species (Gustafson et al., 2009). With the rise in human populace, the demands of worldwide food production have steadily increased, and wheat being a rich source of energy and proteins could serve as a potent crop in the appraisal of food security (Foulkes et al., 2010; Rasheed et al., 2017; FAO, 2018).

Future food security poses a serious challenge, and holistic researches aiming at bread wheat as a vital food security crop are of immense significance. Historically, the wheat yield potential has been achieved by the proportional increase in agricultural inputs and by the availability of new arable land, whereas future gains, however, will rely heavily on genetic improvements (Ramirez-Gonzalez et al., 2018; Borrill et al., 2019). Therefore, approaches that integrate food security with deep understanding of the wheat genomic improvements hold immense promise. Holistic approaches are warranted for transforming agriculture in such a way to support sustainable food security as well as to tackle the challenges posed by climate change (Borrill et al., 2019; Varshney et al., 2018; Mujeeb-Kazi et al., 2019).

Nonetheless, predictions on future food insecurity/shortages are getting tougher due to the variable nature of the climate, and the recent failure to maintain global food production in line with population growth is corroborated by rising food prices (FAO, 2014). Prolonged increases in food prices will eventually lead to social unrest, particularly in the developing countries (Abberton et al., 2016). Furthermore, agricultural ecosystems convert raw materials such as light, water, CO_2, and nutrients into carbohydrates, proteins, etc. However, the changing climate affects the availability of the raw materials and thereby influences plant growth and yield and is critical for cereal crops like wheat because of its wider role in food supply (Hatfield and Dold, 2018). For wheat, yield and nutrient quality are the ultimate traits, and both are likely to be affected by climate change. Furthermore, the emergence of new virulent strains of pathogens, heat, drought, and salinity stresses are likely to further jeopardize wheat cultivation (Mujeeb-Kazi et al., 2017).

To fast forward the rate of genetic gains and mitigate climate change impacts, meeting the targets of food production would require integration of multidisciplinary research (Varshney et al., 2018; Mujeeb-Kazi et al., 2019). Since the birth of agriculture, crop improvements have been largely influenced by the demands for improved quality (taste or aroma as in rice) or higher yield potential and this compromised on other useful diversity (Tariq et al., 2018). In addition, the key pillar of our agricultural history—domestication—has been the replacement of native species by cultivars together with genetically limited introductions of nonnative species. These, in conjunction with extension of agricultural production during and after the Green Revolution, are the probable bottlenecks that have reduced crop traits diversity (Abberton et al., 2016; Rasheed et al., 2017).

Novel plant breeding and improvement procedures are urgently required to exploit the unused allelic variation for combating complex stresses to deliver and mitigate some of the worst scenarios of climate change while ensuring sustainable crop production (Abberton et al., 2016; Rasheed et al., 2018). For wheat, a broad coverage of promising and high-throughput phonemic as well as genotypic approaches is being rapidly developed (see Mujeeb-Kazi et al., 2019). Persistent advances in wheat productivity will be ascertained by integrated approaches of combining genetic improvement along with management practices (Hatfield and Dold, 2018). Moreover, advances in DNA sequencing and genomic prediction tools and their cost effectiveness have shown tremendous promise in wheat breeding and improvement. It is anticipated that the interplay of cross-disciplinary approaches will result in the delivery of climate change ready crops in less time (Varshney et al., 2018; Ramirez-Gonzalez et al., 2018; Borrill et al., 2019).

3. Genetic diversity as a means to mitigate major wheat yield and future adaptation constraints

Modern agriculture is reliant on the cultivation of a few highly productive crop species that were domesticated from wild by our ancestors some 10,000 years ago (Tanksley and McCouch, 1997). Today, for almost 80% of their caloric intake, mankind is dependent on fewer than a dozen of angiosperm species. Furthermore, we only exploit a fraction of the genetic diversity that exists within each of these domesticated species (McCouch et al., 2013). This diversity seems not enough to secure the future food concerns in the face of intensifying yields demands or climate change. However, the exact series of events of how plants were domesticated is yet to get unfolded. It is very probable that strong selection pressure resulted in rapid changes in plant species (Islam et al., 1981; Gill and Raupp, 1987; Mujeeb-Kazi and Hettel, 1995; Ali et al., 2016). Selective propagation of lines containing only favorable mutations and giving less emphasis to adaptive traits for adverse environments would have resulted in restricting the genetic base of plant populations, and that continues to this day (Fig. 2.1).

Following domestication, the genetic variation in crop plants has continually narrowed down by modern plant breeding. Extensive backcrossing and selection of the elite lines although has produced high-yielding pure crop varieties but has resulted in loss of useful diversity (Qi et al., 2007; Mujeeb-Kazi et al., 2013). In almost all plant species including wheat, new varieties are virtually derived from crosses among genetically related modern varieties—excluding the ancestral species. Nonetheless, such practices have dramatically reduced the genetic base of crop species (Schwarzacher et al., 1992; Tanksley and McCouch, 1997; Rasheed et al., 2018).

Wheat is an important staple food, and its cultivation is an important element of the global food security. However, plant breeders have been remarkably successful in developing high-yielding wheat cultivars that have kept nourishing the growing population. Yet, the limited genetic diversity renders wheat to deadly epidemics, and this jeopardizes the potential of wheat crop in sustainable agriculture (for details, see Tanksley and McCouch, 1997). Wheat production and quality are negatively affected by various biotic (virus, bacteria, fungi, insects, etc.) and abiotic stresses (heat, salinity, drought, cold, heavy metals, etc.), thereby hampering global wheat productivity (Ali et al., 2016; Mujeeb-Kazi et al., 2013; Tariq et al., 2018). For instance, modeling studies have indicated that for each degree rise in temperature, 6% decrease in wheat production was likely to occur (Asseng et al., 2017). Hence, it is imperious to widen the genetic base and breed stress-tolerant wheat genotypes for increasing food production as well as for future food security (Masood et al., 2016; Rasheed et al., 2017; Mujeeb-Kazi et al., 2019).

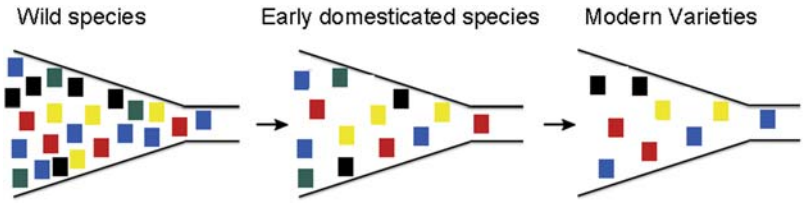

FIGURE 2.1 Schematic representation of the available genetic diversity available in wild species, early domesticates, and modern varieties. *Modified from Tanksley, S.D., McCouch, S.R., 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277 (5329), 1063–1066; Bevan et al. (2017).*

4. Wide hybridization: exploiting genetic diversity of the alien genes for bread wheat improvement and adaptation to emerging stresses

Historically, when wheat cultivation was dominated by land races, there was enough variation. However, intense selection for greater yield has, although, purified desirable alleles for higher yield, in the process, useful genetic variation particularly for stress tolerance/resistance got narrowed (Mujeeb-Kazi and Asiedu, 1990; Ali, 2012; Tariq et al., 2018). However, genetic restoration of wheat is possible by exploiting genetic resources that are available within the three gene pools of wheat (Islam et al., 1981; Schwarzacher et al., 1992; Ali et al., 2016). The primary gene pool is constituted by species with homologous genomes to wheat, and variation from these resources may be introduced through direct hybridization (Mujeeb-Kazi and Bernard, 1982; Schwarzacher et al., 2011). Diploid species of the section, Sitopsis and the *Triticum-Aegilops* polyploids, with at least one of the three genomes homologous to wheat are grouped into the secondary gene pool. Transfer of genes between the two genomes (wheat and secondary gene pool species) takes place through direct crosses or through special manipulation strategies (Mujeeb-Kazi and Hettel, 1995; King et al., 1997). Likewise, wild or cultivated *Triticeae* species, with nonhomologous genomes to wheat, constitute the tertiary gene pool. These species are rich sources for wheat improvement, being distantly related gene transfer is not possible by homologous recombination and requires special techniques such as irradiation, callus culture-mediated translocation, or *ph* manipulations (Kruse, 1974; Islam et al., 1981; Sharma and Gill, 1983a,b; Mujeeb-Kazi and Bernard, 1985; Qi et al., 2007; Mujeeb-Kazi et al., 2017).

Maintenance of useful genetic diversity in breeding programs is utmost vital, and this ensures sustained production as well as minimizes the risks of disease epidemics. Agronomists and breeders have been largely successful and have overcome the challenges of genetic bottlenecks in wheat through wise utilization of both the wild (alien) and cultivated *Triticeae* species with desirable variation (Wells et al., 1973; King et al., 1997; Divis et al., 2006; Wang et al., 2008). The first attempts of wheat-wide crosses are dated back to Wilson where the first wheat and rye hybrid was developed (Wilson, 1876). Similarly, report of doubling wheat—rye hybrids complement (or Triticale) was given by Rimpau (1891). Since then, many hybrids involving wheat with other *Triticeae* members have been produced systematically and studied (Farrer, 1904; Kihara 1937; Kruse, 1974; Sharma and Gill, 1983a,b; Mujeeb-Kazi and Bernard, 1985; Graybosch et al., 2009; Rasheed et al., 2018). Besides hybrids, there are plentiful illustrations of gene transfers into bread wheat for improved grain quality and/or resistance, extending the genetic base of wheat germplasm (Mujeeb-Kazi and Kimber, 1985; Jiang et al., 1994; Sharma, 1995; Heslop-Harrison, 2010; Gill et al., 2011; Carvalho et al., 2009; Schwarzacher et al., 2011). Various annuals and perennials of *Triticeae* members from the three gene pools have proven as mighty sources in tackling genetic bottlenecks of conventionally developed wheat cultivars by transferring quality as well as disease resistance traits (Mujeeb-Kazi and Rajaram, 2002).

In wide hybridization, bread wheat is used as a maternal parent (Fig. 2.2), and hybrids are obtained following well-established protocols (Mujeeb-Kazi and Hettel, 1995). This F_1 hybrid plantlet is usually self-sterile but often is female fertile supportive of easy BC_1 production. However, in rare cases, pollen mother cells may undergo restitution division (meiotic restitution) producing unreduced gametes. Similarly, the sterile F_1 hybrids on colchicine treatment results in fertile amphidiploids (King et al., 1997). Extensive backcrossing follows the production of amphidiploids (between wheat and alien species) till individual alien chromosome addition lines are obtained. The entire alien chromosomal arms may be introgressed into wheat by exploiting the centric breakage fusion property of univalents (for further details, see Mujeeb-Kazi and Hettel, 1995). The effectiveness of introgressed chromosomal segment/s is determined by the substituted chromosomal segment/s of wheat genome, and in cases, the alien chromatin may depress essential agronomic or end-use quality attributes. However, such linkage drag effects are buffered to a higher degree in polyploid species compared with their diploid ancestors (Qi et al., 2007; Ali, 2012; Ali et al., 2016). Still, wheat-alien compensating translocations with minimal alien chromatin with the desired gene are of immense importance, as they would introduce the desired character and will have less likelihood of linkage drag (Forsström et al., 2002; Friebe et al., 2009; Gill et al., 2011).

Due to the presence of three main crossability genes *kr1kr1*, *kr2kr2*, and *k3k3* on homoeologous group 5, most intergeneric hybrids of the *Triticeae* species have been produced within the *T. aestivum* cv. Chinese Spring backgrounds (Mujeeb-Kazi and Asiedu, 1990). Another gene, i.e., the *Kr4/kr4*, has been identified and mapped to chromosome 1A (Zheng, 1992; Luo et al., 1993). The presence of dominant *Kr* alleles normally prevents crossability, whereas the recessive *kr* alleles fail to prevent interspecific hybridization (Molnár-Láng, 2015). Literature survey indicates to extensive reporting on gene transfers for bread wheat improvements, where crosses are made between wheat and closely as well as distantly related species. Successful gene transfers have been achieved from members of diverse genera including (but not limited to) *Triticum*, *Secale*, *Aegilops*, *Hordeum*, *Thinopyrum*, *Lophopyrum*, *Agropyrum*, *Psathyrostachys*,

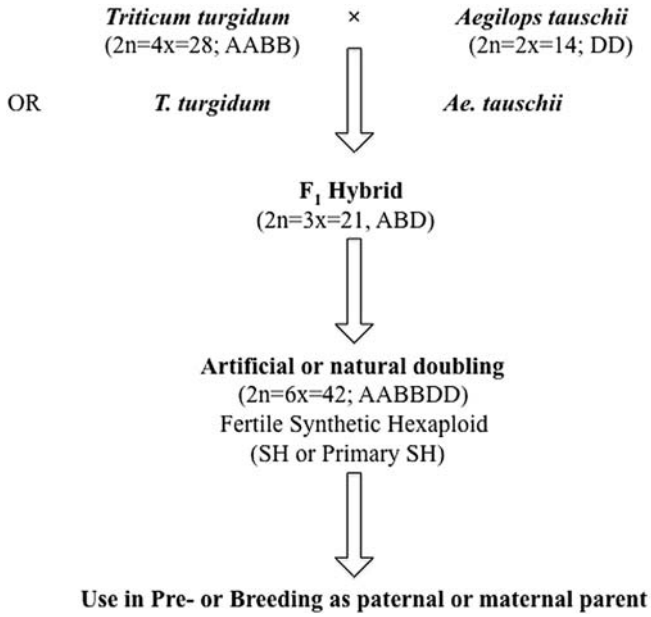

FIGURE 2.2 Production of D-genome synthetic hexaploid wheats (2n = 6x = 42, AABBDD) from crosses between durum wheat (AABB genome) with *Aegilops tauschii* (D genome). For additional details, see Mujeeb-Kazi et al. (2017).

Elymus, *Leymus*, and *Dasypyrum* etc. (Mujeeb-Kazi and Hettel 1995; Gupta, 2016). Here, we focus with examples on the use of wheat-rye (1RS), wheat/*Thinopyrum intermedium* (4JS), and D-genome synthetic hexaploid wheat (SHW) line diversity that exhibit the potential to address sustainable food security as well as to confer resilience against biotic and abiotic constraints under change climates.

5. Potential of wheat-Rye chromatin for bread wheat improvement

Alien chromatin deriving from the short arm of rye chromosome (1RS) into wheat is the most widely used rye translocation for increasing the genetic base of wheat. This chromatin carried genes for resistance to powdery mildew, stem rust, green bug, and wheat curl mite as well as genes for enhancing grain protein and grain yield in wheat (Singh et al., 2018; Howell et al., 2019). The 1RS has been transferred to the wheat homoeologous group 1 of wheat (i.e., 1A, 1B, and 1D); compared with the T1DL.1RS. The T1AL.1RS and T1BL.1RS translocations are extensively used and having the greatest of impacts in bread wheat development (Graybosch, 2001). The first T1AL.1RS translocation was derived from "Insave" rye (via triticale Gaucho) and was found in the wheat line "Amigo," whereas the second T1AL.1RS translocation was reported in the germplasm line GRS1201, and this is differentiated from Amigo translocation due to its Secalin variability. Interestingly, the GRS translocation was traced to the same rye source (Insave) as the Amigo, indicating to the intraspecific variation in Insave rye genes present on 1RS (Porter et al., 1994; Sebesta et al., 1995; Friebe et al., 1996).

For T1BL.1RS translocations, at least three independent origins are reported. Notably, two 1R(1B) substitution lines, i.e., "Zorba" and "Salzmunder Bartwiezen" were produced in Germany. The substitution line "Zorba" and "Salzmunder Bartwiezen" gave rise to a number of T1BL.1RS translocation lines. Similarly, "Kavkaz," a T1BL.1RS derivative of Salzmunder Bartwiezen, was produced in Russia and was widely distributed in different national and international wheat breeding programs. The Kavkaz T1BL.1RS translocation is probably the most important one in terms of its worldwide impact on wheat breeding and production. The Salzmunde translocation reportedly was derived from "Petkus" rye, while the "Zorba" translocation can be traced to crosses with triticale (Zeller and Hsam, 1983; Hanušová et al., 1996; Schlegel and Korzun, 1997). Third T1BL.1RS translocation was reported from Japan in wheat "Salmon" where the origin of rye material was derived from octaploid triticales (Zeller and Hsam, 1983). The T1DL.1RS translocation was induced in Australia, incorporating 1RS from "Imperial" rye. The Kavkaz 1BL.1RS and Amigo 1AL.1RS translocations most frequently appear in wheat cultivar improvement programs (see Graybosch, 2001). Notably, most of the CIMMYT material developed in the mid-1970s in Mexico carried the T1BL.1RS translocation in their pedigrees; breeders in CIMMYT took advantage of this translocation by

combining the IRS (derived from winter wheat Kavkaz) with spring wheats (Mettin et al., 1973; Mujeeb-Kazi et al., 2017). The origin is traced from a winter/spring cross-derivative that generated Veery "S" with the pedigree parents being Kavkaz, Buho, Kalyansona, and Bluebird giving rise to famous cultivars Seri, Ures, Glennson, Genaro, dwarf Veery 10, Pak 81, and others. This is an example that has made a major impact more than any other contribution of alien chromatin on wheat productivity across diverse mega environments globally. Since then, approximately 300 cultivars and germplasm lines carrying T1BL.1RS have been released (Schlegel, 1997; Rabinovich, 1998; Graybosch, 2001).

Enhanced grain yield and stability is attributed to the widespread use of 1RS in wheat improvement programs. Further, selection for disease resistance is another most likely reason of its distribution (Mujeeb-Kazi and Bernard, 1982, 1985; Ali et al., 2016). More importantly, the 1RS existed in diverse pedigrees of lines that wheat breeders would consider "good" parents, and this significantly enhanced the chances of 1RS's inheritance. Nonetheless, 1RS is also associated with linkage drag due to the presence of Sec-1 locus and having negative impacts particularly with regard to end-use quality (Graybosch, 2001). The introduction of 1RS compensates for the loss of the short arm of at least one wheat homoeologous group 1, resulting in loss of some important wheat quality genes (Zeller and Hsam, 1983; Schlegel, 1997; Rabinovich, 1998). Furthermore, all 1RS genes are no longer effective.

Linkage drag associated with 1RS varies with genetic background and judicious selection of parents while introducing the 1RS into wheats—the effects may be minimized. Furthermore, size of the 1RS chromatin may be reduced by induced recombination (Mettin et al., 1973; Mujeeb-Kazi et al., 2017). Still in some cases, the 1RS undergoes spontaneous recombination that may break the association of useful gene within a block containing genes that negatively affects wheat quality (see Ali et al., 2016). Thus, it is likely that the 1RS will continue to introduce novel variation and enrich bread wheat genome against emerging stresses and make an impact on wheat breeding for decades to come.

6. Potential of wheat—*Thinopyrum* hybrids in bread wheat improvement

Members of the genus *Thinopyrum* (referred to as wheatgrasses) are perennials in habit and are long known as excellent sources of providing allelic diversity against biotic and abiotic stresses. *Thinopyrum* species can hybridize to wheat, making them potential sources of novel genes for wheat improvement (Ali et al., 2016). Member of the *Thinopyrum* group have been effectively used for the introduction of novel variation against a number of stresses (Li and Wang, 2009). These transfers vary in size from small segments to chromosomes addition lines (Wells et al., 1973; Sears, 1973, 1977; Mujeeb-Kazi and Hettel, 1995; King et al., 1997; Qi et al., 2007; Ali et al., 2016). Earliest hybrids of wheat × *Thinopyrum* were developed some 80 years ago by Dr. N.V. Tsitsin in the 1920–30 (Tsitsin, 1965). Later on, wheat—*Thinopyrum* hybrids resulted in many progeny lines that are still maintained by the US Department of Agriculture. The "Zhong" series represent one of the vastly exploited wheat-*T. intermedium* hybrids that were produced in China (Sun, 1981). Although *Thinopyrum* species have displayed robust resistance against many wheat diseases (Friebe et al., 2009), early attempts of hybrid development did not aim on disease resistance but focused on perennial wheat (Tsitsin, 1965). Among the fungal diseases, Fusarium head blight, leaf rust, stem rust, and yellow rusts pose serious challenges to wheat production. Similarly, the recent rise in temperature has not only increased the prospects of heat stress but also increased selection of pathogen to heat adaptation (Garrett et al., 2006; Milus et al., 2009).

Members of the *Thinopyrum* group have genes for wheat improvement against major biotic (*leaf rust*, *stem rust*, *powdery mildew*, *Tapesia yallundae*, *eyespot*, *wheat streak mosaic virus [WSMV]*, *wheat curl mites*, *and its vector*, *barley yellow dwarf virus*, etc.) and abiotic (*waterlogging*, *salinity*, *heat and frost tolerance*, etc.) stresses (Friebe et al., 1996; Witcombe et al., 2007; Wang et al., 2008; Li et al., 2019). Initial efforts of transferring disease resistance gene from wheatgrass were for bunt resistance (Larter and Elliott, 1956).

Since the 1960s, at least 15 genes for resistance to fungal or viral stresses have been introduced from *Thinopyrum ponticum* and *T. intermedium* in the form of chromosomal segments (Li and Wang, 2009). The first gene that was successfully transferred from the wheatgrasses was *Lr19* that conferred leaf rust resistance (Sharma and Knott, 1966). This gene was mapped to the long arm of chromosome 7Ae#1 of *T. ponticum* and was introgressed into the wheat cultivar Agatha as T7DS·7DL-7Ae#1L (Friebe et al., 1994). Another translocation that carried the T7DL-7Ae#1L·7Ae#1S segment conferred resistant to leaf rust, but the locus was different from *Lr19* and was later on designated as Lr29. Resistance gene *Lr24* resides on the long arm of *T. ponticum* chromosome 3Ae#1 (Sears, 1973, 1977). Similarly, *Sr24* is located on *T. ponticum* 3Ae#1L, cointrogressed into wheat as a block with *Lr24*. The chromosomal segment 7Ae#1L that carried *Lr19* also carries *Sr25* for resistance to stem rust (McIntosh et al., 1977). WSMV is a potential threat for what cultivation that could limit wheat production; the virus has spread across all major

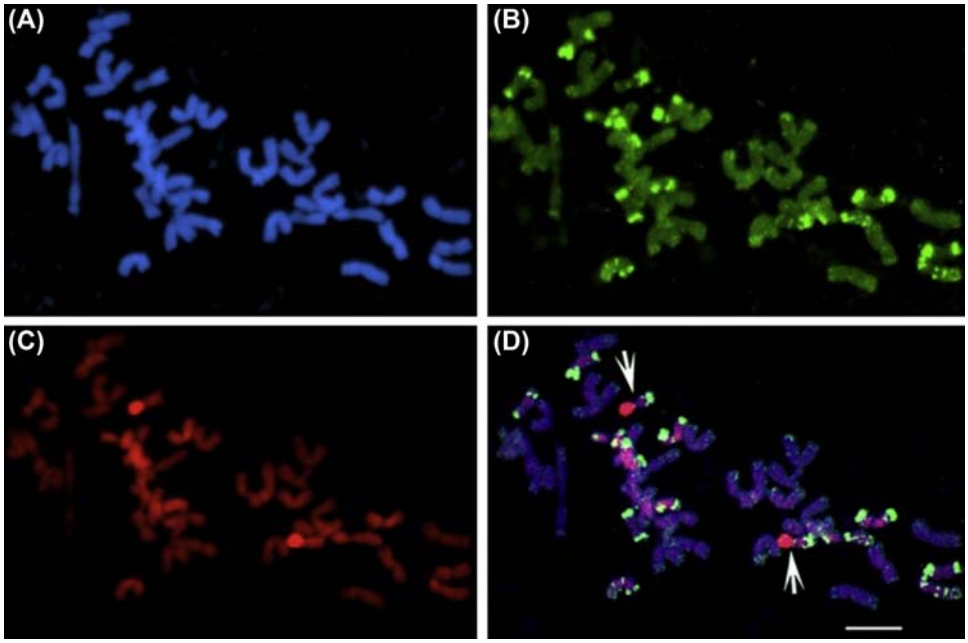

FIGURE 2.3 Root-tip (somatic) metaphase chromosomes of the WSMV (wheat streak mosaic virus)-resistant line Mace (2n = 42). (A) Wheat chromosomes fluoresce blue with DAPI. (B) Hybridization pattern of the dpTa1 DNA sequence labeled with digoxygenin 11-dUTP (detected in green). (C) In situ hybridization of the total genomic DNA from *Thinopyrum intermedium* labeled with biotin 16-dUTP (detected in red). (D) Overlay of A, B, and C images; alien chromosomal arm is indicated by arrows. Bar represents 10 μm.

wheat-growing countries. "Mace" was the first cultivar that could resist WSMV and was not associated with any linkage drag (Graybosch et al., 2009). Mace carried *T. intermedium* chromosome substituting the small arm of wheat chromosome 4D (Fig. 2.3) indicating to one of the most extensively used resistance sources against WSMV (Ali et al., 2016). Similarly, wheat lines of the same pedigree devoid of this *T. intermedium* chromatin are susceptible to WSMV (Fig. 2.4). Furthermore, members of the *Thinopyrum* group are well adapted to drought, high temperatures, wind abrasion, soil salinity, and nutritional imbalance (Friebe et al., 1996; King et al., 1997; Witcombe et al., 2007; Li and Wang, 2009). All these features make *Thinopyrum* an excellent source for future genetic gains in wheat against biotic and abiotic stresses and to develop more resilient wheat cultivars for sustainable agriculture (Li et al., 2019).

7. Potential of D-genome synthetic hexaploid wheat's lines in bread wheat improvement

The bread wheat is an allohexaploid with three distinct but genetically related subgenomes (i.e., A, B, and D). The allohexaploidy of wheat originated from interspecific hybridization of three diploid ancestors followed by spontaneous chromosome doubling (Sears, 1973, 1977; Ogbonnaya et al., 2013; Mujeeb-Kazi et al., 2017). Thus, the natural route of wheat polyploidization could be exploited, by combining the genomes of tetraploid wheat (AABB) and *Aegilops tauschii* (DD) to develop SHWs (see Fig. 2.2). Since the late 1980s, these SHWs have been produced in numbers exceeding a thousand largely at CIMMYT that possess spring and winter habit and are being distributed globally for the introgression of useful diversity in wheat cultivars (Mujeeb-Kazi and Hettel, 1995; Gupta, 2016). Ogbonnaya et al. (2013) have reported other locations where primary SHWs have also been produced. Besides, D-genome (AABBDD), A-genome (AABBAA) (*Triticum urartu*, *Triticum boeoticum*, and *Triticum monococcum*), and B-genome synthetics from the Sitopsis section ($AABBB^{S}B^{S}$) have also been produced at CIMMYT, Mexico. Nonetheless, due to its user-friendly characters and perfect homologous pairing, the D-genome synthetics are considered the priority choice for increasing the genetic base of wheat (Mujeeb-Kazi and Asiedu, 1990; Masood et al., 2016). In breeding programs, SHWs could be crossed onto recipient wheat cultivars that allow recombination across the A, B, and D genomes. Breeders prefer using this bridge-crossing mode to access the diversity of the D genome, as both intra- and interspecific hybridization aspects are covered. Therefore, these SHWs have the potential to address food security and deliver under climate change scenarios (Tariq et al., 2018).

SHWs represent one of the most effective breeding programs for the utilization of alien genes for wheat improvement. The untapped genetic diversity of the SHWs can be crossed with one or more bread wheat cultivars, followed

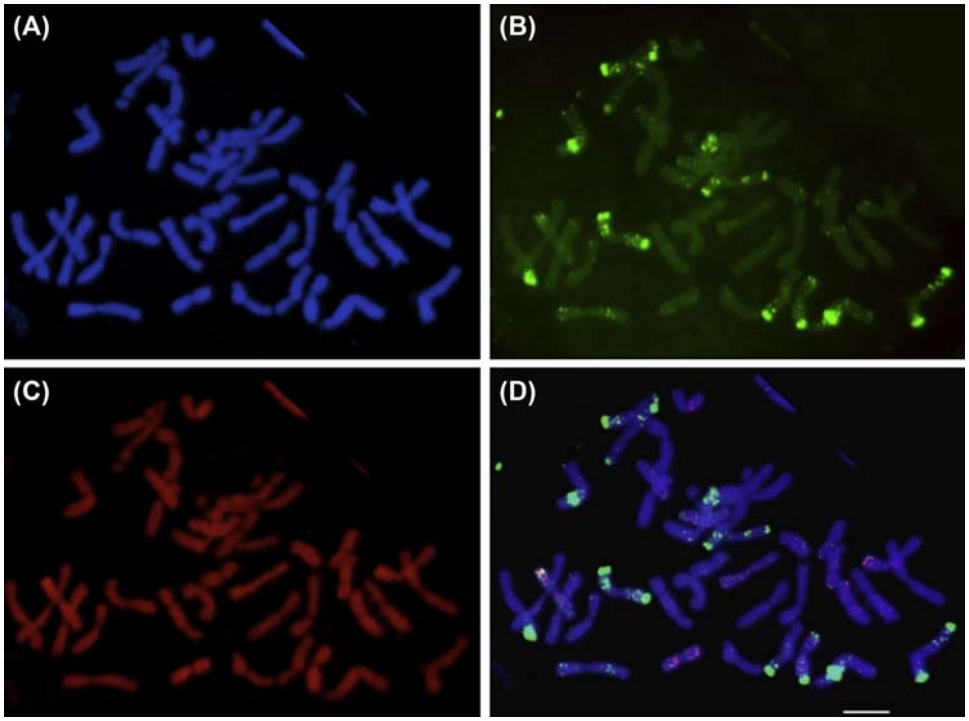

FIGURE 2.4 Root-tip (somatic) metaphase chromosomes of the reference WSMV (wheat streak mosaic virus)-susceptible line Millennium (2n = 42). (A) Wheat chromosomes fluoresce blue with DAPI. (B) Hybridization pattern of the dpTa1 DNA sequence labeled with digoxygenin 11-dUTP (detected in green). (C) In situ hybridization of the total genomic DNA from *Thinopyrum intermedium* labeled with biotin 16-dUTP (detected in red); no *T. intermedium*-origin segments were detected. (D) Overlay of A, B, and C images. Bar represents 10 μm.

by repeated backcrosses (Mujeeb-Kazi et al., 2004, 2017; Rasheed et al., 2017), resulting in synthetic backcross-derived lines (SBLs). These SBLs exhibit significant yield increases as well as offering resistance to almost all major wheat production constraints. SHWs following screening for stresses having resistances/tolerances may be used to widen the genetic base of wheat against a number of biotic (*leaf blotch*, *glume blotch*, *crown rot*, *yellow leaf spot*, *leaf blight*, *powdery mildew*, *Karnal bunt*, *green bugs*, *and Hessian fly*) and abiotic stresses (*including drought*, *water logging*, *frost*, *heat*, *and salinity*). Moreover, SHWs offer resistance to preharvest sprouting, having large kernels, heavy spikes, and higher concentration of both micro- and macronutrients (Schachtman et al., 1992; Calderini and Ortiz-Monasterio, 2003; Van Ginkel and Ogbonnaya, 2007; Ogbonnaya et al., 2013).

In several countries including Pakistan, the SBLs have shown 5%−40% increase in yield (Mujeeb-Kazi et al., 2004; Ogbonnaya et al., 2007). In China, use of synthetic wheats started in 1995, and since 2003, four varieties have been released including Chuanmai 42 that outyielded the commercial check variety by 23%. Since 2006, this SHW variety has been grown on >100,000 ha (Yang et al., 2009). Moreover, attempts have been made and "super wheat," was developed from SHWs, having 30% higher yield and carried tolerance against a number of biotic and abiotic stresses (Mujeeb-Kazi et al., 2004). Indisputably, the development of "Vorobey" involving SHW was a major breakthrough in wheat breeding after "Veery," which carried the 1RS chromatin. Vorobey outperformed and yielded up to 8 t/ha. Moreover, several SHWs having 1000 kernel weight in access of 60 g have been identified (Mujeeb-Kazi et al., 2004, 2017; Ogbonnaya et al., 2013; Gupta, 2016). All these traits make the D-genome SHWs excellent sources and highlight the widespread global use of this invaluable diversity for improving wheat tolerance/resistance to several biotic and abiotic stresses (Rasheed et al., 2018).

8. Advances in high-throughput genotyping and phenotyping platforms for rapid development of superior lines

Virtually, all crops including wheat need to be more tolerant to mitigate the impacts of future climate change hazards. With the recent advancements in high-throughput genotyping and phenotyping platforms as well as whole-genome sequencing at affordable prices becoming instrumental, immense promise is in the offing for identifying

alien genes for wheat improvement (Abberton et al., 2016; Mujeeb-Kazi et al., 2019). The driving forces of the current genomic revolution are the advances in next-generation sequencing technology, and it is probable that within the next few years, all major crops will get benefits of the sequence-based genomic improvement (Rasheed et al., 2018). Additionally, approaches that allow multigeneration outputs per season will accelerate trait screening and discovery of favorable alleles. Nonetheless, high-throughput phenotyping allows screening large populations to identify desirable phenotype(s) that are subsequently genotyped using SNP chips, GBS, or DArTseq platforms. Similarly, mutation breeding (MutRenSeq) allows rapid gene cloning from wheat wild relatives and, with efficient gene editing tools such as CRISPR/Cas9, will have major implications in exploitation of alien genes to produce climate-resilient crops (Abberton et al., 2016; Rasheed et al., 2017). Bread wheat genome is very large and complex, and it has on average three copies of every gene coming from three diploid parents (Ali et al., 2016; Borrill et al., 2019). Although these three copies are highly similar, little is known if they are carrying out the same or different functions, understanding this will enable wheat breeders to accelerate wheat improvement. More recently, it was shown that 30% of wheat triads (genes with an A, B, and D homoeologs) have unbalanced expression (i.e., the expression level of the A, B, and D are quite different). Understanding the inheritance of unbalanced expression of the three homoeologous genomes will lay the groundwork to breed improved wheat varieties (see Ramírez-González et al., 2018). With the availability of wheat reference genome, it is likely that the evolutionary pathway that paved the way for wheat origin and domestication will be fully deciphered that will enable us to capitalize on complex traits such as domestication and will allow us to introduce diversity for increased yield or tolerance that could not be selected in natural environments and safeguard our future through increased food security (IWGSC, 2018).

9. Summary and way forward

Alien species carry invaluable wealth of genetic resources; so far, major part of this diversity remains untapped. Over the recent years, limitations in transfer of alien chromosomes carrying desirable genes have been overcome to a greater extent. We are fortunate to be living at a time when genomic tools and required infrastructure are available for modifying the genetic potential of plants to respond to a range of stresses. To get maximum benefits of these opportunities, integration of several disciplines is required to see these advances are translated in farmers' fields. Despite the fact that breeders have been remarkably successful in developing climate-resilient crops, challenges ahead are tough. The impacts of climate change are likely to be different depending on species response; therefore, tailored solutions seem a realistic approach. Unified policy for developing climate change ready crops in a cost-effective and rapid manner needs to be pursued. Potential lines with higher yield and adaptation to extreme conditions need global distribution, realizing the dire need to safeguard future food supplies and address climatic resilience. Cutting edge science is delivering technologies that are superimpressive. These need to be blended with smart exploitation of "selected" genetic resources that well recognize time-bound output as well as target deadlines. Specifically, alien diploids have distinct advantages over the higher ploidy resources (particularly the allopolyploids) for having excellent resistant/tolerant characteristics and relatively easy genomic manipulations. Such relatives that fit the wide hybridization definition supported by superb homologous recombination give their usage greater priority and should get usage priority for swift wheat improvement outputs. If done astutely (new technologies and selected resources), we will have a win−win situation, which will lead to emerge a holistic well-integrated crop improvement operation, catalyzing selective filial breeding generation advances with utmost efficiency. The ultimate measure of success will reside in maximizing yield, reduction of widespread production gaps, and development of cultivars that are robust, possessing beneficial alleles that govern the huge spectrum of attributes that are embalmed in a cultivars' genetic configuration for all major stresses, which makes varieties productive and sustainable in combating major production constraints. What thwarts our seeing the annual productivity increases that are projected and are vital for achieving food security targets of 2050? The answer is embedded in effectively combatting the numerous constraints that are prevalent or may emerge via exploiting cost-effective cutting-edge efficient technologies coupled with innovative breeding protocols, choice of parental material, cognizance of the output delivery time frame, and above all an integrative modus operandi that functions in unison and advances in tandem.

Acknowledgment

Hazara University, Mansehra, Pakistan, and Higher Education Commission of Pakistan are deeply acknowledged for their overall support.

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CHAPTER

3

Assessing climate change impacts on wheat production in Turkey and various adaptation strategies

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OUTLINE

1. Introduction

Turkey is a Eurasian country encircled by seas on three sides: the Black Sea to the north, the Aegean Sea to the west, and the Mediterranean Sea to the south. The elevation increases from west to east. The western parts of the mountainous regions and the coastal areas are generally rainier than the other regions. Turkey is located between the subtropical zone and temperate zone. The fact that the three sides are surrounded by seas, the extension of the mountains, and the diversity of the landforms causes three different types of climate in the country (Türkoğlu et al., 2016). While Turkey's Mediterranean and Aegean coastal regions are warm and dry in the summer, they are under the influence of mild Mediterranean climate, which is warm and rainy in winters. The Black Sea coastal region has the characteristics of a temperate marine climate. Because of the blocking of the sea effects by the North Anatolia and Taurus mountains, the continental climate, which is hot in summers and cold in winter, is seen in inland areas.

Turkey is located at the east of the Mediterranean Basin, which is identified as one of the most vulnerable regions to climate change (Intergovernmental Panel for Climate Change (IPCC), 2007a). The Mediterranean region has been identified as one of the "hot spots" of climate change in the future, and it is reported that precipitation will decrease in this region, the amount of precipitation will increase in the Black Sea coastal regions, and Mediterranean and Aegean coastal regions will have drought. In addition, it is indicated that in the future there will be a decrease in Turkey's water resources, and the rainfed agriculture will be negatively affected by increasing drought and aridity caused by climate change (Giorgi, 2006; IPCC, 2007a, 2013; Önol and Semazzi, 2009). It has been identified with many pioneering studies and projects that climate change will adversely affect grain production and water resources (it is expected to be significantly decreased in this century) in the Konya Basin, where the main wheat production is carried out in Turkey's inland areas and, also agriculture and water resources in Seyhan Basin, which feeds one of the main cotton production lowlands, Çukurova (Şen, 2013).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00003-0

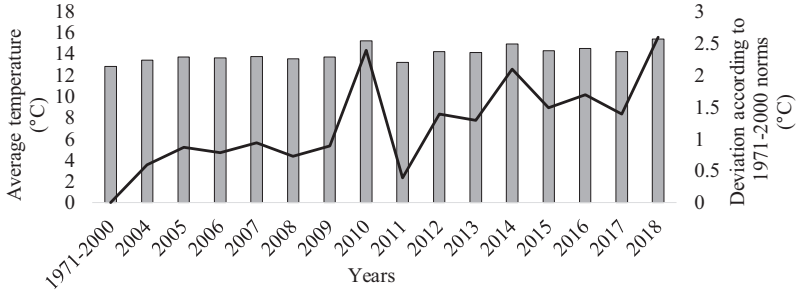

FIGURE 3.1 The average temperature in Turkey and temperature deviations according to the norms of 1971–2000. *Based on Turkish State Meteorological Service 2010. Climate evaluation in 2010. https://www.mgm.gov.tr/FILES/iklim/2010-yili-iklim-degerlendirmesi.pdf and Turkish State Meteorological Service, 2018. Climate Evaluation in 2018. https://www.mgm.gov.tr/FILES/iklim/yillikiklim/2018-iklim-raporu.pdf.*

It was indicated in researches, projects, and observations that the temperature increases at almost every place in Turkey, temperature increases more in summer, the hot seasons get longer, and the number of natural disasters increases. When the temperatures of the 1960s or 1970s were compared with the average summer temperature of the 2000s, the difference was found to be about 1.5°C. Spring and autumn temperatures have also increased in recent years, but increases are not as high as in summer. The hottest years were 2010 and 2018 with a deviation of 2.39°C and 2.59°C, respectively (Fig. 3.1).

Statistics have shown that Turkey has also experienced the highest number of natural disasters between the 1960s and 2010 depending on the temperature changes. It was stated that the drought of 2007 and 2008 caused a decline in yields of some crops at the southeastern part and the western part of Turkey, particularly (Şen, 2013). While wheat production was determined as 22.6 million tons in 2015 according to Turkish Statistical Institute data, production in 2018 was determined as 20 million tons due to the extreme drought experienced in April 2018 (Chamber of Agricultural Engineers, 2014; Turkish Grain Board (TGB), 2018) (Table 3.1). Therefore, the deficit was supplied with imports from other countries. However, high food prices due to low yield caused by drought affected the country's budget negatively. The most important reason for the progressive reduction of wheat production in Turkey is shown as a reduction of rainfall due to global warming and drought. Since these cases may occur more in the future, they will threaten food security more in Turkey.

The increases in temperature have many effects on the yield depending on the growth of the crop and the growth stage in which the product occurs. Higher temperatures generally accelerate crop growth rates, resulting in a shortened growth period and low crop yields (Hatfield et al., 2011). Temperature increases can prolong the vegetation period and may reduce the risk of frost, particularly in areas where crop cultivation is limited to low temperatures (Trnka et al., 2014; Rötter et al., 2013). On the other hand, higher temperatures during the sensitive growth stages of plants may cause heat stress, which may cause various effects.

In a study, it has been shown that high temperatures can cause yield losses in wheat due to the frequency and level of stress (Porter and Gawith, 1999). In the case of cereals such as wheat, for example, the heat stress generated by the maximum temperatures threshold values above 34°C increases the leaf senescence and this accelerates the maturity more than the average temperature effect on the phenology alone (Asseng et al., 2011). In addition, high temperatures result in increased transpiration rates and a reduction in water use efficiency (Ray et al., 2013). Due to the reduction of net photosynthesis, plants respond to a very high vapor pressure gap by closing their stomata. Finally, depending on the optimum temperature that is specific to the crop and the current temperature regime, warmer temperatures can stimulate or adversely affect photosynthesis (Sanchez et al., 2014).

Wheat is cultivated in the whole country in Turkey, including Central Anatolia, Southeast Anatolia, and Thrace predominately. The phenological stages of wheat are sowing, germination, foliation, tillering, bolting, heading, flowering, ripening, and harvesting (DMI, 2005). While a temperature increase of 1°C does not cause great changes in people's daily lives, this value corresponds to 60 days-degree in 2 months and may have the capacity to shift phenological stages. It is thought that the significant temperature increase in Turkey after the 1990s has brought the phenological stages of field and horticultural crops forward. In a climate index study, it was determined that the growing season length in Turkey increases an average of 21 days per century (Şensoy et al., 2013). Increasing temperatures accelerate plant growth in the central northern latitudes (Kadıoğlu and Şaylan, 2000). A trend of 40 days per 100 years forward shifting was found in heading and harvesting dates of wheat in Turkey (Türkoğlu et al., 2016). This situation shows that the increasing temperatures shift the phenological stages to the earlier times. The shortened development period has negative effects on grain filling, grain number per spike, and grain weight (GW) in

TABLE 3.1 Wheat production in planted acres from 2000 to 2018 in Turkey.

Years	Planted wheat acre	Production (million tons)
2000	94.000.000	21.0
2001	94.000.000	19.0
2002	93.000.000	19.5
2003	91.000.000	19.0
2004	93.000.000	21.0
2005	92.500.000	21.5
2006	84.900.000	20.0
2007	80.977.000	**17.2**
2008	80.900.000	**17.8**
2009	81.000.000	20.6
2010	81.034.000	19.7
2011	80.960.000	21.8
2012	75.296.394	20.1
2013	77.726.000	22.1
2014	77.000.000	19.0
2015	78.668.807	22.6
2016	77.719.450	20.6
2017	76.688.790	21.5
2018	76.700.000	**20.0**

Based on Chamber of Agricultural Engineers, 2014. Wheat File. http://www.zmo.org.tr/genel/bizden_detay.php?kod=23218&tipi=17&sube=0 and Turkish Grain Board (TGB), 2018. Cereal Sector Report. http://www.tmo.gov.tr/Upload/Document/hububatsektorraporu2018.pdf.

cereals. Thus, the increase in temperature affects the quality of the crop besides the shortening in the phenological periods. In addition, the shift of phenological stages to the forward will bring the irrigation problem.

Wheat is grown under rainy conditions in Turkey's arid and semiarid regions. Therefore, water scarcity caused by climate change is expected to be the main limiting factor in production. It has been reported that a 6°C increase in both maximum and minimum air temperatures leads to a 30% reduction in wheat yield (Tatar, 2016). It was reported that Turkey's population is 80 million according to data of 2016, and it is expected to exceed 93 million in 2050. It is stated that annual wheat consumption per capita is around 213 kg (Atar, 2018; Turkish Statistical Institute, 2017). It is estimated that the grain consumption per capita will fall well below this value by 2050 (Alexandratos and Bruinsma, 2012). Thus, it is considered that in 2050, to feed this growing population of 13 million, Turkey will need 3 tons of wheat crops, and it is noted that Turkey will cease to be self-sufficient in wheat production (Turkish Statistical Institute, 2017). It is observed that the findings of the study on wheat were confirmed by some local projects. In the Konya-Karapınar project, it is stated that wheat yield decreased due to the very dry season of 2011−12 March and April. In the same study, it was also stated that climate change should be analyzed for wheat, and climate monitoring is mandatory (Soylu and Sade, 2012). Wheat farming is carried out in approximately 67% of the area under cereal cultivation in Turkey, and 63% of the production is obtained from the dry agricultural areas. Therefore, precipitation is an important factor for the growth of this plant. Accordingly, it is inevitable that wheat farming will have great difficulty due to the decrease in rainfall in the future (Aydın and Sarptas, 2018). In the evaluation of wheat agriculture in 2014 by the Chamber of Agricultural Engineers (Turkey), it was reported that there might be significant problems in wheat production in the future. The effects of climate change are expected to intensify in the coming years, and droughts will be more frequent and severe especially in wheat production areas in Turkey. Implementation of higher grain yield strategies under drought conditions is related to two main approaches: (1) reproduction of tolerant and highly efficient genotypes and (2) increasing the efficiency of agronomic

water use (Fischer, 1999). Early-maturing wheat genotypes can also avoid seasonal drought stress in the rainfed wheat production system.

2. Crop adaptation strategies to extreme climate stresses

Wheat crops are grown in a variety of agricultural–ecological conditions, from temperate to subtropical climates. In these areas, there are significant climate differences such as temperature and relative humidity, and wheat crops vary widely seasonally. Synergistic interactions between heat and drought reduce the productivity of wheat more than any stress. Concurrent drought and temperature stresses are more harmful than temperature stress alone. The cultivation of new cultivars that are tolerant to abiotic stress is seen as a solution that will facilitate the coping with negative environmental problems (Kaur et al., 2016). There are various strategies that help the adaptation of plants to climate changes (Table 3.2).

2.1 Cultural methods

The use of drought-resistant cultivars, changes in planting time, and planting and cultivation of new crops are important strategies for a better adaptation of crop plants to reduce the danger of climatic variability and to assure food security. Another plant adaptation approach is the crop management techniques that have the ability to enhance crop development under various environmental stresses. The choice of planting time, planting frequency, and optimum irrigation are important techniques to overcome weather conditions. Fertilizers are also considered as one of the important factors to reduce the effect of global warming and support the plant for better adaptability. Providing a significant amount of energy to plants is considered to be beneficial to maintain and increase the fertility of the soil (Henderson et al., 2018) (Table 3.2).

Plant polyamines (PAs) have been found to provide tolerance to stress conditions such as high and low temperatures, salinity, hyperosmosis, hypoxia, and atmospheric pollutants (Garcıa-Jimenez et al., 2007; Liu et al., 2007)

TABLE 3.2 Strategies for climate change adaptation.

Adaptation strategies		
Cultural methods	Drought–resistant cultivars	
	Cultivation of new crops	
	Crop management techniques	Planting time
		Planting frequency
		Optimum irrigation
		Fertilizers
	Breeding	
	Use of exogenous elicitor (e.g., plant polyamine [PA], osmoprotectans, phytohormones)	
Crop simulation models	Parametric (model) and nonparametric methods are used	
	Quantitative estimates	
	e.g., CERES-Wheat Model, AgroMetShell Model, Global Circulation Model	
Molecular methods	Divergence analysis	
	Quantitative trait locus analysis	
	Marker-assisted selection: Accelerate wheat breeding process	
	Induction and regulation of stress-specific genes	
	Gene silencing	
	Transcriptional factors	
	Omics approaches	

(Table 3.2). It was determined that resistance to drought was increased, and the yield increased by 44% in plants whose poly-(ADP ribose) polymerase level was decreased (Brookes and Barfoot, 2008).

Breeders are trying to develop and select new cultivars of agricultural crops, which are more suitable to a specific environment by using the available resources in the most optimal way. However, it is also suggested that the cultivars recommended for use at present will not be suitable if the climate changes. It is stated that it is usually about 10–15 years for a new cultivar to be cultivated if the target traits are known and the environment in which new lines will be tested is available. However, breeders are likely to face with changing climatic conditions in the near future in which field trials will be conducted. In addition, it is not known which wheat traits might be important in 15–25 years. With global warming, changes in climate and extreme weather events are likely to affect agricultural crops; however, it is not clear how much yield losses will be and whether breeding is necessary for new stress-resistant cultivars (Semenov and Halford, 2009).

2.2 Crop simulation models

Regardless of the development of agricultural techniques, climatic factors continue to affect agricultural production significantly. Temporal and spatial changes of climate factors cause serious fluctuations in agricultural production, and a large loss of crop occurs. For this reason, it is a necessity to obtain the necessary information about the climate of the region before making agricultural activities. Crop prediction is the way in which crop yields and production quantities are usually reported several months before harvesting takes place. Parametric (model) and nonparametric methods (definitive methods) are used for crop estimation (Şimsek et al., 2007) (Table 3.2). The main component of all early warning systems is estimations. Estimations should cover four aspects of food security (availability, continuity, accessibility, and bioavailability) (FAO, 2001), should be as high as possible (consistency decreases as the estimation period increases), and should give decision-makers sufficient time to take action against warnings (Archer et al., 2003). The FAO Agricultural Meteorology Unit has established a crop prediction methodology backed by continuously updated information on plant conditions in FAO's Global Information and Early Warning System, starting from 1974, and is constantly evolving. Today, this methodology helps to estimate crop yields and production quantities several months before harvest.

Two important stress factors, such as temperature and drought, have a high potential effect on wheat yield due to global warming. For this reason, modeling techniques that can be used to identify future threats for wheat growth under climate change and to identify component properties and genes that can be used to improve wheat genetics are described. These techniques will support breeding programs in a rapidly changing climate.

Crop simulation models are increasingly used in basic and applied researches in plant sciences (Debaeke and Aboudrare, 2004; Porter and Semenov, 2005; Sinclair and Muchow, 2001). Simulation models provide the best known approach to improve our understanding of complex plant processes affected by weather conditions and other environmental factors. They are useful in guiding basic research by providing quantitative estimations and highlighting the gaps in knowledge about the subject. Along with high-resolution climate scenarios based on global climate models, crop simulation models are widely used to assess the effect of climate change and to identify potential future threats (Carbone et al., 2003; Olesen et al., 2007; Richter and Semenov, 2005).

Most of the global climate models, in this century, estimate that there is an increase in summer drought and winter wetness in most of the northern middle and high latitudes regions where Turkey has also been located. Also, it is expected that there will be significant increases in the frequency and size of extreme weather events and in the temperature (IPCC, 2007b). Semenov (2007) reported that heat waves would increase significantly in frequency (in order of magnitude), length, and intensity by the end of the century. It is stated that extremely high temperatures might cause a negative effect on the flowering phase, which is one of the most sensitive stages of plant development. This might result in a significant decrease in grain yield, and the excessively high temperatures might completely destroy a harvest.

Elbehri (2015) states that many factors such as climate change and changes in other gas concentrations such as atmospheric CO_2 and ozone will shape crop productivity in the future as well as improvements in agronomic management and technology. However, in the assessment studies of climate change on crop production, only a few factors affecting crop yields are considered. These are changes in climate variables (most notably temperature and precipitation), CO_2 concentration, and technical development or adaptation options (White et al., 2011). Experimental progress has enabled researchers to incorporate and evaluate the effect functions of atmospheric CO_2 concentration in their crop models. In all crop models, the effects of temperature on various ecophysiological processes such as phenology, light use, photosynthesis, and respiration, dry matter allocation to different plant organs and

evapotranspiration are considered. However, only a few models consider the effects of heat stress along with maximum temperatures above certain threshold values, for example, accelerated leaf senescence or effects of various grains on floret mortality/spikelet fertility. All commonly applied crop models take into account the water balance and the effect of crop water shortage. However, there are significant differences in controlling the simulation of soil water dynamics of various models (Van Ittersum et al., 2003). The increasing number of models includes the effect of nitrogen stress on plant growth and nitrogen utilization efficiency (Kersebaum, 2007). Turkey is a developing country, and yet it is at the beginning stage of studies for plant–climate model implementation and development. The number of studies on this subject is limited in Turkey. Şaylan et al. (1998, 1995) have identified the effects of global warming using plant–climate models in their works and emphasized the things that can be done in Turkey. It has been revealed how to determine the agricultural meteorological effects of environmental change with models (Şaylan and Özen, 1997). The CERES-Wheat Model has been tested in Çukurova conditions to determine water–yield relationships (Sezen, 1998). Wheat yield in Turkey was estimated using AgroMetShell Model, and the relationship between the predicted yield values and generated values was determined by Şimsek et al. (2007). Çaldağ and Saylan (2005) used the Crop Environment Resource Synthesis (CERES)-wheat growth simulation model to investigate the effects of climate change on crop growth in Turkey (Table 3.2). The results showed that biomass and grain yield showed an upward trend with the combined effects of increased solar radiation, air temperature, and CO_2, whereas the differences in precipitation showed a negative correlation with plant yield and biomass accumulation. The effects of high atmospheric CO_2 concentration and climate changes in Turkey on the winter wheat yield were investigated using Global Circulation Model (GCM), and wheat yields have been determined to decrease more than 20% in all emission scenarios and time periods. It shows that wheat yield in Thrace region will decrease by 15%–20% due to climate change (Özdoğan, 2011). Kapur et al. (2007) used a regional climate model to estimate the effects of climate change on wheat production in the Çukurova Basin and concluded that there was a 35% decrease in precipitation and a 2.8°C increase in the average temperature. In another study using the data of the climatic parameters of the present and 2070 projections, it was stated with the applied model that the future climate suitability would diminish significantly and the wheat would be subject to considerable change and contraction (Aydın and Sarptas, 2018). In Turkey, a wheat yield prediction model for predicting the yield based on regional panel data was used, and the results showed that wheat production would decrease by between 8% and 23% at the end of 2100 (Eruygur and Özokçu, 2016). When all these crop models are analyzed, it is seen that the temperature increase in Turkey would cause more dry soil and lead to lower yields, and it could increase the market price of wheat, which is the main ingredient of many food products. It is important to use crop simulation models to systematically analyze the effect of technological change on historical yield trends or to represent future yields (Matthews et al., 2013). Crop modeling scenarios can make a significant contribution to numerous areas. For example, it can be used to assess adaptation options for crops under climatic change. It can be used to suggest how the breeding should be targeted to match the crop cultivars to future climates better or how management practices should be changed for crop and crop systems to improve the performance of crops under climatic change, or it can be used to determine how existing crops/cultivars will perform in the future.

2.3 Molecular and genomic approaches

Molecular control mechanisms for abiotic stress tolerance are based on activation and regulation of stress-specific genes (Bechold and Field, 2018). It was stated that the characterization of genetic diversity for plant phenology in wheat could help to adapt breeding programs to local environments and to optimize wheat phenology for climate change (Dubcovsky et al., 1998; Law et al., 1978; Whittal et al., 2018; Yan et al., 2003). Wheat can coordinate its flowering period with changing season to avoid freezing temperatures, high temperature stress, and drought stress that can damage flower organs. Wheat flowering time can be determined by two basic environmental clues: low temperature and photoperiod (insusceptible and sensitive) that categorize wheat genotypes in winter or spring. The main genetic factors affecting such phenological features in wheat are VRN-1, VRN-2, and VRN-3, the vernalization response genes that control the need for a cold time to pass from vegetative to reproductive phase, and the photoperiod sensitivity genes that determine the plant response to day length. VRN-1 and VRN-3 cause flowering when they are dominant. While recessive mutants of VRN-2 accelerate flowering, it was stated that VRN-1 has the main effect on the transition from the vegetative stage to the reproductive phase. It has been determined that photoperiod genes play an important role in determining the flowering time and adaptation of winter wheat (Dubcovsky et al., 1998; Law et al., 1978; Whittal et al., 2018; Yan et al., 2003).

The divergence analysis is considered to be a very important method in the development of new cultivars based on genetic distance and similarities. Local cultivars developed by traditional farming methods for genetic research are important resources. For example, a local wheat type kept in the database has a broader genetic variance and is an important basis for stress resistance, as it contains cultivars that can be adapted to various environmental stresses (Lopes et al., 2015).

Recently developed techniques have provided faster identification and characterization of heat/drought-dependent genes. Developments in molecular biology create new opportunities for the molecular development of modern wheat. Natural variants of modern species harbor a great source of potential stress-related genes and have an enormous potential for wheat development. The identification and successful isolation of a single locus related to drought are generally challenging due to the complex genomic nature of wheat. The polyploid structure of the wheat genome due to the repetition of DNA sequences also complicates molecular analysis due to the repetition of DNA sequences (Barnabás et al., 2008). Today, with the introduction of molecular methods, plant breeding has gained a biotechnological dimension. Molecular markers are used effectively in the breeding of quantitative characters with complex inheritance controlled by multiple genes. Molecular markers are developed from genes that are active regions of the DNA or DNA sequences that do not have any genetic coding functions. The analyses such as phylogenetic analysis, quantitative trait locus (QTL) analysis (Table 3.2), genetic mapping, marker-assisted selection (MAS) (Table 3.2), gene isolation strategies, characterization of gene sources, determination of parents, identification of culture cultivars, and determination of genetic relationship can be carried out with these markers (İsçi, 2008). The transfer of desired genes between cultivars or species has accelerated by the integration of DNA marker techniques to plant breeding. Analysis of quantitative properties, which are controlled by many genes such as tolerance to drought and cold, yield, quality, resistance to diseases and pests, is carried out. MAS provides a strategy to accelerate the wheat breeding process.

Omics approaches provide useful resources for explaining the biological functions of any genetic information for crop renewal and development. Genetic and transcriptomic analyses are used to identify phenotypes in different environmental variability relationships. Genomics also enables the investigation of the molecular mechanisms underlying abiotic stress resistance. These approaches assist in the development of crops compatible with climate change for better yield and production under different climate changes (Raza et al., 2019; Roy et al., 2011). This was done precisely in durum wheat researches. Turkey is one of the largest durum wheat (*Triticum turgidum* L. var) manufacturers in the Mediterranean region. The main environmental constraints limiting durum wheat production in this region are drought and extreme temperatures. Omics technology has also been used in the tolerance studies of durum wheat against the drought (Habash et al., 2009). The regions of the genes that encode quantitative characters controlled by the cumulative effects of a large number of genes, such as yield, located on the chromosome are called QTLs. With QTL mapping, it is possible to find the genes that determine the targeted yield traits, and sometimes, one or more genes that cause a disease or disorder can be detected (Das, 2015). Many traits such as plant height, flowering time, yield, quality, and resistance to certain disease pests are controlled quantitatively. Gene regions of quantitative properties are called QTLs. The location of QTLs can be determined using DNA or molecular markers, and their distribution within the genome can be revealed and mapped. Knowing the location of these genes in the genome is very important for plant breeding studies. The determination of the location of QTLs for hereditary properties, which have agricultural significance, has led to genetic manipulations and gene transfers between organisms (İsçi, 2008). The discovery of molecular markers and the chromosome maps derived from them enabled genetic control of quantitative traits. Because quantitative traits are affected by a large number of genes, it is important to know the location of these genes in the genome. By applying the method known as QTL analysis in a suitable population, the location of the relevant genes in the specific chromosomal region can be determined, the magnitude of the effects can be estimated, and the effect of the gene can be determined whether it is additive or dominant. These are the initial steps in the regulation of genes in breeding programs to obtain superior cultivars (Asins, 2002). QTL examination of yield-related traits of the crops under stress conditions allows the development of new cultivars that can better adapt to abiotic stress (Kole et al., 2015). Increasing GW continues to be an important target of many wheat-growing programs. Although there are many studies reporting QTL for increased GW, few genes have been identified as the basis of this trait. Avni et al. (2018) made QTL analysis for increased GW using a population of recombinant inbred lines derived from crossing between wild emmer wheat and durum wheat (This cultivar is grown in especially Konya-Karaman and Southeast Anatolia in Turkey; it has 7000−8000 years of history and high gluten content.) cultivars. The results showed that the rich genetic diversity of wild wheat and the TtGRF4-A candidate gene have the potential to increase wheat yield in breeding programs.

Transgenic methods that enable the transfer of only the desired loci, by preventing the transfer of genes that reduce the crop yield, from a source organism to elite wheat varieties are shown as an alternative to the ongoing breeding programs. Up to now, transcription factors have been the most attractive targets for transgenic wheat development due to their roles in stress-related multiple pathways. Plants can adapt to stress conditions by altering the expression of genes that respond to stress. Several genes have been identified for the drought stress response. It has been shown that many transcription factor families play an important role in drought and salinity tolerance in wheat plants. These include the NAC (Manickavelu et al., 2012), C_2H_2 zinc finger (Kam et al., 2008), bZIP (Cao et al., 2012), and WRKY (Okay et al., 2014) families. The transcription factor of Arabidopsis WRKY30 (AtWRKY30) was cloned and expressed in wheat. As a result of the overexpression of AtWRKY30, an increase was determined in plant growth, biomass, gas exchange properties, chlorophyll content, relative water content, proline content, soluble protein content, soluble sugar content, and activity of antioxidant enzymes, and it was shown as a candidate gene, which has tolerance against heat and drought stress (El-Esawi et al., 2019). Baloğlu et al. (2014) reported that the expression of TaMYB33 and TaWLIP19 genes in the drought-tolerant Kızıltan-91 (Turkey) (*Triticum turgidum* ssp. *durum*.) and medium-resistant Yüregir-89 (Turkey) (*Triticum aestivum*) cultivars was higher than einkorn wheat (Turkey) (*Triticum monococcum*). It has been monitored that after the transfer of barley late embryogenesis abundant (LEA) protein to wheat by particle bombardment, it has a better drought tolerance when it is overexpressed. In another recent study, using a new technique that combines *Agrobacterium*-mediated genetic transformation with twofold haploid technology, overexpression of barley HVA1 resulted in drought tolerance increase in bread wheat (Chauhan and Khurana, 2011). Therefore, genes encoding LEA proteins have emerged as attractive candidates for drought tolerance engineering.

Success in the development of advanced wheat varieties with genetic engineering depends on the stable and predictable expression of the added gene. In addition, gene silencing, which refers to the suppression of a gene's function by a cellular mechanism, rather than by genetic modification, is a common phenomenon in the production of transgenic plants. Today, this mechanism is considered a powerful method for determining the function of any gene in the cell and for obtaining transgenic plants resistant to various abiotic stress factors such as nutrient stress, drought, cold, salinity, heavy metal, and oxidative stress. In recent years, high temperature has become very important for plants with global warming. As a result of the studies, it was observed that protected 9 miRNA from 32 miRNA families were related to high temperature in wheat (Xin et al., 2010). Bulut (2016) has identified changing microRNA profiles based on tissue and stress duration as well as detection of the microRNA repertoire of wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*) (Özkan et al., 2010; Shewry, 2009) grown in Diyarbakır-Karacadağ territory in Southeastern Anatolia region, which is the gene center of this wheat species that was domesticated more than 10,000 years ago. They have shown as an important resource for future drought-resistant crop development studies.

New researches have focused on studying wheat tolerance at the proteomic level to target different proteins and understand their role in stress. Changes in the gene expression of plants and in the levels of various enzymes and proteins involved in metabolic pathways occur during growth, development, or exposure to the environmental changes (Hakeem et al., 2012). This illustrates the importance of analyzing the wheat proteome to understand the molecular basis of heat tolerance in some wheat varieties. In fact, precise and accurate proteome analysis techniques are used as powerful tools in exploring genes and pathways involved in the response to abiotic stress in plants (Kosová et al., 2011). Thus, key proteins, enzymes, and metabolic pathways identified in tolerant wheat lines are considered to be a potential target for the design of tolerant wheat varieties. In recent years, the application of high-yielding "omic" strategies on the *Triticum* species, which have a different tolerance to drought, revealed that genes associated with stress are involved. In addition, drought-related molecules were identified using various bioinformatics, molecular biology, and functional genomic tools, and their roles in drought tolerance were investigated. With the recent developments in sequencing technologies, a large part of the genome sequence of bread wheat has been determined through the efforts of ITMI (International *Triticeae* Mapping Initiative) and IWGSC (International Wheat Genome Sequencing Consortium). The presence of the whole wheat genome sequence will contribute to studies that continue to explore the large allele sources in drought/heat-tolerant wild germplasm, and this will also lead to improved marker development, genome analysis, and large-scale experiments (Kaur et al., 2016).

There are many studies explaining the effects of climate change on crop yield. However, despite the fact that food security is a critical aspect, the impact on the nutritional value of crops is much less noticeable. Grain protein concentration, which is the ratio of the amount of cereal protein to the grain yield, is an important feature affecting the quality of nutrition, the end-use value, and the baking properties of wheat flour (Shewry and Halford, 2002). Globally, wheat provides 20% protein for humans. The concentration and yield of

cereal protein depend on a combination of factors such as the genotype of the crop, soil, crop management, atmospheric CO_2 concentration, and weather conditions (Nendel et al., 2009). The increased CO_2 concentration alone can increase the total amount of protein in the grain (Broberg et al., 2017) but decreases its concentration (Broberg et al., 2017; Myers et al., 2014). The grain protein concentration increases with drought stress and high temperatures as a result of decreasing starch accumulation (Triboi et al., 2006). Asseng et al. (2019) investigated the effects of CO_2, water, nitrogen (N), and temperature on wheat protein concentration, which is a significant determinant of wheat quality for human nutrition, depending on the varying climatic conditions in the world's major wheat-producing regions as part of agricultural model comparison and improvement project (AgMIP), and they suggested that grain and protein yields are expected to be low and more variable in most of the low rainfall areas. It was found that the global wheat yield was increased by 7% and the protein yield was increased by 2% in the genotypes adapted to temperature (and also by taking into account the changes in CO_2 and precipitation). The development and selection of cultivars mostly should aim to increase the yield and quality of the crop in the current climatic conditions. Thus, it is considered as important to carry out studies aiming to increase the quality of wheat as well as its yield.

3. Conclusion

In the future, climatic change events, which have the increment probability in frequency, duration, and intensity in Turkey, have the potential to threaten food security by affecting wide areas. These climate irregularities, which are common in recent years, are considered as one of the most important obstacles to the increase in wheat production. Therefore, it is important to raise people awareness and to be included in educational activities in terms of adaptation to climate change. Development of various agricultural projects, which describes the negative effects of climate change on water resources, is required to ensure the sustainability of management strategies and agricultural production with the objectives of efficient use and conservation of all groundwater and surface water resources in Turkey. In addition, research and development activities (agronomic, especially the limited number of biotechnological and molecular studies, etc.) should be further encouraged, and production should be supported by ensuring the development of wheat species that are fertile, high quality, and more resistant to the conditions such as natural disasters, temperature, drought, diseases, and pests, which will occur due to climate change.

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CHAPTER

4

Cellular mechanism of salinity tolerance in wheat

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OUTLINE

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00004-2

1. Introduction

Wheat (*Triticum aestivum* L.) is an essential crop in all over the world. About 2 billion people (almost 36% population of the world) are using wheat as food. Wheat contains almost 55% of the carbohydrates and 20% of the food energy (Breiman and Graur, 1995). Therefore, different varieties of wheat are grown all over the world in accordance with different environments.

The main areas producing wheat were China, India, United States, Turkey, Pakistan, Russian Federation, France, Ukraine, Canada, Argentina, Kazakhstan, Australia, Germany, and United Kingdom (FAO, 2002) in 2002. Most varieties of wheat belong to hexaploid wheat (*T. aestivum*), also called bread wheat and are important for making bread. The largest part of the wheat flour produced is used for bread making. Wheat that grows in environment is commonly of hard type. In addition to 11%–15% protein part, this wheat also contains hard gluten (elastic protein). In hexaploid wheat, haploid DNA content is almost 100 times larger than the genome of *Arabidopsis*, almost six times more than that of maize and almost 40 times more than that of rice (Bennett and Smith, 1976; Amuruganathan and Earle, 1991).

Many environmental conditions affect the growth of plants, e.g., temperature, drought, water logging, nutrient depletion, and salinity. For different soils, water accumulation and salts are indivisibly interlinked. For many countries like Pakistan, irrigation water consists of high contents of sodium (high ratio of sodium absorption) which might be the reason for deterioration in structure of textured soils. Less leakage of water causes salinity problems, and extra water enhances falling of crops (Qureshi and Barrett-Lennard, 1998).

Increased resistance of crops against salt is required for the production of food in many parts of the world. Tolerance of crops to salt should be improved due to the poor irrigation system in agriculture. This will help us to reduce the cost of irrigation water and dispose of the salts (Pitman and Lauchli, 2002). In the dry land farming, we can improve salt tolerance, hence increasing the yield with saline soil.

In areas of low rainfall where subsoil contains many salts, we can increase tolerance of salt in the crops. Excess salt was applied and responses of plants to high salinity were studied for almost two eras (Flowers et al., 1977; Greenway and Munns, 1980; Plant and Bray, 1999; Hasegawa et al., 2000; Zhu, 2002). Salinity-tolerant algae growing in seas have been observed over a decade (Karsten and Kirst, 1989). Salt tolerance of crops may have a great impact on crops that are growing in the high salt soil. Salt in subsoil remains the main limitation of agriculture in all semiarid regions (Table 4.1).

1.1 Wheat in Pakistan

According to different studies, wheat production was forecasted by Azhar et al. (1972) in Pakistan. Azhar et al. (1972) assessed a function and production of wheat in the province of Pakistan. They estimated the region's total wheat production in December and January and a monthly return of local varieties, white wheat, fields, manure, and rainwater by using data, from 1962 to 1963 and 1971 to 1972.

TABLE 4.1 History of wheat.

10000 BCE: Wheat grains are being used for about thousands of years as food of humans. Wheat was grown in pits.	6700 BCE: This was stone age. Humans used rocks to grind the grain of wheat.
5500 BCE: The ability to grow grains causes the humans to come close and communicate instead of hunting and wandering.	3000 BCE: In the start, Egyptians used yeast to produce loaves. By chance, they also made the first oven-baked bread.
200 BCE: Then Romans used the power of animals for grinding of wheat.	168 BCE: Then Romans make pastoral.
85 BCE: In Asia, water mills were introduced.	CE 1180–1190: The windmills were also reported in France and England.
1700–1800: As the time advanced and people moved from villages to cities, a great industrial revolution occurred.	1850–1900: Gregor Mendel took experiment on 28,000 pea plants and made "Law of inheritance" which is now, modern genetics.
1900 onwards: Crops breeding and genetics have advanced and increased the wheat quality and yield.	21st century: Most advanced genetics, in which it is discussed how crop resistance will be improved.

They came to know that the observed output and the guessed values are very interlinked to each other. The distance in these two amounts was again lessened for irrigation in barani areas. Azhar et al. (1974) checked production of wheat forecast in 1973–74 again. In order to compare it, they also included the 1972–73 forecasts. These data were used in the classification of their district. The results showed that the calculation increased from the final estimate of 1972–73 wheat.

Pervez et al. (2005) also studied an estimation in area and manufacturing of wheat in Pakistan for up to 2022. He used the data of last 30 years for area and wheat production in order to make models. According to ARIMA model, the production of wheat would be increased to 29,784500 tonnes in 2022. The larger area and more productivity depend on proper government policies about the cultivation of wheat in the country.

1.2 Soil salinity

The most important nonbiotic problem that affects germination, growth, and production is salinity of the soil. When the pH of soil solution increases above 8.5, crop yield becomes low. The addition of salt can maintain the osmotic potential of water. As a result, availability of water to root cells decreases.

Plants have the ability to tolerate salts, grow, and complete their life cycle on another media which comprises very high absorptions of mixed salts. Halophytes are the plants that can survive and grow properly on very high concentrations of salt in the area under plant canopy, in which zone, roots are present. Halophytes can tolerate salts, so they can be obligate or facultative. Obligate halophytes are identified by less similarity in appearance of different varieties and comparative growth rates, which can increase almost 51% in seawater. Whereas, facultative halophytes are found in less salted environments with the edges between salted and nonsalted highlands and are identified due to presence on edges and are different in physiology which make them strong enough to survive in both saline and nonsaline conditions.

1.3 Effect of salinity on plants

The main environmental factor limiting the development and production in plants is salinity (Shrivastava and Rajesh, 2015). Plant death and less production are the harmful results of high salts, which can be seen in many plants. Most of the plants have established procedures, either remove salt from their cells or bear its high concentration in the cell. All main procedures like photosynthesis, synthesis of protein, energy and lipids are disturbed due to the salt stress in plants.

The first response due to salinity is the reduction in the expansion of leaf surface as stress intensifies and stops the growth of the plant. Growth restarts as the stress decreases. The process of photosynthesis primarily provides carbohydrates and other substrates required for the growth of a cell, and the photosynthetic rate is usually slow for plants in contact with salts, especially when the salt is NaCl. Salt stress biology and plant response to the high salinity has been discussed for over 2 decades (Flower et al., 1977; Hasegawa et al., 2000; Zhu, 2002).

1.4 Effect of salinity on wheat

Salt effect on seed germination is generally considered as a decline in germination percentage at a given time in the seed. The growth of the plant is slowed down due to high salt concentration. Less seedling germination is also due to the salinity of the soil. When the salinity is controlled, the phenomenon of germination restarts and development of plant takes place properly without any stress.

In wheat genotype, the differences in resistance to salts were used to check the theory that the growth response to salts has two stages. In the first stage, there will be a huge reduction in the growth rate due to salts that are present outside the root, that is, “osmotic” response. In the second stage, it will also cause an extra decrease in the growth due to the salinity that has established toxicity level in the plants, that is, a “specific saline response.” If this model is correct, i.e., the ability of some wheat varieties to have different genotypes that can remove salt or withstand more concentration of salt, then they should not be affected by salt stress for some period.

2. Cellular mechanisms of salinity tolerance in wheat

Growth and yield of plants are affected by salinity, a major environmental factor (Allakhverdiev et al., 2000). The damaging effects of saline conditions on plants result in their death and loss of productivity. To overcome this effect, plants move salts outside their cells or bear their occurrence inside the cells by distinct processes. Photosynthesis, protein production, energy and lipid catabolism are affected due to saline soils.

Wheat (*T. aestivum*) is a temperately salt-tolerant crop (Maas and Hoffman, 1977). Wheat will produce low yield in saline conditions (100 mM NaCl), whereas, rice (*Oryza sativa*) will perish before development. After prolonged periods of salt treatment (250 mM NaCl), barley, a strong salt-tolerant crop (*Hordeum vulgare*) dies. Durum wheat is weak in salinity tolerance than bread wheat (Maas and Hoffman, 1977; Salt Tolerance Database reproduced on USDA-ARS, 2005).

2.1 Biochemical indicators of salinity stress

At the cellular level features and indicators are present that relate to salinity. Salt-tolerant crop plants have distinct processes for salinity tolerance (Levitt, 1980; Hasegawa et al., 1986, 2000; Rains, 1989; He and Cramer, 1993; Amzallag, 1999). Mechanisms to tolerate salinity have to be elucidated at the cellular level for understanding their complete involvement at the plant level. Such understanding at cellular and tissue level would then help in developing salt-tolerant cultivars (Mansour and Salama, 2004) (Fig. 4.1).

2.2 Protoplasmic characteristics under salinity stress

Protoplasm resistance to salinity is associated with salt tolerance of several halophytes and glycophytes. Experiments are conducted on saline conditions using living protoplasm of cells to study salinity effects at the cellular level (Mansour and Salama, 2004). The protoplasmic features taken into consideration during such experiments are the following:

2.2.1 Plasma membrane permeability

The part of the cell that first interacts with saline soils is plasma membrane, and its permeability is linked with membrane lipid environment and lipid−protein correlation. The responses of various genotypes vary in saline conditions, and evidence supports that it is due to the differing permeability of plasma membranes in their salt tolerances (Mansour, 1997).

Tissue leakage is observed in salt-sensitive cultivars due to the injury of the plasma membrane in response to salt stress. Plasma membrane is not affected by the osmotic aspect of salinity. Cell membranes under salt stress are

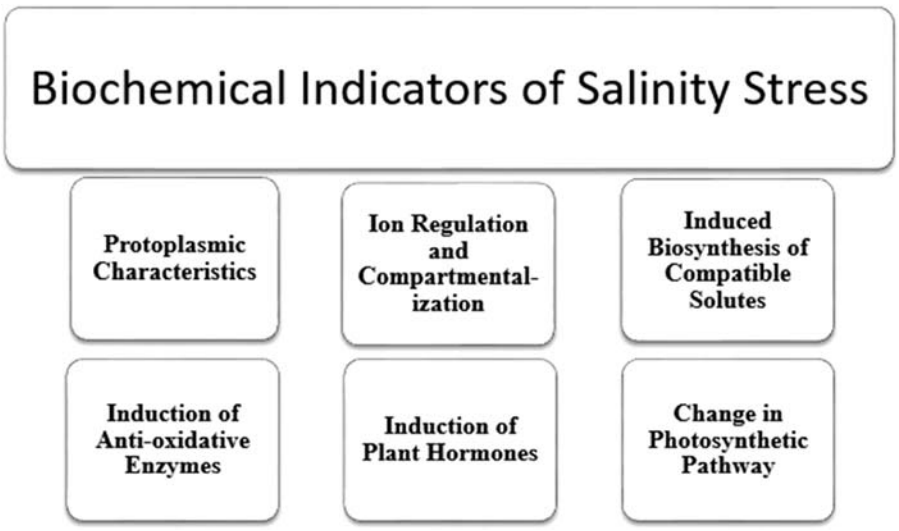


FIGURE 4.1 Biochemical indicators of salinity stress.

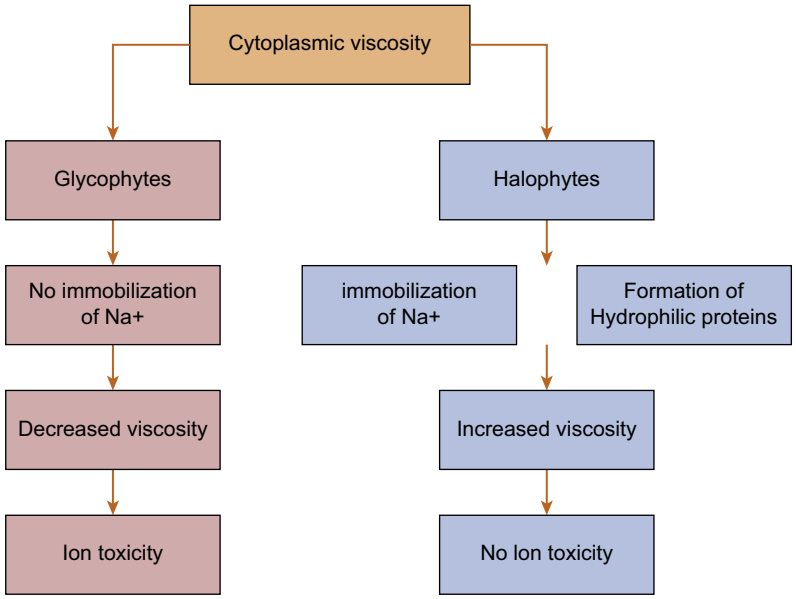


FIGURE 4.2 Cytoplasmic viscosity under different conditions.

affected due to salt ions (Leopold and Willing, 1984; Mansour et al., 1993a; Mansour, 1995b, 1997). Membrane permeability is an important indicator to study salt stress and its tolerance, as no reduced growth or severe chlorosis was observed with different membrane permeabilities (Mansour et al., 1993a; Mansour, 1997). Due to salinity, lethal lesions appear on membranes of salt-sensitive plants, which have membrane defensive functions and also such plants accumulate agents (e.g., proline, etc.) under salt conditions. Thus, plasma membrane provides assistance to plants so that they can adapt to salt stress. The difference in permeability may be due to changes in lipid contents of the plasma membrane. This is ensured by the evaluation of plasma membrane lipids that indicate changes in lipids. In saline environments, cellular homeostasis and membrane integrity is improved by such changes that are absent in glycophytes. The change in the extent of infiltration of membrane lipids and membrane volatility in both glycophytes and halophytes due to salt stress regulate salt ions permeability (Mansour and Salama, 2004) (Fig. 4.2).

2.2.2 *Cytoplasmic viscosity*

Under salinity stress, the cytoplasmic viscosity is studied by Russian scientists. In normal conditions, different genotypes have different cytoplasmic viscosities (Slonov, 1986; Udovenlco and Evdokimov, 1970; Mansour et al., 1993c; Mansour and Stadelmann, 1994; Mansour and Salama, 1996b). Hydrophilic proteins or other cytoplasmic macromolecules are present in the cytoplasm or may be produced under saline conditions and result in increased cytoplasmic viscosity of salt-tolerant species. The cytoplasmic viscosity of glycophytes is lower than the tolerant species and also decreases in the presence of salts. Differences in cytoplasmic structure and properties in both halophytic and glycophytic genotypes are consistent with the proteins synthesized in the cytoplasm under salt stress (LaRose et al., 1989; Hurkman et al., 1991; Plant and Bray, 1999; Hasegawa et al., 2000).

Na^+ concentration in cytoplasm might be 100 mM despite compartmentalization of salt ions to vacuoles. So, salt ions concentration must be lower than the concentration accepted by cytoplasm, thus, salt ions have little importance (Cheeseman, 1988). The ion poisonousness in the cytoplasm of halophytes is alleviated by immobilizing Na^+ in a limited volume of cytoplasm, so protoplasm is also protected from ion toxicity. Salt-sensitive plant species are unable to immobilize sodium ions, so they have low cytoplasmic viscosity and increased levels of salt ions in the cytoplasm. Changes in cytoplasmic viscosities in the presence and absence of salt stress indicate differences in cytoplasmic features that relate to salt tolerance (Mansour and Salama, 2004) (Fig. 4.3).

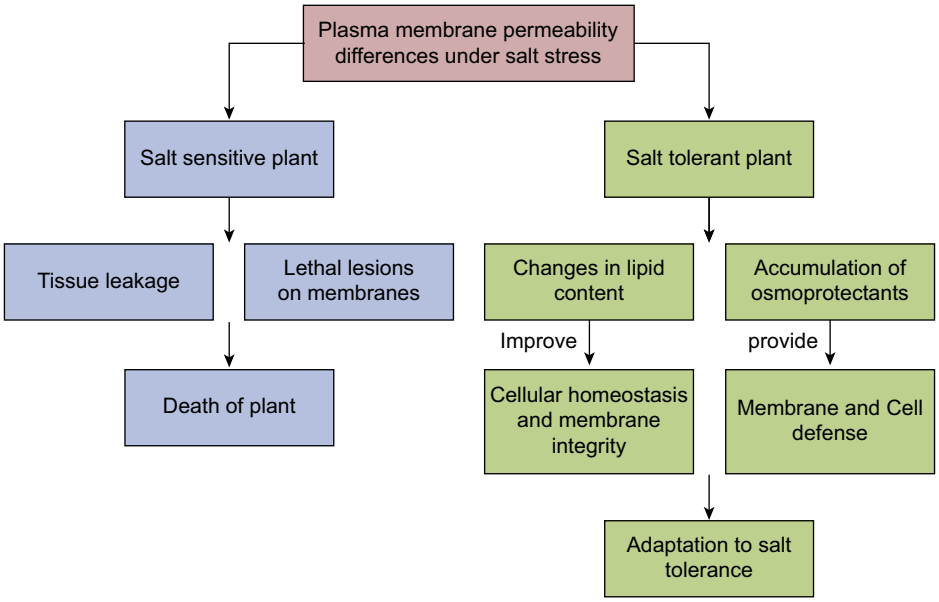


FIGURE 4.3 Difference in plasma membrane permeability under salinity.

2.2.3 *Cytoplasmic streaming*

Cytoplasmic streaming has not been evaluated widely in a stress situation such as salinity. The working of actin−myosin systems that require ATP as energy is linked with cytoplasmic streaming. In salt-sensitive plants, streaming is high in the absence of salt stress (Mansour and Stadelmann, 1994). In salt-tolerant plants, cytoplasmic streaming is low, may be due to low ATP pool and other factors such as free Ca^{++} in the cytoplasm that affect streaming (Okazaki and Tazawa, 1986). This fact might have a positive impact on salt-tolerant cultivars with low streaming in a way that less ATP is used under salinity and more ATP remains available for carrying out essential metabolic processes. In the presence of salinity, plants adapt to such conditions by lowering their metabolic activity and so the growth of salt-tolerant plants is reduced due to slow cytoplasmic streaming (Kuiper et al., 1988; Mansour and Salama, 1996a). It seems that slow cytoplasmic streaming may be beneficial in salty surroundings (Fig. 4.4).

2.2.4 *Cell Solute potential*

The cell solute potential in glycophytes and halophytes decreases in mediums with high salt content (Kingsbury et al., 1984; Kingsbury and Epstein, 1986; Mansour et al., 1993b; Mansour, 1994; Mansour and Salama, 1996a). Decline in cell solute potential leads to dropping of osmotic potential in the outer environment of cells. Increase in solute potential leads to osmotic adjustment based on the accumulation of ions in cells (Kingsbury et al., 1984; Kingsbury and Epstein, 1986; Mansour and Salama, 1996a). When ion compartmentalization is absent in salt-sensitive cultivars, the decreased cell solute potential leads to drastic effects under saline conditions. Greater Na^+ builds up in salt-sensitive plants (Kingsbury and Epstein, 1986; Matsushita and Matoh, 1991). An active cellular reaction to salinity to circumvent damaging effects of toxic ions on the cytoplasm is to sequester them in the vacuole, and it is associated with salt tolerance (Greenway and Munns, 1980; Gorham et al., 1985; Kingsbury and Epstein, 1986).

Both tolerant and sensitive cultivars adjust osmotically and have no alteration in cytoplasmic considerations under decreased cell solute potential. Osmotic adjustment maintains high water content in the cytoplasm that is found in many genotypes, but the mechanism of avoiding toxic effects of ions is different. Salt-tolerant species are efficient in maintaining compartmentalization of ions in vacuole due to a transport protein, tonoplast Na^+/H^+ antiporter. This protein gets activated in salt-tolerant species and accumulates ions in the vacuole (Mansour and Salama, 2004). Osmotic adjustment is not an effective tool to study salt tolerance and for selection purpose in breeding programs.

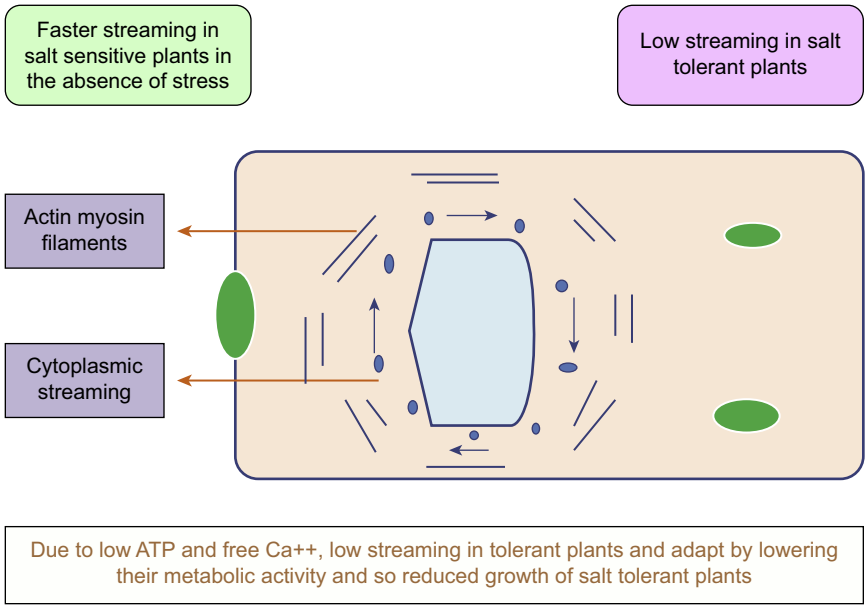


FIGURE 4.4 Cytoplasmic streaming in salinity-tolerant plants.

2.2.4.1 Ion regulation and compartmentalization

Stress can interfere with the homeostasis, so in cases like this, ion uptake and compartmentalization play a significant role for plant survival and growth (Adams et al., 1992). Plants cannot withstand high levels of salts in their cytoplasm. So, in saline conditions, they adapt by gathering extra amounts of salts inside the organelles like vacuole or sectionalize the salt ions toward various tissues to assist cellular activities (Reddy et al., 1992; Zhu, 2003). In glycophytes, sodium uptake is lower. Sodium goes to the older tissues that play a role as storage compartments and are then removed (Cheeseman, 1988). Compartmentalization is done through Na^+/H^+ antiporter, an enzyme involved in stimulation of salt (Apse et al., 1999). During stress conditions, plants have less Na^+ concentration as compared to K^+ concentration in the cytosol. It is done by the regulation of potassium and sodium ion carriers, and pumps of H^+ that give dynamic energy for transport (Zhu et al., 1993) (Fig. 4.5).

2.2.5 *Compatible solutes biosynthesis*

Stability of ions can be maintained when the cytoplasm gathers low molecular compounds called compatible solutes because they do not hinder the reactions (normal) of the system (Yancey et al., 1982; Ford, 1984; Ashihara et al., 1997; Hasegawa et al., 2000; Zhifang and Loescher, 2003). They come as a substitute for water in the biochemical reactions. Glycine betaine (GB) (Rhodes and Hanson, 1993) and polyols (Ford, 1984) are included in the compatible solutes. When the plant is under the stress of salt, carbohydrates like sugars (sucrose, fructose, fructans, glucose) are accumulated (Parida et al., 2002). Their basic role includes osmotic adjustment, osmoprotection, carbon storage (Parida and Das, 2005), and, most importantly, scavenging of radicals.

Polyols work in two ways, i.e., osmoprotection and osmotic adjustment. Under stress conditions, functions of nitrogen include salinity, maintaining pH of cell, osmotic adjustment, cell detoxification, protection of cellular macromolecules, storage of nitrogen, and free radicals scavenging (Mansour, 2000). The compatible solutes can save enzymatic activities of several molecules when the plant is under saline stress. They have less impact on the balance of charge, pH of cytosol, or organelle luminal compartments. These osmolytes are synthesized by modification of basic intermediary metabolites. Mostly, this modification/diversion is initiated by stress. For example, in higher plants, GB is made from choline by some chemical reactions that are mediated by betaine aldehyde dehydrogenase and choline monooxygenase (Rhodes and Hanson, 1993).

2.2.6 *Induction of antioxidative enzymes*

Water deficit is caused in plant cells as a result of salt stress because it hinders many of the normal plant processes (Greenway and Munns, 1980; Cheeseman, 1988). It leads to the formation of reactive oxygen species (ROS) like

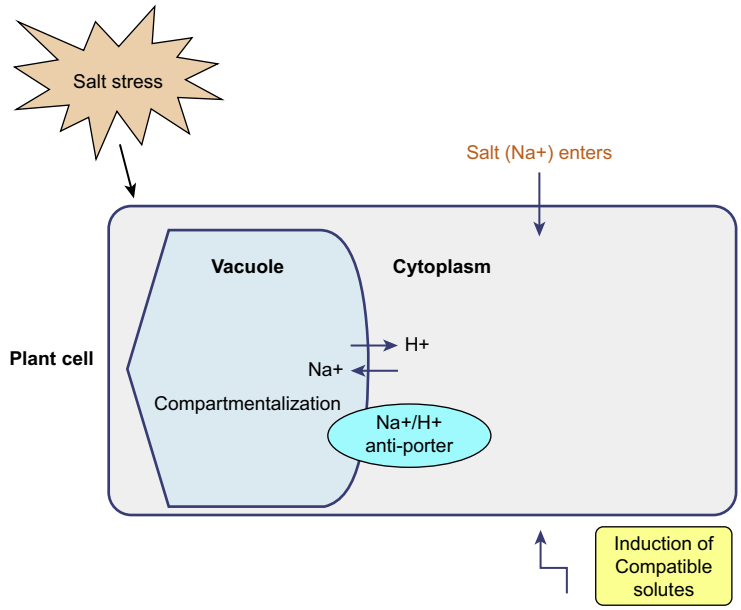


FIGURE 4.5 Ion regulation during salinity stress.

hydrogen peroxide, hydroxyl radical, superoxide (Halliwell and Gutteridge, 1985), and singlet oxygen (Elstner, 1987). Species of oxygen negatively affects the metabolism because they cause damage to lipids (Fridovich, 1986; Wise and Naylor, 1987), nucleic acids, and proteins (Fridovich, 1986; Imlay and Linn, 1988).

During photosynthesis, the internal O_2 concentration is high and chloroplast may produce activated oxygen species (Asada and Takahashi, 1987). H_2O_2 and O_2 are produced due to O^{2-}. Many antioxidants in plants help them to cover themselves against the reactive oxygen species. The superoxide dismutase converts O^{2-} to H_2O_2. H_2O_2 is broken down by a variety of catalases and peroxidases (Chang et al., 1984). Ascorbate-specific peroxidase can detoxify H_2O_2 because chloroplast lacks catalase enzyme apparently (Chen and Asada, 1989) through the ascorbate–glutathione cycle (Halliwell and Gutteridge, 1986). Under salt stress, the functioning of the antioxidative enzymes, such as ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase (POD), and superoxide dismutase rises and an association between level of enzymes and salinity tolerance is observed (Gossett et al., 1994). The synchronization among the assembly of ROS and the antioxidants functioning is affected when plants face stress, such as temperature extremes, chemicals, drought salinity, that causes oxidative damage (Spychalla and Desborough, 1990). Plants that contain a high amount of antioxidants are resistant to this oxidative damage (Fig. 4.6).

2.3 Induction of plant hormones

ABA and cytokinins are increased when the plant is under high salinity stress (Thomas et al., 1992; Vaidyanathan et al., 1999). Abscisic acid is involved in the alteration of genes that are regulated by salt stress (de Bruxelles et al., 1996). ABA-inducible genes play an essential role in the processes of salt tolerance in rice (Gupta et al., 1998). In less salt-tolerant wheat *T. aestivum* L., the salt tolerance is increased when they are given slow exposure to the stress of salt rather than a sudden shock (Noaman et al., 2002).

2.3.1 Change in photosynthetic pathway

As a result of salt stress, photosynthesis is inhibited because salt stress reduces the H_2O_2 potential. Some halophytic plants (*Mesembryanthemum crystallinum*) that have the ability to grow under salt stress but still avoid salinity transfer their C3 mode of photosynthesis to CAM (Cushman et al., 1989). This shift enables to reduce and lessen water deficit by opening stomata at night, thus reducing the loss of water by transpiration during continued salinity conditions. In salt-tolerant plant species like *Atriplex lentiformis*, there is a transfer from the C3 to the C4 pathway in response to high salt stress (Zhu and Meinzer, 1999). Chlorophyll level is measured in plant species including

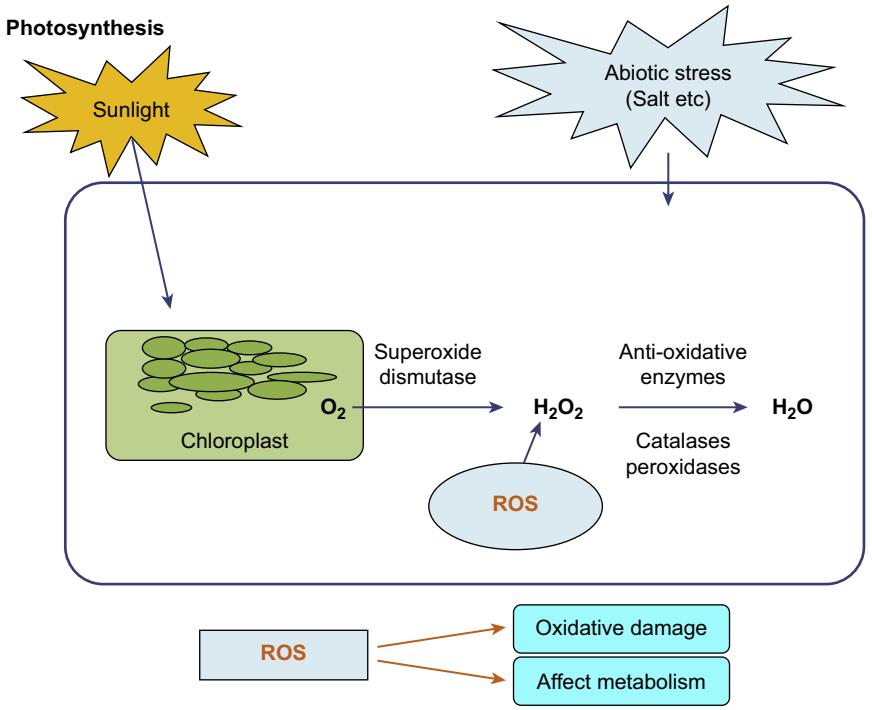
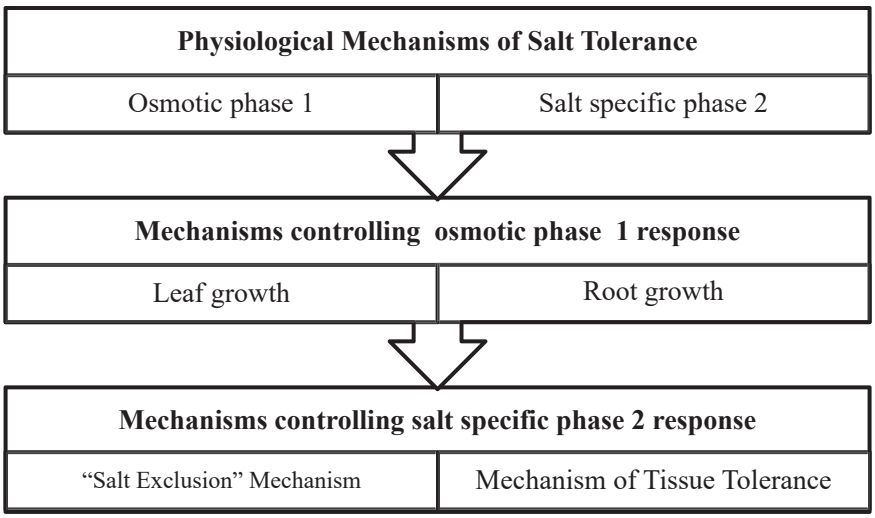


FIGURE 4.6 Antioxidant enzyme activity during salinity stress.

wheat by chlorophyll fluorescence measurement of Fv/Fm. It is a quick approach and can handle large numbers. Chlorophyll level is also measured through SPAD meter. It is more cost-effective.

3. Physiological mechanisms of salt tolerance



3.1 Salt and osmotic specific effects on growth

Plant growth in soil water is inhibited due to two reasons:

1) Plant's reduced ability to uptake water.
2) Injuring the cells of transpiring leaves by entering transpiration stream, thus reducing the growth.

These two effects lead to a two-phase growth response to salinity.

3.1.1 *Phase 1*

In the first stage of response which is depicted in the form of growth is due to the effects of the external salts. Salt solution in soil reduces the growth of the leaf blade and also affects the growth of roots (Munns, 1993). Cellular responses and catabolic reactions that are involved in general plants are pretentious by drought. Neither chloride ions nor Na^+ concentration accumulated in the plant cells inhibits the growth of tissues; phloem meristem is largely supplied by the salt that can be excluded and quickly transferred to the vacuoles (Fig. 4.7).

3.1.2 *Phase 2*

In the second stage (Munns, 2005), the response of growth is due to the toxic effect of salts present in plants. The salt that is absorbed by the plant accumulates in older leaves and starts to move in the leaves which are involved in the transportation of water for a longer time. This enhances the amount of Na^+ and Cl^- to a great extent and hence the death of leaves takes place. The damage is caused possibly due to the excessive amount of salt which cannot be classified by the cells in their vacuoles. Salts are then quickly produced in the cytoplasm and stop enzyme functions. As a result, they may accumulate in the walls of the cell and cause water deficiency in the cell.

The death rate in leaves is important for the existence of plants. If many new leaves are constantly being produced with the ratio that is greater than the ratio with which older leaves are dying, then sufficient amount of photosynthesizing leaves will be present that plant for proper flowering and seeds, though less in numbers. However, if the rate of dying older leaves is more than the newer leaves, the plant could not continue to produce more seeds. In annual plants, competition is always present at the time of flowering and seeds production, till the area of leaf is suitable for supplying the proper photosynthate. Moreover, for perennial species of plants, a chance is present for entering the resting stage and hence can survive in stress conditions.

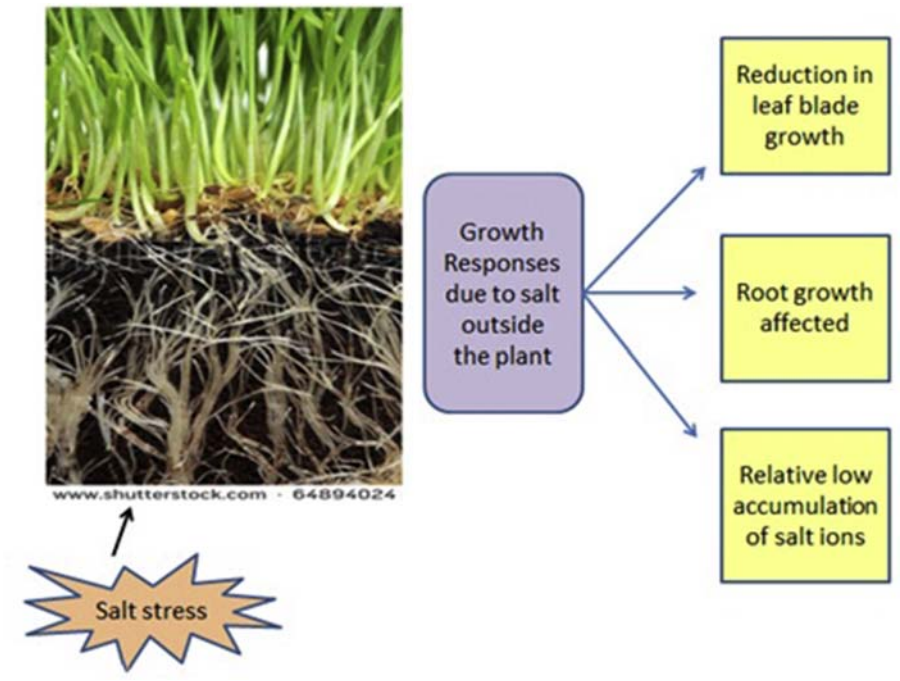


FIGURE 4.7 Plant growth response against salinity.

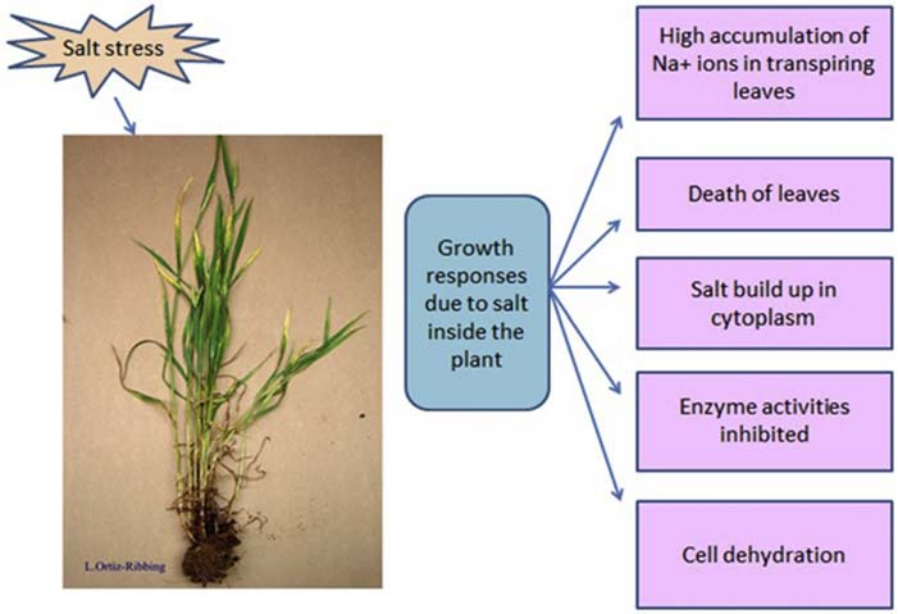


FIGURE 4.8 Growth response against internal salinity stress.

In short, reduction in growth at start is due to the osmotic effect of salts which is present on the outer side of the roots, and continuous reduction in growth is due to the failure to stop salt from increasing up to the poisoned levels in leaves involved in transpiration (Fig. 4.8).

3.1.3 *Mechanisms of controlling leaf and root growth (response of phase 1)*

Many mechanisms control this phase of growth, and the response is not specific for salts. The reasons involving this are linked with the stress of water. The sign for its support is that Na and Cl ions are present in less toxic absorptions in the growing cells, leaves (Hu and Schmidhalter, 1998), and roots (Jeschke, 1984; Jeschke et al., 1986). The wheat that is growing in 120-mM NaCl, Na ions in the tissues of growing leaves were at most only 20 and 10 mM only for rapidly growing regions and Cl^- about 50 mM only (Hu et al., 2005).

Water position, regulation of hormones, and supply of photosynthetic material apply main control all over the plants growth in dry or salted soils, which is a big problem that has been discussed many times. There are many processes which indicate that hormonal signals are controlling growth in saline soils instead of water. Indication for this theory is that the enlargement of leaves in salted soils with the passage of time and days does not show any response for an increase of water level in leaves (Munns, 2002). Through these experiments, we conclude that chemical signals are starting through roots in dry or salted soils that lessen the growth of leaves. These are known as root signals. ABA is an important applicant for that signal because this is present in xylem and its concentration increases with the stress of drought and salinity (Cramer and Läuchli, 1986). However, there is no definite proof showing that merely ABA signal is originating from roots (Dodd, 2005). Furthermore, in the xylem sap, the source of ABA is not known (Munns and Cramer, 1996). Cell division controls by the division of cells, and diversity can be seen from the appearance of leaves, which have a small area but are thicker, which indicate the change in cell size and shape (James et al., 2002). Leaves from that plants treated with salts have a high weight and area ratio. It means that the efficiency of transpiration has increased. An important feature is that they cJames et al., 2002an tolerate dry and salted soils. Controlled cell division with hormones and elongation is also apparent in the roots. In many kinds of literature, it has been cleared that root elongation rates and initiation of adjacent roots are affected by salinity (Rubinigg et al., 2004) (Fig. 4.9).

3.1.4 *Mechanisms for controlling the effects of salinity (phase 2 responses)*

Some species cannot remove salts properly with the help of transpiration stream. With the passage of time, they must adapt other methods to control the salts left behind in the leaves when water evaporates. The concentration of salts in older leaves is higher than those in new leaves. The concentration of salts increases continuously to the extent that kills the cells in older leaves, unless the salts are cataloged in vacuoles, hence shielding the cells from the toxicity

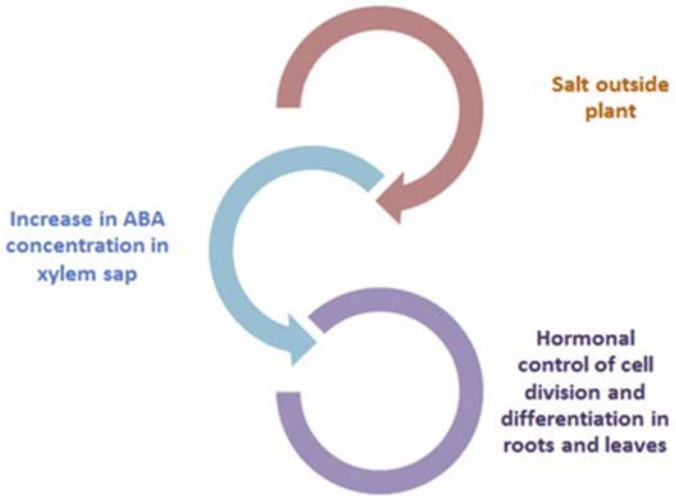


FIGURE 4.9 Response of phase 1.

of ions. The idea that salts should be removed from the tissues or sorted in the vacuoles of cells was generated by the findings of biochemists that enzymes of halophytes do not accept the high absorptions of NaCl. Mechanisms for the salt-specific structures are therefore of two main types: those plants that can minimize the entry of salts into them, called "salt exclusion," and others which can reduce the salt concentrations in the cytoplasm, called "tissue tolerance." In halophytes, procedures are present; they can "dismiss" the salts properly and the cells can also catalog the salt in their vacuoles. The , in which salt glands or bladders excrete salts, permit them to grow well in salted soils.

Cytosol of roots absorbs Na^+ probably in the order of 10−30 mM (Tester and Davenport, 2003). The cytosolic absorptions of leaves for Na^+ are still unknown, but most probably are less than 100 mM (Wyn Jones and Gorham, 2002). The concentration at which Cl^- becomes toxic is not much known.

4. Salt exclusion mechanism

A strong relationship is present in the elimination of salt and acceptance of salt in many plant species (Lauchli, 1984; Flowers and Yeo, 1986; Munns et al., 2003), freshly checked for rice (Lee et al., 2003; Zhu et al., 2004) and wheat (Poustini and Siosemardeh, 2004). Some plant species, like citrus, in which Na ions are held in roots or stems, have a powerful connection between Cl^- elimination and tolerance of salts.

Roots should remove most Na ions and Cl ions that mix in the soil solution increasing a number of salts in the shoot-up to the toxic levels with the passage of time. Transpiration rate of water in plants will increase 50 times more than they hold in leaves (Munns, 2005). If a plant grips 1:50 of the salt in soil solution (i.e., it excludes 98%), then the concentration of salt in the shoot will never be more than the concentration in soil and the plant can grow properly in salted soil (Munns, 2005). In the majority of plants, 98% of the salt is removed from soil solution, permitting only 2% to pass in the xylem vessels of shoots (Fig. 4.10).

In bread wheat, a high Na^+ concentration (98%) is eliminated in surrounding soil, so its concentration does not build up in leaves to > 50 mM (Husain et al., 2004). Durum wheat genotypes were given salt treatment for nearly 4 weeks, and then tolerance was evaluated as shoot dry matter (Munns and James, 2003). In general, the greatest dry matter is produced by those genotypes that have a low concentration of Na^+, few injured leaves, and a low ratio of living to dead leaves (Munns et al., 2006a,b).

Salt directed from leaves to phloem helps in maintaining lesser salt concentration. However, it appears that the concentration of salt that is retranslocated from leaves is low as compared to the concentration imported in the transpiration stream. Although salt in the nearby roots are removed, salt in the leaves remains for a long time which results in above retranslocation. The salt exclusion from phloem to a large extent is observed in more salt-tolerant species, but low salt-tolerant species do not follow such criteria as explained through ion measurements in phloem sap (Munns et al., 1986, 1988). As salt is excluded from phloem, it confirms that salt is not moved into developing parts of the shoot. From younger leaves, salt is transferred to the dividing/growing and lengthening tissues in the shoot (Layzell et al., 1981) (Fig. 4.11).

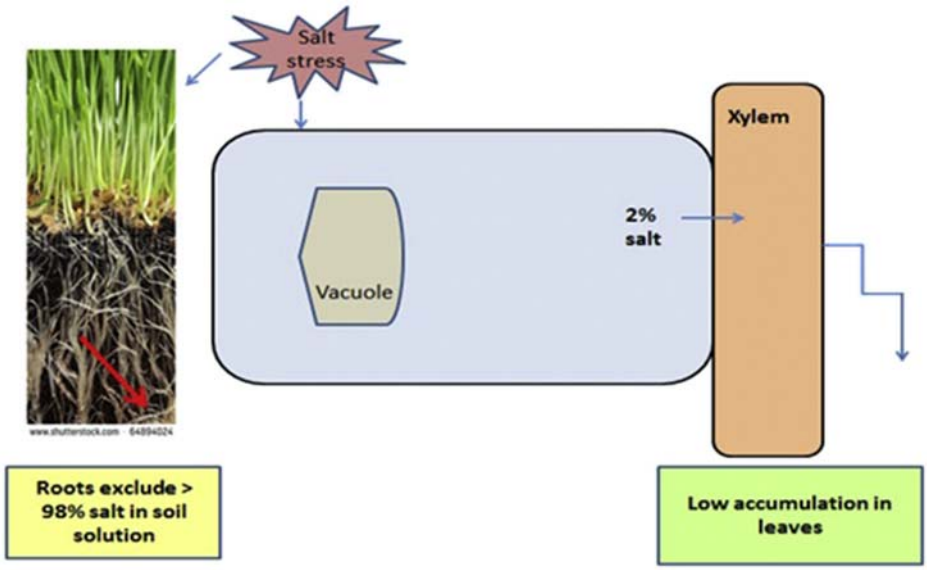


FIGURE 4.10 Salt exclusion mechanism.

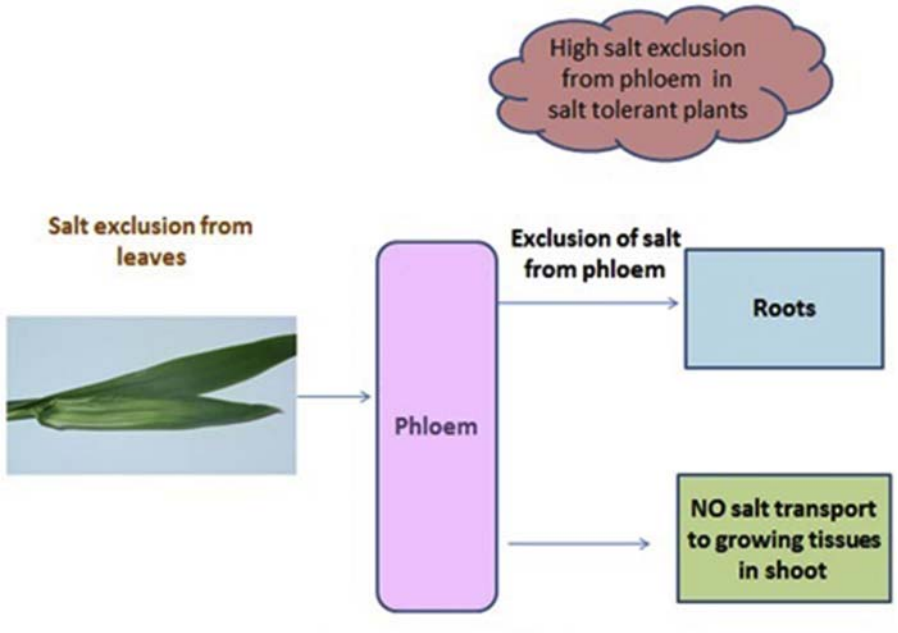


FIGURE 4.11 Salt exclusion.

4.1 Regulation of salt exclusion at cellular and complete plant level

Na^+ transport in salt-sensitive species to tolerate salinity is based on following:

1. Transfer of salt in roots, leaf sheaths, or stem xylem.
2. In roots, filling with the xylem by xylem parenchyma cells.
3. Salt accumulation in the phloem.
4. Root cells in the cortex and central part of the root (stele) load salt selectively.

Two durum wheat genotypes (Line 149 and the cultivar 'Tamaroi') with different rates of Na^+ buildup were used in a study to evaluate above four transport points for sodium exclusion (Munns et al., 2000). Na^+ accumulation in leaf blade, controlled by two major gene loci, is described by genetic studies (Munns et al., 2003). Such genetic variations

examined the capacities of unidirectional 22Na^+ transport and total Na^+ buildup to determine physiological traits (Davenport et al., 2005). The genotypes show no variations at the last control point, that is, the root cells (Davenport et al., 2005). The genotypes show many differences as the rate of transfer of salt in xylem was much reduced in the salt-tolerant genotypes and in the ability of the leaf sheath to isolate sodium ions as these transfer to the leaf. From shoots to roots, no considerable recirculation of sodium was observed (Davenport et al., 2005). The leaf sheath sequestration and xylem loading are distinct genetic characters that interrelate to control leaf blade Na^+.

4.2 Development in salt tolerance of durum wheat genetically using sodium exclusion trait

On farms with high salt stress, cultivation of durum wheat is restricted because durum wheat is salt sensitive. Sodium exclusion trait was used to expand the salt tolerance of durum wheat (Gorham et al., 1990a,b; Dvořak et al., 1994). In bread and durum wheat, salt stress tolerance is related to their ability to select K^+ over Na^+ and to low transfer rate by which salt is moved to shoots (Gorham et al., 1990a,b; Husain et al., 2004). Five ancient *Triticum turgidum* subspecies were considered and their genetic differences were examined to bring the salt exclusion trait into current durum wheat genotypes. Genotypes that are involved in low Na^+ absorption in leaves and have high K^+/Na^+ refinement were selected. Due to large genetic differences, a traditional variety named Line 149 was chosen for breeding (Munns et al., 2000).

The action of Na^+ exclusion feature on avoiding leaf damage and improving crop productivity was assessed using two durum wheat genotypes (Line 149 and 141) with different rates of Na^+ transportation to leaves (Husain et al., 2003). The loss of chlorophyll occurred more rapidly in older leaves of high-Na^+ genotypes than in leaves of low-Na^+ genotypes. The low-Na^+ trait enhanced productivity (>20%) in glasshouse experiments at temperate salt stress (Husain et al., 2003). Though, growth was not enhanced at extreme salinity. This ensures that there might be other characters that are significant along with salt exclusion at extreme salt stress.

Genotypes with low and high Na^+ buildup were crossed, and segregating populations were developed. Genetic analysis of such populations specified two genes that follow Mendelian pattern to give very low rates of Na^+ buildup (Munns et al., 2003). Two genes are not known yet. It is expected that one gene is involved in recovering Na^+ from the xylem in roots and leaves, and the other gene is involved in the loading of Na^+ in the xylem in the roots (Davenport et al., 2005). These genes work in a coordinated manner and result in low Na^+ loading in leaves.

With the help of quantitative trait locus, RFLP and AFLP, genetic location for the low-Na+ trait was identified and located on chromosome 2A (Lindsay et al., 2004). Many markers related to the gene are identified at QTL nominated as Nax1 (Na^+ exclusion). To select low-Na^+ genotypes of durum wheat in breeding program, microsatellites markers are used, as these are linked to low sodium character in many varieties of different genetic backgrounds (Lindsay et al., 2004).

5. Other characters for salt tolerance (mechanism of tissue tolerance)

When salt reaches in the shoots, plants can partition it either by holding it into leaf base or stem or moving it toward older leaves from younger ones. This strategy is employed by those species that are unable to eliminate salt (98%) from the transpiration stream. Traits other than salt exclusion can be used to achieve tolerance to the osmotic effect of salt in surrounding environment, having a greater impact than the salt definite effect on growth and yield. These traits or characters involve osmotic adjustment, water-use efficiency, and physiological patterns that utilize water and lead to earlier flowering in plants. Such traits were used to develop tolerant lines of wheat and barley (Colmer et al., 2005).

Plants that are unable to eliminate salt (98%) from transpiration stream must have the ability to sectionalize it in vacuoles, thus guarding the cell wall against desiccation by salt accumulation and cytoplasm from ion poisonousness (Flowers and Yeo, 1986). Otherwise, the death of cells may occur due to high salt content that builds up in older leaves. So, to avoid this damaging effect, salt must be sequestered in the cell vacuole. Compatible solutes mount up in the different organelles of the cell including cytoplasm, so they help to maintain osmotic pressure of salt in the vacuole (Munns, 2005).

5.1 Screen for tissue tolerance to Na^+

To find tolerant lines of durum wheat against high salinity and Na^+ content in leaves, these genotypes were given salt treatment for 21 days and those genotypes with least leaf injury were selected (Munns and James, 2003). This

trait (least leaf damage) is linked with highest leaf Na^+ content. Total leaf sodium ion content does not link with a fraction of damaged leaf, so there might exist variability at the genetic level to tolerate salt at cell-specific level. To evaluate salt tolerance in leaves, some sodium ions in dead leaves are calculated. High Na^+ concentration per percentage damaged leaves is associated with the high capability of tissue tolerance to Na^+ (Munns and James, 2003).

6. Improving salinity tolerance

The population of the world is increasing day by day, but the quantity of available food is getting limited compared to this increasing rate (Varshney et al., 2011). The increasing population, shrinking agricultural land, and increasing industrialization are the major causes of the shortage of food supply. The main advantage of producing salt-tolerant plants would be the production of crops in salinity affected areas.

When the water-soluble salts gather in the soil, it leads to salinization (USDA, 1998). According to United Nations Environment Program, approximately 50% of cropland in the world is salt-stressed (Yokoi et al., 2002). Out of all the land that is irrigated, 20% of it is under salt stress (Yeo, 1999), except for the countries like Argentina, Egypt, and Iran where this figure goes up to 30% (Zink, 2003). Salt stress has negative impact on the wheat phenological aspects such as rate of root growth (Neumann, 1995), leaf number, leaf rate expansion (El-Hendawya et al., 2005), root/soot ratio (El-Hendawya et al., 2005), and yield of total dry matter (Pessarakli and Huber, 1991; El-Hendawya et al., 2005). As far as dry matter is concerned, wheat genotypes with high Na^+ content produced low dry weight than wheat with low Na^+ content (Munns et al., 2006a,b). In cases when salinity becomes very high, it would result in plant death (Niu et al., 1995; Yeo, 1998; Glenn et al., 1999). Any abiotic stress like salinity, temperature, drought, etc. will directly affect the plant's phenotypic characteristics and productivity. The yield or productivity can be increased by breeding stress-tolerant crops. There is some limitation in the success rate of breeding because of the following reasons:

(1) Several genes control the stress tolerance, but their selection at the same time is difficult (Richards, 1996; Yeo, 1998; Flowers et al., 2000).
(2) Sometimes undesirable genes get incorporated during the process of breeding, so efforts are needed to eliminate this limitation (Richards, 1996).
(3) There is a shortage of selection processes especially in the case of field conditions (Ribaut et al., 1997).

Genetic engineering can develop tolerant plants to different stresses. This approach is a precise and fast way to achieve the tolerance against stress, as compared to classical breeding (Cushman and Bohnert, 2000). Through the process of genetic engineering, we can avoid several limitations like the transfer of unwanted chromosomal regions, and also several genes can be transferred to the crop of interest at once.

7. Mannitol

In many plants, mannitol is produced, but not in wheat. Studies have shown that *Arabidopsis* and genetically engineered tobacco (*Nicotiana tabacum*) showed improved growth by mannitol-accumulation when grown under stress (Tarczynski et al., 1992, 1993; Thomas et al., 1995). Normally mannitol is not synthesized in wheat, but when mtlD expressed under the influence of promoter named ZmUbi-1 promoter, tolerance toward salinity and water stress was observed. In a study by Davis et al. (1988), it is revealed that when the mtlD gene of *Escherichia coli* was introduced into wheat, its role in tolerating water and salinity stress can be observed. There is a change of fructose-6-phosphate to mannitol-1-phosphate by the action of mannitol-1-phosphate dehydrogenase that is encoded by gene mtlD (Thomas et al., 1995). After this, mannitol-1-phosphate produces mannitol with the help of phosphatases.

In this approach to produce transgenic plants, two constructs were used, i.e., pTA2 that contained mannitol-1-phosphate dehydrogenase producing gene (mt1D) and the other pAHC20 that is without it (Davis et al., 1988). In the presence of stresses like PEG and NaCl, the growth of calli containing the pAHC20 construct was reduced by 40%, while the calli-containing pTA2 had no influence on growth. Due to the PEG and NaCl stresses, mt1D gene containing calli had 81% and 118% mannitol, respectively.

There is an improvement in mannitol accumulating plants because it works by scavenging the hydroxyl radicals and stabilizing the macromolecular structures (Smirnoff and Cumbes, 1989; Crowe et al., 1992; Shen et al., 1997a, 1997b). ROS can breakdown the biological molecules by reacting with them. They can also damage nucleic acids, leading toward causing damage to the plant (Smirnoff, 1998). Mannitol's significance as a scavenger of the hydroxyl

radical is observed in vivo and in vitro (Smirnoff and Cumbes, 1989) using transgenic tobacco (Shen et al., 1997a). In this case, mannitol saves the plants against stress by protecting the ferredoxin, glutathione, thiol-regulated enzyme, phosphoribulokinase, and thioredoxin from hydroxyl radicals (Shen et al., 1997b). The molecular structures are stabilized by the formation of hydrogen bonds.

The increased accumulation of mannitol may cause a negative impact on plants. There would be more divergence of carbon to mannitol biosynthesis. The carbon that is normally used for Suc synthesis will deplete and in turn, will lead to depletion of Suc pool, causing a deleterious effect on the growth of plants. This happens because carbon diverges to mannitol biosynthesis. As the excess of everything is bad, this happens in the case of mannitol too. It is a compatible solute but when it reaches high amounts, it gets dangerous for plants, and they cannot tolerate it.

7.1 The DREB transcription factors

The main function of DREB transcription factors is their involvement in the regulation of many stress-regulated genes that play a significant role in the responses to abiotic stimuli (Agarwal et al., 2006; Hussain et al., 2011). DRE cis elements were identified in *Arabidopsis* (Shinozaki, 1994), approximately 40 homologs of the DREB gene from nearly 20 types of plants have been reported and one DREB gene can be induced by multiple stress factors (Lata and Prasad, 2011; Lata et al., 2011; Khan, 2011).

As DREB transcription factors are involved in stress tolerance to abiotic factors, plants were transformed with about 20 different DREB transcription factors along with the constitutive promoter CaMV35S or the stress-inducible promoter rd29A that can tolerate multiple abiotic stresses (Lata and Prasad, 2011). These factors work when DRE/CRT cis-acting elements bind in the promoter regions and can be used to make transgenic plants (Shinozaki, 1994; Kasuga et al., 2004).

Many of these downstream genes encode proteins like LEA proteins, osmoprotectants, lysophospholipase C, protease inhibitors, cold acclimation proteins, glucose transporter proteins, and transcription factors. These genes were identified using cDNA microarrays and play important roles in plant stress tolerance (Lata and Prasad, 2011; Khan, 2011; Nakashima et al., 2009; Maruyama et al., 2004).

In a study by Zhang et al. (2010), the transgenic wheat line T349, overexpressing gene GmDREB1 showed high salinity tolerance than the wild types. They showed improved seedling growth in saline conditions. High salinity results in osmotic stress and further salt intake and osmotic stress can lead to accumulation of ROS that would raise the osmotic stress (Boo and Jung, 1999; Hasegawa et al., 2000). As mentioned above, these factors show their role in abiotic tolerance by binding to DRE/CRT cis-acting elements of many stress-related genes (Agarwal et al., 2006; Hussain et al., 2011).

These factors face abiotic stress tolerance when they bind to DRE/CRT cis-acting elements in the promoter regions of many stress-related genes, as they play significant roles in plant stress tolerance (Agarwal et al., 2006; Hussain et al., 2011). Upregulation of methionine synthase in T349 shows that it plays a significant part in improving the tolerance to salt in transgenic wheat by regulating the osmotic balance. Methionine is formed with the help of methionine synthase. This happens when a methyl group is transferred to homocysteine from 5-methyltetrahydrofolate. It is a process that takes place in methyl cycle which is active, and it is also known as the source of single carbons (Hanson et al., 2000).

That methionine is then changed into S-adenosyl methionine (SAM) with the help of SAM synthetase. SAM provides the methyl group for several metabolites, which includes methylated polyols, GB, and polyamines, under high salinity conditions. Methylated polyols and GB are the compatible solutes that accumulate in the cytoplasm. As a result, the osmotic balance is regulated under salt stress (Bohnert and Jensen, 1996; Takabe et al., 1998). This indicates that the upregulation of methionine synthase in T349 involves improving the ability of transgenic wheat to tolerate salt by regulating the osmotic balance. Glyceraldehyde-3-phosphate dehydrogenase (GPD) was also upregulated in T349 under salt stress, along with methionine synthase. GDP is an enzyme that is important in glycolysis gluconeogenesis pathways. Carbon is metabolized away from glycerol when there is increased GPD activity. This would lead to glycolysis and ATP formation, providing compatible osmolytes and the energy required for osmotic stress tolerance.

7.2 Glycine betaine

GB, as an osmolyte and enzyme-protectant, can protect the stability of the membrane under the influence of salt stress, thus improving the salinity tolerance of the plant. GB, a glycine derivative, in response to drought and salinity,

gets accumulated in the chloroplast and plastid of plants. In some cases, GB gathers to high levels that may lead to osmotic pressure (Munns and Tesser, 2008), but generally, plants gather this in low concentration. When GB is present in low concentrations, it helps to stabilize the quaternary structures of enzymes and many other complex proteins. With the ROS scavenging process, it protects the photosynthetic machinery.

A study conducted by Zhang et al. (2010) revealed that genetically engineered maize that have *E. coli's* betA locus, which encodes choline dehydrogenase, had high GB buildup due to stress conditions. Enzyme choline dehydrogenase (CDH), produced due to the expression of betA, carries out the oxidation of choline to betaine aldehyde, which then leads to oxidation of betaine aldehyde to glycine betaine with the help of same given enzyme (Welin et al., 1999). BetaA gene is also transferred to cotton and maize, leading to more accumulation of GB. This accumulation resulted in reduced membrane damage, an increase in the enzyme activities and high tolerance and resistance to several stresses as compared to wild-type plants (Quan et al., 2004a, 2004b; Lv et al., 2007).

In the transgenic lines L2 and L3, which comprised high amounts of GB, the K^+/Na^+ ratios were also higher than the WT. This shows that when there is a high accumulation of GB, it would lead to protection of membrane integrity and also protect the macromolecules from losing their stability. This is beneficial because it maintains the normal metabolism and helps to retain K+ in cells when it is under salt stress (NaCl). GB accumulation stabilizes and retains the activity of macromolecules by avoiding the ROS-induced damage (Liang et al., 2009), saving complex proteins from damage (Mamedov et al., 1993; Allakhverdiev et al., 1996), and improving membrane integrity (Sakamoto and Murata, 2001, 2002).

8. Future perspectives

As the population of the world is increasing at a high rate, time will come when there would be less food as compared to a population that needs it for survival. As crops face biotic and abiotic stresses, their yield is affected negatively. This would have a direct impact on the survival of man. By using the approaches like genetic engineering, crops can be grown in stressed environments like high salinity, osmotic pressure, temperature, etc. In this way, a good yield is obtained that might fill up the need for more food.

9. Conclusion

High salinity affects the plant development and leads to impaired growth. Wheat is an important crop, and if it is affected due to some biotic and abiotic stress that would have a direct impact on the economy. Nature has its ways to deal with the stresses that would have an impact on normal growth. In wheat, there are cellular mechanisms that enable it to survive. In extreme cases, when the stresses become high, the approach of genetic engineering comes into use. This approach will not only help the plants to survive, but it will also help to solve the problem of limited food available to mankind.

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CHAPTER

5

Salt-regulating genes in wheat

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OUTLINE

1. Introduction

Wheat is considered the third largest crop of the world. As of 2008, out of all the globally cultivated land for wheat, 43.6% is occupied by Asia, 27.6% by the whole Europe, 18.5% by America (continent), 6.1% by Oceania, and 4.2% by Africa (Ali and Khan, 2014). Despite the growing human population, the production rate of wheat did not increase significantly from 1991 to 2008. The total wheat production in 2008 was 689.95 MMT (million metric tons) as compared with 546.88 MMT in 1991 (Ali and Khan, 2014). According to estimates, the top 10 global wheat-producing countries had an annual wheat production of 606 MMT during 2013–14 (Cooper, 2015).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00005-4

The wheat crop has origins in the Levant region of the Near East and the Ethiopian Highlands. As the grain could be cultivated easily on a large scale and stored, human establishments were formed, ultimately leading to the beginning of the human civilization. Human population increased in the Assyrian and the Babylonian Empires, collectively known as the "Fertile Crescent" (Cooper, 2015). Out of various varieties, bread wheat is especially of practical importance. It fulfills 20% of the world's daily food requirements in terms of calories. Due to recent advances in agriculture and improved selective breeding techniques, the yield of wheat crop has doubled over the past 40 years (Berkman et al., 2012). However, due to increased global demand, the requirements are not being fully met. Furthermore, new approaches are required to increase the yield and quality of wheat.

Bread wheat contains compounds such as vitamins, proteins, and minerals that are required for proper growth and development (Brenchley et al., 2012). With the expansion of agriculture and rising trend of human settlement, it is among the widely cultivated crops owing to its promising yield and economic benefits. Recently, genetics have made possible to produce a heat-tolerant form of bread wheat (Ullah et al., 2018).

There are different types of wheat cultivars characterized according to their requirements (winter wheat and spring wheat). Wheat is used as a texture. Wheat containing gluten, also known as hard wheat, is used for making bread, cakes, and biscuits. Also, it is rich in different types of proteins, carbohydrates, and vitamins especially vitamins B and E. It can be refined to make starch and wheat germ oil. It is also used to make animal food (Hussein et al., 2018). According to FAO estimate, all the different types of wheat production were about 650 million metric tons in 2010. China, France, India, and the United States are leading producers of wheat. In 2050, the wheat production has to be increased up to 60% to meet the food requirement. The crux of the matter is to realize how much important wheat is for the growing population and how much more important it will be in years to come. As of 2012, in the past 20 years, unfortunately, there has not been enough increase in the production of wheat to meet the challenges of growing world population (Mcguire, 2013). The present yield of wheat is not enough to ensure food security in the face of growing population, and by 2050, the global demand of wheat is expected to increase by 60% (Tadesse et al., 2017).

Wheat genome has been described as a complex one (Liu et al., 2012), and scientists increasingly focus on wheat for the analysis of its complex genome and also for the improvement in yield and quality. The genome of wheat is allopolyploid. There are different types of wheat, some are diploid (2×) such as *Triticum monococcum*, some of the types are tetraploid ($4\times = 28$) e.g., *Triticum turgidum*, and some are hexaploid ($6\times = 42$) e.g., *Triticum aestivum*. The important types of wheat including *T. turgidum* L. and *T. aestivum* L. are cultivated as the major food crop worldwide (Baum et al., 2009). The annual cultivation of *T. turgidum* is almost 25 million tons (Li et al., 2018).

There are various biotic and abiotic stresses that have been posing threats to the wheat crop globally, leading to the decrease in productivity and quality of the crop. Biotic stresses are imposed due to the infection by other organisms such as fungi, viruses, and bacteria, e.g., wheat stem rust caused by fungus *Puccinia graminis tritici.* Similarly, stress caused by a virus in the form of wheat yellow rust leads to its poor yield. Stresses imposed by bacteria include leaf blight and bacterial sheath rot. They also decrease wheat crop production (Singh et al., 2008). To make situation worse, there are also some abiotic stresses that steadily affect the crop but remain unidentified for a long time.

Abiotic stresses including salt stress, heat, cold, oxidative stress, and drought are a serious threat to agriculture (Guo et al., 2014; Raza et al., 2019). According to an estimate, the loss in crop productivity due to these abiotic stresses is about 20% (Kreps et al., 2002). Abiotic stress leads to changes in gene expression due to cellular dehydration (Cook et al., 2004). Salt stress has been identified as a principle limiting factor in wheat cultivation as well as its yield. According to an estimate, 20% of the land is used for agriculture and 50% of cropland in the world is affected due to salt stress (Munns and Tester, 2008), and it has been predicted that there will be a loss of 30% land in the next 25 years due to salinity (Wang et al., 2003). Salts present in soil affect the living mechanisms by intruding the metabolic processes such as photosynthesis, lipid metabolism, growth, and protein metabolism at all plant levels, and all the stages of development such as germination, seedlings, and vegetative stages are affected by salt-induced stress (Evelin et al., 2009). Normally, a high concentration of the salt produces toxicity of the ions and also imposes osmotic stress (Munns, 2002). Hence, increased concentration of different ions, such as sodium (Na), chlorine (Cl), calcium (Ca), potassium (K), bicarbonates, nitrites, and sulfates, causes lowering of water content of soil. Consequently, roots cannot take water in adequate concentration. Therefore, increased salt concentration results in the disturbance of ion homeostasis in the plant cells. As a result, various harmful substances, such as osmolytes, including glycine—betaine, also proline, derivatives of oligosaccharides raffinose, and high-molecular-weight proteins that are hydrophilic in nature from the LEA superfamily are produced (Azooz et al., 2011; Ahmad et al., 2012c).

High salt concentration triggers different harmful processes, such as membrane disorganization, increased production of toxic metabolites, and elevated ROS production. Salinity causes low nutrient uptake, resulting in reduced grain protein, fat, and fiber substances in the wheat (Abbas et al., 2013). Seed germination is the most vulnerable

plant growth stage to be affected by salt stress (Farooq et al., 2009). Moreover, chlorophyll cannot perform its proper function, hence leading to degradation and death of plant cell as a result of hyperosmotic and hyperionic stress (Ahmad et al., 2011). Inhibition of the plant development due to salts in soil is due to two main reasons: Firstly, it diminishes water uptake capability of plants, which prompts reduced development, i.e., the low water impact of high salt concentration, and secondly, salt may move to the transpiration mechanism of plants and, in the long run, harm the cell of leaves that are carrying out the process of transpiration, thus prohibiting plant development. This is the salt-specific or particle overabundance impact of high salt concentration (Munns, 2002).

2. Plant responses against high salt concentrations

All the developmental stages in the life of plants are controlled by a combination of physiological responses, which might lead to diminished growth and yield. Plants respond to high concentration of salts in multifarious ways, but the two main phases are as follows:

i. The principle stage of developmental reaction caused by the impact of high salt is from the outer side of a plant. Salts present in growth medium minimize leaf development and, to a certain extent, root development. The cell processes and metabolic pathways are like those of drought-affected plants. Na^+ or Cl^- never gather in the developing tissue at a concentration that stops the development of the tissue. Phloem provides food to the meristematic tissues, where salt is effectually omitted. Hence, it can be accumulated in fast elongating cells that are coming to their xylem via their vacuoles.

ii. Lateral phase in the development stages is caused by harmful high salt impact in the inner cells of plants. The salt reaches the old leaves along with its transportation in the transpiring leaves for a long period bringing about higher sodium and chlorine fixations, as a result causing leaves' death. This may be due to increased cellular capacity to accumulate salt in the vacuole. After this, salts will move quickly toward cytoplasm of the cell, thus stopping catalyst reactions. On the other hand, they may accumulate in the plasma membrane and cause the water to leave from the cell.

2.1 Leaves and shoot growth control mechanisms

Plant responses that control the growth of shoot and leaves are not particular of the salt concentrations, but they seem to be connected with waterborne stress factors, as it shows that sodium and calcium levels fall in leaves and roots under drought, ultimately leading to destructive results (Fricke, 2004). When exposed to high concentration of the salts, the developmental control of plants is mainly due to hormonal regulations and transport of proteins. Over the time, the hormone pathways are recommended as opposed to relations of water control development in soils having high levels of salts (Fig. 5.1).

2.2 Root signal pathways

Tests showed that during drought and high salt concentrations, compounds originated from roots diminish leaves development. Harsh salt stress causes reduced nutrient uptake by the roots (Hu and Schmidhalter, 2005).These are considered to be root signal pathways. Notwithstanding, abscisic corrosive is the main signal generated by the roots under stress (Dodd, 2005). Concentration of osmotic stressors can affect the magnitude of cellular damage made during wheat production, which may eventually lead to an overall compromised yield of the crop. Ethylene-responsive factors via gene classification in wheat are shown to be critical for wheat production under stressful environmental conditions (Abhinandan et al., 2018).

3. Hormone regulation in salt stress

The dry weight of leaves from salt-treated plants is proportionately high, which implies that transpiration rate of these leaves is higher. Hence, it is necessary to maintain optimum hormone control of cells that are undergoing division and extension in the roots. Literature has demonstrated that high salt stress has a variance impact on the rate of root elongation (Rubinigg et al., 2004; Pan et al., 2019).

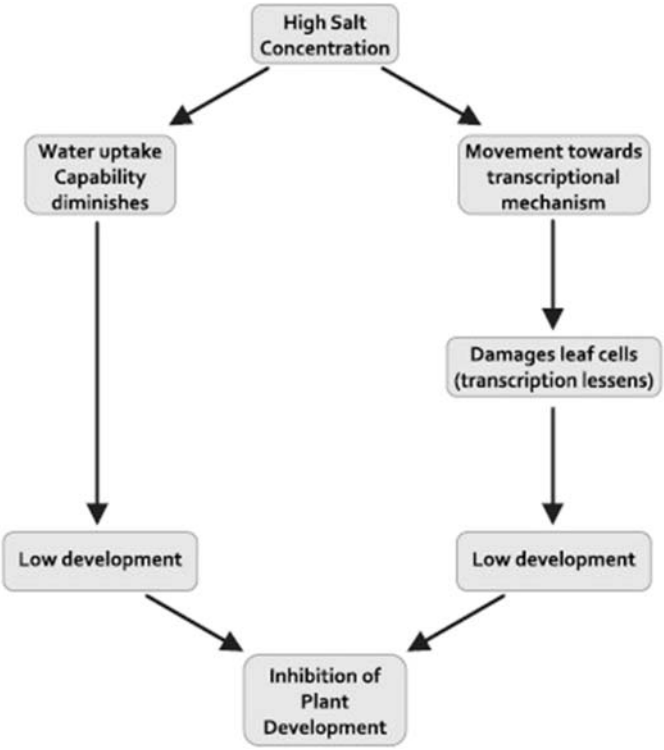

FIGURE 5.1 Effect of high salt concentration in plants.

Mechanisms that help control high stress of salts are of two types: one helps to limit the uptake of salt contents from soil in plants, whereas the other mechanism minimizes the amount of the salt inside the cell (Tester and Davenport, 2003).

3.1 Salt exclusion

Roots eliminate the excess concentration of sodium and chlorine dissolved in growing media of soil, or salts present in shoots that can potentially reach poisonous levels with time. Plants remove around 50 times more salts as compared with water in leaves (Munns, 2005). On the off chance that plant performs in just 1/50 of salt concentration from the soil (i.e., avoids 98%), increase of salt concentration in shoot will never increment as compared with that present in soil, and plant can still live indefinitely in high salt soil (Munns, 2005). Ion exclusion, tissue tolerance, and salt tolerance are the three major features that plants employ to adapt to salinity stress (Roy et al., 2014). Once the salt enters into the root system, there is subsequent activation of various signal cascades that produce ionic tolerance by limiting Na^+ entry into the root and decrease the overall translocation of Na^+ (Isayenkov and Maathuis, 2019).

About 98% of the salt is eliminated by the plants in soil solution, allowing only 2% to be transported in xylem to the shoots. Bread wheat excludes more than 98% sodium in soil, leaving its amount in leaves more than 50 mm (Husain et al., 2004). On the contrary, chlorine removal varies from species to species. Transport from leaves toward phloem may help to keep low salt concentrations; however, it shows moderately little retranslocation of salt concentrations from leaves, inside the transpiration stream. This effect was observed apropos to the continuity of salt after they were removed around the roots in leaves. Estimations of particles inside the phloem sap of plants have demonstrated that the species that greatly tolerate salt stress prohibit the sodium and chlorine from the phloem to an extensive degree, in contrast to less tolerant species. However, salts stacked in the phloem in lower leaves may move to the roots as shown in Fig. 5.2.

Phloem from young leaves may head toward the meristematic and elongated tissues of shoots. Various species represent a strong relationship between salt prohibition and salt resistance (Munns and James, 2003; Tester and Davenport, 2003). The accompanying segment demonstrates how characteristic variety of wheat in sodium barring can be employed to present a novel source of high salt concentration tolerance at a commercial level. To understand

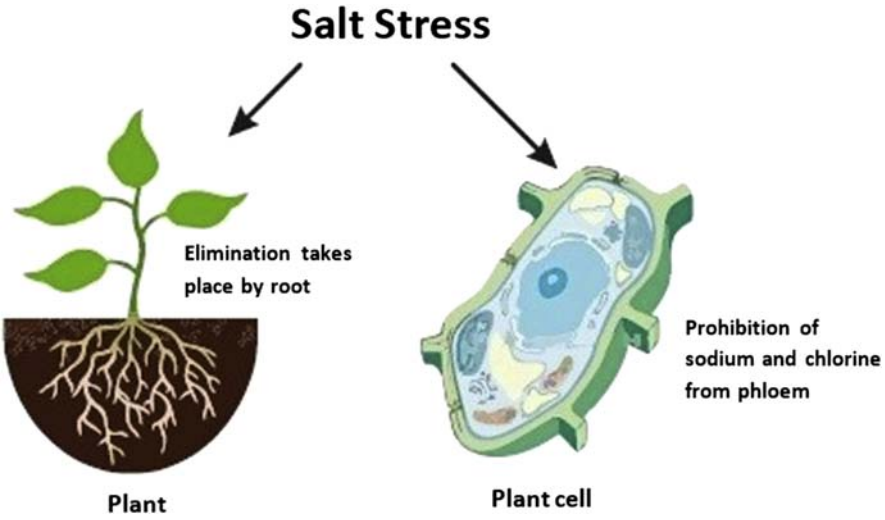

FIGURE 5.2 Salt exclusion.

the energy costs of salt stress tolerance in crop plants, there is a need of biophysical modeling of how salt and water are transported into the cells, roots, and leaves by integrating the already known transporters and ion gradients (Tyerman et al., 2019).

3.2 Effects of abscisic acid on salinity tolerance

ABA is a vital phytohormone whose function in plants is to tolerate high salt concentrations. It is perceived as a hormone that is upregulated due to the shortage of soil water around the root. Salinity stress causes water loss, ultimately increasing the levels of ABA in shoots and roots (Popova et al., 1995). The positive association of ABA aggregation to salt tolerance (Fig. 5.3) has been in any metabolic event credited to the increase of K^+, Ca^{2+}, and good solutes. For example, proline and sugars, in root vacuoles, neutralize with the uptake of Na^+ and Cl^- (Gurmani et al., 2011). ABA is a basic cell factor that regulates the outflow of various salt and water shortage responsive genes. Fukuda and Tanaka (2006) showed the impacts that ABA has on two genes, namely, Hvp1 and Hvp10, involved in vacuolar H^+ inorganic pyrophosphatase and of Hvvha-A, respectively (Fukuda and Tanaka, 2006). The experiment was designed to determine the purpose of the reactant of vacuolar H+-ATPase in *Hordeum vulgare* under salt stress. ABA treatment in wheat impelled the expression of Mapk4-like TIP-1 and GLP-1 qualities under salt stress (Keskin et al., 2010). A recent study demonstrated that a nuclear protein, GmWRKY16, which has the capability of transcriptional activation, is found to enhance salt tolerance through an ABA-mediated pathway in *Arabidopsis thaliana* (Ma et al., 2019).

4. Salt stress triggers the upregulation of Taaoc1, implicated in improving salinity tolerance

Evidences confirm that abiotic stress triggers the alpha-linolenic acid (ALA) pathway in plants (Lenka et al., 2011). RNA transcriptional studies, in particular, have revealed the salt stress-induced expression of genes involved in ALA metabolism (Liu et al., 2012; Wu et al., 2019). In one study, cv SR3 hybrid wheat plants were treated with NaCl or PEG (polyethylene glycol). Transcript levels of *TaAOC1*, a gene that expresses an allene oxide cyclase that participates in the ALA pathway, were measured subsequently (Zhao et al., 2014). The mRNA levels of TaAOC1 gene were elevated about 8−15 times, clearly detectable within 30 min of treatment. Afterward, it was essential to determine the effects of JA (jasmonic Acid) and ABA on the TaAOC1 transcription. Upon exogenous introduction of JA, TaAOC1 transcript levels were elevated more than 150 times. ABA treatment conferred similar results, although comparatively less induction was observed. TaAOC1 expression contributed to providing tolerance against salt stress. The study established that the synthesis of JA is an integral part of the metabolism pathway as it improves tolerance against salinity stress. However, a functional AtMYC2 is required for this process. Along with TaAOC1,

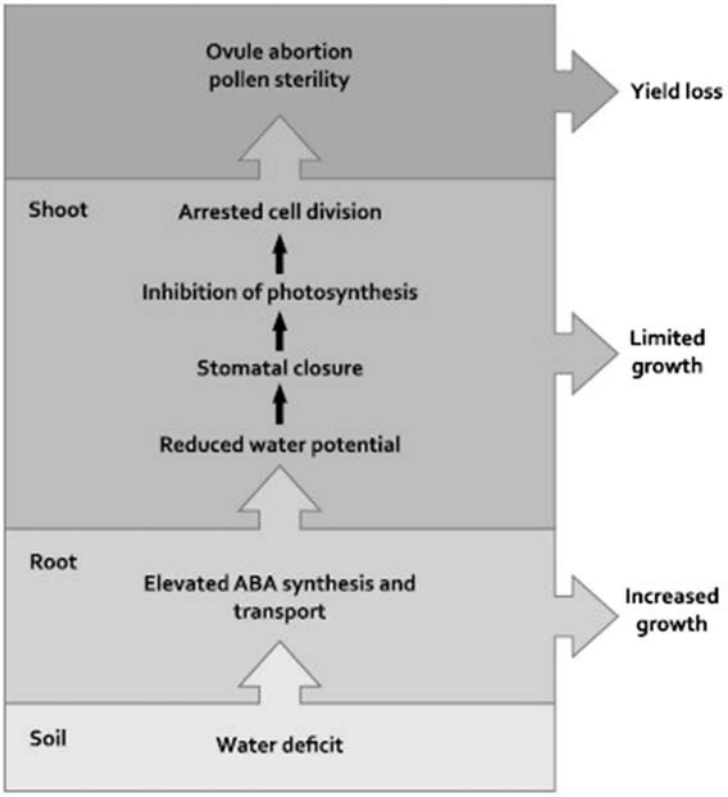

FIGURE 5.3 Effect of abscisic acid hormone.

TaOPR1 encodes for two main enzymes of the ALA metabolic pathway. A recent study shows that TaAOC1 and TaOPR1 cause salt tolerance through both ABA- and JA-dependent pathways to increase expression of MYC2, an important component of salt stress response-signaling cascade (Wang and Xia, 2018).

4.1 Effects of upregulation of *Tachp* on tolerance against salt-induced stress

TaCHP gene encodes CHP-rich zinc finger protein with three distinct C1 (DC1) domains and the resultant ability to bind two zinc ions. The domain-containing proteins have a regulatory function. Microarray data suggested that *TaCHP* (a CHP family gene) is differentially expressed in SR3 as compared with JN177. *TaCHP* transcript levels were raised in SR3 roots as opposed to JN177 roots in the case of both stressed and nonstressed conditions. However, leaves lacked significant *TaCHP* mRNA according to the data (Li et al., 2010). Interestingly, *TaCHP* gene was found to be downregulated by ABA and salt stress in wheat; contrastingly, it plays a positive part in salt resistance in transgenic Arabidopsis (Li et al., 2010; Hou et al., 2018). The gene was found to be upregulated in SR3 as opposed to normal JN177 even during salt-induced stress. Analysis from real-time PCR and reverse transcription (RT)-PCR have authenticated that *TaCHP* was initially repressed after introducing salinity stress for 30 min, but later its levels became constant. In the JN177 roots, *TaCHP* was expressed significantly lesser, but the initial decline in the mRNA levels was also observed (Li et al., 2010).

The study proved that the production of *TaCHP* in SR3 is linked to defense against salt-induced stress. Abnormal *TaCHP* expression was reported to enhance the accumulation of *DREB* products. Moreover, *TaCHP* may also have a potential role in the cross-talk mechanism between the ABA pathway and other signaling pathways involved against different plant-specific stresses.

4.2 Overexpression of Gmdreb1 in transgenic wheat has enhanced salt tolerance

Genetically engineered plants have a potential to provide tolerance against abiotic stresses, including salt stress. DREB (dehydration responsive element binding), a transcription factor, upon binding to *cis*-acting elements of

responsive genes, controls the expression of downstream signaling genes that contribute to provide tolerance to abiotic stress (Agarwal et al., 2006; Wei et al., 2009). DREB1 is a transcriptional regulator that has been shown to play a significant role in triggering responses against abiotic stress (Mizoi et al., 2012; Feuj et al., 2018). A study proved that another transcription factor GmDREB1 gene upregulation was associated with enhanced salt tolerance in the transgenic wheat (*T. aestivum* L.) varieties T349 and T378 (Jiang et al., 2014). The various parameters such as radicle number, radicle length, and coleoptile length were found to be higher in the genetically modified wheat lines as compared with the normal wild-type Jimai 19 control. This finding indicated that improved growth of the transgenic wheat at the germination stage is potentially due to upregulation of the GmDREB1 gene in a salty environment. Another study found 13 novel allele variations of TaDREB1, which are DRE-binding proteins that function as transcript activators. Out of all variations, TaDREB1-D transcript expression level was detected in wheat seeds under salinity stress (Liu et al., 2018).

4.3 Mannitol accumulation improves growth in transgenic wheat against abiotic stresses

Research on model transgenic plants has affirmed that mannitol accumulation can relieve abiotic stress. Mannitol, a colorless sweet-taste alcohol, is not naturally produced by all plants. Using the techniques of genetic engineering, scientists inserted an MtlD gene encoding mannitol-synthesizing enzyme from *Escherichia coli* into wheat (*T. aestivum* L. cv Bobwhite) (Abebe et al., 2003) in the quest to ascertain whether the newly acquired ability to synthesize (and accumulate) mannitol would alleviate abiotic stresses such as drought and salinity stress. Mannitol synthesis is enhanced in plants under stress conditions, and this synthesis is attributed to the action of NADPH (Gupta and Huang, 2014). Mannitol-1-phosphate dehydrogenase, the enzyme encoded by the introduced gene, catalyzes the formation of mannitol-1-phosphate from fructose-6-phosphate. Mannitol-1-phosphate then finally forms mannitol. Calli and other parts of the transgenic wheat plant were used to determine the potential to alleviate water and salt stresses. Their study established that low concentration of mannitol was successful in achieving better growth against salt and water stress. However, they reported that mannitol accumulation itself was not adequate to protect against stress through lowering of osmotic potential (Abebe et al., 2003). They attributed the enhanced tolerance of the transgenic wheat to other protective functions of mannitol. However, the research did not negate the possibility of osmotic effects in meristems and other regions of the plant. In a recent study, mannitol-treated detoxification efflux carriers (DTX)/multidrug and toxic compound extrusion (MATE) overexpressing lines, which are important translocators of ABA, showed increased root growth compared with wild type, signifying higher tolerance to osmotic stress (Lu et al., 2019).

4.4 Snac1 gene from rice contributes to tolerance against abiotic stresses in transgenic wheat

Efforts have been made to identify and manipulate the stress-induced genes to improve tolerance of plants to various abiotic stresses, including salt stress. Notably, gene SNAC1 (that encodes NAC transcription factor) from rice plant was found to be stimulated by stress; hence it was inserted into wheat plant to observe its effects in wheat (Saad et al., 2013). The resulting transgenic wheat varieties were carefully analyzed and studied under different stress conditions. An enhanced ABA sensitivity and an increased ability to withstand salinity and drought was reported in the wheat plants expressing the SNAC1 gene, indicating that this gene has a possible role in contributing toward tolerance in bread wheat against drought conditions (Saad et al., 2013).

4.5 Differential gene expression of Hkt genes in high salt concentration promotes tolerance against salt stress

Evidence of salt stress-induced differential gene expression provides an opportunity to elucidate the role of possible stress-induced genes and to determine their markers. This approach may prove fruitful for the production of salt-tolerant varieties of wheat crop in the future. Studies proved that differential gene expression occurred in two varieties of bread wheat, namely, Kharchia65 (most salt-tolerant variety of bread wheat) and HD2329 (salt-sensitive variety) (Singh et al., 2015). This can help us understand the mechanism that promotes tolerance against salt stress. HKT alleles have been found to be essential for tolerance against salt-induced stress. Two HKT genes (TaHKT2; 1.1 and TaHKT2; 3.1) were found to be differentially expressed in Kharchia-65 and HD2329 (Singh et al., 2015). Moreover, activation of antioxidant enzymes was also different in the two varieties of bread wheat. This proves the intrinsic defense responses against salt stress. The expression pattern of recent gene TaHKT2; 3.1 has been generated, and its potential role

explored. The study establishes a relationship between salt tolerance and the differently observed molecular patterns. A study conducted on various wheat genotypes also revealed that Kharchia-65 is the most salt-tolerant genotype and is known to attain different genetic and epigenetic mechanisms for regulatory HKT genes expression and uses inbuilt physiological and biochemical traits to tolerate salt stress (Kumar et al., 2017).

4.6 *Taopr1* overexpression in the face of salinity improves salinity tolerance in *cv* SR3 *wheat*

Wheat SR3 exhibits a considerable level of salinity tolerance. This can be attributed largely to enhanced performance of the scavenging systems against ROS (reactive oxygen species) (Wang et al., 2008). Salinity stress triggers an increased expression of a variety of genes in *cv* SR3, including a *TaOPR1* gene that encodes an OPRI protein (Liu et al., 2012). Research shows that TaOPR1 depends on ABA for its response toward salinity stress (Dong et al., 2013). Salinity stress-induced *TaOPR1* upregulation conferred improved tolerance to salinity. This effect was observed in wheat and Arabidopsis (in heterologous form of expression). This tolerance mechanism potentially works by controlling the signaling pathways of both ABA and ROS but is believed to remain uninfluenced by the JA synthesis and signaling.

According to microarray analysis, the transcriptional levels of both cv SR3 and cv JN177 were same 30 min after treating them with 200 mm NaCl. However, within a day, the mRNA levels of cv SR3 plants rose and became almost four times that of cv JN177 plants (Dong et al., 2013). Real-time PCR also supported this analysis as it showed that *TaOPR1* mRNA levels increased considerably in cvR3 compared with cv JN177 after NaCl treatment. High salinity triggers the production of ABA and ROS. Upon introducing hydrogen peroxide (10 mm) and ABA 100 μm, the *TaOPR1* transcripts were the same as observed during salt-induced stress, with cv SR3 being more responsive than cv JN177 (Dong et al., 2013). The study established that stress triggers TaOPR1 expression and the upregulation of this gene in cv SR3 plays an important role in stress tolerance. Salinity-induced gene upregulation was negatively influenced by the application of norflurazon, which inhibits ABA production. The inhibition suggested that stress-responsive TaOPR1 transcription requires ABA.

To determine whether TaOPR1 had any effect on salinity tolerance, it was introduced in both JN177 and Arabidopsis ecotype Columbia. Of 12 independently generated wheat lines, 2 wheat lines were selected due to adequate TaOPR1 expression. The two selected wheat lines and the control line cv JN17 were grown in hydroponic nutrient solution known as Hoagland liquid medium. After adding 200 mM NaCl, cv JN17 became limp, while the transgenic wheat lines continued to display turgidity (Dong et al., 2013). Moreover, their roots and shoots elongated, indicating improved growth under these conditions.

4.7 Sbpip1-mediated improvements in salinity tolerance in transgenic wheat

Salicornia bigelovii Torr is an euhalophyte that requires an increased concentration of sodium for proper growth. It is believed that it has developed adaptations to cope with the saline environment. It possesses a unique gene SbPIP1 that belongs to plasma membrane major intrinsic gene family. SbPIP1 was inserted into the wheat plant of cv. Ningmai 13, and the transgenic wheat was carefully analyzed during germination to determine its potential for tolerating salt stress. The analysis confirmed that the transgenic wheat lines exhibited appreciable salt tolerance as compared with Ningmai 13 (Yu et al., 2015; Mujeeb-Kazi et al., 2019).

Research was conducted to elucidate the mechanism behind SbPIP1 gene-mediated enhanced salt tolerance. Both the transgenic and normal wheat lines were treated with excess salt (Yu et al., 2015). Characteristic features such as the MDA content, proline content, and the contents of soluble proteins and sugars were determined and compared between the SbPIP1-upregulated wheat lines and the control wheat lines. The results revealed the details of SbPIP1-mediated salt tolerance in conjunction with the observations.

The results indicated that SbPIP1 upregulation triggered a rise in osmolyte proline, decline in the MDA content, and acceleration of the sugar biosynthesis in the initial stages. On the contrary, no effect was observed on the regulation of soluble protein synthesis (Yu et al., 2015). Moreover, the results indicated that SbPIP1 plays a role in improving the salt tolerance by promoting the buildup of proline, increasing the production of soluble sugars (initially), and increasing the antioxidant response. The results reaffirmed SbPIP1's key role in the promotion of salt tolerance in wheat.

4.8 *Atnhx1* expression in transgenic wheat plants shows tolerance toward salinity-induced stress

Various studies have exploited expression of specific genes in wheat to identify their role in salt tolerance, including a gene that encodes for *Arabidopsis thaliana* vacuolar Na^+/H^+ antiporter, AtNHX1, which showed

improved germination and increased wheat grain yield when investigated under saline stress (Asif et al., 2019). A study focused on the *Agrobacterium*-mediated *AtNHX1* gene transformation of two hexaploid wheat cultivars to ascertain the possibility of tolerance against salinity-induced stress (Moghaieb et al., 2014). An effective system was used to achieve speedy transformation without involving tissue culture techniques. One-month-old young plants of two transgenic wheat lines from Gemmiza-9 were selected and exposed to varying levels of sodium chloride. Experimental analysis suggested that upon increasing the concentration of NaCl, the morphological features were highlighted in both plants (Moghaieb et al., 2014). Comparison of morphological features of transgenic plants with negative controls confirmed that they showed improved growth under salinity imposed stress. The normal control plants inhibited growth at 300 mM NaCl concentration, embracing death at 350 mM concentration, while the transgenic plants continued to grow under increasing salt concentrations. Increasing salt concentration leads to decreased dry weight in both wild and transgenic plants, but the reduction of plant weight in wild-type plant was more significant under the same conditions. The study demonstrates that the transgenic wheat plants (expressing AtNHX1 gene) showed a buildup of Na^+ levels in their leaves in response to increasing NaCl concentration. This suggests that the expression of this gene contributed to enhance tolerance against salt-induced stress. Moreover, increased NaCl concentrations lead to K depletion in the leaves. There is a considerable difference in K levels between the normal and transformed plant leaves, under salt stress. While Na competes for binding to K-binding sites, cytosolic K concentration is lowered. The findings authenticated that AtNHX1 expression improves salt tolerance, potentially by increasing sodium ion concentration inside the cells and by continuously maintaining the balance between sodium and potassium ions.

4.9 Role of Myb transcription factors in salt-induced stress

MYB transcription factors in the wheat are also involved in the tolerance response of plant against high salinity conditions (Amirbakhtiar et al., 2019; Dong et al., 2018). This physiological adaptation is acquired by plants to avoid damage to their cells due to a high concentration of salts. Studies state that MYB genes are helpful for tolerance of salinity in different genomes. The important MYB gene, TaMYBsdu1, shows overexpression in the leaves and root of wheat under long-term salt stresses. This confirms that TaMYBsdu1 may be an important factor involved in the salt stress adaptation of wheat. Zhang et al. (2016) introduced MYB transcription factor that was homologous to Arabidopsis AtMYB333 and found it as an important gene for maintaining salt tolerance in the root of bread wheat (Zhang et al., 2016).

4.10 *Tastg* role in salt tolerance

A newly identified gene, known as TaSTG (*T. aestivum* salt tolerance gene), can be expressed by wheat under high salt concentration, suggesting its potential role in stress regulation. Recent experiments with genetically modified rice and *Arabidopsis* exhibiting overexpression of TaSTG has shown salt tolerance more than that of wild-type gene control mechanism (Wang et al., 2013). Seedlings obtained from genetically modified Arabidopsis show a normal rate of germination even in high concentration of salts. The chlorophyll level, solvent sugars, and proline are elevated in the genetically modified *Arabidopsis* than the normal plants. Moreover, the concentration of sodium (Na^+) and malondialdehyde in plants was essentially lower in those species having an overexpression of TaSTG (Wi et al., 2006).

4.11 Role of *SOS* gene in salinity

Salt overly sensitive (SOS) stress signaling pathway plays major role in ion homeostasis and salt tolerance (Hasegawa et al., 2000; Yang and Guo, 2018). The combination of different type of stresses, such as ionic stress, oxidative stress, and osmotic stress, leads to salt stress. Salt is the major abiotic stress across the globe. Na^+ has its roles to play in different mechanisms inside the cell such as photosynthesis, metabolism, cytosolic enzyme activity, and so on. Plants acclimatize to the adverse conditions by undergoing various modifications to their immune system for the survival and growth. The three main processes include prevention of Na^+ inflow, discrimination of Na^+ in the vacuole and Na^+ discharge.

4.12 *SOS1* gene

This *SOS* gene is involved in salt tolerance as it maintains ion homeostasis. It plays its role either directly or indirectly. There are four types of *SOS* gene: *SOS1*, *SOS2*, *SOS3*, and *SOS4*, respectively. *SOS1* and *SOS2*, also called as

serine/threonine protein kinases, are activated by *SOS3;* the Ca^{++} binding protein. *SOS4* plays its role in regulation and transportation of Na^+. An antiporter known as Na^+/H^+ antiporter is also present, which is encoded by the *SOS1* gene. *SOS2* and *SOS3* complex plays a role in the regulation of activity and functions of *SOS1* gene, which subsequently activates Na^+/H^+ antiporter to perform its function. Specifically under salt stress conditions, *SOS4* gene is expressed (Shi and Zhu, 2002). The *SOS4* gene is only involved in salt tolerance and does not play any part in the *SOS2* and SOS3 pathway as shown in Fig. 5.4.

Genes other than *SOS1* gene are also involved in immunity mechanism in wheat against the salt-induced stress. The expression of genes such as betaine aldehyde dehydrogenase and pyrroline carboxylate synthetase is enhanced. For the transfer of Na^+, it is loaded into xylem in roots. It is stored in vacuoles to perform its functions. However, excessive Na^+ stored in the vacuole results in Na^+ stress. Now, *SOS1* gene plays its function by unloading Na^+ from the root xylem, ultimately resulting in lesser destruction of leaves by Na^+ stress. Another study investigated the expression of *TaSOS1* gene in root, sheath, and blade in the wheat seedlings, and it was found that salinity led to increased expression of *TaSOS1* gene, thereby improving salt tolerance (Ghassemi et al., 2018).

4.13 Salt-regulated genes in root

Roots have an exceptional capability to control sodium Na^+ and chlorine Cl^- levels. Surprisingly, their ion concentration never rises with time. To the contrary, at higher salt concentration, the level of sodium and chlorine decreases as compared with the outside. Diverse durum and bread wheat genotypes present in high salt concentration areas were found to have small concentrations of sodium and chlorine, i.e., ranging from 50 to 150 mm (Husain et al., 2004). Roots aggregate natural salts to keep up cells in turgor state, so that organic compounds such as proline or sucrose that tolerate salts are also increased in their level as shown in Fig. 5.5.

Transporter mechanisms maintain the upregulation of sodium and chlorine from extracellular environment. Genes involved in this mechanism are grouped in the vacuoles. Sodium enters passively into cells of root from soil having high salt in it. Stacking of the xylem tubules is ought to be expanded by the levels of sodium chloride salts. Sodium efflux may increase drastically, attributed to an antiporter. For example, SOS1 pathways are activated, and cell membrane pumps protons. In a similar way, potassium gates and symporters in the plants, such as HKT1, is potentially upregulated to keep potassium (K^+) balance (Ali et al., 2019).

Sodium gates that transport sodium, for example, nonselective negative ion gates, might be downregulated. Cation/H^+ antiporters that control the normal level of organelles may be upregulated. In the absence of depolarization effect, sodium does not enter the xylem, but potassium can enter with the support of receptors. For example, xylem potassium stacking can occur by dynamic instead of passive transport. Some types of potassium channels having best permeability for potassium as compared with sodium might be upregulated during the process. Elongation of roots may be regulated by different genes that participate in signal transduction pathways during cell division. The action of methods that integrate and also convey signals by hormones may be changed at the tip of the root. Moreover, "signals from roots" cap have an effect on transpiration, thus potentially resulting in the stomatal closure as well as decrease in leaf extension levels (Maathuis et al., 2003).

Salt stress frequently upregulates genes that show response against antioxidant reactions, for example, ascorbate peroxidase and glutathione reductase (Ueda et al., 2004). These are normally expressed in stress conditions, to varying degrees. Different transcriptional factors are modified by stresses. Chen et al. (2002) presented an extensive literature that reviewed levels of mrRNA in 402 factors involved in transcription in different tissues of plant after various biotic and abiotic stresses (Chen et al., 2002). After studying replication and different stages of the plants development, this study revealed that around 15% of this process occurred in roots, and some of this was only specific for root (Chen et al., 2002). Besides, some were not prompted by salt stress but stimulated by abiotic stress in broader terms.

Deficiency of calcium is a typical issue relevant with salt readings (Cramer, 2002). Ca^{2+} movement (centralization of ionized and hydrated calcium) is brought about by addition of salt concentrations down to the soil. Hence, uptake of Ca^{2+} affects membrane permeability for different negatively charged ions, and eventually the plant development (Tester and Davenport, 2003).

As an example, if half-quality Hoagland's answer (having 2 mm calcium) has added supplement media, i.e., 100 mm sodium chloride or above, chemical action of calcium would be around one-third of the total concentrations that is below the level that is needed for natural processes. Low calcium activity caused the deviation of the root membrane from normal functioning, indicating that calcium is required for optimum performance under stress conditions.

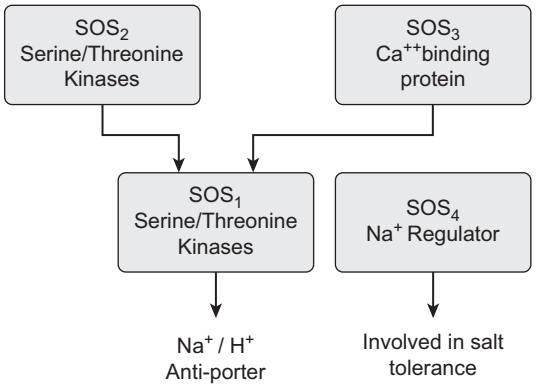

FIGURE 5.4 Role of *SOS* gene in salinity.

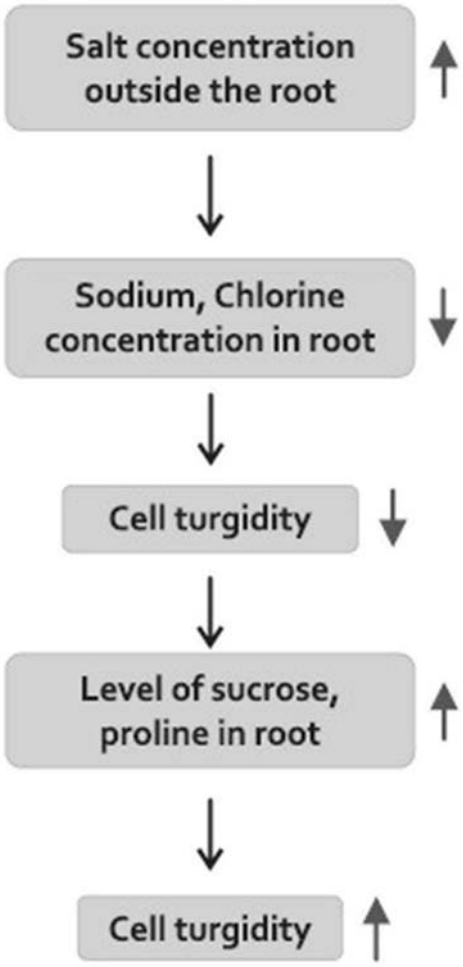

FIGURE 5.5 Salt regulation in root.

5. Salt-regulating genes in leaves

Genes present in mature leaves for the adaptations of high salt concentration have many functions. They control process of photosynthesis and circadian rhythms of stomatal opening/closing, help to avoid sodium lethality, and play a role in maintaining turgor. They can also direct leaf arrangements. These are produced by food originating from roots and other highly growing areas from the different parts of plants (Munné-Bosch and Alegre, 2004).

Solute requirement increases with spam of time in adult leaves. Sodium and chlorine levels maximize to the concentrations that should be appropriated in vacuoles of cells, or they may be lethal. The action of NHX1 must be high. Also, the pumps for proton need to activate them. Likewise, the requirement for protective materials increases as time passes, as progressively more seasoned leaves appear with higher concentrations of sodium and chlorine fixations and a less capability for carbon fixation. Genes involved in the synthesis of antioxidant compounds are upregulated. In all stress conditions, ROS production remains increased, especially when plants are exposed to the high intensity of light (Suzuki and Katano, 2018). However, photosynthesis rate is constrained by stomata opening and closing. Compounds, for example, superoxide dismutase, ascorbate peroxidase, and glutathione reductase, may also be upregulated (Milla et al., 2003).

6. Conclusion

Wheat crop has nutritional and economic importance. The large-scale production of wheat prompted the expansion of human settlements, ultimately leading to the beginning of the human civilization (Cooper, 2015). Since the beginning of the human population, wheat has been cultivated extensively. Due to advancements in the agriculture sector, the annual production of wheat has increased (Berkman et al., 2012). However, due to increasing global demand, wheat production needs to be increased to fully meet the requirements of the growing world population. There are different varieties of wheat such as bread wheat, durum wheat, Einkorn wheat, and so on. Wheat is not only a texture rather it is one of the widely used source of protein and animal food.

Wheat, like other cultivated crops, is exposed to abiotic stresses such as salinity, drought, and oxidative stress. These environmental stress factors have a negative impact on the wheat quality and yield. Salt stress or salinity is particularly an important factor responsible for low yield and loss of valuable land. Moreover, high salt concentration alters physiological as well as biochemical processes in plants (Ahmad, 2010; Ahmad et al., 2011, 2012a, 2012b, 2012c). In response to these adverse conditions, the plants develop adaptation features. Notably, salt exclusion principle is brought into effect, effectively removing salt from the plants. Biochemical pathways are activated, leading to enhanced gene expression implicated in enhanced tolerance against salinity conditions. Hormonal regulation (ABA treatment) and maintenance of ionic balance are also essential to maintain plant immunity (Hatmi et al., 2018). Furthermore, certain enzymes are activated that are involved in antioxidation responses. Both genetic and environmental factors work in collaboration to dampen the effect of salt-induced stress. More research needs to be conducted to elucidate the detailed biological mechanisms involved in stress regulation. Manipulation of intrinsic biological pathways activated under salt stress and ascertaining their complex mechanisms will help develop salt-tolerant wheat crops in the future.

To conclude, high concentration of salts is one of the largest threats posed to crops worldwide and is believed to become worst in the future. The unfavorable impact of high salt concentration on wheat can be seen at the whole crops levels regarding plant production and economical loss of the food crops. Some wheat varieties are more adaptable than others and strive more for survival in high salt concentrations. Detailed information of different mechanisms can be employed to have an understanding of wheat responses to salt stress. The study provides basics on how wheat regulates and tolerates the high concentration of the salts to keep up an ideal harmony between salt uptake and regulation. Hereditary mechanisms and environmental adaptations work collaboratively to render plant tolerant to salinity stresses imposed on the crops.

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CHAPTER

6

Role of osmoprotectants in salinity tolerance in wheat

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OUTLINE

1. Introduction

Wheat (*Triticum aestivum* L.) is a major food crop throughout the world with annual crop yield of about 736 million metric tons (FAO, 2015), and therefore scientists focus on it greatly for the analysis of complex genome along with the development of strategies for the improvement in wheat crop yield and quality. Wheat genome is the most complex one among other food crops that are used as a source of energy and other nutrients. Pakistan being a major wheat producer had annual production of 24.2 million tons during the year 2012–13 and was predicted to cross 25 million ton mark for the year 2013–14 (Government of Pakistan, 2012). Wheat belongs to Poaceae family that includes monocots along with other cereals crops (Clayton and Renvoize, 1986).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00006-6

1.1 Genome organization

Wheat genome is an allopolyploid that comprises three different ancestral genomes that are named as A, B, and D. These A, B, and D wheat ancestral genomes originated from wild grasses of *Aegilops* genus (McFadden and Sears, 1946). Each of these ancestral genomes consists of seven pairs of homologous chromosomes (Hussain et al., 2010). Some of the wheat like *Triticum monococcum* is diploid and has two sets of chromosomes, but there are others that are tetraploid ($4\times = 28$) and hexaploid ($6\times = 42$) as well. *T. monococcum,* also referred to as common line wheat, is diploid with AA genome composition. Of all these different wheat varieties, tetraploid wheat *Triticum turgidum* L. and *T. aestivum* L. are of great importance, as they are being cultivated as a major food crop worldwide (Baum et al., 2009). Other than A, B, and D genomes, there are some other genomes present in some of the wheat species that includes S, T, U, N, and C genomes. This classification of wheat genomes was done by Morris and Sears in 1967 using many cytogenetic strategies.

Bread wheat (*T. aestivum* L.), one of the wheat crops, is being cultivated on a major area of land. It has hexaploid (AABBDD) genome, and its three different ancestral genomes have originated from the wild wheat of *Aegilops* and *Triticum* genera. D genome of *T. aestivum* is proposed to be originated from *Aegilops tauschii Coss* as confirmed by the phylogenetic analysis done by Petersen et al. (2006), and according to that analysis, it was also confirmed that *Triticum urartu* (AuT) contributed the A genome to bread wheat. Von Buren (2001) proposed *Aegilops bicornis* to be the donor of B genome to bread wheat, but due to the similarity between B and S genomes, some species containing S genome were also proposed to be the possible donor of B genome (Huang et al., 2010). Durum wheat (*T. turgidum*) is one of the main tetraploid (AABB) wheat having 28 chromosomes that is cultivated and commercialized as well. Its annual yield production worldwide is about 25 million tons and is considered to be highly rich in protein content (Bushuk and Rasper, 1994). Origin of bread wheat and other related species has been a subject of great study for the last 10 years, and phylogenetic analysis based on small molecular fragments has led to the revolution in cytogenetic analysis of *Triticum* genus (Farris, 1983).

Einkorn wheat (*T. monococcum*) has a diploid genome (AA) and is considered to be one of the earliest wild wheat, as early as 7500 BCE. It is mostly wild, used to be domesticated in the past era and is considered to be evolved from *Triticum boeoticum* (AA) due to the genomic resemblance. Cytogenetic analysis was also done on the base of 288 bp AFLP marker by Heun et al. (1997) which confirmed the proposed statement. The introduction of bioinformatics tools in phylogenetic studies of wheat genome has revolutionized the pace and precision in finding the exact relation among ancient and present wheat varieties.

1.2 World production

Wheat crop is one of the most widely cultivated crops globally and fulfills the food requirements of almost half of the world population. When compared with the other food crops like maize, rice, etc., wheat leads not only to the aspect of acreage but in production as well. That is the reason wheat has been centrally focused on the genomic and cytogenetic studies to make a better understanding of complex crop for the purpose of improvement in yield. Wheat provides 55% and 20% of carbohydrates and calories, respectively, to the world population (Breiman and Graur, 1995). Wheat consumption in different countries differs due to differences in the cultures and climate. Countries like Pakistan, India, Australia, Russia, Afghanistan, and Iraq have 80% or more dependence on wheat than on other grains (Global grain consumption map, 2011). Optimum conditions are necessary for the cultivation of the wheat crop. At 25°C, wheat is shown to have maximum production provided that it is grown on water and nutrient-rich land. Considering the current production of wheat, it needs to be increased by 60% till the year 2050 to meet the requirements of the world population.

In the agriculture sector of Pakistan, wheat contributes about 25% of crop sector value becoming a major contributor to the sector (Faruqee et al., 1997). When we look at the gradual increase in wheat production in Pakistan during the last 50 years, it has increased in doubling manner. But for the last 2 decades, there has not been enough increment in yield resulting in shortage of food to Pakistan population (FAO, 2015). Wheat has been a major source of income to the rural areas. According to Pakistan Agriculture Research Council (PARC), wheat consumption was 120 kg per person annually that was among the highest consumption rate throughout the world (Khan, 1989). Province of Punjab is a major producer of the wheat crop and comprises major land suitable for irrigation among other provinces. About 40% of the cultivated area of all crops was used for the cultivation of wheat during the year 2011−12. Wheat was cultivated on about 6,483,000 hectares of total cultivated land, and cotton covered the second highest area of cultivation (Punjab Development Statistics, 2011−12).

1.3 Stress effects

Plants being motionless creatures face limited possibilities for their survival under drastic variations in their surrounding environment (Kuiper, 1998). Some biotic and abiotic stresses have been affecting the wheat crop

worldwide leading to the decline in production as well as quality. Biotic stresses are not as much prevalent when compared to the one that is posed by changes in plant surroundings (Hussain, 2015). Biotic stress is induced by the infection or attack by any other organism like bacteria, viruses, or fungi. Wheat stem rust that is caused by a fungus *Puccinia graminis* results in major production losses throughout the world. It was first reported in Uganda and named as Ug99 (Singh et al., 2008). Other bacterial infections like bacterial leaf blight and bacterial sheath rot are also an important limitation in the way of increasing worldwide wheat production. Wheat yellow rust is another threat for the wheat which is caused by a virus leading to massive losses throughout the world.

In contrast to biotic stresses that are easily identified, abiotic stress steadily affects the crop yield without being identified for a long period. Abiotic stresses such as heat, cold, salinity, drought, and oxidative stress are serious threats to the agriculture. Heat stress due to elevated temperature leads to a loss in wheat yield and quality severely (Danish et al., 2019). The biotic stresses account for about 10%–20% yield loss worldwide, while abiotic stresses like salinity, drought, and heat cause 50% yield loss in the agriculture sector (Kreps et al., 2002). The plant being immobile is left with the only defense mechanism of bringing about the change in their proteomic composition and other developmental changes to adapt them in their surrounding environment. Stresses like heat, cold, salinity, and drought causes cellular dehydration which affects plant gene expression in a similar way that can help scientists to analyze it (Cook et al., 2004).

Due to rapid climate change and reduced annual rainfall worldwide, drought stress has been considered to cause the drastic detrimental effects on the yield of major food crops like wheat (Lucas et al., 2017). Drought occurs when a specific land or region faces very low precipitation as compared to the average rainfall in that season. This results in massive effects on the groups, people, environmental sector, and agriculture sector of that region (Danish and Zafar-ul-Hye, 2019). Pakistan, being a major wheat producer and ranked 8th globally, requires a good amount of rainfall. But for the last few years, some regions are facing low rainfall, leading to induction of drought stress and a decline in wheat yield. The wheat crop does not solely rely on rainfall, but the glacier water is another source of water. But due to elevated temperature, glaciers are melting leading to the reduced water tank (Hussain et al., 2004). Increased drought stress leads to the reduction in quality and increase in ash content of wheat (Rharrabti et al., 2003). In Pakistan, due to drastic change in rainfall climate pattern, low rainfall results, leaving crops dependent on the river or underground water. Rainfed areas that are solely dependent upon rainfall are facing drought stress due to low rainfall than the required amount. Some of the wheat varieties have been produced that are drought tolerant and grown on rainfed areas. Tijaban-10, a drought-tolerant wheat has been introduced to some of the rainfed regions of Baluchistan province of Pakistan and has been reported with high crop yield (Jahangir et al., 2013). Another drought-tolerant wheat variety Raj has been introduced to the province of Khyber Pakhtunkhwa (KPK) and improvement in yield to about 50% has been achieved by introducing this wheat cultivar (Mirza et al., 2003).

Drought is the leading factor involved in the reduction of productivity of wheat crop throughout the world (Boyer, 1982; Timmusk et al., 2018). Wheat is mostly grown on the area with an average rainfall of 30–113 cm each year. Tetraploid wheat (*Triticum durum*) is considered to be more tolerant as compared to hexaploid wheat (*T. aestivum*) (Waines, 1994). Low water level in plants leads to the loss of osmotic potential that cause changes in morphology of cells and tissues. Under water-deficit environment, wheat brings about change in its proteomic content leading to a reduction in the loss of further water by transpiration. If exposed for a long period, drought stress leads to the reduction of chlorophyll content and also causes instability of the membrane.

1.4 Nutritive value of wheat kernel

Wheat is often considered primarily as a source of energy (carbohydrate), and it is certainly important in this respect. However, it also contains significant amounts of other important nutrients including proteins, fiber, and minor components including lipids, vitamins, minerals, and phytochemicals which may contribute to a healthy diet (Shrewy and Hey, 2015). Wheat is a particularly important source of dietary fiber, with bread alone providing 20% of the daily intake in the UK, and well-established relationships between the consumption of cereal dietary fiber and reduced risk of cardiovascular disease, type 2 diabetes, and forms of cancer (notably colorectal cancer) (Shrewy and Hey, 2015). Wheat shows high variability in the contents and compositions of beneficial components, with some (including dietary fiber) showing high heritability. Hence, plant breeders should be able to select for enhanced health benefits in addition to increased crop yield.

2. Salinity

Drought and, majorly, salinity are among the most unfavorable abiotic environmental factors directly affecting agricultural productivity in arable land (Ashraf et al., 2012; Babgohari et al., 2013; Niazi et al., 2014). Salinity is

recognized as one of the serious soil degradation determinants. Of the world's total area, 6.5% is saline, and before now, almost 20% of the area under cultivation has been moved into salinity-affected area (Hakim et al., 2014; Oyiga et al., 2016). In these days, it has become a fact that these unfavorable abiotic stresses can lead ultimately to a continuum of physiological, morphological, molecular, and biochemical changes during plant productivity and growth (Wang et al., 2003). Either essential heavy metals (above threshold) or nonessential and other soil withering factors (e.g., soil salinity) are significant in subterritorial restriction of plant productivity and growth (Hayat et al., 2014). There are many studies in which consequences of salinization upon different processes like photosynthesis at different physiological stages of the plant has been investigated. (Yeo et al., 1985; Dionisio-Sese and Tobita, 2000; Senguttuvel et al., 2014). Such kind of research has shown that there exists an inverse relation between salinity and chlorophyll content (Priyanka et al., 2015). Soil salinity is a main environmental constraint that causes devastating growth losses in glycophytes (salt-sensitive plants), most crop species are glycophytes (Greenway and Munns, 1980). On the other hand, salinity or drought stress triggered C3 to CAM photosynthesis switch in halophyte plants like *Mesembryanthemum crystallinum*, that is linked with hypermethylation of satellite DNA (Dyachenko et al., 2006; Wang et al., 2014). Due to abiotic factors, average yield losses increase by 65%−87% in agricultural productivity (Niazi et al., 2014). In 2005, Flower and Flower reported that three-fourth earth is occupied by saline water. In the entire world, an area of about 8×10^8 ha is saline affected (Munns, 2005).

Arid regions of the world are worst affected by salinity followed by semiarid regions. About more than 6 million hectares are salt affected (Chatrath et al., 2007). High sodium absorption ratio in the majority of irrigated areas of Pakistan damages the soil structure and checks the water infiltration which leads to salinization and water logging (Qureshi and Barrett-Lennard, 1998). In Pakistan, sodium chloride (NaCl) is a major salt present in the saline soils (Mushtaq and Rafiq, 1977), and other salts are also present, such as sodium sulfate, sodium carbonate, etc. It was observed that about 1.2 million acres are categorized as slightly saline and 0.27 million acres are moderately saline in the Red River Valley (RRV). Slightly and moderately saline soil have caused 15%−50% productivity losses, respectively (Hadrich, 2011). Wheat is one of the most top- ranking cereal crop and a glycophyte crop. Soil salinity has significantly affected the wheat growth, productivity, and grain yield (Garg and Gupta, 2000). Once the NaCl enters the plant, Na^+ and Cl^- must be eliminated from the soil solution through roots. Otherwise, it accumulates slowly in plant shoot leading to a toxic level. After accumulation, transpiration rate increases approximately 50 times than retaining in leaves (Munns, 2005).

In graminaceous crops, salt toxicity is due to Na^+ specifically, which causes damages in the cytosol (Tester and Davenport, 2003). During plant growth, when Na^+ concentration is accumulated to a high level in the cytoplasm, Na^+ toxicity is more usual in leaf than roots. Accumulation of Na^+ in the cytoplasm and also in the nucleus leads to inhibition of many physiological processes like transpiration, respiration, leaf turgidity, and osmoregulation. High Na^+ concentration also inhibits the enzymatic activities (Munns et al., 1983; Kumar et al., 2017) and transcriptional factors (Xue, 2002). The effect of different concentrations of saline water on wheat was observed showing that 99 mM NaCl in irrigation water induces noticeable thickness in mesophyll tissue, increases flag leaf blade, and reduces the hairs and motor cells number on lower epidermis. It was also observed that NaCl treatment in irrigation water has reduced the xylem tissue thickness, the peduncle diameter, and stomata number on peduncle, as well as some hairs of the main shoot (Aldesuquy, 1998; Aldesuquy and Mickky, 2014).

Plant water is reduced by high Na^+ concentration, which is the major reason to create water stress in plants. Secondly, it causes severe ion toxicity in glycophytes than halophytes because Na^+ is not eagerly sequestered in vacuoles. Finally, it causes nutrient imbalance and deficiencies, and it may also retard plant growth and molecular damages, finally leading to plant's death (Hayat et al., 2014). Osmotic stress which leads to homeostasis disturbance is due to drought and salinity and also enhances the production of reactive oxygen species (ROS) (Seppänen et al., 2000; Zhao and Zhang, 2006; Moghadam et al., 2012). Later, it was also seen that high Na^+ concentration badly affected the seed germination, vegetative growth, seedling growth, flowering and fruit sets on plants which ultimately led to economic yield loss and poor productivity (Cavusoglu et al., 2007).

It was also observed relevant to the plants that high salt treatment causes physiological disruptions like reduced epidermis thickness and leaf rolling in *Imperata cylindrica* (Hameed et al., 2009). Mesophyll thickness, epidermal thickness, spongy cell diameter, palisade cell length and diameter in cotton and bean plants are observed due to the high concentration of salinity (Longstreth and Nobel, 1979). High salt concentration also reduced the chloroplast number, as well as smaller intercellular spaces in potato leaves (Bruns and Hecht-Buchholz, 1990; Aldesuquy and Mickky, 2014). The impact of a plant hormone 28-homobrassinolide (HBL) in overcoming the effects of metal cadmium (Cd) and NaCl toxicity on wheat plants solely was against the synergy (Hayat et al., 2014). Ahmad et al. (2010) conducted an experiment on wheat plant by stressing it with different levels of saline solution. He observed gradual yield declines, such as number of spikes per plant, number of tillers, yield of straw, grain yield, number of

grains per plant, and weight of 1000 grains, and finally, the yielded grains contained less phosphorus, calcium, potassium, nitrogen, and magnesium contents, but higher sodium content when compared with control plants (Ahmed et al., 2008). Soil salinity may be solved by soil reclamation and drainage with freshwater. However, due to highly affected land, these ways of solution appear unreliable and laborious (Qureshi and Barrett-Lennard, 1998) to which, limited availability of freshwater is an additional factor, especially in agriculture (Hamdy, 1996; Mojid et al., 2012). Plants have a natural mechanism to survive under unfavorable environmental conditions (Zhu, 2001). Many scientists have conducted many experiments to investigate the plant cells response to salinity, and three basic strategies of plants have been determined in this regard (Gonneau et al., 2001). First strategy is the active Na^+ influx prevention; second, wilting of plant stem and leaves; and finally, activation and expression of tolerant salt genes to avoid cellular dehydration (Mauch and Dudler, 1993; Schefe et al., 2006).

Abscisic acid (ABA) has a vital regulatory role in the plant as a response to salt and drought stresses (Mauch and Dudler, 1993). ROS are imbalanced due to salt and drought stresses, and these ROS are produced by electron transport chain (ETC) of mitochondria and chloroplast (Frova, 2003; Lo Piero et al., 2009). ROS is also reported essential for cell signaling pathways (Van Breusegem et al., 2001). It is also observed that glutathione-s-transferases (GSTs) provide protection against different stresses (Luan, 2002; Jain et al., 2006). GSTs have been grouped into many categories based on active site residues as well as amino acid sequences, including tau, phi, lambda, theta, zeta, elongation factor 1 gamma ($ef1_y$), dehydroascorbate reductase (DHAR), and tetra chloro-hydroquinone-dehalogenase (TCHAD). Most GSTs belong to tau and phi groups (Edwards and Dixon, 2000; Dixon et al., 2002, 2008; Niazi et al., 2014). Some glycophytes show tolerance to saline soil either by expelling out the Na^+ from the cell via cell membrane or sequestering it into the vacuole (vacuolar antiporter), in exchange of H^+. For this purpose, Na^+/H^+ antiporter proteins play a significant role in expelling the Na^+ out of cytosol through the cell membrane to maintain low salt concentration under saline conditions (Blumwald et al., 2000). Ratner and Jacoby in 1976 initiated research studies on Na^+/H^+ antiporter proteins. Later, Apse et al. (1999) identified the vacuolar and plasma membrane Na^+/H^+ antiporter genes in plants. Under salt stress condition, vacuolar volume of plant cells also increases (Gaxiola et al., 1999; Mimura et al., 2003) which increases the capacity of plant cells vacuole to sequester Na + into the vacuole at the maximum rate.

Crop plants have long been tackling salt tolerance by traditional breeding methods (Noble, 1983; Xue et al., 2004). Recently, traits of salt tolerance have been transferred to wheat from remote grass and phylogenetically related species (Wei et al., 2001; Wang et al., 2014). A novel strategy has been used to introduce Na^+/H^+ antiporter genes for improving salt tolerance in subcellular parts of the plant. The overexpression of vacuolar Na^+/H^+ antiporter genes *AtNHX1* from *Arabidopsis thaliana* have also shown the dramatic improvement in salinity tolerance in transgenic *A. thaliana.* This gene has been observed as a powerful vacuolar Na^+/H^+ antiporter in leaves of *Arabidopsis* (Xue et al., 2004). A substantial improvement in salt tolerance after overexpression of vacuolar Na^+/H^+ antiporter gene in tomato (Zhang and Blumwald, 2001), *Brassica napus* (Zhang et al., 2001), and rice (Ohta et al., 2002) was observed. By overexpression of plasma membrane Na^+/H^+ antiporter gene, there was a significant reduction in cellular Na^+ level (Shi et al., 2002; Gao et al., 2003).

It has been also shown that the plasma membrane antiporter genes salt overly sensitive 1 (*SOS1*) or *SOD2* overexpression was obtained as a result and the transgenic *Arabidopsis* was highly tolerant to salt. These results demonstrated that antiporter transgenic technology has potentially enhanced the agricultural growth and productivity in salt stress, but there was no field trial of the transgenic plant that has been observed to date. A transgenic wheat was made by transformation of vacuolar Na^+/H^+ antiporter gene of *Arabidopsis AtNHX1* with constitutive promoter using *Agrobacterium*-mediated transformation, which showed improved growth and germination in saline soil. The biomass production, grain weight, germination, growth, and yield of transgenic plants were observed to be significantly improved (Xue et al., 2004).

Deleterious effects of saline soil on germination and growth can also be overcome with seed priming with plant growth regulator. Hormone movement from roots to leaves is mainly affected by saline soil, ultimately reducing the plant growth (Azooz et al., 2004; Aldesuquy and Mickky, 2014). Mustard, gram, and wheat crops are less salt tolerant. In plants, salt tolerance is regulated by many genes that are linked to each other (Munns, 2005).

Through conventional breeding, limited improvement has been achieved because many genes are involved in salinity tolerance (Saade et al., 2016). Many techniques have been utilized to make salinity-tolerant plants, like *in vitro* selection, conventional breeding, hybridization, assessment of morpho-physiological traits, halophytes, genetic transformation, and marker-assisted selection smart engineering of genetic resources for enhanced salinity tolerance in crop plants (Arzani and Ashraf, 2016). Although the nature of salt tolerance is polygenic, by the introduction of a single gene or some genes, also the salinity tolerance is enhanced (Reynolds et al., 2005). In wheat, a lack of genetic diversity among breeding lines has been recognized as a major constraint to future yield increases. Species

belonging to bread wheat's secondary and tertiary gene pools shows higher level of genetic variability and are a significant source of genes to broaden its genetic base (Arzani and Ashraf, 2017). Novel genes introgression from progenitors and related species has been broadly employed to improve the agronomic traits of hexaploid wheat (Winfield et al., 2015). It is reported that Na^+ expulsion from the shoot is due to salinity tolerance of crop to Na^+ (Munns, 2002). Salt tolerance gene is responsible for Na^+ exclusion from leaves in wheat (Husain et al., 2003). For salt tolerance, *Thinopyrum* chromosome 5 Eb carried dominant gene (Forster et al., 1987). The gene for salt tolerance is also transmitted from D genome of *Aesquarrosa* (Gorham et al., 1997). 4D chromosome recombined with 4B also showed the improved K^+/Na^+ ratio and on chromosome 4DL, locus *Kna1* has regulated the Na^+ exclusion in the shoot. Under the saline conditions, the chromosome that possesses *Kna1* locus has more yield and biomass, as compared to species with control plant. This confirmed that *Kna1* was responsible for salt tolerance (Dvořák and Gorham, 1992). On 5A chromosome of bread wheat, many genes are controlling abiotic stress, but at the distal end of 5A, there is a salt tolerance gene (Simon-Sarkadi et al., 2007).

Another strategy to achieve increased salt tolerance is through the maintenance of Na^+/K^+ homeostasis, as increased Na^+ disrupts K^+ uptake and cytosolic enzyme sensitivity. It has been reported that the low Na^+ concentration regulation is chiefly attributed to the activity of K^+ and Na^+ transporters and H^+ pumps, and the SOS2−SOS3 protein kinase pathway along with the Na^+ transporter SOS1 initiates the secretion and sequestration of toxic Na^+ in *Arabidopsis* cells (Zhang et al., 2016).

3. Osmoprotectants

Osmoprotectants, also known as compatible solutes or compatible osmolytes, are a group of organic molecules that are polar, have no charge and have soluble nature (Fang and Xiang, 2015). These solutes protect cells and organelles from dehydration and even at high concentration, do not interfere with the biochemical mechanisms taking place in cell and via continuous influx, maintain osmotic balance within the cell (Hasegawa et al., 2000). They provide a defensive mechanism in plants from stress through different means such as contribution toward osmotic adjustment, detoxification of ROS, stabilization of membranes, and native structures of enzymes and proteins (Blum, 2017). Numerous ecological factors causes stress in plants and consequently, a decrease in crop yield, but salinization is a major venturesome in this aspect (Priyanka et al., 2015). Osmotic stress, as a consequence of higher salt concentrations outside the root, inhibits cell expansion, water uptake and development of plant. Subsequently, high Na^+ ion uptake into leaves enhances leaf chlorosis, necrosis, and mortality due to diminished photosynthesis (Hussain et al., 2017). Salinity complied with osmotic stress, ion toxicity, as well as oxidative stress and imbalance of hormone (Ashraf et al., 2012). Plants developed different physiological and biochemical processes to continue to live in soils that have high salinity that includes (1) compartmentalization and ion homeostasis, (2) ion transport and uptake, (3) intracellular synthesis of small organic molecules called osmoprotectants, (4) activation of enzyme and biosynthesis of compounds having antioxidant properties, (5) polyamines synthesis, (6) production of nitric oxide (NO), and (7) modulation of hormones (Gupta and Huang, 2014).

3.1 Types of osmoprotectants

Each osmoprotectant is distinct from other by charge, shape, size and protects the various osmotically sensitive structures and molecules in the cell (Garcia et al., 1997). Osmoprotectants include proline (Hoque et al., 2007; Ahmad et al., 2010), trehalose; quaternary ammonium compounds (QACs), such as alanine betaine, glycine betaine (GB), choline-O-sulfate, hydroxyl pro betaine, proline betaine, and pipecolate betaine (Rhodes and Hanson, 1993; Khan et al., 2000; Wang and Nii, 2000); sugar especially sucrose (Bohnert et al., 1995; Kerepesi and Galiba, 2000); and polyols (Ford, 1984; Popp et al., 1985; Ashraf and Foolad, 2007; Saxena et al., 2013). Chemically, osmoprotectants are of three types: (1) betaines (fully *N*-methylated amino acid derivatives) and related compounds such as dimethyl sulfoniopropionate (DMSP) and choline EO sulfate; (2) certain amino acids like proline and ectoine; (3) and polyols and nonreducing sugars such as trehalose (Rontein et al., 2002).

3.2 Concentration of osmoprotectants in plant

These osmoprotectants are prepared and stored in different concentrations among different plant species. Some compatible osmolytes within the cell are controlled either by preparation of the solutes by irreversible mechanism or

by a combination of different pathways, some involving synthesis and other involving degradation. Their amount increases with the increase in external osmolarity (Gupta and Huang, 2014). Hence, increasing osmolytes concentration helps in maintaining osmotic balance and is therefore crucial for growth and development in salt stress (Gupta and Huang, 2014). Plants protect themselves from salinity by transporting excess salt either to vacuole or accumulating it in older tissues that sacrificed eventually (Reddy et al., 1992; Zhu, 2003). The level of osmoprotectants in a plant depends on external osmolarity. Plants that naturally accumulate osmoprotectants in cells have typically 5−50 μmol g-1 fresh weight (∼6−60 mM on a plant water basis) and are elevated during exposure to salinity stress since biosynthesis and accumulation is usually to some extent stress-induced (Rhodes and Hanson, 1993; Bohnert et al., 1995). Osmoprotectants are mainly accumulated in the chloroplast, cytosol, and other organelles (Rontein et al., 2002). Such elevated concentration of osmoprotectants has a significant and pivotal role in maintaining cell turgor and osmotic balance by water uptake under salt stress (Rhodes David and Samaras, 1994).

3.3 Salinity and osmoprotectants

Salinity and drought adversely affect agriculture, reducing growth, development, and yield of a crop. Drought and salinity are principal scourges on crop yield and quality around the globe (Rontein et al., 2002; Nemat Alla et al., 2019). Increasing the resistance of crops to these osmotic stresses was one of the first objectives of plant metabolic engineering (Le Rudulier et al., 1984; Mauceiri et al., 2018). Moreover, it remains a major goal till today (Sakamoto and Murata, 2001). Intracellular synthesis and accumulation of organic osmolytes are the principal effective mechanisms to reduce the harms from salinity and osmotic stress.

There are many ways that plant uses to cope and overcome drought and salinity. One way is to biosynthesize and accumulate small, organic molecules that are soluble in nature, electrically neutral compounds that are compatible with cytosol, and nontoxic even at higher concentration. Osmoprotectants can prevent destabilization of intracellular membranes and stabilize the normal folding of proteins against the impairing effect of solutes and salts when their concentration is enhanced (Yancey, 1994).

The protective mechanism of the biosynthesis of osmoprotectants involves exclusion of organic osmolytes from hydration sphere of proteins (Timasheff, 1992). These circumstances favor cellular proteins thermodynamically for presenting reduced surface area to water. In contrast, if osmoprotectants are not synthesized, salt successfully enters the hydration sphere and disrupts normal folding of proteins by interacting directly with their surfaces (Kosar et al., 2019). In dry or saline environments, osmoprotectants can therefore, serve both to raise cellular osmotic pressure and to protect cell constituents. Their protective effects also extend to temperature extremes and other stresses (Nemat Alla et al., 2019). Among different mechanisms, one simple way of osmolytes action is to hinder ion entry into the cytosol, while the other way is to elevate ion excretion from sensitive parts of the cell because the ions and the organic molecules added are absorbed through the roots. K^+ is an essential macronutrient for plant's growth and for maintaining high K^+/Na^+ ratio in shoot, which has been suggested to be a major strategy adopted by plants to cope with salt stress (https://www.frontiersin.org/articles/10.3389/fpls.2017.01151/full Hamamoto et al., 2015; Liang et al., 2017).

Ana Beatriz Carcia, in his experiment, has shown that plants synthesize and accumulate different compatible solutes when they encounter NaCl stress; one among them is proline (Pro). He identified some alternations in solute concentration in sodium chloride stressed rice *(Oryza sativa* L.), along with other osmoprotectants. He observed a small amount of trehalose accumulated in roots of rice after 3 days stress (Garcia et al., 1997).

3.4 Effect of external osmolarity on plants

Some of the proteins made during stress believed to serve as osmoprotectants (Delauney and Verma, 1999; Bartels et al., 1991; Vernon and Bohnert, 1992). When dispensing externally, these molecules have been found to keep plants safe from some of the harm and damage that result due to excess salinity or drought (Krishnamurthy, 1991). There is evidence that shows polyols, sugars, and proline concentration in plants are increased to favor the osmotic potential in the cell when salinity in the soil surrounding the plant roots increase (Pollard and Jones, 1979). When water is reduced, membranes and enzymatic structures undergo change, thus decreasing membrane's integrity and enzymatic activity. High concentration of osmoprotectants maintains osmotic balance and protects enzyme activity and membrane integrity (Schwab and Gaff, 1990; Genard et al., 1991). Osmoprotectants use various mechanisms to preserve and protect cell integrity. Evidence also shows that when plants are supplied with different osmoprotectants, these substances alter the physiology and morphology of plant organs like blade and sheath (Garcia et al., 1997).

Plants possess redox regulatory mechanisms by employing different enzymatic and nonenzymatic antioxidants to scavenge ROS (Tanveer and Shabala, 2018).

3.5 Trehalose

Trehalose is an important osmoprotectant. It is a nonreducing disaccharide that plays an important role in mantling osmotic balance, metabolic homeostasis and enhances salinity stress tolerance in different organisms (Turan et al., 2012). In trehalose biosynthetic pathway, glucose part is transferred to glucose-6-phosphate from UDP-glucose after being catalyzed by an enzyme, trehalose-6-phosphate synthase, yielding uridine diphosphate and trehalose-6-phosphate. Afterward, dephosphorylation of T-6-P by trehalose-6-phosphate phosphatase yields trehalose (Cabib and Leloir, 1958; Goddijn and Smeekens, 1998). Production of trehalose can be used as a stress-reducing strategy as it promotes growth in plants in the presence of both drought and high levels of salt (Mosequeda et al., 2019). Higher concentrations of trehalose has been found in root nodules of *Phaseolus vulgaris* and *Medicago truncatula* in response to drought and salt stress, showing critical role of trehalose in signaling during plant—bacteria interactions by promoting plant yield, growth, and better adaptation to harsh conditions. Recent studies shows that exogenously applied trehalose may play an important role in the recovery of reduced D1 protein synthesis and protect it from heat-induced photoinhibition in wheat (*Triticum aestivum* L.) by reducing ROS production and decreasing membrane lipid peroxidation through the change of antioxidants and by enhancing gene transcript level of related antioxidant enzymes during heat stress (Luo et al., 2018). Trehalose when applied exogenously causes the changes in the metabolism of sugar, protects the plants from desiccation by water recovery and maintains enzymes, proteins from aggregation, and lipid membranes (Mohamed et al., 2018).

3.6 Mannitol

Genes from model plant *Arabidopsis* have been transcribed in various other plants to increase their resistance to salt stress. One such example is of tobacco, in which *AtTPS1* gene heterologous expression from *A. thaliana*, enhanced resistance to various abiotic stresses like drought, salinity, and temperature (Almeida et al., 2005). Gene from *Escherichia coli* encoding mannitol is ectopically expressed in wheat and increased salt stress resistance owing to the defensive action of mannitol (Abebe et al., 2003). In another experiment, transgenic *Arabidopsis* plants were produced by transferring celery's mannose-6-phosphate reductase (*M6RP*) gene that produces mannitol. These plants were showing enhanced resistance in wild-type *Arabidopsis* when exposed to salinity stress (Sickler et al., 2007).

3.7 Glycine betaine

When dehydration stress encounters plants, the pathways for GB synthesis are activated in response and has most abundantly occurring QAC in plants (Venkatesan and Chellappan, 1998; Mansour, 2000; Mohanty et al., 2002; Yang et al., 2003). QACs include various organic osmolytes like GB (N, N, N-trimethyl glycine), proline betaine, choline-O-sulfate. Among them, GB plays an important role in osmotic adjustment in plants. Biosynthesis and accumulation of this osmolyte is found in different organisms, like mammals, bacteria, marine invertebrates, haemophilicarchae bacteria, and plants (Rhodes and Hanson, 1993).

The chloroplast is rich in GB where it adjusts osmotic balance and protects membranes of thylakoid, resulting in sustaining photosynthetic efficiency (Robinson and Jones, 1986). Concentrations of GB are not uniform in all tissues of a plant or all plants of a specie, rather it differs significantly in organs and various plant species. When the plants that retain less concentration of GB are exposed to salinity stress, they start synthesizing GB at the elevated level. Thus, they are known as a natural accumulator of GB (Storey et al., 1977). While in various other plant species, GB is not evident under stressful or normal conditions.

Biosynthesis of GB takes place via different pathways in plants, such as choline monooxygenase which catalyzes the conversion of choline to betaine aldehyde, which yields GB by dehydrogenase activity of betaine aldehyde dehydrogenase. Other pathways are known to comprise steady N-methylation of glycine, but earlier one (from choline to GB) has been found in all plant species that show accumulation of GB (Weretilnyk et al., 1989). Rhodes found that most plants showing salt tolerance accumulate the considerable level of GB (Rhodes and Hanson, 1993).

The biological functions of GB have been studied extensively in higher plants, such as spinach, sugar beet, barley, and maize (Chen and Murata, 2008). Transgenic plants have been generated by cloning genes transcribing GB synthetic enzymes. The role of GB in improving salinity resistance is also depicted by the extracellular implementation

of GB in various plant species resulting in enhanced yield and plant growth (Mäkelä et al., 1999). It is quintessential to find an optimum concentration of GB depending on the crop species for the best possible stress tolerance results. For instance, at increased concentrations, GB is more sensitive for the broad-leaved species like bean, tomato, and grape than for the cereals. Hence, the proper GB concentration should be used, so as to get the maximum benefit of osmotic adjustment in different plant species (Roychoudhury and Banerjee, 2016).

3.8 Proline

Proline acts as an important osmolyte, which exists in plant cells in free form and have high water solubility, low molecular weight and is neutral in charge in the physiological pH range. Plant cells tend to accumulate soluble osmoprotectants to diminish the effects of osmotic stress caused by salt stress, especially the biosynthesis of proline is clearly activated. Thus, the proline content can be used as a physiological index of resistance of plant to stress tolerance.

Various research studies have shown that in different abiotic stresses, different plants respond by increasing proline level (Hayat et al., 2014; Muhammad et al., 2015). Proline, in plants, maintains osmotic balance and has a significant osmoprotective role. A wheat gene *Ta-UnP*, was amplified in laboratory, showed significant improvement in the salt tolerance of transgenic *Arabidopsis* and rice. After stress due to salinity, the content of proline in transgenic *Arabidopsis thaliana* was substantially increased, thereby maintaining the osmotic potential and protecting plant cells from stress conditions (Liang et al., 2017).

Proline is manufactured from its originator glutamic acid under drought and stress conditions (Delauney and Verma, 1993). In an experiment, tobacco plants have been engineered for drought and salinity resistance trait by enhancing proline production that was achieved by altering feedback inhibition mechanism of an enzyme that limits the rate of reaction in the biosynthetic pathway of proline (Hong et al., 2000). It has been studied recently that transgenic *Nicotiana tabacum* L. engineered with the *OsP5CS1* and *OsP5CS2* genes enabled the genetically modified plants in various abiotic stress environment to accumulate the increased level of proline and protect the cells from oxidative damage (Zhang et al., 2014; Muhammad et al., 2015). In other studies, engineered petunia and pigeon pea with the gene *P5CS* accorded tolerance to drought and salt, respectively. Transformed petunia builds up a high level of proline that made the plant tolerant to drought for 14 days duration. Similarly, in transgenic pigeon pea, four times increased proline content was observed under 200 mM NaCl stress. Therefore, transgenic plants showed more growth and chlorophyll content under salt stress conditions (Yamada et al., 2005; Surekha et al., 2013; Mohammad et al., 2015).

Two enzymes play an important role in the biosynthesis of proline, that is, pyrroline-5-carboxylate synthase (5PCS) and pyrroline-5-carboxylate reductase (P5CR). P5CR is the rate-limiting enzyme in proline biosynthesis in plants and is controlled at the transcriptional level (Liang et al., 2017). The enzymes that play a significant role in the biosynthetic pathway of proline are P5CR and pyrroline-5-carboxylate synthase (5PCS) (Ashraf and Foolad, 2007).

Proline also contributes as an osmolyte in maintaining subcellular structure, such as membranes and proteins and also has a pivotal role in osmotic adjustment (Srinivas and Balasubramanian, 1995). When stress condition is over, proline undergoes rapid breakdown to yield a significant amount of reducing agent that favors oxidative phosphorylation in mitochondria and supports ATP production from regaining stress and recovery of physical damage induced by stress (Hare and Cress, 1997; Hare et al., 1998).

Proline is one of the well-known osmoprotectants accumulated to high levels under saline conditions. In wheat plants, in response to drought or salinity stress, proline accumulation normally occurs in the cytosol where it contributes substantially to the cytoplasmic osmotic adjustment. It is generally believed to play role as a shield against salt damage (Mahboob et al., 2016). Proline deposition mostly occurs in the cytoplasm, when plants suffer from salinity or drought. Hence, in cytosol, it plays a pivotal role in maintaining osmotic balance (Leigh et al., 1981; Binzel et al., 1987; Ketchum et al., 1991). For better growth of crops under salt-stressed conditions, various research tools are being tried to counteract the effects of salinity like exogenous application of osmoprotectants such as proline is well known to induce abiotic stress tolerance in plants.

4. Conclusion

Wheat is one of the world's major food crops. Wheat being an important food across the globe experiences a lot of biotic as well as abiotic stress. In the surrounding environment, stress due to salinity is the one of the key factors that results in limitation of crop growth and yield. The development, growth, and yield of crops were all inhibited in saline soil. The classical procedures have been unable to ensure food security in the face of growing. Exploring osmoprotectants provide an alternative to the classical procedures. These compounds can be best made use of under salinity stresses. Research on the wheat salt tolerance gene can lead to the use of saline soil and expand wheat planting area, thereby increasing wheat yield. The development in genomic knowledge and technology has

provided new horizons and foundations for genetic improvement of complex traits such as drought and salt tolerance. Researchers have performed considerable research on the salt tolerance genes of wheat and have had breakthroughs but still there is need of thorough research on physiological and biochemical adaptation of plants to salt, combined with genetic engineering, which will further explain the plant salt-tolerance mechanism and provide sufficient theoretical guidance for the future cultivation of salt resistant crops. Thus, this calls out for a need to explore mechanisms that might lead to an improvement in its yield and quality.

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CHAPTER

7

Salt responsive transcription factors in wheat

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OUTLINE

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00007-8

1. Introduction

World population count is rising progressively with a pace of about 1.1% increment a year. At the present moment, there are around 7.7 billion people sharing this sphere which are anticipated to rise with 10% increment at the end of next decade (8.5 billion in 2030), 9.8 billion till 2050 (26% increment), and 10.9 billion (42% increment) by the end of the ongoing century (United Nations Organization, 2019). It is inferred that demands for primary life necessities will increase steadily with such speedy increment in human population. The utmost and life-sustaining need among all the primary life necessities is for food.

Approximately 275 crops are consumed as sources of food by humans (Tilman et al., 2011) but among all these food crops; wheat, maize, and rice are utilized in high quantities as staple food worldwide—a reason why these three cereal crops are collectively termed as the "Big Three Cereal Crops" (Shewry, 2009). Nevertheless, wheat among big three cereal crops is an unambiguously significant crop due to its eminent nutritional value, special genome organization, and high quantity consumption (Cooper, 2015).

1.1 Nutritional value of wheat

Wheat alone is source of 20% total calories among all calories consumed by humans in a year (Waines and Ehdaie, 2007). A wheat grain constitutes mainly around 70% carbohydrates (starch) and up to 15% proteins (gliadin and glutenin) (Slade et al., 2012). Out of the total wheat produced globally, approximately 65% are utilized as human diet, while remaining quantity is disseminated as feed for livestock (~21%), seed source (~8%), and roughly 6% as industrial raw material (Shewry and Jones, 2005). These deliberations render the cause of growing more and healthy wheat to satisfy the dietary requirements for arousing population.

1.2 Genome organization of wheat

Wheat genome is allopolyploid; having several sets of chromosomes, thus making the wheat's genome as one of the complex genomes for study and research (Liu et al., 2012). Employing genetic manipulations or similar techniques within polyploid genomes for studying cellular mechanisms and finding solutions for problems like abiotic stress tolerance, improving yield, and enhanced quality becomes more complicated in such large pool of genetic contents. The ploidy level varies among wheat varieties, which may be diploid (2x) such as *Triticum monococcum*, tetraploid (4x) *Triticum turgidum*, and hexaploid (6x) *Triticum aestivum* (Baum et al., 2009). Tetraploid *T. turgidum* (4x) and hexaploid *T. aestivum* (6x) are still commonly grown wheat varieties across the world which are alternatively known as durum wheat and bread wheat, respectively (Thuillet et al., 2005). These polyploid wheat varieties arose as a result of several scientific and domestication processes such as hybridization, selection, and crossing.

The modern-day durum wheat arose from *dicoccoides* specie of *T. turgidum* which is conceived as wild ancestor because it was first wheat specie domesticated in Near East realm (Maier, 1996). New species of *T. turgidum* like *durum* and *dicoccum* arose as it spread across the Europe (Buckler et al., 2001).

The modern-day bread wheat (*T. aestivum*) contains three diploid genomes, named as A, B, and D genomes, which arose from a series of crossings among grasses of *Aegilops* with wheat genera *Triticum* (Zohary et al., 1969). Both the ancestral *Triticum urartu* and *Aegilops speltoides* contained diploid set of chromosomes ($2x = 14$ chromosomes). Crossing of A-genome from *T. urartu* with B-genome of *A. speltoides* led to a hybrid genome (AB) which after doubling resulted in a viable tetraploid (AABB) known as "wild emmer" that contained 28 chromosomes (Chen et al., 2013). Further crossing of AB-genome of "wild emmer" with D-genome from diploid *Aegilops squarrosa* (14 chromosomes) resulted in a 42-chromosome hexaploid known as *T. aestivum* which contained three ancestral genomes (AABBDD) in diploid form (Levy and Feldman, 2002), and this hexaploid *T. aestivum* is today's commonly grown bread wheat.

1.3 Global production of wheat

Achieving the mounted healthy wheat production has been a target since green revolution (Pingali, 2012). This strive made possible to maximize wheat production. As inferred, during past 30 years (1985–2015) wheat production raised from about 500 million tons (2.39 tons per hectare in 1985) to approximately 736 million tons in 2015 with yield value of 3.66 tons per hectare, shown in Table 7.1 (FAO, 2019).

TABLE 7.1 Wheat production statistics in past 30 years from 1985 to 2015.

Sr.	Year	Wheat production (million tons)	Wheat yield (tons per hectare)	Total arable land (million hectares)	Reference
1	1985	499.53	2.39	1394.54	FAO (2019)
2	1995	544.36	2.77	1404.41	FAO (2019)
3	2005	626.94	3.12	1405.84	FAO (2019)
4	2015	736.98	3.66	1425.92	FAO (2019)

As understood from Table 7.1, both the wheat production and yield increased significantly over the past 30 years primarily on the account of technological advents and agricultural interventions (Khush, 2001), but the volume of total arable land did not rise prominently (FAO, 2019). The reasons behind slow increment in availability of arable land include several environmental factors—collectively referred to as abiotic factors. Abiotic factors, also known as abiotic stresses, entail the nonliving environmental factors that adversely affect the plant health, growth, and yield. Such factors include primarily the accumulation of salts (salt or salinity stress), water deficiency (drought stress), depleted amount of nutrients (nutrient deficiency), temperature variations (high- and low-temperature stresses), and presence of toxic elements in soil (heavy metal stress). It is figured that all of these stresses are collectively accountable for 80% annual loss among total yield losses (Lobell et al., 2009). However, salinity is a more striking factor among all abiotic stresses because it is not only a threat to plant health, growth, and yield, but it also spreads continuously over arable lands thus reducing the availability of arable lands for cultivation purposes.

1.4 The problem statement and possible solution

The annual wheat production has boosted so far, yet, 87%–110% more wheat production is required by next 30 years (till 2050) to feed the fast-growing world population (Ray et al., 2013; Tilman et al., 2011). Two logical approaches can be adopted to achieve mounted production of healthy wheat: (1) make more land arable out of unarable lands using soil management practices which will thus provide more space/soil for growing more wheat resulting in elevated yield (Gregory et al., 2002), (2) make wheat able to not only withstand the unfavorable soil condition but also can grow better in such harsh conditions of unarable lands (Golldack et al., 2011). Converting unarable soil into arable on large scale is laborious, difficult, costly, time-consuming, as well as this process is restricted by rapid urbanization, deforestation, and industrialization (Gregory and George, 2011). However, the latter option of altering the plants is more suitable to achieve high wheat yield upon the unfavorable land because this approach is less laborious, easy to achieve, economical, and less time-consuming—a reason why extensive research has focused on genetic alteration of wheat to make them tolerant against salt-affected soils.

1.5 Salt responsive transcription factors in wheat

Plethora of genes gets activated due to salt stress in wheat. According to a report, about 5996 genes showed differential expression in wheat after treated with salt stress (Kawaura et al., 2008). The resultant gene's products act in a concerted way to protect the plants from the detrimental effects of stress conditions. Achieving tolerance to an abiotic stress is a very complicated process because stress affects multiple stages of plant development (Chinnusamy et al., 2004). However, the common role among such complicated processes is played by transcription factor(s) (TF or TFs) that regulate transcriptional activation or suppression of responsive genes (Singh et al., 2002; Golldack et al., 2011), as shown in Fig. 7.1.

It becomes axiomatic that manipulating the role of TFs will allow driving the molecular mechanisms according to requirements. Potential wheat TF families involved in stress-responsive pathways include *WRKY*, *NAC*, *MYB*, *bHLH*, *AP2/ERF*, and *bZIP*. These TFs are widely known to modulate expression of stress-related genes through binding to their promoters in a sequence-specific manner thus alters the gene expression (Hu et al., 2006). In common wheat; 59, 161, 53, and 48 genes are reported to encode different members of *AP2/EREBP*, *MYB*, *NAC*, and *WRKY* families, respectively, under salt stress (Kawaura et al., 2008). However, a major part of their functional genomics involved in abiotic stresses is unknown and are limited to the analysis of only a few TFs. One of the major reasons behind this gap for study is the complex and huge (six fold) genome of wheat (Mujeeb-Kazi et al., 2019). Despite the fact that naturally wheat is less tolerant to high salt concentration, yet, some of wheat cultivars do exhibit remarkable

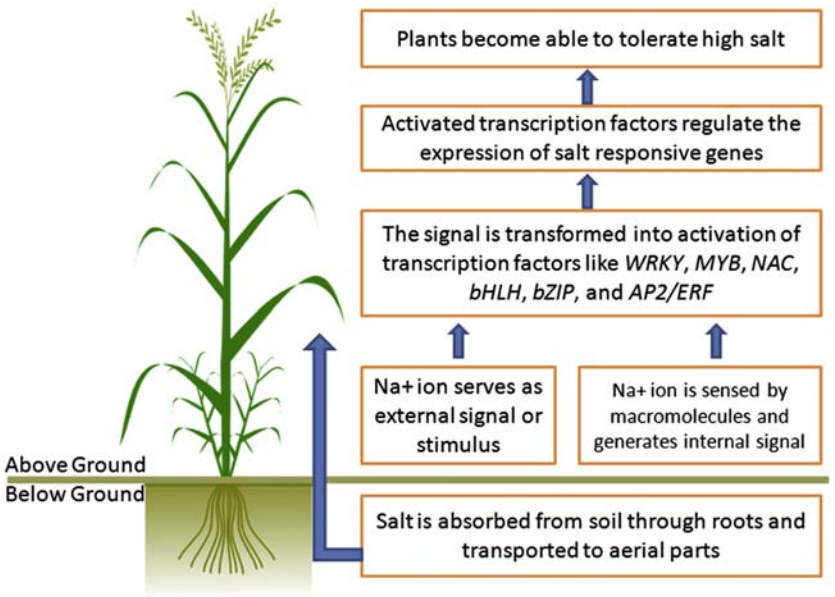

FIGURE 7.1 Transcription factors response to salt transported across the wheat plant from soil through roots to shoots.

tolerance against salinity stress (Xia et al., 2003). Characterization of novel TFs encoding genes from such tolerant cultivars to understand their regulatory role in interacting stress responsive pathways will open up new avenues for engineering wheat as well as other important crop plants against salinity stress (Kawaura et al., 2008; Golldack et al., 2011).

Applying the genetic manipulations in wheat primarily relies on identification and regulation of key responsible genes as well as detailed understanding of their responsive mechanisms happening inside the wheat cells under salinity stress. Although much studied, yet, it is motive to conclude the so far conducted studies of salt responsive genes and their mechanisms in both normal as well as stressed conditions. Such schematic studies will broaden the knowledge about gene functioning, stress-responsive mechanisms and effects of stresses upon plants—all of which shall contribute toward the efforts for developing stress-tolerant plants.

Keeping in view of these indices, this chapter is dedicated to emphasize on evaluating molecular and biochemical properties of six highly salt-responsive TF families (*MYB*, *WRKY*, *bHLH*, *NAC*, *bZIP*, and *AP2/ERF*). Also, their roles in molecular pathways of wheat under salt stress are explained with examples from each TF family.

2. MYB transcription factor gene family

MYB TF family is among the well-known plant TF families that are reported to exhibit vital functions in several molecular processes under favorable as well as stressed conditions in several plants including wheat (Yanhui et al., 2006; Zhao et al., 2018). "C1" was the first *MYB* gene isolated from *Zea mays* (Paz-Ares et al., 1987). So far, over 200 *MYB* TFs have been identified in rice and *Arabidopsis* genomes (Rahaie et al., 2010; Zhang et al., 2011). Differential features of this TF family have been exploited at wide scale, including number of *MYB* genes, sequencing, evolution, and their functions in different plants (Yanhui et al., 2006; Weltmeier et al., 2006; Wilkins et al., 2009). Research has revealed that *MYB* family has a major role under biotic stresses, abiotic stresses, signaling mechanisms, and hormonal synthesis through regulation of gene expression (Li et al., 2019). These genes also participate in many cellular metabolic pathways, enlargement of the cell, and cell cycle regulation (Ma et al., 2009).

2.1 Molecular and biochemical characterization of MYB proteins

MYB protein family is identified through a conserved domain known as *MYB*. This domain possesses 1−4 imperfect tandem repeat(s) (R) at N-terminal region, and each of these repeats is 50−53 amino acids long (Dubos et al., 2010; Zhao et al., 2018). The primary sequence of each repeat has three tryptophan residues or phenylalanine in some cases, which are placed at a regular distance and collectively contribute to the formation of the hydrophobic

core. Three α-helices are present in *MYB*; two α-helices at C-terminal region form a structure known as helix–turn–helix (*HLH*) that helps in recognition and binding to a specific site (C/TAACG/TG) of the DNA major groove (Ogata, 1998). Though extensive studies have been conducted for characterization and gene expression of *MYB* family in many plants including wheat, yet, much more has to be unveiled about mechanism of action of *MYB* family particularly in wheat under salt stress.

2.2 Classification of MYB TFs

MYB family is classified into four subfamilies on the basis of repeat(s) in *MYB* domain. There are four repeats in 4R-*MYB*, three consecutive repeats (R1R2R3) in 3R-*MYB*, two repeats in R2R3-*MYB*, while *MYB*-related type usually, not as fast rule, possess single repeat (Agarwal et al., 2006; Dubos et al., 2010) as shown in Fig. 7.2.

The *MYB*4R proteins having four repeats are less common in plants (Dubos et al., 2010). The largest *MYB* gene family is R2R3-type in plants and has a multidimensional role in the regulating gene expression. Common examples include control of morphogenesis and cell shape (Herman and Marks, 1989); role in abiotic and biotic stresses (Abe et al., 2003; Seo and Park, 2010); responses to salicylic acid, abscisic acid, gibberellic acid (Gocal et al., 1999) (Murray et al., 2003), and jasmonic acid (Lee et al., 2001). *MYB*1R is reported to have roles in circadian rhythms (Schaffer et al., 2001); morphogenesis of cells (Simon et al., 2007); and also in secondary metabolism (Matsui et al., 2008). On the contrary, *MYB*3R make a small subfamily.

2.3 Role and significance of MYB TFs in salinity tolerance

In a strive to investigate salinity-responsive genes in common wheat by Kawaura et al. (2008), they studied the microarray analysis of stress-regulated genes and monitored the transcriptomes response of short-duration salt stress in wheat (Kawaura et al., 2008). They grouped, annotated, and characterized the genes with differential expression featuring salt response. Moreover, uniqueness of salt response in wheat with the special reference to the TFs was also investigated. The TF genes from wheat genome were monitored using microarrays to study expression analysis and genes showing upregulation exceeded the number of downregulated genes. 42 *MYB* genes out of 161 genes were noticed to be salt responsive. Most of these genes were verified to be transiently up- or downregulated.

In another study, 10 *MYB* TFs encoding genes from wheat were studied against salinity (Rahaie et al., 2010). Two inbred recombinant lines possessing variable level of tolerance to salt were used to study pattern of *MYB* genes

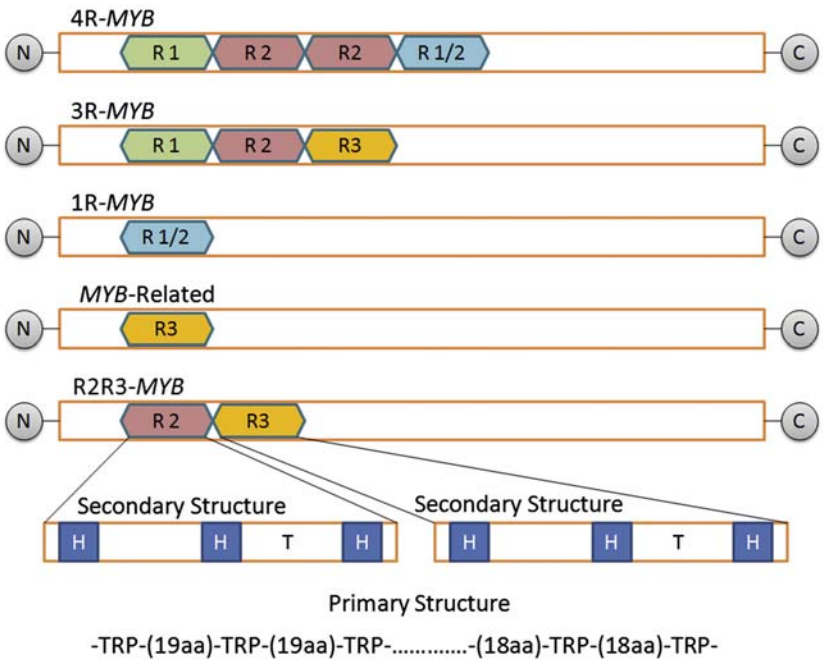

FIGURE 7.2 Structure of *MYB* transcription factors classified on the basis of number of (R) repeats. *aa*, amino acid; *C*, C-terminus; *H*, helix; *N*, N-terminus; *T*, turn; *TRP*, tryptophan.

expression. Quantitative RT-PCR analysis showed constant upregulation of four *MYB* genes in the seedling's roots of both lines when exposed to salt stress for short duration. While, three *MYB* genes in both recombinant inbred lines were upregulated after prolonged treatment with salt. However, in both lines, a single *MYB* gene (*TaMYBsdu1*) showed upregulated pattern when subjected to salt stress for the long and short periods. *TaMYBsdu1* (salt stress upregulated gene) also had higher expression level under long-term drought stress. *TaMYBsdu1* showed lower expression level in salt susceptible plants than salt-tolerant plants. Hence, it was recommended that *TaMYBsdu1* be significant for improving tolerance against drought as well as salinity stresses.

Cai et al. (2011) reported that *TaMYB3R* gene had an important role in water scarcity, cold, and salinity stresses in wheat (*T. aestivum* L.) (Cai et al., 2011). They designated a *MYB* gene cloned from wheat (*T. aestivum* L.) as *TaMYB3R1* having three conserved *MYB* domain repeats. *In silico* (bioinformatics) analysis revealed high sequence similarity of *TaMYB3R1* protein with other plant *MYB3R* proteins. This *MYB* protein is more similar to the rice gene *OsMYB3R2* that is upregulated under salt stress. It was concluded that *TaMYB3R1* might also take part in abiotic stress regulation in wheat. Elevated *TaMYB3R1* expression in response to plant hormone abscisic acid (ABA) was observed in onion. Abiotic stresses like salinity, cold, and drought upregulated the *TaMY3R1* expression which remained high under salinity and cold stress (Cai et al., 2011). It was observed that *TaMYB73* improved tolerance against salinity in *Arabidopsis thaliana* by ectopic expression of this wheat *MYB* gene.

A new wheat *MYB* gene *TaMYB73* has also been reported through results attained after specific targeting of probe in cDNA microarray. Results showed that *R2R3*-type *TaMYB73* has transactivation action with higher level of salt response. Application of NaCl, phytohormones, and many other stresses like GA and ABA indicated that stress-responsive elements are located in the promoter site. It was also further established that overexpression of this *MYB* gene improved chloride (NaCl, KCl, and LiCl) tolerance in *Arabidopsis*. However, it did not respond to mannitol. This study suggested that *TaMYB73* is a significant *MYB* TF that takes part in tolerance against salt stress somewhat by regulating stress-responsive genes that improve ionic resistance (He et al., 2012).

The full-length cDNA of *TaPIM1*, a *MYB* gene, was isolated from wheat (*T. aestivum* L.). The transcription level of *TaPIM1* increased considerably against drought, salt stress, and fungal pathogen (*Bipolaris sorokiniana*). This *R2R3*-type *TaPIMP1* encodes 323-amino acid long protein and localized in nucleus affirmed by transient expression experiment. A functional complement tobacco (*Nicotiana tabacum* L.) cultivar W38 transformed with *TaPIM1* confirmed by RT-PCR showed elevated expression. The lines that expressed *TaPIMP1* were analyzed for their ability to tolerate drought and salt stress and to resist pathogen. As opposed to normal tobacco plants, the functional complement tobacco showed significant tolerance to drought and salt stress, as well as improved resistance to the fungal pathogen. Transgenic lines showed substantially higher activities of phenylalanine ammonia-lyase (PAL) and superoxide dismutase (SOD) as compared to wild-type tobacco plants, proving the significant role of *TaPIM1* against diverse range of stresses in wheat (Liu et al., 2011).

An effective way for studying functional gene is isolation of full-length cDNA from wheat. Zhang and coworkers revealed a set of *MYB* genes that responded to multiple stresses in wheat (Zhang et al., 2011). They isolated 60 cDNA with full-length sequences encoding *MYB* proteins. For understanding the functions of wheat *MYB* genes under abiotic stresses, *A. thaliana* plants overexpressing a stress-responsive gene, *TaMYB32* was analyzed. According to their findings, improved salt tolerance in *Arabidopsis* by overexpression of *TaMYB32* has been observed.

Wild emmer wheat was analyzed on salt stress along with other environmental stresses by Chen and his coworkers (Chen et al., 2013). They screened several wild emmer genotypes and came up with potential salt-tolerant lines. Their performance under salt stress was investigated through TF expression in wild emmer and cultivated wheat. Among four genes: *NAC8*, *NAC2F*, *MYB2A*, and *MYB3R*, which were expressed under salt stress in wild emmer wheat, two *MYB* genes (*MYB2A* and *MYB3R*) were identified to play an essential role in eliciting a response against salt stress. In contrast, *MYB73* gene expression was found to be unexpectedly downregulated, signifying that *MYB73* gene may be serving through unlike mechanisms regulating the salinity tolerance in wild emmer and cultivated wheat. Also, in wild emmer expression of four genes including *NAC2F*, *NAC8*, *DREB3A*, and *MYB2A* were higher (1.5- to 3.7- fold) as compared to cultivated wheat treated with salt. However, *MYB3R* exhibited comparatively lower expression in both genotypes as compared to *MYB2A*. Expression of *MYB3R* was 4.5-fold lower in cultivated wheat than that in wild emmer. Their study indicated that antioxidative system in salinity-tolerant emmer wheat is more enhanced as opposed to common wheat.

Baloglu and his group (2014) found *MYB* TF gene, *TaMYBsdu1*, which confers tolerance to wheat under both salinity and drought stresses (Baloglu et al., 2014). They identified that another *MYB* protein gene, *TaMYB33*, in two wheat cultivars (Kiziltan-91 and Yuregir-89) that play role in short-term abiotic stress exposure which may be induced by severe osmotic stress. Gene expression of some TFs genes including *TaWLIP19* (a wheat version of *bZIP*), *TaMBF1*, *TaWRKY10*, *TaMYB33*, and *TaNAC69* were analyzed in three *Triticum* species (*T. aestivum* cv.

(Yuregir-89), *T. turgidum* cv. (Kiziltan-91), and *T. monococcum* (Siyez)). It was found that all genes are upregulated in all three cultivars of wheat under salinity stress except *TaMYB33* in Siyez. Their work provides a comprehensive analysis of gene expression that is quite valuable information for understanding the regulation of these TFs proteins under abiotic stresses in modern cultivars and ancient einkorn wheat. Also, identified TFs might be used for molecular plant breeding by determining cultivars as drought or salinity-susceptible and/or tolerant.

Another *R2R3*-type *TaMYB19MYB* gene was identified and analyzed in Chinese spring wheat by its nulli-trisomic lines. It has been found that *TaMYB19* is located on three different chromosomes of a wheat genome. The expression analysis revealed that these genes behave similarly in response to different biotic and abiotic stresses. The *TaMYB19-B*, which is present on chromosome B has overexpression under different environmental stresses including excessive salinity (Zhang et al., 2015).

3. WRKY transcription factor gene family

In plants, *WRKY* TF gene family encodes *WRKY* proteins is known to regulate the transcriptional activities of genes. *WRKY* proteins are central components of signaling pathways in the execution of defense responses against diverse stresses in plants (Rushton et al., 2010). For example, in several plant species, regulatory role of *WRKY* genes have been observed against bacterial infection (Dellagi et al., 2000; Du and Chen, 2000), fungi (Chen et al., 2002), oomycetes (Beyer et al., 2001), viral infection (Yoda et al., 2002), wounding (Hara et al., 2000), radiation (Izaguirre et al., 2003), hormonal (Chen and Chen, 2000; Du and Chen, 2000; Yang et al., 1999), mechanical (GUS-Mayer et al., 1998), drought (Qiu and Yu, 2009; Rizhsky et al., 2002), cold (Huang and Duman, 2002), and salinity stresses (Qiu and Yu, 2009; Seki et al., 2002). Since last two decades, the role of *WRKY* TFs in plants is being investigated extensively (Gupta et al., 2019). The first identification of *WRKY* TF as a DNA binding protein from sweet potato has accelerated much research in this area (Ishiguro and Nakamura, 1994). Since then, many members of *WRKY* gene family have been reported from higher plants like rice (Liu et al., 2005), *Arabidopsis* (De Pater et al., 1996), barley (Sun et al., 2003), potato (Dellagi et al., 2000; Beyer et al., 2001), tobacco (Chen and Chen, 2000; Hara et al., 2000; Kim and Zhang, 2004), coconut (Mauro-Herrera et al., 2006), cotton (Xu et al., 2004) and sugarcane (Lambais, 2001). Moreover, the identification of expressed sequence tags (ESTs) of *WRKY* in sequence data of ferns and mosses confirms their occurrence in lower plants as well.

3.1 Molecular and biochemical characterization of *WRKY* proteins

The *WRKY* TF gene family is among the 10 major TF-gene families that are identified specifically in plants so far (Ülker and Somssich, 2004). The *WRKY* proteins are so named because of the presence of conserved DNA-binding domain(s) known as *WRKY* domain(s) (Eulgem et al., 1999, 2000). Presence of 60-amino acid long one or two *WRKY* domains characterizes the *WRKY* proteins (Hara et al., 2000). At the N-terminal end of *WRKY* domain, a highly conserved sequence of seven amino acids WRKYGQK also known as heptapeptide and a unique zinc-finger-like structure with either *Cys2His2* or *Cys2HisCys* sequence at its C-terminal end marks the *WRKY* domain (Eulgem et al., 2000; Gupta et al., 2019). Structural studies (Fig. 7.3) indicate that *WRKY* domain consists of four beta strands forming an antiparallel beta-pleated sheet and is involved in DNA binding while conserved Cys/His residues form zinc-binding pocket at one end of the beta-sheet (Yamasaki et al., 2005).

TFs also known as transacting factors act by binding specific DNA sequence motifs present in cis-acting element, promoters, or enhancers, and regulate gene expression (Eulgem et al., 2000). In *WRKY* TFs, the conserved heptapeptide sequence recognizes and binds with high affinity to the consensus sequence C/TTGACC/T of W-box residing the genes promoter region mostly involved in defense responses (Eulgem et al., 2000; Zhou et al., 2008; Rushton et al., 1996). However, some *WRKY* proteins having an affinity for different DNA sequence motifs have been

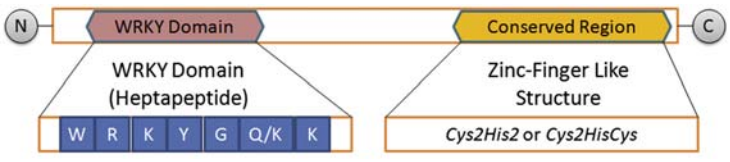

FIGURE 7.3 Basic structure of *WRKY* TFs.

observed. For instance, *NtWRKY12* and *GmWRKY21* with WRKYGKK-type domain binds WK-boxes (TTTTCCAC) rather W-box (Van Verk et al., 2008; Zhou et al., 2008).

3.2 Classification of *WRKY* TFs

The *WRKY* proteins are members of *WRKY* TFs superfamily (Riechmann et al., 2000; Eulgem et al., 2000). Despite the presence of highly invariant heptapeptide structure in *WRKY* domain, the overall sequence of *WRKY* proteins varies greatly. Depending on the number of *WRKY* domains and zinc-finger structure sequence pattern, *WRKY* superfamily is divided into four groups, group I consists of *WRKY* TFs having two *WRKY* domains and zinc-finger structure of either *Cys2His2* or *Cys2HisCys* type, group II members have one *WRKY* domain and *Cys2His2* structure; group III includes one *WRKY* domain and *Cys2HisCys*, whereas group IV that contains rice *WRKY* TFs having one *WRKY* domain but lacking distinct zinc-finger-like structure. Group II is further divided into five subgroups, IIa to IIe, which share the same conserved short motifs (Eulgem et al., 2000).

3.3 Role and significance of *WRKY* TFs in salinity tolerance

Despite the versatile role in different important biological processes of plants, *WRKY* genes and their functions are less explored in wheat. Houde and colleagues identified 28 ESTs corresponding to *WRKY* genes that were differentially expressed when wheat was exposed to different abiotic stresses (Houde et al., 2006). However, Wu et al. (2008) reported and analyzed spatial and temporal expression of 15 cDNAs having a complete open reading frame (ORF) from wheat (*T. aestivum* L.) line 3338 encoding putative *WRKY* proteins under different abiotic stresses (Wu et al., 2008). These *WRKY* cDNAs were predicted to be ranging from 621 bp to 1416 bp in length via sequence analysis tool. Phylogenetic analysis revealed that these 15 wheat *WRKY* proteins belong to three groups. Seven *WRKY* proteins fall into group II which in turn is further divided into four subgroups. Whereas, six and two *WRKY* proteins belong to III and I groups, respectively. Despite having conserved *WRKY* domain in most of the members, sequence variation within conserved domain does exist in some of the members. This sequence variation implies that wheat genome encodes many *WRKY* proteins each having a specific role in growth and development depending on wheat species. Also, it was described that these 15 *TaWRKY* genes express differently in different tissues and developmental stages. Eight among 15 *TaWRKY* genes were found to express differentially under different abiotic stresses applied to wheat seedlings. However, among eight genes, only two *WRKY* genes, *TaWRKY10* and *TaWRKY19-a*, were found to upregulate under high salt concentration (10% NaCl), and their expression continued to increase up to 40 min after treatment.

Detailed analysis demonstrated the identification of 43 unigenes encoding putative *WRKY* TFs from EST database of wheat and their expression was studied against different abiotic stresses. Among 43 *WRKY* uni-genes amplified from wheat (*T. aestivum* L. cultivar Xifeng 20), the role of *TaWRKY2* and *TaWRKY19* was further explored because of their induction against multiple stresses. Bioinformatics analysis revealed that both of these *WRKY* genes belong to group I, possess two *WRKY* domains and execute defense response mainly against abiotic stresses. Moreover, the presence of nucleolar organizing signal suggests that these are localized in nucleus and act as nuclear proteins. Functional analysis of these two *WRKY* genes was carried out by their heterologous expression in *A. thaliana*. Seedlings of 7-days-old transgenic *Arabidopsis* lines overexpressing *TaWRKY2* showed minor epinastic phenotype as opposed to mock plants (Col-0) when treated with 150 mM NaCl. Salt-stressed transgenic plants overexpressing *TaWRKY2* showed better recovery and survival rate (80%). Bolting rate was high and had longer inflorescence as compared to salt-treated wild type (WT) plants after transferred to soil under normal conditions. Furthermore, as compared to Col-0 (WT) plants, reduced level of malondialdehyde (MDA) and reduction in relative electrolyte leakage was observed. These constitute important factors indicating damage as a result of abiotic stress was noted in salt-stressed transgenic lines. Reduced relative electrolyte leakage and MDA are the strong indicators of *TaWRKY2* conferring great tolerance to transgenic lines under salt stress. Similarly, salt-treated transgenic *Arabidopsis* plants overexpressing *TaWRKY19* showed great growth recovery (>94% survived) when compared with WT, where survival rate was 47% under normal conditions on shifting in pots. Also, reduced MDA and relative electrolyte leakage in *TaWRKY19* overexpressing transgenic plants proves its involvement in enhancing salinity tolerance. Both of the genes *TaWRKY2* and *TaWRKY19* confer salinity tolerance by regulating genes present downstream in the signaling pathway—a characteristic feature of most *WRKY* proteins (Niu et al., 2012).

Further study reported the isolation and characterization of *TaWRKY79*, a salinity-induced *WRKY* gene that belongs to wheat group II *WRKY* TF. The characteristic *WRKY* domain of *TaWRKY79* showed high similarity with those

of *HvWRKY38*, *OsWRKY71*, *AtWRKT25*, and *AtWRKY33* genes induced under different abiotic stresses. RT-PCR detected the fast and elevated level of *TaWRKY79* transcript in 2-week-old wheat seedling treated with 200 mM NaCl (for 0.5 h) posttreatment. Heterologous expression of *TaWRKY79* promoter:GUS fusion in *A. thaliana* showed high GUS expression in leaves of 10-days-old transgenic seedlings after 3h treatment with 100 mM NaCl. Thus, it was confirmed that promoter region of *TaWRKY79* has such cis-elements able to respond to salt stress. Constitutive expression of *TaWRKY79* under 35S promoter into *A. thaliana* resulted in increased tolerance to salinity when exposed to NaCl and LiCl. Transgenic *A. thaliana* plants developed longer primer roots in response to ionic stress as opposed to wild-type plants. In transgenic *A. thaliana*, genes responding ABA showed upregulation indicating that *TaWRKY79* TF works in an ABA-dependent pathway that helps in enhancing salinity stress tolerance (Qin et al., 2013).

Wang et al. (2013) characterized 10 *WRKY* genes identified in *T. aestivum* L. cv. Chinese Spring genome (Wang et al., 2013). However, only *TaWRKY10*, an important TF encoded by the wheat genome was further investigated because of its induction in response to multiple stresses like PEG6000, sodium chloride (NaCl), cold (4°C), and hydrogen peroxide (H_2O_2). Southern blot analysis revealed that wheat genomic DNA has three copies of *WRKY10* gene. *TaWRKY10* protein is targeted to the nucleus because of the presence of nuclear localization signal, where it may act as a transcriptional activator. Seeds from transgenic tobacco plant lines showing heterologous expression of *TaWRKY10* were subjected to different stresses like mannitol, NaCl, and H_2O_2. Transgenic lines, when treated with 100 mM NaCl, showed high germination rate that ranged from 93.8% to 96.8% as compared to 90.5% and 91.5% for wild-type and vector control (VC) plants, respectively. Under different concentrations of NaCl, transgenic tobacco lines showed an increase in root length as opposed to WT and VC plants with halted root growth, thus indicating the role of *TaWRKY10* during seed germination and root elongation in increasing tolerance against NaCl stress. Studies also showed that transgenic tobacco plants overexpressing *TaWRKY10* were more tolerant toward salinity and drought as compared to control plants. Phenotypic analysis revealed that transgenic tobacco lines were taller, having greater survival rates and exhibited low yellowing of leaves as opposed to control plants following 3 weeks of drought and 400 mM NaCl treatment. Substantially, high level of proline, soluble sugar, relative water content (RWC), and low level of MDA and ROS was noted in transgenic tobacco lines as compared to WT lines as a defensive mechanism against drought and salinity stress. Thus, indicating the role of *TaWRKY10* in conferring tolerance to drought and salinity by transcriptional activation of other osmotic and oxidative stress–related genes (Wang et al., 2013).

Later on, the role of *TaWRKY10* was evaluated in three different species of wheat (*T. aestivum* L. cv Yuregir-89, *T. turgidum* L. cv Kilziltan-91, and *T. monococcum* L. cv Siyez) under high salt and drought stress along with other TF-encoding genes. Expression analysis of *TaWRKY10* gene under salinity stress and drought was determined using RT-PCR. It was observed that transcriptional activity of *TaWRKT10* was upregulated in all three species of wheat after treatment with drought and salinity stress as opposed to mock plants. This study provides insight regarding the expression analysis of *TaWRKY10* in different genotypes of wheat and serves as a mean for distinguishing cultivars showing susceptibility and tolerance against salt and drought stresses (Baloglu et al., 2014).

4. *bHLH* transcription factor gene family

Basic helix-loop-helix (*bHLH*) proteins constitute a superfamily of TFs having vital and dynamic functions in eukaryotes. Despite the fact that *bHLH* proteins play a diverse role in regulating different life processes, to date, only a few *bHLH* genes from plants have been described and functionally characterized as opposed to animal *bHLH* genes (Hegedus et al., 2003). The first plant protein described to have *bHLH* sequence motif was Lc protein, the R gene product from maize for controlling anthocyanin biosynthesis (Ludwig et al., 1989). Phylogenetic analysis based on sequence comparison of full-length protein across various eukaryotic groups resulted in the division of *bHLH* genes into six clades (A to F). All the plants *bHLH* proteins described so far belong to the B group depending on their ability to bind to G-box and participate in transcriptional activation of genes involved in biosynthesis pathways (anthocyanin synthesis), phytochrome signaling network, and developmental pathways (Mol et al., 1998).

4.1 Molecular and biochemical characterization of *bHLH* proteins

The distinctive feature of *bHLH* TFs gene family is 60-amino acid-long domain having two parts with distinct functions. The N-terminal end of the domain which binds with DNA is 15 amino acids long with six basic amino

acids known as a basic "b" region. The basic region of *bHLH* proteins recognizes and binds to the consensus sequence (5′-CANNTG-3′) of core element known as E-box, the G-box (5′-CACGTG-3′) being the most common core element. Moreover, the regions surrounding the core element may also participate in determining the specificity of the binding site. While the *HLH* part of the domain forms two amphipathic alpha-helices with a loop of variable length separating them. Specificity of interaction for any particular protein partner lies in alpha helices, and interaction between alpha helices of two *bHLH* proteins causes homodimers or heterodimers formation. Dimers binding to E-box of target gene cause their transcriptional activation (Cabrera and Alonso, 1991; Van Doren et al., 1992). Phylogenetic analysis of *bHLH* gene sequences from different plant species reveals that the overall sequence similarity is very low between evolutionary clades; however, the only evolutionary conserved feature they are sharing is a *bHLH* domain.

4.2 Role and significance of *bHLH* TFs in salinity tolerance

In the salt-tolerant wheat mutant, RH8709-49, cDNA microarray analysis revealed a significant increase in the expression level of a novel salt responsive gene *TaSRG* after 12 h of salt treatment. Bioinformatics analysis showed that the deduced protein possesses a *bHLH* domain. Moreover, both the gene and the deduced protein share significant homology with rice and *Arabidopsis* homologous relatives. Yeast one-hybrid experiment revealed that *TaSRG* product activates the transcription of the *lacZ* reporter gene and hence possesses transcriptional activity. The role of *TaSRG* was further analyzed in roots and leaves of mutant wheat plants exposed to different stresses like ABA, PEG, NaCl, and cold. It was observed that ABA and NaCl strongly induced the expression of *TaSRG*. The transcript level of *TaSRG* was reported to increase up to 7.2-fold after 6hours ABA treatment in leaves of mutant wheat plants as compared to mock plants. Whereas, following 12 h of salt treatment, 1.8-fold increase in expression of *TaSRG* in roots of mutant wheat plants was observed as opposed to control plants. Overexpression of *TaSRG* conferred enhanced salt tolerance ability to transgenic *Arabidopsis* plants, whereas T-DNA insertion *Arabidopsis* mutants were sensitive to salt stress. Mutant rice plants with downregulated *OsSRG*, a homolog of *TaSRG*, showed a dramatic decrease in survival rate and chlorosis under salt stress as opposed to mock plants (He et al., 2011). Plants facing high salt concentration show a high ratio of K^+/Na^+ and high proline content profile which enhance their salt tolerance ability (Cuin et al., 2008). *TaSRG* overexpressing *Arabidopsis* lines showed a higher ratio of K^+/Na^+ and high proline contents as compared to wild-type and T-DNA mutant plants, both of which usually increase in plants under salt stress. Thus, it strongly confirmed the role of *TaSRG* as a TF for regulating the expression of genes that confer salt tolerance to plants (He et al., 2011).

Yang and team reported the isolation, cloning, and characterization of a *bHLH* protein encoding gene from wheat (*T. aestivum* L. ca. Shinxin 828) genome and designated it as *TabHLH1*(Yang et al., 2016). *TabHLH1* encodes a protein of 480 amino acids, and in silico analysis confirmed that it possesses a conserved *bHLH* domain, a characteristic feature of *bHLH* TF family. Functional analysis of *TabHLH1* was analyzed by its heterologous expression in tobacco plants under different stress conditions. Under salt stress, upregulation of *TabHLH1* was observed, and growth rate of transgenic tobacco plants was better as compared to wild type. Moreover, the different physiological parameters measured like proline and soluble sugar content were higher in *TabHLH1* overexpressing transgenic plants. All these experiments show the involvement of *TabHLH1* gene in conferring tolerance against salinity stress to transgenic plants.

5. NAC transcription factor gene family

NAC TFs consist of extensive proteins group including *NAM*, *ATAF*, and *CUC*, hence named collectively as *NAC* TFs (Guérin et al., 2019). *NAC* proteins are discovered to be available in various classes of plants including small plants as well as in yielding plants (Lindemose et al., 2014). This family has many proteins that profoundly monitored the domains that are associated with the DNA binding and located at a variable C-terminal and N-terminal ends (Olsen et al., 2005; Ernst et al., 2004). Initially, *NAC* TF was obtained from three proteins, named as no apical meristem (*NAM*), *CUC2* (cup-shaped cotyledon), and *ATAF1-2* that have a comparable DNA-binding domains. *NAC* TFs are considered to be involved in different parts of plant growth. A couple of cases are *NAM* and *CUC1-2* from *Arabidopsis* and *Petunia*, respectively. These play a role in controlling the meristematic cells formation and *NAP* from *Arabidopsis*. This goes about as a selected gene of *AP3/PI* and works in the division of cell and cell development in petals, stamens, and *AtNAC1* that interfere in auxin signaling to advance parallel root improvement. As of late,

a couple of *NAC* TFs are accounted for to assume a crucial part in abiotic stresses, including salinity and drought, as well as in developmental processes, like directing senescence, cell division, and wood structuring.

Also, various *CUC*, *ATAF*, and *NAM* proteins are found to partake in plant reactions to pathogens, viral diseases, and natural boosts (Kim et al., 2007). Three *NAC* genes in *Arabidopsis*, *AtNAC072*, *AtNAC019*, and *AtNAC055*, were observed to induce under drought and salinity, and more expression of this gene as in transgenic *Arabidopsis* plants showed the improved stress tolerance contrasted with the wild type.

5.1 Molecular and biochemical characterization of NAC proteins

Usually, *NAC* proteins impart a rationed *NAC* domain at N-terminal end (150 amino acids) and an expanded transcription regulatory (TR) area at the C-terminal end (Ernst et al., 2004). However, a couple of varieties in the structure have likewise been recognized. These unusual *NAC* proteins can encode just the *NAC* domain (Christiansen et al., 2011) or two tandemly rehashed *NAC* domains (Krogh Jensen et al., 2009). *NAC* proteins consist of conserved *NAC* domain that is located at the N-terminus end, contains approximately 150−160 amino acid residues and is divided into five subdomains (Ooka et al., 2003). The function of the *NAC* domain relates to its location in the nucleus, its binding with DNA and the formation of heterodimers or instead homodimers with other proteins that contain *NAC* domains (Olsen et al., 2005). *NAC* proteins may possess regions at the C-terminal end that are greatly divergent in functions (Ooka et al., 2003) and are involved in the control of any differences in transcription activation of *NAC* protein (Krogh Jensen et al., 2009). These proteins are deviating C-terminal regions, usually operating as functional domains and acting as transcriptional activators or repressors. The large C-terminal regions have protein-binding activity; C-terminal *NAC* domains bind calmodulin proteins in *Arabidopsis*(Kim et al., 2007), and this indicates that the mechanism is much complicated for transcriptional regulation by *NAC* proteins.

The transcription regulatory regions, by and large lying at the much-veered C-terminal end, can either initiate (Lu et al., 2006) or suppress transcription (Yamaguchi et al., 2010). The transcription regulatory region (TRR) has a few motifs that are group-specific as well as rich in repeats of proline-glutamine, serine-threonine, or else acidic buildups. For instance, the transcription regulatory regions in *NAC* proteins of rice have 10 C-terminal motifs. An alternate extensive study has uncovered that these motifs are saved for a known subgroup of *NAC* subfamilies, yet differ over the distinctive subfamilies (Shen et al., 2009). In this manner, these are conferring variety of roles to *NAC* proteins. Also, on account of unnecessary low complexity sequences, transcription regulatory regions have a high level of intrinsic disorder (ID) and neglect their solitary stable three-dimensional arrangement (Kjaersgaard et al., 2011). Such adaptability empowers them to interface with distinctively selected protein, and transcriptional activity makes this protein a model for systematic analysis. Some *NAC* proteins have protein tying capacity in their transcription regulatory regions (Kleinow et al., 2009). A helical trans-membrane motif exhibited in some *NAC* proteins (like *NTLs*) is in charge of plasma film or endoplasmic reticulum layer mooring (Seo et al., 2009). Up to now, 18 NTLs have been recognized in *Arabidopsis*, seven in maize (*Z. mays*), five each in rice (Kim et al., 2007), which may assume critical administrative parts under natural signals.

5.2 Regulation of NAC TFs

Latest research has supplied intriguing cases of regulation of genes at the transcriptional level. Investigations have shown that the procurement of pluripotentiality includes the performance of a few quiet *NAC* genes (Naqvi et al., 2010). A part in dedifferentiation is as per *NAC* quality capacity in meristem advancement. An alternate illustration is the *Z. mays* endosperm gene *nrp1* that belongs to *NAC* protein family and is managed by gene-specific design. Consequently, alleles are silenced, which are transmitted from parents permitting maternal control of endosperm advancement (Li et al., 2011).

MicroRNAs (miRNAs) are little administrative RNAs that combine with selected mRNAs giving posttranscriptional restraint of the targets (Hegedus et al., 2003). Examining through bioinformatics recommended that TFs are included within cell destiny and being targeted by microRNAs in plants (Jeong et al., 2009). *Arabidopsis NAC* mRNAs, including *NAC1*, *CUC2*, *CUC1*, *At5g61430*, and *At5g07680*, were at first anticipated and focused by parts of the microR164 gene family (Jeong et al., 2009) and *CUC2*, as well as, *CUC1* mRNAs had been indicated to be cut inside their miR164 complementary site (Kim et al., 2008). Likewise, articulation of microR164 unsusceptible renditions of *CUC2* as well as *CUC1* mRNAs and overexpression of microR164 demonstrated that microR164 is essential for fitting regulation of *CUC2* and *CUC1*. MiR164 is controlling cleavage of *NAC1*, *At5g61430*, as well as *At5g07680* be likewise located, further exhibiting the significance of later transcriptional control of particular gene belonging to *NAC* family (Seo and Park, 2010).

NAC TFs are regulated in diverse processes including stress response, growth, and development by binding to the promoter region of responsive genes. The wide-ranging response of *NAC* has been reported in several plants. Three *NAC* TFs (AtNAC072, AtNAC055, and AtNAC019) enhances drought tolerance in *Arabidopsis* through binding to ERD1-promoter region (Tran et al., 2004). Other *NAC* TFs from *Arabidopsis* have shown responses to salt stress, promotes root development (He et al., 2005) and regulation of germination under hypoxia (Christianson et al., 2009). In barley, *NAC* TFs are studied to have responsive role against pathogen attach and drought stress (Jensen et al., 2007; Delessert et al., 2005; Lu et al., 2006). Several *NAC* TFs are responsive to multiple stresses including drought and salinity (Hu et al., 2006, 2008; Gao et al., 2010; Nakashima et al., 2007). Similarly, in wheat, several *NAC* TFs like *TaNC4* and *TaNAC69-1* among reported till date has shown regulatory response against multiple abiotic stresses including salinity (Xia et al., 2010a, 2010b). Overexpressing these TFs enhances plant's defense against several stresses.

5.3 Role and significance of NAC TFs in salinity tolerance

Plant-specific *NAC* TFs have been accounted for part in various stress responses and growth activities (Guérin et al., 2019). Six genes encoding *NAC* TFs had been identified in wheat (*T. aestivum*) named as *TaNAC7*, *TaNAC4a*, *TaNAC6*, *TaNAC2a*, *TaNTL5*, and *TaNAC13*. These are characterized into three categories: development-related *NAC* TFs and *NTLs*, stress-related *NAC* TFs, and membrane-associated *NAC* TFs determined through the phylogenetic investigation. All *TaNAC* were initiated by one or a few sorts of stress treatments, including lack of hydration, saline conditions, and low temperature though diverse genes indicated distinctive interpretation levels. All these *TaNAC* except *TaNAC7* had been demonstrated to have transcriptional initiation action in the yeast strain *AH109* by transactivation examination (Tang et al., 2012).

Broad range studies of *NAM* attributes encourage the practical explanation of this extensive family to portray many other *NAC* TFs in wheat (*T. aestivum*) (Uauy et al., 2006; Waters et al., 2009). Xia and coworkers identified *TaNAC8* belonging to *NAC* TFs from *T. aestivum* that responded to both biotic and abiotic stresses (Xia et al., 2010a). They further distinguished *TaNAC4*TF gene responsive to biotic and abiotic stresses (Xia et al., 2010b). *TaNAC69*, a member of *NAC* TFs family was more expressed by environmental stresses including salinity in *T. aestivum* (Xue et al., 2006). *TaNAC8* reveals high similarity to rice *OsNAC8* with a domain of *NAC* protein located at N-terminal and interlayer helices motifs at the C-terminal end. It is affirmed by yeast hybrid assays that C-terminal area of *TaNAC8* served as activator of transcription. Abiotic stress analysis like high salt stress, lack of hydration, and freezing temperature prompted *TaNAC8* appearance recommending that *TaNAC8* may work like activator of transcription in *Triticum* defense responses to environmental stresses.

Along with abiotic stresses, *NAC* TFs are also responsive to plant hormones including ABA, a-naphthalene acetic acid, and 1-aminocyclopropane-1-carboxylic acid (He et al., 2005). Transgenic trials showed that *TaNAC2* helps in achieving tolerance to water deficiency and salt stress in model plant *Arabidopsis*. Morphological measures showed that overexpressing *TaNAC2* possess a potential role in enhancing tolerance to abiotic stresses in crop plants (Mao et al., 2012). Wheat is potentially improved with the help of biotechnological approaches; a new gene designated as *TaNAC67* in bread wheat was expressed in *Arabidopsis* and subjected to diverse environmental stresses to analyze changes under stress. Gene expression revealed that *TaNAC67* is responsible for inducing tolerance to temperature, salinity, and drought (Mao et al., 2014).

6. *bZIP* transcription factor gene family

Basic region/leucine zipper (*bZIP*) is an important plant TF family that plays vital role in many environmental as well as biotic stresses. Biochemical, genetic, and molecular studies of this TF family reveal that *bZIP* are involved in regulation of many plant developmental processes including tissues and organ differentiation (Silveira et al., 2007; Shen et al., 2007), elongation of cells (Fukazawa et al., 2000), pathogen defense (Thurow et al., 2005; Kaminaka et al., 2006), osmotic control (Satoh et al., 2004; Weltmeier et al., 2006), metabolism (Baena-González et al., 2007), hormone and sugar signaling (Uno et al., 2000; Nieva et al., 2005), unfolded protein response (Liu et al., 2007; Iwata and Koizumi, 2005), light response (Ulm et al., 2004), and gene regulation of seed storage protein (Lara et al., 2003). Primarily, 50 *bZIP* genes of plants were grouped into five families by similarities among their *bZIP* domains (Vettore et al., 1998). Later on, investigation of *Arabidopsis* genome determines the presence of 81 distinctive *bZIP* proteins (Jakoby et al., 2002). Further comprehensive research discovered up to 77 *bZIP* proteins that are encoded by the *Arabidopsis* genome (Vincentz et al., 2003).

In wheat, 187 *bZIP* TFs were identified through in silico analysis (Li et al., 2015). They further identified 96, 98, and 107 *bZIP* TFs from *Aegilops tauschii*, *T. urartu*, and barley genomes, respectively. Among these identified genes, 69.4% *bZIP* TFs from *T. urartu* were orthologues of 68.8% *bZIP* TFs from *A. tauschii*. It was revealed that wheat shares more similarity in their phylogeny with *Brachypodium* and barley as compared to *A. tauschii* and *T. urartu*. On these phylogenetic studies, wheat *bZIP*s were classified into 14 groups, while 48 *bZIPs* expressed differentially, confirmed through microarray analysis. Closely evolved genes shared similarity in their structures. Out of 23 selected *TabZIPs*, 15 possessed LTR elements in the promoter region. 21 of these 23 *TabZIPs* were responsive to cold stress. However, expression of all the selected genes was tissue specific (Li et al., 2015).

6.1 Molecular and biochemical characterization of *bZIP* proteins

Basic region/leucine zipper (*bZIP*) TFs possesses basic domain for DNA binding and a leucine zipper for dimerization purposes. The characteristic primary sequence of *bZIP* domain that gives rise to adjacent amphipathic alpha-helices have two distinctive regions, the N-terminal part is known as basic region that is 16 amino acids long and consists of a nucleus targeting sequence accompanied by a conserved N-x7-R/K sequence motif for DNA binding, while the part toward C-terminus is characterized by the presence of leucine or other equivalent hydrophobic residues, forming hepta repeat. During DNA binding, the homo- or hetero-dimerization with its partner takes place by hydrophobic residues interaction via coiled-coil structure that provides stability to the unit. All the eukaryotic organisms analyzed so far, have *bZIP* proteins and the DNA sequence motif recognized by the *bZIP* proteins is characterized through the presence of ACGT core. However, plants *bZIP* proteins bind A-box with TACGTA sequence, C-box having GACGTC sequence, and G-box with CACGTG sequence preferentially (Jakoby et al., 2002).

6.2 Classification of *bZIP* transcription factors

Arabidopsis bZIP genes were categorized (*AtbZIP*) into 10 groups. In every group, the basic region is characterized by having similar sequences. However, leucine zipper region has sequences of variable sizes and positions (Jakoby et al., 2002).

Likewise, a grouping of 47 *bZIP* proteins was carried out by Liao and group in soybean along with 75 *AtbZIP* proteins (Liao et al., 2008). This resulted in classifying the *bZIP* proteins into 10 groups parallel to *Arabidopsis* (Liao et al., 2008). As this grouping is based on conserved domains, it might be helpful for dividing the *bZIP* TFs of crop plants based on their functions. However, not a direct relation between protein function and the arrangement of *bZIP* domains exists (Jakoby et al., 2002).

6.3 Role and significance of *bZIP* TFs in salinity tolerance

Interpretation examination of gathering of *bZIP* genes under long salt stress condition into a differentiating variety of wheat through converse technique, Northern blot demonstrated that *bZIP1* is more expressed in a vulnerable variety; Chinese Spring and less expressed in an unsusceptible cultivar I, under salt stress. A bioinformatical study using BLAST-X demonstrated that present quality's protein possesses two homologs in Arabidopsis (*AtZIP56*) and wheat (*TaABF*). Earlier work demonstrated that messenger RNA of *TaABF* gathers with *PkABA1* mRNA (ABA impelled protein -kinase) amid wheat granule development, torpidity formation, and *TaABF* transcripts build momentarily throughout imbibition of torpid grains. Instead of *PKABA1* mRNA, other *TaABF* transcripts are particularly seen and not extraordinarily delivered in vegetative tissues under ABA application or abiotic stress (Rahaie et al., 2010). Recently, the *bZIP* TFs protein has been isolated from *T. aestivum* and called as abscisic acid-responsive element binding protein 1 (*TaABP1*). This *bZIP* is upregulated in drought stress, so it is thought to have a vital role in environmental stresses, including drought and salinity in wheat.

TabZIP60 was taken and mapped from the genome with three similar sequences in wheat. Its analysis showed that *TabZIP60* protein is present in the nucleus and also involved in inactivation of transcription. *TabZIP60* genes are subjected to ABA treatment, low temperature, glycol, and salinity. Its overexpression showed that they improve tolerance against all abiotic stresses including salinity (Zhang et al., 2015).

From recent in silico analysis, 191 *bZIP* TFs were identified in *T. aestivum* (Agarwal et al., 2019). It is well established that *bZIP* TFs have diverse set of functions including stress response and developmental processes through regulating downstream genes expression. Such plant-specific *bZIP*s adhere to DNA containing ACGT with core

cis element, ABRE for instance. These elements include TACGTA (A-box), GACGTC (C-box), CACGTG (G-box), AACGTT (T-box), and TGA(G/C)TCA (GCN4 motif) (Fujita et al., 2005).

7. *AP2/ERF* transcription factor gene family

The *AP2/ERF* (APETALA2/ethylene responsive factor) is a superfamily of plant-specific TFs comprising four major subfamilies: (1) *AP2* (APETALA2), (2) *RAV* (related-to-ABI3/VP1), (3) *ERF* (ethylene responsive factor), and (4) *DREB* (dehydration-responsive element-binding protein). It is known to have roles in several developmental processes as well as against various environmental stimuli. In the beginning, these were considered to be plant specific, but later on studies disclosed the presence of *ERF/AP2* domain in proteins of *Cyanobacteria*, protists, and fungi (Weltmeier et al., 2006). Proteins with *AP2* domain belong to *HNH* class of endonucleases (Weltmeier et al., 2006). That is why it was hypothesized after identifying this TF group was identified in *Cyanobacteriaum* that this gene might be eventually evolved into plants from *viral endonucleases and cyanobacteria* (Magnani et al., 2004; Licausi et al., 2010).

AP2/ERF comprises large group of *TFs* expressed in plant species, such as, 167 genes in rice (Sharoni et al., 2011) and 145 in *Arabidopsis* (Sakuma et al., 2002). Initially identified in *Arabidopsis* (Jofuku et al., 1994) and followed by *N. tabacum* (Ohmetakagi and Shinshi, 1995), they are known to act by binding to *ERE* (Ohmetakagi and Shinshi, 1995). *AP2/ERF* domains are composed of about 60 amino acid residues with higher homology (Weigel, 1995). It was revealed from structural analysis through NMR that *AP2/ERF* TF domain α-helix at C-terminal while 3-stranded β-sheet at N-terminal which identifies the target region (Allen et al., 1998).

Many *AP2/ERF* proteins have been reported from angiosperms, gymnosperms, and microorganisms as well (Magnani et al., 2004; Shigyo et al., 2006; Xu et al., 2007). Several *DRE/ERFs* proteins have been isolated from wheat, barley, and soybean (Xu et al., 2008a, 2008b). The role of *AP2/ERF* proteins is known to be in reproductive and vegetative developments, proliferation of cells and plant responses to hormones, biotic, and abiotic stresses (Nakano et al., 2006; Licausi et al., 2010; Sharoni et al., 2010). Hence, it is essential to study fundamental processes of the stress signals transmission so that *AP2/ERF* regulation can be manipulated for improving stress resistance in crop plants.

7.1 Molecular and biochemical characterization of *AP2/ERF* proteins

AP2/ERF TFs are comparatively less exploited TFs characterized by the presences of *AP2/ERF* DNA-binding domains that have direct interaction with different DNA sequence motifs present in the promoter region of many downstream genes. These motifs include GCC box and/or *DRE/CRT* (C-repeat element). Sakuma and his coworkers (2002) classified *AP2/ERF* TFs into five subfamilies based on similarity and number of DNA-binding domains; *AP2* (APETALA2), *ERF*, *DREB* (dehydration-responsive element binding protein), RAV (related to *ABI3/VP1*), and others (Sakuma et al., 2002).

Detailed in silico analysis to identify *AP2/ERF* TFs through their binding pattern using *DREB2A* and *DREB1A* established that these proteins possess greater affinity for binding with core sequence (A/GCCGAC) of *DRE* (Sakuma et al., 2002). To be more precise, confirmed by evaluating upregulated genes promoters in transgenic plants, *DREB2A* binds to sequence ACCGAC while *DREB1A* adheres to A/GCCGACNT (Sakuma et al., 2006; Maruyama et al., 2004). On the other hand, *ERF* possesses higher affinity toward their core sequence AGCCGCC (GCC-box) (Fujimoto et al., 2000). Despite these findings, exceptions are reported as well. For instance; *TINY* belonging to *DREB* subfamily and A-4 subgroup have the potential to bind to both GCC-box and DRE (Sun et al., 2008). Similarly, *DREB2* from A-2 subgroup (HvDRF1) belonging to barley binds to TT/ACCGCCTT (Xue and Loveridge, 2004). An A-3 subgroup member ABI4 (ABA-insensitive 4) protein in *Arabidopsis* and maize bind to *ABRE* (coupling element) while expression of RD29A (ABA-independent) protein is regulated by *DRE* (Yamaguchishinozaki and Shinozaki, 1994). These results indicate precise regulation of *AP2/ERF*.

7.2 Role and significance of *AP2/ERF* TFs in salinity tolerance

Numerous *DREB1*-like genes are inserted into plants by transformation for enhancing various abiotic tolerances in crops including tobacco and wheat. Transgenic wheat expressing the cotton gene *GhDREB* showed enhanced tolerance to elevated salt stress, drought, and low-temperature stress, gathering larger amounts of sugar in soluble form and chlorophyll in leaves after stress induction. No phenotypic contrasts were seen between nontransgenic

controls and transgenic plants, which proposed that *GhDREB* may be utilized to enhance wheat tolerance against stress through genetic engineering (Gao et al., 2009).

In another study, *TaERF3*; wheat TF was found responsive to salt and drought (Rong et al., 2014). In this study, four overexpression lines of TaERF3 were established and characterized for their function. The *TaERF3*-transcript level in wheat cultivar "Yangmai" was rapidly induced after being exposed to NaCl and PEG. As observed from phenotype, overexpressed lines performed significantly well in tolerating salt as well as drought stress compared to wild type. In all overexpressing lines, the proline and chlorophyll contents were prominently high while stomatal conductance and H_2O_2 content were remarkably reduced as compared to wild-type plants. Further, viral-induced gene silencing procedure was adopted to generate mutants. These mutant lines, through RT-PCR, showed that expression of 10 stress responsive gene reduced while expression of these 10 genes was enhanced in *TaERF3* over-expressing lines. It was observed through electrophoretic mobility shift assay that *TaERF3* protein interacts with promoter regions at *cis*-element GCC-box, which further activates stress-responsive genes. It was concluded that *TaERF3* regulates activation of stress-responsive genes and thus positively regulates responses of wheat to drought and salt (Rong et al., 2014).

8. Conclusion and future prospects

Plants survive, being sessile, in such environment where they continuously encounter with a variety of stress conditions that cause reduction in their growth potential and yield production. Nature has granted plants with highly evolved genome to face and cope with prevailing adverse situations as an adaptation to their sessile existence. This adaptation is in their complex signaling networks that enable them to respond to different stresses. Responses to stresses involve intricate, interconnected pathways whose regulation mainly depends on the genes encoding TFs. Different TFs and their interacting partners have been identified from various plant species under different stresses. However, very limited information regarding the involvement of TFs in abiotic stresses is available in economically important crop plant species, particularly in wheat, whose production is mainly hampered by the stressful environment, especially soil salinity. Among the most important TF gene families identified so far in plants, some members of *WRKY*, *bHLH*, *NAC*, *MYB*, *bZIP*, and *AP2* are involved in eliciting responses against abiotic stresses in wheat. Different research groups have reported the identification and characterization of some salinity-induced TFs which confer tolerance to wheat. This has helped in gaining some understanding of the intricate mechanisms of tolerance against salinity stress. In future, with the help of more versatile and robust techniques, the up- and downstream interacting partners will be detected. This will further assist in manipulating the genome of salinity-sensitive wheat cultivars and other economically important agricultural crop plants species in future. Also, development of crop varieties and cultivars with high tolerance to environmental stresses and their successful cultivation, especially in areas with more frequent stress conditions will alleviate hunger, a major problem that is associated with increasing population. Current research shall focus on identifying more TFs responsive to salt. Focusing, exploiting, and manipulating such TFs through biotechnological techniques will allow producing salt-tolerant wheat and thus will eventually help to fulfill global food requirements.

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CHAPTER

8

Molecular mechanism of drought tolerance in wheat

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OUTLINE

1. Introduction

World is presently witnessing massive changes in climate and temperature owing to global warming, and this has majorly affected the agriculture sector. It is estimated that, by 2025, around 1.8 billion people will face absolute water shortage, thereby depriving 65% of the world's population of sufficient crop supply. Crop tolerance to water stress is

https://doi.org/10.1016/B978-0-12-819527-7.00008-X

a complicated parameter. Hence, drought-tolerant and stress-resistant high-yielding crops are highly preferable (Fleury et al., 2010). The increasing demand on existing resources is not feasible in today's time; therefore, there is a desperate need of high-yielding stress-resistant crops to maintain balance between crop produce and increasing human consumption. Since several decades, the focus of research has been diverted toward drought, as it is considered to be the most adverse abiotic stressor that limits the global crop productivity with its ginormous impact on the overall plant's growth and development (Lesk et al., 2016). Drought, however, is accompanied by the challenges due to its complex quantitative trait nature. Plants exhibit multifarious responses to cope with drought stress that includes morphological, physiological, biochemical, and molecular adaptations (Fahad et al., 2017). Extensive studies in different species indicate that an increase in reactive oxygen species (ROS) can be caused by drought stress due to which the oxidative balance of the cell can be altered (Dat et al., 2000). Rise in the generation of ROS is a general signal triggered under conditions of drought, and this expression is regulated by the antioxidant gene expressions triggered by the activation of superoxide dismutase (SOD) and catalase (CAT) (Jiang and Zhang, 2002). Ultimately, transpiration decreases significantly under drought stress, which then leads to slow heat loss from the leaves that causes leaf temperature to rise. As a result, carbon dioxide (CO_2) concentration and photosynthesis process are increased, thereby affecting plant growth. Finally, the outcome of these downstream processes leads to improved efficiency of water use by plants. Some of the studies have also verified an increase in plant development with high concentration of CO_2 (Gifford, 1979; Kimball et al., 1995; Curtis, 1996; Manunta et al., 2002). Furthermore, alternative oxidase (AOX), a respiratory terminal oxidase, plays a substantial role in protecting chloroplast and optimizing photosynthesis under drought stress (Dahal and Vanlerberghe, 2017). It is also believed to play a key role in sustaining mitochondrial respiration in plants during drought conditions. To overcome heavy crop yield losses due to drought, it becomes obligatory to explore and exploit multipart strategies involved in developing resilient crop varieties.

Plant varieties with high drought tolerance are considered as most suitable for drought-related research. On that account, a well-known research model in this direction is wheat crop. Wheat (*Triticum aestivum* L.) is one of the main staple crops globally, grown on a vast area of land under diverse conditions, covering 17% of the total cultivated land (Lv et al., 2018). Among all cereal crops, wheat is a rich source of protein. It is widely consumed in several parts across the globe, making it an important constituent of regular diet. It provides 20% of total calories to feed 30% of the world population (Lobell and Gourdji, 2012; Shiferaw et al., 2013).

The environmental stressor such as drought is the major limiting factor for crop production and is being profoundly detrimental at all stages of growth, reproductive phases, flowering, grain development, and yield of wheat, which have even led to yearly losses with an average of 5.5% (Ma et al., 2017; Zampieri et al., 2017). There is mounting evidence to support the direct impact of drought on the grain weight, its productivity, and protein quality. The natural progenitors of cultivated crops, which harbor drought tolerance characteristics lost during cultivation of modern lines, provide a better option to be used in the improvement of latest crop varieties (Ashraf et al., 2009). Similar progenitor of modern wheat *Aegilops tauschii* is considered more drought tolerant than *Triticum* and wild emmer wheat (*T. dicoccoides*) species and, therefore, provides the most promising source of drought-related genes and gene regions to be used for developing resistant wheat crop varieties.

Current efforts are focused on producing high-yielding *Triticum* species under water stress environment. Recently, the utilization of drought-tolerant wild species, application of the functional genomics, transgenic technologies, and the rapid advances in molecular biological techniques have facilitated drought-related studies (Ahmed et al., 2014). This results in a significant progress in the identification of drought-related genes and its associated regions, enabling the categorization of some of its molecular aspects. Drought tolerance in wheat through genetic improvement is possible with conventional and mutation breeding (Nezhadahmadi et al., 2013). Accordingly, this chapter summarizes diverse aspects of drought stressor including the recent researches pertaining to drought, its current status in wheat (*Triticum* species), its morphophysiological state in plants, a brief synopsis on the identification of drought-tolerant markers by omics and quantitative trait loci (QTLs) mapping, and a comprehensive description on drought stress mechanisms with primary focus on molecular drought-tolerant mechanism in wheat.

2. Drought

Drought is one of the main abiotic environmental stresses affecting crop productivity worldwide (Timmusk et al., 2018). About 60% of land on the globe belongs to arid or semiarid zones. The importance of developing drought-resistant species is increased due to the uneven distribution of rainfall and water shortage (Danish and Zafar-ul-Hye, 2019). This goal can be achieved by a complete understanding of the genetic and molecular basis of drought resistance. About one-third of the world's potentially viable land suffers from water deficit or drought, which

periodically reduces crop yield. Meteorological event in the absence of rainfall for a period, long enough to cause moisture depletion in the soil and consequently decrease in water potential of plant tissues, is termed as drought (Fatima, 2014). The consequence of low crop yield is caused due to restricted full genetic potential expression of that plant, thereby acting as a serious limiting factor in agricultural production as it prevents the crop from reaching the genetically determined theoretical maximum yield. High temperature and desiccation or water stress are the key factors that affect crop yield (Barnabas et al., 2013; Danish et al., 2019). As far as wheat is concerned, it is cultivated in both irrigated and rainfed areas where the major factors that limit its productivity and stability are drought and salinity (Morris et al., 1994). Moreover, drought stress is a major limitation to bread wheat productivity and its yield stability (Fábián et al., 2019). Physiological responses to drought include closing of stomata, significant reduction in the photosynthesis activity, a prominent oxidative stress, an altering integrity of cell wall, and production of toxic and fatal metabolites (Zvi and Blumwald, 2011). This is all accompanied by signal recognition of roots and loss of turgor pressure with a reduction in water potential of leaf, stomatal conductance to CO_2, internal CO_2 concentration, and growth rates (Nezhadahmadi et al., 2013). Measurements of drought tolerance are done by maintaining the membrane integrity. Cysteine expressed in wheat leaf and its proteolysis activity rises under water-deficit conditions. Growth is among one of the physiological processes sensitive to drought and is affected by reduction in the turgor pressure (Zhu, 2002). A low turgor pressure in water stress quenches cell expansion and growth. Turgor pressure higher than the cell wall yield causes cell expansion (Munns, 2002). Plant responds to water deficiency by osmotic adjustment in its physiology (Fatima, 2014).

2.1 Identification of drought-tolerant molecular markers

Due to the complex nature of stress-related dehydration genes, large-scale identification of drought-related QTLs or genes is necessary. Molecular markers are exclusively used for locating drought-related genes for genome mapping and tagging. Marker-assisted selection (MAS) technique is inexpensive and more suitable than phenotype-based selection and is currently the only option to combine characteristics by gene pyramiding (Tester and Langridge, 2010). DNA-based markers can be derived from QTL and permit selection already in the seedling stage. QTLs for drought-tolerant traits have been identified in the past decade in wheat (Kumar et al., 2012), rice, maize, and other crops.

For marker search, metabolite and expression profiling methods are used. New breeding markers based on transcript or metabolite abundance can be derived from multiparallel methods such as expression and metabolic profiling. Metabolites were measured on the Golm Metabolomics platform (Degenkolbe et al., 2013). In previous studies, genes that were differentially expressed have been identified in many plants genotype of contrasting drought tolerance and thus could be marker candidates for drought tolerance (Degenkolbe et al., 2009). The ideal marker should correlate positively with drought tolerance in a wide range of genetic backgrounds. For complex traits such as drought tolerance, studies have shown that markers will indicate traits contributing to drought tolerance rather than overall tolerance (Tester and Langridge, 2010). Therefore, ideally, the marker transcript concentration or metabolite will correlate with one or several traits contributing to drought tolerance in a wide range of cultivars.

Molecular markers track the presence of QTLs for drought tolerance by linking DNA markers to the QTL (Saintenac et al., 2013). It is known that plants respond to drought-related stress by altering their gene expression and protein production. Some of the proteins that are expressed under the state of drought include dehydrin, vacuolar acid invertase, glutathione S-transferase, and late embryogenesis abundant (LEA) proteins (Close, 1996; Pnueli et al., 2002; Trouverie et al., 2003; Anderson and Davis, 2004). Omics studies and QTL mapping of yield-related traits are used for the identification of stress-tolerant molecular markers. These markers provide significant aid in screening cultivars for drought tolerance/sensitivity and/or improvement of drought tolerance in wheat (Budak et al., 2013).

The application of molecular markers such as RAPD (randomly amplified polymorphic DNA) is preferably used to detect polymorphism of genetic material of agriculturally significant drought-tolerant cultivars (Shah et al., 2009). Molecular markers help in a direct measure of genetic diversity and go beyond indirect diversity measures based on geographic origin or agronomic traits. Simple sequence repeats are highly polymorphic in wheat and are suitable for the discrimination of genotypes. They are generally genome abundant, specific, and codominant and cover all 21 wheat chromosomes. They have been successfully employed to characterize genetic diversity in seed bank collections of improved wheat germplasm and wild relatives (Li et al., 2000). The germplasm improvement and genetic diversity is the key to durable and sustained production of wheat. The principal objective of molecular characterization of germplasm is to enrich the gene pool of cultivated wheat varieties by tapping the vast genetic resources

available in the plant's wild relatives (Shah et al., 2009). Therefore, the best option for yield improvement and yield stability under soil moisture−deficit conditions is to develop drought-tolerant crop varieties through molecular approaches.

2.1.1 Omics technique

Recent progress in technology has led to the development of high-throughput sequencing tools to discover and exploit plant genomes for producing improved crop varieties. In this perspective, the high-throughput "-omics" research period has arisen with most promising views for crop improvement. The main purpose of these omics-related approaches is to decode the entire genome to have better understanding of plant molecular responses, which will in turn provide precise strategies for crop improvement (Jain et al., 2019). Study of an organism's genes, transcripts, proteins, and metabolites is collectively called as "omics." The three main omics approaches are genomics, proteomics, and metabolomics, which serve the purpose of unraveling the whole genetic expression, proteins, and metabolites, respectively (Krugman et al., 2011).

Tolerance to abiotic stress involves transcription factors (TFs) that are similar in both monocot and dicot plants, and some molecular mechanisms of drought tolerance have been described broadly (Yamaguchi-Shinozaki and Shinozaki, 2006). It consists of signal transduction cascade and transcription activation/regulation, functional protection of proteins by LEA proteins (e.g., dehydrins) and chaperone proteins (e.g., heat shock proteins), accumulation of osmolytes (proline, glycine betaine [GB], trehalose, mannitol, *myo*-inositol), induction of chemical antioxidants (ascorbic acid and glutathione), and enzymes reducing the toxicity of ROS (SOD, glutathione S-transferase). Homologous genes of these different classes were also identified in transcriptomic experiments comparing wheat lines grown under well-watered and water-stressed conditions.

In case of drought, omics technique assists in identification of crucial genes regarding drought. Profile studies data and genomic sequence information are essential for understanding drought response mediated by differential accumulation of drought-related components (Jain et al., 2019). High-throughput profiling identifies drought-tolerant markers of different wheat species by these techniques (Thomason et al., 2018). Bread and durum wheat drought-induced transcripts and proteins with varying sensitivities for drought have also been identified using omics technique (Krugman et al., 2011). Methodologies used range from cDNA microarrays to cDNA-amplified fragment length polymorphism (AFLP). 2D gels, mass spectrometry, and chromatography techniques are used for differential protein identification (Krugman et al., 2011). Proteomic profiles of durum wheat embryos have been established owing to the fact that these embryos sustain germination during extreme conditions of desiccation (Irar et al., 2010). The metabolomics profiling has revealed that the drought-resistant genotype is characterized by the higher accumulation of tricarboxylic acid cycle intermediates and drought-related metabolites including glucose, trehalose, proline, and glycine. The integration of metabolomics and transcriptomics results has indicated that drought adaptation includes efficient regulation and signaling pathways that lead to effective cell homeostasis, carbon metabolism, and bioenergetic processes (Irar et al., 2010).

Lately, advancement has been made in detecting key regulators of water stress tolerance in wheat through the help of transgenic approaches. A recent field research observing at the effect of drought on transcriptome of wheat that changes during reproductive stages detected more than 300 differentially expressed genes involved in many critical mechanisms including floral development, photosynthetic activity, and stomatal movement (Ma et al., 2017). A common response to drought stress involves differential expression of cytochrome P450, proteinase inhibitors, heat shock proteins, dehydrins, glutathione transferase, and regulatory proteins such as TFs. Multiple TFs, such as basic leucine zipper (bZIP), NAC, and WRKY were expressed differentially in a water stress−tolerant wheat genotype compared with the susceptible genotype (Ergen et al., 2009). Transcriptomic and proteomic investigation of a pale green durum wheat mutant under water-deficit stress indicated expression modulation of numerous genes encoding antioxidant enzymes, photosystem components, and enzymes responsible for metabolism of carbohydrates and the tricarboxylic acid cycle that may be essential in addressing drought resistance in wheat (Kulkarni et al., 2017). Similarly, a number of other transcriptome and proteome profiling and genetic manipulation studies have identified candidate genes with prospective roles in tolerance mechanisms during drought conditions.

Microarray assays and RNA sequencing−based gene expression analysis act as vital tools in the past to determine response of wheat plant to multiple abiotic stresses such as drought stress. These assays have showed some unexpected results such as reduction in the expression of glutathione-related genes following water conservation in a tolerant synthetic wheat line (Mohammadi et al., 2007) or proline accumulation in a drought-sensitive emmer wheat line, suggesting that some pathways/mechanisms rely upon type of stress applied, genotype, and the duration and

intensity. Advances in this field have provided insights into the molecular basis of various crucial processes involved in plant stress responses and thus opened up new outlook and chances for improving crop plants.

2.1.2 *Quantitative trait locus mapping*

Locations where some genes influence the phenotype of a quantitatively inherited trait are named as QTLs. Genetic variations of a crop can be explored through polygene (QTL mapping) (Ashraf et al., 2008). Drought tolerance is a complicated polyploidy trait with complex quantitative phenotypes. Recently yield QTLs in hexaploid durum wheat have been identified via linkage analysis and associated mapping (Kumar et al., 2010). QTLs for drought tolerance in wheat have been determined through yield-related measurements under desiccated conditions (Maccaferri et al., 2008). These studies have revealed that drought tolerance and yield are two complex traits involving multiple loci, genotypes, and environmental interactions. Moreover, numerous yield-related QTLs have been mapped using wheat (*T. aestivum* L.) RAC875/Kukri doubled haploid (DH) populations that have matured under various environmental conditions. In the first study, inbred populations were evaluated under drought, heat, and high production potential to detect genetic loci for grain yield (GY), yield components, and key morphophysiological traits (Bennett et al., 2012a). In another study, QTL-associated regions for GY and physical grain quality were assessed in 16 fields (Bennett et al., 2012b). A multienvironmental analysis provided a basis for fine mapping and cloning of the genes linked to a QTL related to yield (Bonneau et al., 2013). Recent studies along with the new advances in DNA sequencing technology and the developed approaches of coupling linkage analysis with "omics" studies have indicated that the data generated from such studies will find their way into practical wheat-breeding programs regarding drought (Fleury et al., 2010; Habash et al., 2009). The common steps involved in QTL analysis are evaluation of phenotype of a large population for the presence of polymorphic markers that are followed by population genotyping and lastly statistical analysis to detect the loci that are affecting the targeted trait (Bennett et al., 2012c). QTL for water stress tolerance has some disadvantages as well that includes a large number of genes, genetic or environmental interactions, and mapping population use that is flawed. These drawbacks have restrictions for high-yield QTL mapping under drought condition (Gupta et al., 1999). In wheat, the QTLs for yield and yield-related traits in water stress and biomolecules involved in signaling pathways have been mapped. Inheritance of abscisic acid (ABA) aggregation and circulation in plants is not simple, and numerous genes/QTLs are involved in it. On the long arm of the 5A chromosome between *Xpsr575* and *Xpsr426* loci, a major QTL for ABA production was mapped, in single chromosome substitution line and their subsequent F_2 and DH populations. Development by substitution lines was done from hybridization of high and low ABA producing Chinese Spring' and "SQ1" genotypes (Quarrie et al., 1994). From this QTL, it has been seen that strong linkage with *Dhn1/Dhn2* locus represents a direct connection between ABA accumulation and early flowering-based water stress tolerance in wheat plant (Ibrahim et al., 2012). Mapping of nine QTLs in wheat in response to exogenously applied salicylic acid (SA), ABA, and ethylene signifies the presence of potential genes taking part in signaling in these regions (Castro et al., 2008).

Multiple QTLs linked to ABA buildup in leaves were mapped in an F_2 population developed from the cross of contrasting genotypes for ABA production. But one novel QTL was linked to both higher ABA content and smaller leaf size due to genetic linkage between the genome regions. The QTL location was a homoeolog of the major wheat gene *Vrn1* that codes for a number of tillers, ABA accumulation, and leaf size (Quarrie et al., 1997). A major QTL for ABA production was mapped on chromosome 6D in an F_2 population. This QTL region has several genes for ABA responsiveness, seed dormancy, and regulation of LEA proteins that protect the cell machinery under drought stress; a major QTL for higher GY (21%), wider flag leaf, and chlorophyll content on 7A chromosome was mapped in a DH wheat line by using psp3094 SSR. Exogenous ABA application activated this QTL, suggesting that genes in this region might be involved in ABA signaling (Quarrie et al., 2007). Mapping of four homologs of *Arabidopsis* ABA signaling genes (*TmABF*, *TmVP1*, *TmERA1*, and *TmABI8*) in a wheat population derived by crossing *Triticum boeoticum* and *Triticum monococcum*. The position of these QTLs was on chromosome 3Am, 4Am, and 5Am (Nakamura et al., 2007).

Seven QTLs for ABA production in response to drought on chromosomes 2A, 3A, 1B, 7B, and 5D were detected in an F_4 population at a field capacity of 33%. The most significant QTLs for ABA content were located on chromosomes 3B, 4A, and 5A on the marker location of *Wmc96*, *Trap9*, and *Barc164* (Barakat et al., 2015). In another study, five main QTLs for ABA responsiveness were mapped on chromosomes 1B, 2A, 3A, 6D, and 7B in a wheat recombinant inbred line population. A QTL located on chromosome 6D contributed 11.12% to variation for ABA in comparison with 5%–8% input by other QTLs. Expression analysis identified allelic differences in QTLs for three ABA-responsive Cor/LEA protein–coding genes, *Wrab15*, *Wdhn13*, and *Wrab17*. In ABA-treated seedlings, the expression of these genes was influenced by QTLs present on chromosomes 2A, 7B, and 6D (Kobayashi et al., 2010). In conclusion, several QTLs for ABA production and downstream signaling pathways have been mapped

in wheat, but most of the studies have not focused further on this aspect. We recommend the use of functional genomics tools along with QTLs to identify the genes located in QTL regions.

3. Responses of plant's metabolic machinery toward water stress

Water deficit or drought is one of the many factors to which plant's metabolic machinery responds (Osakabe et al., 2014; Thomason et al., 2018). Photosynthesis, stomatal activity, enzymes, adenosine triphosphate (ATP) synthesis, respiration, and many other important phenomena taking place in plants are adversely affected by physiological stress, and if the stress is prolonged, plant growth and productivity are severely affected. Among different biochemical responses, osmolyte biosynthesis and function, water flux control, and membrane transport of ions for maintenance and reestablishment of homeostasis are considered to be affected in particular (Hasegawa et al., 2000).

3.1 Gene regulation

Under drought stress, some genes are activated to cope with water unavailability. Research shows that same genes are activated in drought stress as in the case of cold stress, but their mode of action is different. The signaling mechanisms that are controlled by gene expression enable plant responses to drought stress (Thomson et al., 2018). These mechanisms involve signaling factors and TFs that are regulated transcriptionally or posttranslationally in response to water stress. The population structure and size for genetic analysis must be carefully assessed. Germplasm should be selected based on the possibility that the lines will yield valuable new genetic combinations of direct and instant relevance to breeding programs developing cultivars for the target environment. Breeding for water stress tolerance in wheat plant is still in the initial stage, and therefore, more attention is given to the genetic improvement of wheat regarding heat stress (Shelden and Roessner, 2013). In recent years, several studies have been done to find out wheat genotypes tolerant to heat stress. Selection for drought tolerance should not have a significant negative effect on other selection targets in a breeding program, such as maturity, height, disease resistance, and grain quality. The use of elite varieties in the targeted environment has some benefits: the lines can be used directly in a breeding program. Moreover, alleles discovered in nonelite germplasm might not lead to improvement because it was already selected during the development of elite wheat cultivars. The presence of genetic variation in wheat is crucial to identify the contrasting parents for classical breeding (Shelden and Roessner, 2013). Significant genetic variation in wheat for drought tolerance has been identified for selection of diverse parents. The cross-hybridization of wheat diploid progenitors generates drought-tolerant synthetic hexaploid wheat with introgression of several novel drought-tolerant genes (Zhang et al., 2005).

Under water stress, plant machinery shifts its focus to ABA production for downstream activation of signaling and tolerance mechanisms, which lowers the grain filling and yield. Therefore, the balance between yield and drought tolerance needs to be examined (Alvarez et al., 2014). ABA content has been used as selection index for screening wheat under water deficit, and contrasting parents for its production have been crossed. ABA is a key phytohormone, and ABA signaling is a major part of the drought response regulatory networks; moreover, ABA-independent pathways are also involved in this process (Shinozaki and Yamaguchi-Shinozaki, 2000). The complexity of ABA-dependent and ABA-independent pathways in drought stress signaling networks has been extensively analyzed at cellular level but not at the intercellular level (Iqbal et al., 2019). Intercellular signaling in response to water deficit provides a comprehensive understanding of plant responses and adaptation to drought stress (Bray, 1993).

Choice of a suitable breeding strategy to develop water-deficit stress-tolerant cultivars is the key step for an effective breeding program. Therefore, strategies that can transfer specific genes, exploit wild relatives of crops, identify and transfer genes with ease, require less time, and labor to develop cultivars are of great value (Hussain, 2015). The advances in genetics, genomics, and functional genomics have enabled researchers to combine one or more advantages of different strategies to develop drought-tolerant wheat. Here, we have described the advances in these methods.

3.2 Effect of drought on photosynthesis

Drought highly affects photosynthesis being carried out in plants, and as a result, usually, there is a decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence, and a reduction in food production

(Farooq et al., 2009). In wheat plant, the rate of photosynthesis decreases with the temperature rise above 30°C as the optimal rate of photosynthesis is around 25°C (Thomason et al., 2018). Smaller stomata size and increased density in flag leaves of wheat plant were found to be linked with water stress tolerance in wheat varieties (Shahinnia et al., 2016). Around 40 genes in *Arabidopsis* are known to regulate development and patterning of stomata. Interestingly, larger stomata and smaller density leads to better transpiration efficiency (TE) in *Arabidopsis*, whereas in wheat, smaller stomata and high density promotes higher TE (Kulkarni et al., 2017). Molecular genetic understanding of genes and linkages for size, stomatal patterning, and density regulation in wheat will allow modulation of stomatal index in wheat and improve TE under drought stress.

In drought stress, both stomatal and nonstomatal activities are affected, which clearly shows that, together with carbon dioxide ($CO_{2)}$ uptake, other processes are also being damaged. The role of drought-induced stomatal closure is very important, as it limits CO_2 uptake by the leaves, because in such dehydrating conditions, CO_2 can cause increased susceptibility to photodamage (Lawlor, 2009). Drought stress produces many changes in plant's regular mechanisms. Some of them include change in photosynthetic pigments and components, damage in photosynthetic apparatus, and altered or reduced activity of enzymes of Calvin cycle, resulting in crop yield reduction (Sharifi and Mohammadkhani, 2015). Along with these factors, loss of balance between the production of ROS and the antioxidant defense is also an important factor that inhibits the growth and photosynthetic ability of plants (Guan et al., 2000). This imbalance causes the accumulation of ROS that induces oxidative stress in proteins, membrane lipids, and other cellular components. Components of photosynthesis affected by drought are mentioned in the following sections.

3.2.1 Stomatal oscillations

Stomata openings cover only about 5% of the leaf surface area, but they are involved in around 70% water transpiration by plants. Stomata is the aboveground control point for the carbon dioxide (CO_2) entry for photosynthesis and water exiting from plants through the process of transpiration (Shahinnia et al., 2016). As a response to water stress, the stomata closes that lowers leaf water potential, decreased carbon assimilation, oxidative stress, and higher canopy temperature (Yokota et al., 2002). Improved maintenance of stomatal control over transpiration process is crucial for fighting photosynthesis inhibition under dehydration stress. Stomatal density and stomatal size determine the stomatal pore area per leaf. Important genetic variation for stomatal density and size has been reported in wheat plant (Kulkarni et al., 2017). Understanding of genes regulating stomatal patterning and size at molecular level in wheat is essential, as this information could be productively employed to improve TE under drought stress.

All plants respond to acute water deficit by closing their stomata to prevent water loss by transpiration. As a result, either leaf's turgor pressure or water potential is decreased, or low humidity atmosphere is created (Khazaei et al., 2010). When water concentration is low, plants respond by closing stomata that result in a decrease in the inflow of CO_2 into the leaves (Azhand et al., 2015). This spares more electrons for the formation of ROS. With the decrease in transpiration, the amount of heat that is supposed to be dissipated increases. Research shows that stomatal responses are dependent on soil moisture content rather than leaf water status (Sharifi and Mohammadkhani, 2015). On the basis of these studies, it can be deduced that stomata respond to chemical signals like ABA that is produced by dehydrating roots even when water content in leaves is sufficient (Blum, 1996). High temperature of the sap increased by environmental conditions via transpiration promotes the ABA accumulation and reduces stomatal activity. ABA alters the plant's physiology and plays regulatory role in senescence process and assimilates remobilization. In another study, it was seen that exogenous application of ABA at anthesis increases soluble carbohydrates in shoots that at the time of maturity were transported to grains (Travaglia et al., 2007). Increased cytokinin concentration in the xylem sap directly promotes stomatal opening and affects the sensitivity of stomata toward ABA (Wilkinson and Davies, 2002). Hence, it is clear that stomata respond progressively toward drought, resulting in the overall decrease in photosynthesis (Davies and Zhang, 1991). However, stomatal activity is controlled by a number of complex intrinsic and extrinsic factors in addition to soil water availability.

Both stomatal conductance and stomatal index affects carbon isotope discrimination ($\Delta^{13}C$). For example, Drysdale and Rees that are Australian wheat varieties developed for low $\Delta^{13}C$ display higher TE and around 10% better yield under hot and dry conditions (Aktar and Islam, 2017). In environments where crops were able to maintain better water status, the genotypes showed a positive relationship between $\Delta^{13}C$ and yield of grain. Ploidy level is another feature that impacts the stomatal density and size in the wheat genome complex. Comparison between *T. monococcum* (diploid), *Triticum durum* (tetraploid), and *T. aestivum* (hexaploid) was done for stomatal density and size, and results showed a substantial genetic variation for stomatal density. The higher heritability of this trait helps in dissection at molecular level (Kulkarni et al., 2017).

3.2.2 Effect on photosynthetic enzymes

Energy metabolism in plants is dependent on two processes that are photosynthesis and respiration. Drought intensely disturbs the photosynthesis process as a consequence of both diffusive restrictions resulting from stomatal closure and, in some cases, limitations in the biochemical processes that are related to reduce abundance of significant photosynthetic components. Photosynthesis is the most sensitive physiological event, leading to poor growth performance in wheat under drought conditions (Feng et al., 2013). A major effect of dehydration stress is that there is decrease in photosynthesis resulting from reduced leaf area expansion, damaged photosynthetic machinery, leaf senescence that occurs prematurely, and related reduction in wheat yield (Ashraf and Harris, 2013). The heat-induced injury reaction sites are thylakoid lamellae of chloroplast and stroma where metabolism of carbon and photochemical reactions takes place, respectively. In wheat, as a result of drought, thylakoid membranes get disrupted, thereby constraining the normal membrane-associated electron carriers and enzyme activities, which eventually results in lowering the rate of photosynthesis (Ristic et al., 2008). The chloroplast enzymes inactivation, mainly brought by oxidative stress, may also lessen the rate of leaf photosynthesis. Decrease in overall photosynthetic rate due to dehydration stress is often attributed to amplified nonphotorespiratory processes (Ainsworth and Ort, 2010). The researchers opined that hindrance in normal photosynthetic activities is the result of reduced soluble protein, Rubisco, and Rubisco-binding proteins (Hasanuzzaman et al., 2013). Wheat leaf exposed to a high temperature around 40°C either in light or dark leads to a massive change in Rubisco and Rubisco activase enzyme activity, and such changes are not reversible even under dark conditions (Mathur et al., 2011).

In wheat, very severe drought conditions reduce photosynthesis due to a decline in the activity of Rubisco, an enzyme involved in the first major step of carbon fixation (Flexas et al., 2004). In photosynthesizing tissues, photosystem II is much reactive to stress due to heat; however, in photosystem I, it is relatively stable (Mathur et al., 2014). Heat stress firstly damages the intricate phenomena of photosystem II and secondly causes change in the photosynthetic behavior. The activity of the photosynthetic electron transport chain (ETC) is finely tuned to the availability of CO_2 in the chloroplast and change in photosystem II under drought conditions. The reduction of carbon assimilation reduces ROS generation that, in turn, decreases synthesis of protein and inhibits repairing of impaired photosystem II (Akter and Islam, 2017). The sensitivity of photosystem II where higher temperature causes increase in thylakoid membrane fluidity and transport of electron to heat stress are usually seen. It has been shown that temperature greater than 40°C dissociates the light harvesting complex II Chl a/b proteins from the photosystem II. Damaging and disordering of thylakoid membranes due to heat stress is also accountable for the termination of photophosphorylation. At higher temperatures, the key regulatory enzyme of Rubisco, i.e., Rubisco activase, is reported to be dissociated causing a reduction in the photosynthetic capacity of leaf in wheat. Due to dehydration, cells shrink and cellular volume declines, which make the cellular content more viscous that results in increased protein−protein interactions, leading to their aggregation and denaturation (Akter and Islam, 2017). Another effect of drought on cells is the increase in solute concentration, which increases the viscosity of cytoplasm. These solutes may be toxic and deleterious to enzyme activity and might even affect the synthesis and degradation of Rubisco, which actually control its level (Lawlor and Tezara, 2009). Thus, even under drought stress, holoenzyme is relatively stable. The activity of Rubisco is regulated by either its reaction with CO_2 and Mg^{2+} to carbamylate (a lysine residue in the catalytic site) or by introducing inhibitors in the catalytic site (Pinheiro and Chaves, 2011). Tight binding inhibitors can decrease the activity of Rubisco even in the light. A rapid decline in photosynthesis under drought is accompanied by decreased maximum velocity of ribulose-1,5-bisphosphate carboxylation by Rubisco, the speed of ribulose-1,5-bisphosphate regeneration, Rubisco and stromal fructose bisphosphatase activities, and the quantum efficiency of photosystem II in higher plants (Hu et al., 2009). Another trend observed in plants under drought stress is that the caboxylation capability of Rubisco gets greatly declined, and it acts more as oxygenase rather than carboxylase. Other enzymes whose activities are affected by drought stress are phosphoenolpyruvate carboxylase, nicotinamide adenine dinucleotide (NAD) phosphatemalic enzyme, fructose-1,6-bisphosphatase, and pyruvate orthophosphate dikinase (Lawlor and Tezara, 2009). It is a common observation that the decrease in the activity of pyruvate orthophosphate dikinase has been recorded 9.1 times during water stress, which is two to four times greater than other enzymes. It suggests pyruvate orthophosphate dikinase to be the rate-limiting enzyme in photosynthesis under drought stress (Du et al., 2000).

3.2.3 Effects on adenosine triphosphate synthesis

Synthesis of ATP is also influenced by severe or mild drought stress, and along with the photophosphorylation, it can be considered as a limiting factor of photosynthesis. Mitochondria are the unique and important organelles in terms of ATP (energy) production for the eukaryotic cell (Hamilton et al., 2001). The mitochondrion is often one of

the first recognition sites of stress within the cell, as its activities and responses are crucial in maintaining cell viability during these conditions. The mitochondria play a key role in the stress tolerance that has been well documented. ATP, the universal biological energy currency, is produced by the mitochondrial F1F0-ATP synthase complex that is final complex of the ETC (Chandra and Manatt, 2011). This complex generally provides the required ATP for osmoticum synthesis under stress. Communications among the nucleus, mitochondria, and chloroplasts are essential in stress tolerance. Under stress conditions, ATP synthesis does not completely stop, but it gets fairly reduced (Hamilton et al., 2001). Limited ATP maintains electron transport, despite high values of reductant, which results in the increase in demand while less ATP is being produced. Under stress conditions, noncyclic electron transport is downregulated to counter the decreased ATP production, thereby activating cyclic ETC. As a result, a proton gradient is generated, which induces high-energy state quenching (Golding and Johnson, 2003). Hamilton et al. reported that exposure of wheat (*T. aestivum* L.) to aluminum increases the mitochondrial F1F0-ATP synthase complex activity only in aluminum-tolerant genotype.

3.2.4 *Effects on respiration*

Heat stress alters activities taking place in the mitochondria by affecting the respiration phenomenon. The rate of respiration rises when the temperature increases, but at a certain temperature level, it diminishes due to destruction of respiratory machinery (Akter and Islam, 2017). Due to the reduced availability of water in the soil, the rate of photosynthesis is greatly reduced so is the rate of respiration. In wheat, it has been estimated that more than 50% of the daily accumulated photosynthetases are transported to the roots and around 60% of this fraction are respired (Turton et al., 1996). The increased rate of respiratory carbon loss in the rhizosphere due to drought stress affects the ATP production by decreasing it and enhanced the synthesis of ROS (Akter and Islam, 2017). This is because the CO_2 and O_2 solubility and the kinetics of Rubisco enzyme are affected by heat stress. Almeselmani et al. (2012) observed that in flag leaf of wheat, the rate of respiration was significantly higher in heat-prone varieties under drought stress (35/25°C day/night) when compared with that of control (23/18°C day/night). Severe drought conditions have been found to reduce the overall biomass of shoot and root, photosynthesis, and root respiration rate (Saibo et al., 2009). Drought-sensitive spring wheat uses relatively greater amount of glucose to absorb water in severe drought stress. The effects of water stress on respiration, mainly respiration in the light (R_L), are not well understood. In plants, the ETC in mitochondria includes an AOX that is non−energy-conserving terminal oxidase. A number of studies have shown that water stress increases AOX transcript, protein, and maximum capacity in plants.

3.2.5 *Effect of oxidative damage*

Environmental stresses give rise to the generation of ROS. Superoxide anion radicals (O-2), hydroxyl radicals (OH), hydrogen peroxide (H_2O_2), alkoxy radicals, and singlet oxygen (O_{12}) are some of the ROS formed in response to environmental stresses (Hernández and Almansa, 2002). ROS are highly toxic and may react with proteins, lipids, membranes, etc., causing oxidative damage to the cells and disabling their normal functions (Singh et al., 2016). In many plants including wheat, oxidative stress remarkably increased membrane peroxidation and caused decline in membrane thermostability (Savicka and Skute, 2010). Hydroxyl radicals react with almost all cellular constituents. Frequent dehydration stress in plants may result in the accumulation of ROS in plasma membrane of the cell, along with depolarization of cell membrane, trigger of programmed cell death, and initiation of ROS-producing enzyme RBOHD (Mittler et al., 2011). It is shown that all cellular components synthesize ROS, but chloroplasts are considered to be its key source as the excited pigments in thylakoid membrane may interact with oxygen and superoxide species or O_{12}. Miller et al. (2009) found that heat stress increased malondialdehyde content in leaf by 27% and O_2 production in root by 68% at the early stage and 58% at the later stage of development of seedling. However, plants have antioxidant mechanisms for evasion of the excess ROS.

ROS are generated by both enzymatic and nonenzymatic reactions, but availability of oxygen under drought stress regulates separation between these two pathways (Ahuja et al., 2010). Electron O_2 reduction can occur at high oxygen level in case of nonenzymatic reactions, whereas in enzymatic reactions, ROS are formed via mitochondrial ETC (Saibo et al., 2009). Among enzymatic sources of ROS xanthine oxidase, an enzyme responsible for the initial activation of O_2 should be mentioned. The electron donor xanthine oxidase can use xanthine, hypoxanthine, or acetaldehyde, while the latter has been shown to accumulate under oxygen deprivation. The next enzymatic step is the dismutation of the superoxide anion by SOD to yield H_2O_2 (Alvarez et al., 1998). Peroxidases and CATs also play an important role in the fine regulation of ROS production in the cell through activation and deactivation of H_2O_2 (Pei et al., 2000). Several apoplastic enzymes may also generate ROS under normal and stressful conditions. Other oxidases, responsible for the two-electron transfer to dioxygen (amino acid oxidases and glucose oxidase), can contribute to H_2O_2 accumulation (Apel and Hirt, 2004). ROS are formed as by-products in the ETCs of

chloroplasts, mitochondria, and the plasma membrane (Sairam et al., 2005). The plant mitochondrial ETC, with its redox-active electron carriers, is considered as the most probable candidate for intracellular ROS formation. Mitochondria can produce ROS due to the electron leakage at the ubiquinone site, the ubiquinone−cytochrome b region, and the matrix side of complex I (NADH dehydrogenase) (Nohl et al., 2001). Superoxide radical and its reduction product H_2O_2 are potentially toxic compounds and can also combine by the Haber-Weiss reaction to form the highly toxic OH (Sairam et al., 2003). Many reports show the deleterious effects of ROS, whose production is stimulated under water stress (Blokhina et al., 2003). ROS can cause lipid peroxidation and, consequently, membrane injuries, protein degradation, and enzyme inactivation. Oxidative stress may also cause protein oxidation, with a loss of enzyme activity and the formation of protease-resistant cross-linked aggregates (Berlett and Stadtman, 1997). It has been found that oxidatively damaged proteins accumulate in pea leaves when subjected to moderate water stress (Moran et al., 1994). Overall, the production of ROS is linear with the severity of drought stress, which leads to enhanced peroxidation of membrane lipids and degradation of nucleic acids and both structural and functional proteins. Various organelles including chloroplasts, mitochondria, and peroxisomes are the seats as well as first target of ROS produced under drought stress (Singh et al., 2016). Numerous studies have shown that antioxidants ascorbate peroxidase (APX), CAT, SOD, glutathione reductase (GR), and peroxidase (POX) have ameliorating effects of drought stress in wheat plant (Caverzan et al., 2016).

Osmotic adjustment allows the cells to decrease osmotic potential and, as a consequence, increases the gradient for water influx and maintenance of turgor pressure. Improved tissue water status may be achieved through osmotic adjustment and/or changes in cell wall elasticity. This is essential for maintaining physiological activity for extended periods of drought (Kramer and Boyer, 1995). It has been identified that among various mechanisms osmotic adjustment, accumulation of ABA and induction of dehydrins may confer tolerance against drought injuries by maintaining high tissue water potential (Lambin et al., 2001). With the accumulation of solutes, the osmotic potential of the cell is lowered, which attracts water into the cell and helps with turgor maintenance. The maintenance of turgor despite a decrease in leaf water volume is consistent with other studies of species with elastic cell walls (Singh et al., 2015). Osmotic adjustment helps to maintain the cell water balance with the active accumulation of solutes in the cytoplasm, thereby minimizing the harmful effects of drought (Morgan et al., 2002). Osmotic adjustment is an important trait in delaying dehydrative damage in water-limited environments by continued maintenance of cell turgor and physiological processes (Taiz and Zeiger, 2006). The osmotic adjustment also facilitates a better translocation of preanthesis carbohydrate partitioning during grain filling, while high turgor maintenance leads to higher photosynthetic rate and growth (Serraj and Sinclair, 2002).

3.3 Antioxidant defense

The antioxidant defense system in the plant cell constitutes both enzymatic and nonenzymatic components. Enzymatic components include SOD, CAT, peroxidase, ascorbic acid peroxidase, and glutathione reductase. Nonenzymatic components contain cysteine, reduced glutathione, and ascorbic acid. In case of drought stress tolerance, high activities of antioxidant enzymes and high contents of nonenzymatic constituents are important. ROS in plants are removed by a variety of antioxidant enzymes and/or lipid-soluble and water-soluble scavenging molecules (Matsumoto et al., 2001). However, antioxidant enzymes are the most efficient mechanisms against oxidative stress. Apart from CAT, various peroxidases, and peroxiredoxins, four enzymes are involved in the ascorbate−glutathione cycle, a pathway that allows the scavenging of superoxide radicals and H_2O_2. These include ascorbate peroxidase, dehydroascorbate reductase, monodehydroascorbate reductase, and glutathione reductase (Fazeli et al., 2007). Most of the ascorbate−glutathione cycle enzymes are located in the cytosol, the stroma of chloroplasts, mitochondria, and peroxisomes (Del Rıo et al., 1998). Ascorbate peroxidase is a key antioxidant enzyme in plants, whereas glutathione reductase has a central role in maintaining the reduced glutathione pool during stress (Mittler et al., 1999; Pastori and Foyer., 2002). Two glutathione reductase complementary deoxyribonucleic acids have been isolated, one type encoding the cytosolic isoforms and the other encoding glutathione reductase proteins dual-targeted to both chloroplasts and mitochondria in different plants (Wang and Qiu, 2006). Among enzymatic mechanisms, SOD plays an important role and catalyzes the dismutation of two molecules of superoxide into O_2 and H_2O_2, the first step in ROS scavenging systems (Stenseth et al., 2002).

Carotenoids and other compounds, such as abietane diterpenes, have received little attention despite their capacity to scavenge singlet oxygen and lipid peroxy radicals, as well as to inhibit lipid peroxidation and superoxide generation under dehydrative forces (Laguna et al., 2004). Oxidative damage in the plant tissue is alleviated by a concerted action of both enzymatic and nonenzymatic antioxidant systems. These include β-carotenes, ascorbic acid, α-tocopherol, reduced glutathione and enzymes including SOD, peroxidase, ascorbate peroxidase, CAT,

polyphenol oxidase, and glutathione reductase. Carotenes form a key part of the plant antioxidant defense system (Wahid et al., 2007), but they are very susceptible to oxidative destruction. The β-carotene present in the chloroplasts of all green plants is exclusively bound to the core complexes of photosystem I and photosystem II.

3.4 Cell membrane stability

Biological membranes are the first target of many abiotic stresses. It is accepted that the maintenance of integrity and stability of membranes under water stress is a major component of drought tolerance in plants (Martınez et al., 2004). Cell membrane stability reciprocal to cell membrane injury is a physiological index widely used for the evaluation of drought tolerance (Erdei et al., 1996). Moreover, it is a genetically related phenomenon since QTLs for this have been mapped in drought-stressed rice at different growth stages and showed that membrane stability of the leaf segment was the most important trait to screen the germplasm for drought tolerance (Ali et al., 2009). Tolerance to drought has been evaluated as an increase in cell membrane stability under water-deficit conditions. In holm oak (*Quercus ilex*) seedlings, it has been observed that hardening increases drought tolerance primarily by reducing osmotic potential and stomatal regulation, which certainly improves new root growth capacity and cell membrane stability. Variation in cell membrane stability, stomatal regulation, and root growth capacity has been negatively related to osmotic adjustment (Villar-Salvador et al., 2004). The causes of membrane disruption are unknown; notwithstanding, a decrease in cellular volume causes crowding and increases the viscosity of cytoplasmic components. This increases the chance of molecular interactions that can cause protein denaturation and membrane fusion. For model membrane and protein systems, a broad range of compounds have been identified that can prevent such adverse molecular interactions. Some of these are proline, glutamate, GB, arnitine, mannitol, sorbitol, fructans, polyols, trehalose, sucrose, and oligosaccharides (Hoekstra et al., 2001).

3.5 Compatible solutes and osmotic adjustment

One of the most common stress tolerance strategies in plants is the overproduction of different types of organic compatible solutes (Serraj and Sinclair, 2002), and this process is termed as osmotic adjustment. Compatible solutes are low-molecular-weight highly soluble compounds that are usually nontoxic even at high cytosolic concentrations (Pinhero et al., 2001). They protect plants from stress through different means such as contribution toward osmotic adjustment, detoxification of ROS, stabilization of membranes, and native structures of enzymes and proteins (Blum, 2016). By using osmotic adjustment, the organelles and cytoplasmic activities take place at about normal pace and help the plants to perform better functions such as growth and photosynthesis and assimilate partitioning to grain filling. As a mechanism, the osmotic adjustment has been suggested as an important trait in postponing the dehydration stress in water scarce environments (Fang and Xiang, 2015). The osmotic adjustment is accomplished by the accumulation of compatible solutes. Of these, proline is one among the most important cytosolutes, and its free accumulation is a widespread response of higher plants, algae, animals, and bacteria to low water potential. Its synthesis in leaves at low water potential is caused by a combination of increased biosynthesis and slow oxidation in mitochondria (Girija et al., 2002). Despite some controversy, many physiological roles have been assigned to free proline, including stabilization of macromolecules, a sink for excess reductant, and a store of carbon and nitrogen for use after relief of water deficit (Blum and Ebercon, 1976). A correlation between drought resistance and proline buildup in barley plants showed that the resistance to water deficit in barley resulted in accumulation of free proline, which was many folds higher than in the susceptible cultivars. Naidu (1998) has reported that cotton cultivars adapted to water stress conditions accumulated higher GB than the nonadapted ones under drought. In addition to direct protective roles of GB either through positive effects on enzyme and membrane integrity or as an osmoprotectant, GB may also protect cells from environmental stresses indirectly by participating in signal transduction pathways (Jun et al., 2000). Yokota et al. (2002) have reported a higher citrulline accumulation in the wild watermelon leaves assuming that citrulline is located only in the cytosol and constitutes 5% of the total volume of the mesophyll cells. Citrulline is a novel and the most effective OH^- ion scavenger among compatible solutes examined so far. Moreover, it can effectively protect DNA and enzymes from oxidative injuries.

Rapid accumulation of the nonprotein amino acid γ-aminobutyric acid was identified in plant tissues upon exposure to stress many years ago. It acts as a zwitter ion, exists in free form, and has a flexible molecule that can assume several conformations in solution, including a cyclic structure that is similar to proline (Li et al., 2017). The physiological roles of γ-aminobutyric acid in drought tolerance entail osmotic regulation, detoxification of reactive oxygen radicals, conversion of putrescine into proline, and intracellular signal transduction (Kinnersley and Turano, 2000). Drought stress initiates a signal transduction pathway, in which increased cytosolic Ca^{2+} activates $Ca^{2+/}$calmodulin-

dependent glutamate decarboxylase activity, leading to a γ-aminobutyric acid synthesis. Elevated H^+ and substrate levels can also stimulate glutamate decarboxylase activity, leading primarily to γ-aminobutyric acid accumulation (Kinnersley and Turano, 2000). Experimental evidence supports the involvement of γ-aminobutyric acid in pH regulation, nitrogen storage, plant development, and defense, as well as a compatible osmolyte and an alternative pathway for glutamate utilization. After drought stress, the content of proline was more than 50%, and at the end of recovery, the γ-aminobutyric acid content reached 27%.

Trehalose is a nonreducing disaccharide of glucose that also functions as a compatible solute in the stabilization of biological structures under abiotic stress. In nature, trehalose is biosynthesized as a stress response solute by a variety of organisms including bacteria, fungi, algae, insects, invertebrates, and lower plants (Vinocur and Altman, 2005). Capacity to produce trehalose, earlier thought to be absent from higher plants, has now been reported to accumulate in high amounts in some drought-tolerant ferns, the resurrection plant *Selaginella lepidophylla*, and desiccation-tolerant angiosperm *Myrothamnus flabellifolia*. The presence of low amounts of trehalose was demonstrated even in tobacco and many higher plants. Its metabolism may be channelized to enhance drought tolerance in plants. Physiological roles of trehalose include efficient stabilization of dehydrated enzymes, proteins, and lipid membranes, as well as protection of biological structures under desiccation stress rather than regulating water potential (Ashraf and Harris, 2004; Koyro et al., 2012). Karim et al. (2007) have reported that enhanced drought tolerance by trehalose depends on improved water status and expression of heterologous trehalose biosynthesis genes during *Arabidopsis* root development. At a molecular level, exogenously applied trehalose may trigger the ABA-insensitive 4 gene expression but decrease sucrose induction, providing a possible molecular mechanism for the trehalose effect on plant gene expression and growth. Plants can withstand drought stress by conserving cell and tissue water principally by osmotic adjustment, maintenance of the antioxidant defense system for the scavenging of ROS, and keeping the cell membranes stabilized. Improved drought tolerance has been reported in the transgenic plants overproducing trehalose-6-phosphate synthase despite the minute accumulation of trehalose. Thus, the plant growth regulators and polyamines, γ-aminobutyric acid, free amino acids, and sugars also play a vital role in drought tolerance by scavenging the ROS, stomatal regulation and protection of vital macromolecules, and maintenance of the cell water balance.

4. Molecular mechanism of drought tolerance in wheat

Drought tolerance in wheat is a complex intrinsic response that is regulated by an interlinked network of genes, which are synchronized by some key players. At the molecular level, it is mainly regulated at transcription that involves the expression of genes, followed by the regulation at posttranscription, translation, posttranslation, and epigenetic levels (Mohammadi, 2018). Following is the summarized research including identification of drought-tolerant gene and mechanisms of drought tolerance in wheat.

4.1 Identification of genes related to drought tolerance regulation in wheat

In recent years, advancement in the laboratory techniques and computational biology has enabled the researchers to identify some genes associated with drought tolerance in wheat plant. Condense marker mapping of wheat genome has made it possible to recognize genes related to drought tolerance with the help of MAS and QTL (Budak et al., 2013). Gene expression analysis techniques (Northern blotting, Southern blotting, and Western blotting) are very helpful in identification of genes. Real-time PCR followed by gel electrophoresis helps to locate markers related to genes (Chen et al., 2011). AFLP, 2D gels, mass spectrometry, and chromatography techniques are used for differentially expressed protein identification (Krugman et al., 2011). Recently emerging new branch of computational biology has made possible in vitro recognition of genes in the genome of an organism with the help of transcriptomics, proteomics, and metabolomics (Nezhadahmadi et al., 2013).

4.1.1 Transcription regulation

Transcription regulation of drought response genes is one of the important events in the molecular mechanism of drought tolerance in wheat. TFs in response to certain drought-tolerant markers regulate transcription of genes associated with drought-tolerant mechanisms. Regulation is divided into two groups. The first group contains protein-coding genes that protect the plant from the effects of dehydration; it includes genes for regulation of osmotic pressure, transport system of the cell, and cell structure stabilizing proteins and genes of the proteins

important for the protection of essential macromolecules (Shi et al., 2010). The second group contains genes for the regulatory proteins mainly TFs (Shi et al., 2010). Transcription regulation mechanism of drought tolerance in wheat is divided into two groups, i.e., ABA-dependent mechanism and ABA-independent mechanism (DREB-dependent mechanism) (Budak et al., 2013; Shi et al., 2010; Nakashima et al., 2014) (Fig. 8.1). There are various mechanisms that stimulate the plant's development and growth. Such processes are always governed by the hormones released by plants called as phytohormones. Out of five distinctive phytohormones, one is ABA that plays a role in controlling many development and growth characteristics of plants including leaf abscission and inhibition of fruit ripening. ABA is commonly known as the "stress hormone" that reacts to multiple environmental stresses including both biotic and abiotic stress (Zhang, 2014). Wani et al. (2016) critically elaborated the importance of all major phytohormones in plant growth and development as well as abiotic stress tolerance, besides mentioning their engineering for conferring abiotic stress tolerance in transgenic crops. ABA has key roles in numerous cell-based processes, viz., development of seed, vegetative growth, seed under development and sprouting, and reaction to ecological stress (Vishwakarma et al., 2017). ABA is stable under high temperatures so as to get dissolved in boiling water without undergoing degradation. Under water deficit, the plant machinery focus is diverted toward ABA production for activation of downstream signaling pathways and drought-tolerant mechanisms that decrease the grain filling and crop yield. Therefore, there is a need to find the balance between yield and drought tolerance (Xiong and Zhu, 2003).

The rise in de novo biosynthesis of ABA is due to the increase in abiotic stress that plays a role to inhibit its degradation and is thought to be triggered by stress relief. ZEP gene is identified for ABA biosynthesis and has been cloned and expressed in several plant species. This gene is found to be existed in every plant part but is highly linked for basal expression in leaves. In addition, the level of ABA biosynthesis through ZEP gene is regulated in different plant portions during development phases in numerous plant species. The variations in the expression of ZEP genes in different plant species are partly associated to basal transcript levels, which also cover stress induction ability of genes as seen in different experiments (Xiong and Zhu, 2003). ABA substance has been used as selection index for screening wheat under water stress, and contrasting parents for the crop yield have been crossed. Fig. 8.1 represents schematic overview of drought-tolerant mechanism in wheat. The detailed description of different drought-tolerant mechanisms in wheat is given in the following sections.

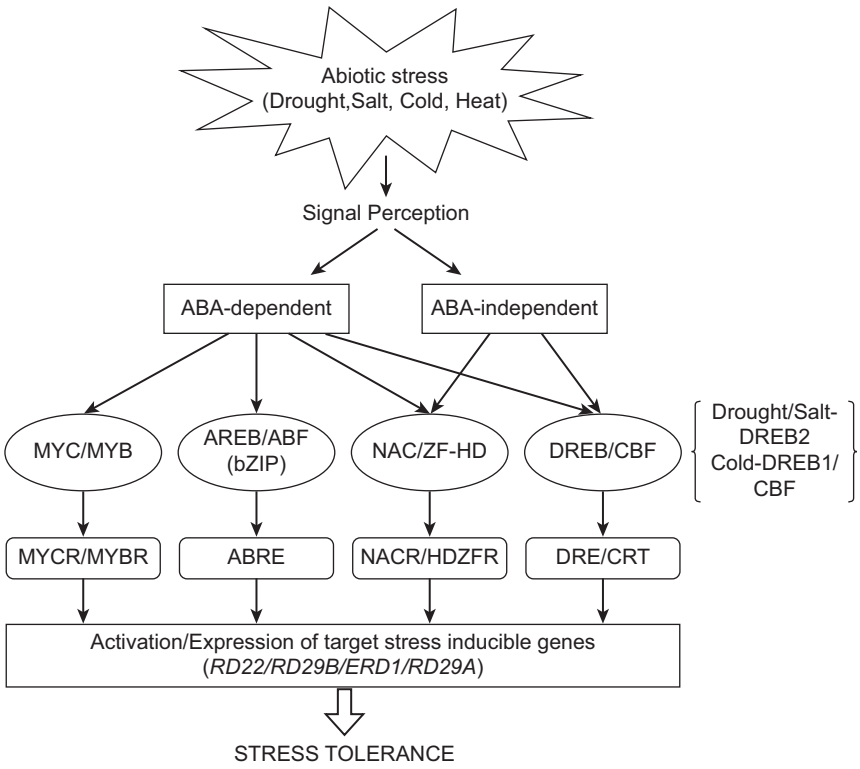

FIGURE 8.1 Schematic overview of abscisic acid (ABA)-dependent and independent mechanisms for drought tolerance in wheat, which regulate different transcription factors. These factors in turn control the expression of different stress-responsive genes in wheat.

4.1.1.1 Abscisic acid–dependent mechanism

ABA is a phytohormone that plays a significant role in growth and maturity by regulating seed dormancy, stress forbearance, and water retention capability of the plant (Leung and Giraudat, 1998; Xiong and Zhu, 2003). ABA is a tiny molecule and classified as a sesquiterpene. It has a nonplanar configuration and has multiple functional moieties. The synthesis of ABA takes place de novo during drying up process, and its degradation occurs during rehydration following dehydration (Vishwakarma et al., 2017). It occurs in plant roots and terminal buds at the top of plant. The C-15 ABA skeleton is commonly found in biosynthetic precursors such as xanthoxin, abscisic aldehyde, and abscisic alcohol as well as oxidized catabolites including phaseic acid, 8′-hydroxy-ABA, and dihydrophaseic acid. The level of ABA produced endogenously is elicited in plant system due to several stress signals. These may include the stimulation of genes that encode for enzymes that form ABA from β-carotene (Vishwakarma et al., 2017).

The quantity of ABA usually increases in response to stress including drought, as ABA acts as a first line of defense against drought (Finkelstein et al., 2002). It has been observed that QTLs of ABA located at chromosome 5A L are responsible for its accumulation in response to stress (Quarrie et al., 1994). As very pivotal role is played by ABA, it becomes important to understand its biosynthesis. The major key player in the biosynthesis of ABA is 9-cis-epoxycarotenoid dioxygenase (NCED), which is rate limiting (Ágnes et al., 2013). Its expression is upregulated in response to drought, and then it regulates the biochemical cascade of ABA biosynthesis (Fig. 8.2). ABA-dependent pathways arbitrate stress adjustment by induction of two TFs: (1) bZIP, i.e., the AREB/ABF (ABA-responsive element–binding protein/ABA-binding factor) and (2) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) (Cramer et al., 2011) (Fig. 8.1). The sucrose non–fermenting-related protein kinase 2 family (SnRK2) comprises plant-specific Ser/Thr kinases, which act as ABA signaling positive regulators. SnRK2s were first reported to be engaged in ABA signaling in wheat plant (Fujii and Zhu, 2012). It is seen from previous researches that some TFs such as AP2/EREBP (ERF) are involved in both ABA-dependent and independent signaling mechanisms. In spite of being two separate and independent pathways, there is plausibly some cross-talk between both (Lata and Prasad, 2011). The AP2/ERF TF family include the ethylene response factors, e.g., a TaERF promotes drought tolerance in wheat with increased proline and chlorophyll levels (Rong et al., 2014). ABA-induced genes and ABA-induced TFs in response to drought in wheat have been described in Tables 8.1 and 8.2, respectively.

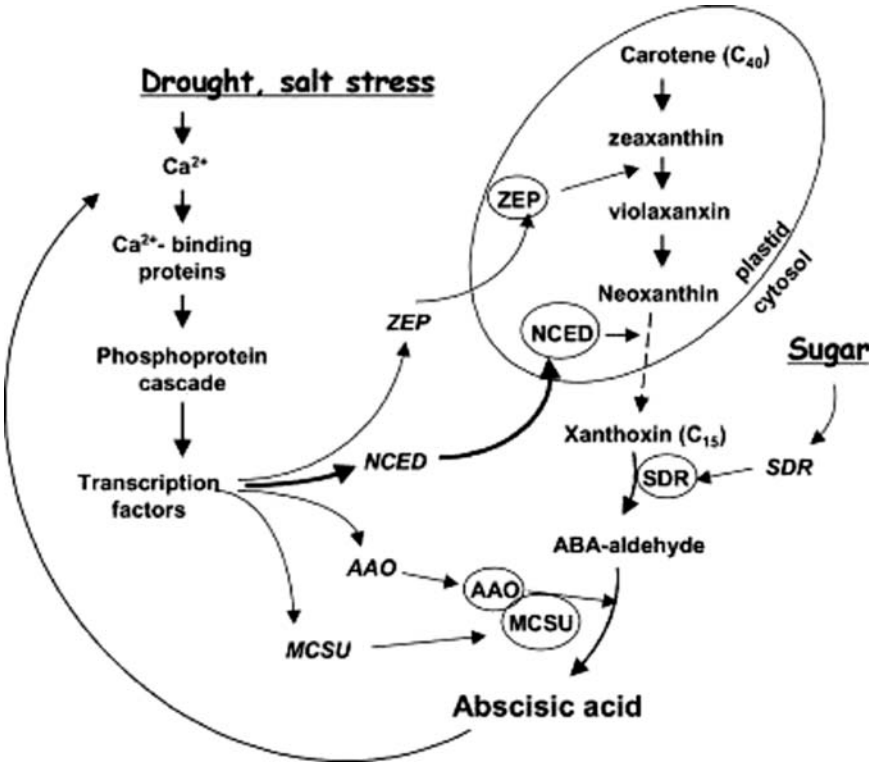

FIGURE 8.2 Schematic overview of drought response in wheat through induction of Ca^{2+}-dependent phosphoprotein cascade, which induces the transcription factors involved in the upregulation of the enzymes needed in the production of abscisic acid (ABA). Among these enzymes, NCED is strongly upregulated. These enzymes regulate the production of ABA from starting substrate C40 carotene. Zeaxanthin is cleaved to ABA. This in turn regulates the self-production of ABA.

TABLE 8.1 List of abscisic acid (ABA)–responsive genes in wheat involved in drought tolerance.

ABA-induced genes	References
Wdhn13	Kobayashi et al. (2008a,b,c), Quellet et al. (1998), Budak et al. (2015)
Wrab17	Kobayashi et al. (2008a,b,c), Quellet et al. (1998), Budak et al. (2015)
Wrab18	Kobayashi et al. (2008a,b,c), Quellet et al. (1998), Budak et al. (2015)
Wrab19	Kobayashi et al. (2008a,b,c), Quellet et al. (1998), Budak et al. (2015)
PKABA1	Aurelio et al. (1999)

TABLE 8.2 List of transcription factors (TFs) responsive to abscisic acid (ABA) in wheat for drought tolerance.

Class	TF genes	ABA response	Reference
bZIP	WLIP19	Yes	Rahaie et al. (2013), Wang et al. (2015)
	TaOBF1	Yes	Rahaie et al. (2013), Wang et al. (2015)
	TaABF1	Yes	Rahaie et al. (2013), Wang et al. (2015)
MYC/MYB	TaMYBsdu1	Yes	Cai et al. (2011), Okay et al. (2014)
	TaMYB33	Yes	Cai et al. (2011), Okay et al. (2014)
	TaMYB3R1	Yes	Cai et al. (2011), Okay et al. (2014)

4.1.1.1.1 ZIP transcription factors ZIP TFs contain two regions, i.e., (1) basic region that contains nuclear localization signals and (2) zipper region that forms a zipper-like confirmation after attaching to DNA (Rahaie et al., 2013). bZIP TFs are also termed as AREB/ABF. Specific sequences known as ABA-responsive element (ABRE) act as *cis*-acting element and are found in association with couple elements at upstream of ABA-induced genes (Kobayashi et al., 2010). These motifs act as a promoter for these genes. AREB/ABF recognizes these motifs and regulates gene expression. It is located in the upstream sequence of Wdhn13, Wrab17, Wrab18, and Wrab19, which are involved in the drought and stress response (Quellet et al., 1998; Takumi et al., 2003). High level of ABA induces protein kinase gene PKABA1 in response to drought and stress (Gómez et al., 1999). This protein kinase acts as a mediator in downregulation of ABA-responsive gene, i.e., gibberellins (Aurelio et al., 1999). Expression level of bZIP TFs that are WLIP 19, TaOBF1, and TaABF1 are found unregulated in response to ABA (Rahaie et al., 2013; Keyser et al., 2010). ABRE is a major *cis*-acting element in ABA-responsive gene expression. Two ABRE motifs are important *cis*-acting elements regulating ABA-responsive expression of the *Arabidopsis RD29B* gene. Two bZIP TFs, AREB/ABF, can bind to ABRE, thereby activating ABA-dependent gene expression (Uno et al., 2000). The AREB/ABF proteins require an ABA-mediated signal for their positive stimulation, as indicated by their reduced activity in the ABA-deficient *aba2* and ABA-insensitive *abi1* mutants and their enhanced activity in the ABA-hypersensitive *era1* mutant of *Arabidopsis*. This phenomenon is very probably due to the ABA-dependent phosphorylation of the AREB/ABF proteins. Overexpression of *ABF3* or *AREB2/ABF4* resulted in ABA hypersensitivity, lowered the transpiration rate, and increased drought tolerance in transgenic *Arabidopsis* plants (Shinozaki and Yamaguchi-Shinozaki, 2000). Recently, transgenic plants expressing a phosphorylated form of AREB1 with multisite mutations displayed induction of many ABA-responsive genes without exogenous ABA application (Uno et al., 2000). These data suggest that such constitutively active forms of TFs rendered by point mutations may contribute to enhancement of drought tolerance in transgenic plants.

4.1.1.1.2 Myelocytomatosis/myeloblastosis transcription factors MYC/MYB was initially first found in virus (Klempnauer et al., 1982). Now, it is evident that these are present in both plants and animals. It is a large

family of TFs containing more than 200 TFs (Rahaie et al., 2013). Its function is associated with overexpression of stress-tolerant genes in response to ABA. The expression level of MYC TFs is found upregulated in response to ABA. The MYB is a member of the MYB protooncogene protein family TF and was first identified in mammalian cells as an oncogene (Klempnauer et al., 1982). The protein contains three domains, namely N-terminal DNA-binding domain, central transcriptional activation domain, and C-terminal domain, which are involved in transcriptional repression (Vargova et al., 2011). MYB TFs represent a family of proteins that contain the conserved MYB DNA-binding domain. Plants contain an MYB protein subfamily that is characterized by the R2R3-type MYB domain (Dubos et al., 2010). MYB proteins are classified based on the number of DNA-binding repeats present in their sequences. The major function of MYB TFs was the regulation of cell cycle and involvement in the regulation of abiotic stress response.

4.1.1.2 Abscisic acid–independent mechanism

The ABA-independent regulons include the CBF/DREB (cold-binding factor/dehydration-responsive element binding), NAC, and ZF-HD (zinc-finger homeodomain) (Lata and Prasad, 2011). The transcriptional regulatory network based on DREBs is induced by dehydration in wheat. There are two known DREB regulons: DREB1/CBF and DREB2 (Edae et al., 2013). The ABA-independent mechanism is controlled by many TFs such as DREB, WRKY, and NAC (Rahaie et al., 2013) whose description is provided in the following sections.

4.1.1.2.1 Dehydration-responsive element-binding factor–dependent mechanism Dehydration-responsive element-binding factors (DREBs) are a large class of TFs related to the AP2/ERF family that shows an immediate response to biotic and abiotic stresses (Sazegari and Niazi, 2012). These TFs bind directly to the DRE/CRT sequence and contain CCGACC-repeat region, in the promoter region of genes (Sazegari and Niazi, 2012; Shinozaki and Yamaguchi-Shinozaki, 2000). This class further contains two subclasses containing DREB1/CBF and DREB2; DREB1/CBF shows response to cold-induced drought, and DREB2 shows response to dehydration-induced drought (Zhou et al., 2010). Drought induces wheat DREB (WDREB2). DREB TFs regulate the expression of rd29A, kin1, and erd10 genes having a function in regulating response to abiotic and biotic stress (Zhou et al., 2010).

A soybean-based DREB gene (*GmDREB*) by gene gun bombardment method using RD29A promoters and ubiquitin, transformed to wheat plant and transgenic plants with both promoters, expressed greater drought and salt tolerance (Shiqing et al., 2005). This enhanced tolerance of the crop was associated with to twofold higher proline production, stay-green phenomenon under drought and survival, and recovery on rewatering (SURV) after water-deficit conditions (Wang et al., 2006). This suggests that signaling pathways play a role in downstream proline production. Transformation of wheat with a cotton-originating DREB (*GhDREB*) improved drought, salt, and freezing tolerance due to higher production of soluble sugars and chlorophyll in leaves (Gao et al., 2009). Transgenic wheat with *DREB1A* was subjected to field screening on the basis of SURV. Although the event was selected in greenhouse, plants showed even higher yield under field drought (Pierre et al., 2012). However, there is urgent need to find out activated genes or expressed proteins by these TFs to thoroughly understand their role in signaling pathways.

4.1.1.2.1.1 WRKY transcription factors The WRKY TFs are a superfamily of regulators that are responsible for controlling various developmental and physiological processes. This family of TFs was initially thought to be plant specific until the recent detection of WRKY genes in nonphotosynthetic eukaryotes (Xie et al., 2005). Proteins of this family contained one or two highly conserved WRKY domains and a zinc finger motif in the C-terminal region (Eulgem et al., 2000). The WRKY domain bound to the W box or sugar-responsive *cis*- acting element found in promoters of target genes (Sun et al., 2003). WRKY TFs function in gene expression regulation in response to biotic and abiotic stress. It has been found in many crop plants (Wang et al., 2015). WRKY TFs are also important in critical plant developmental and physiological functions (Phukan et al., 2016). This gene family has been broadly studied for its part in abiotic stress tolerance mechanism in several plant species, including wheat (Ding et al., 2016). It binds to the W-box in the promoter region of the genes (Chen et al., 2011; Wu et al., 2008). In wheat, expression of genes, WRKY1 and WRKY2 of WRKY TFs, is upregulated in response to stress (Proietti et al., 2011; Rahaie et al., 2010). A direct role of WRKY TFs in drought tolerance is evident from their upregulation at the protein level in response to drought stress (Tripathi et al., 2014). Wheat WRKY TFs, *TaWRKY44* and *TaWRKY93*, were recognized to be critical response factors under heat stress (Wang X. et al., 2015). A functional proof of the function of WRKY in water-deficit stress tolerance of wheat was evident from *TaWRKY10* overexpression in tobacco, which enhanced drought-tolerant response in transgenic tobacco lines with a suggested role as a negative regulator of antioxidant accumulation (Wang et al., 2013). Some of the wheat *TaWRKYs* (*TaWRKY*16, 24, 59, 61, and 82) were found to be differentially expressed in both leaf and root tissues under drought stress (Okay et al., 2014).

4.1.1.2.1.2 NAC transcription factors NAC is the family of TFs that regulates genes during both biotic and abiotic stress. NAC TFs play several important functions not only in plant development but also in abiotic stress responses (Nakashima et al., 2014); they comprise three proteins, namely, NAM, ATAF, and CUC. This family of TFs is well known for its roles in plant development process. All these TFs have highly conserved DNA-binding domains and are well known for various functions during abiotic stress (David et al., 2016).

Abiotic stress alters gene expression and cellular metabolism and also changes plant growth, development, and crop yield. NAC TFs are key machineries during the plant stress and function in complex signaling responses. NAC TFs have been identified in a large number of plants. Transcription profiling and functional analyses provided some direct evidence on the possible participation of NAC TFs in abiotic stress responses. The alterations of NAC genes establish complex signaling process to regulate genes in response to plant stress. This makes them potential candidates for imparting stress tolerance (Hu et al., 2008). It has been found that TaNAC8, TaNAC2, TaNAC4, and TaNAC69 have an important regulatory role in the drought stress (Rahaie et al., 2010).

Wheat TaNAC69 binds to the promoter regions of chitinase enzyme of rice along with zinc finger protein expressed in inflorescence meristem (ZIM) and glyoxalase I, thereby enhancing the stress tolerance by overexpression of these genes. In particular, expression levels of glyoxalase I family genes were matching to that of *Arabidopsis* stress−inducible NACs ANAC019, ANAC055, and ANAC072, which are known for their importance in drought tolerance (David et al., 2016). SNAC1 is induced primarily in guard cells by drought, which in turn upregulates stress-related genes in transgenic rice plants without significant changes to the phenotype and yield (Hu et al., 2009).

4.2 Genetic manipulation of wheat at molecular level for drought tolerance

Some plants show a high degree of tolerance to drought, whereas others may not be successful in resistance toward drought. MAS and QTL mapping enable to pinpoint the genes involved in the drought resistance (Shinozaki and Yamaguchi-Shinozaki, 1997; Marone et al., 2012). With the help of this knowledge, it is now possible to manipulate the genome of a crop at the molecular level for introducing drought-resistant trait. Genetic engineers mainly focus on the manipulation of the genes encoding for organic osmolytes, plant growth regulators, antioxidants, heat shock, LEAs and TFs involved in gene expression (Ashraf, 2010). Significant loss of genetic diversity has occurred at three levels: (1) species level (domestication), (2) varietal level (green revolution), and (3) gene level (breeding cycles). Therefore, breeding techniques for drought tolerance in wheat could be enhanced by integrating transcriptomic, proteomic, metabolomic, and phenomic approaches to further unfold drought-responsive genes and signaling pathways. Lack of a genome sequence, poor genomic resources (Fleury et al., 2010), and failure to integrate such approaches may hinder further understanding of the flow of genetic information influencing drought tolerance in wheat. Advances in sequence-based gene expression analysis through the use of next-generation sequencing techniques could shade more light on the regulatory mechanisms and networks of this polygenic trait (Poland et al., 2012; Edwards et al., 2013). Gene expression analysis and genome-wide transcript profiling under managed stress could increase knowledge on the functions and levels of expression of thousands of drought-responsive genes. To date, several classes of genes have been confirmed to be up- or downregulated by drought stress to enable dehydration avoidance or tolerance in various plant species including wheat.

High wheat crop yield produced through green revolution has lower stress tolerance. It is the time for plant breeders to look back and employ the lost genetic diversity as some wild wheat relatives are potential sources of drought tolerance. For example, wild emmer wheat (*Triticum dicoccoides*) has inter- and intravarietal genetic diversity for water use efficiency and phenology and comprises several genes and QTLs for drought tolerance (Budak et al., 2015). Gene expression studies in emmer wheat identified more than 13,000 expressed sequence tags in response to drought (Ergen and Budak, 2009), and 33 outlier loci for drought tolerance were identified by single nucleotide polymorphism markers. So far, following strategies have been adopted for manipulating wheat for drought response at molecular level (Budak et al., 2015).

4.2.1 Overproduction of organic osmoregulators

Organic osmoregulators play a central role in response to abiotic stress, i.e., drought or dehydration (Ashraf, 2010; Ashraf and Foolad, 2007). Organic solutes overproduce to increase the water retention capability of the crop plant (Ashraf, 2010; Ashraf et al., 2008; Serraj and Sinclair, 2002). Wheat grain comprises about 60%−75% starch of its total dry weight. Heat stress substantially limits starch biosynthesis in grains of wheat but results in a remarkable gain in total soluble sugar and protein (Akter and Islam, 2017). Liu et al. (2011) observed that heat shock treatment above 30°C causes a significant rise of grain starch and restricted the dry matter accumulation in grain of wheat. Around

97% of activity was gone due to the reduction in soluble starch synthase at 40°C, resulting in reducing grain growth and starch accumulation in wheat. High temperature stress (35/27°C) imposed at seedling stage significantly reduces soluble sugar accumulation and biomass yield in wheat (Wang et al., 2013).

Approach to engineer genes of these osmoregulators can be applied to upregulate their expression to induce drought resistance. A pylol, known as mannitol, has an important role in inducing resistance to drought. Many attempts have been carried out to manipulate gene for mannitol to overexpress it (Wu et al., 2008). Mannitol biosynthesis gene, that is, mt1D gene overexpression, has been shown to induce drought resistance in wheat (Wu et al., 2008; Serraj and Sinclair, 2002). GB and other quaternary ammonium compounds are produced excessively in response to drought in wheat (Wu et al., 2008; Abebe et al., 2003). Engineering approaches are being used to manipulate the activity of two enzymes involved in its expression including choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH) (Aldesuquy et al., 2013). Gene of CMO from *Escherichia coli* is incorporated in wheat to induce the overexpression of GB (Wu et al., 2008). There are many other osmoregulators that reduce the negative effects of drought in wheat by regulating the quantity of osmotic solutes in the cells, thus increasing the osmotic pressure, which includes the best example of SA. It is a phenol growth regulator and also induces drought resistance in wheat (Abebe et al., 2003; Quan et al., 2004).

4.2.2 *Overproduction of antioxidants*

ROS are well known for both harmful and beneficial effects depending on their concentration in plants. The role of ROS as signaling molecules involved in processes such as cell cycle, stomatal conductance, development, growth, senescence, programmed cell death, hormonal signaling, and regulation of gene expression has been widely explored (Caverzin et al., 2016). The intensity and duration of ROS signaling also depends on the pool that forms as a consequence of ROS synthesis by oxidants and their elimination by antioxidants. ROS are continuously produced in the plant at a high level (Ahmad and Wani, 2014); however, under normal conditions, antioxidant enzymes, i.e., CAT, guaiacol peroxidase, APX, and SOD, are also produced at high level (Wu et al., 2008; Carvalho, 2008; Hassan et al., 2015). Drought and dehydration cause the accumulation of ROS in the cell (Tartoura, 2010). Transgenic wheat lines are generated in which the expression of the antioxidant enzyme is upregulated to cope with the oxidative stress produced in response to drought (Wu et al., 2008).

Among the various ROS, H_2O_2 is one of the most abundant in aerobic biological systems in higher plants, being highly reactive and toxic. Hydrogen peroxide is considered a signaling molecule in plants that mediates responses to various biotic and abiotic stresses. The biological effect of H_2O_2 is associated to multiple factors, such as the site of production, the developmental stage of the plant, and previous exposures to different kinds of stress; however, the strongest effect on plants is the relationship with its concentration. In wheat, it was observed that seed pretreatment with H_2O_2 enhances drought tolerance of seedlings (Ahmad and Wani, 2014). Additionally, as a result of H_2O_2 pretreatment, wheat aluminum acclimation became better during subsequent aluminum exposure, thereby reducing ROS accumulation.

The exogenous H_2O_2 treatment also protected wheat seedlings from damage by salt stress (Li et al., 2017), and the pretreatment of seeds enhanced salt tolerance of wheat seedlings, decreasing the oxidative damage. In wheat, it was observed that seed pretreatment with H_2O_2 enhances drought tolerance of seedlings. Moreover, H_2O_2 pretreatment improved wheat aluminum acclimation during subsequent aluminum exposure, thereby reducing ROS accumulation (Caverzan et al., 2016). The exogenous H_2O_2 treatment also protected wheat seedlings from damage by salt stress, and the pretreatment of seeds enhanced salt tolerance of wheat seedlings, decreasing the oxidative damage. Thus, considerable evidence suggests that H_2O_2 and other ROS may act as important signal molecules mediating response to stress tolerance in plants. Thus, the processes by which an ROS treatment may protect against various stresses require further study because other pathways (biochemical, molecular, and genetic) can be involved and contribute to tolerance. Importantly, each plant species responds differently to stress condition and under field conditions, and oftentimes, the plants suffer combined stresses. However, ROS signaling mechanisms are potentially significant to any research program targeted at improving crop tolerance to environmental stresses.

4.2.3 *Late embryogenesis abundant proteins*

LEA proteins are the major seed proteins. Their accumulation is a functional adaptation of plants in gaining tolerance against osmotic as well as oxidative stresses. LEA proteins are found in the seeds of a higher plant in response to dehydration. These proteins protect the plant from the adverse effects of dehydration (Hong bo et al., 2005). LEA proteins are members of a large group of hydrophilic, glycine-rich proteins present in a wide range of plant species. This class of proteins are known to be intrinsically disordered in their structures and are mainly expressed under

water deprivation condition. The LEA genes are highly diverse, with wide distribution in the plant kingdom, and have pivotal role in various stress-tolerant responses (Magwanga et al., 2018).

LEA proteins consist of a wide range of molecular masses and mainly accumulate in the second and third phases of seed development, which is when the storage materials accumulated in the seed start to getting dehydrated, thus entering into dormancy phase (Mukherjee et al., 2006). These novel proteins were first identified in the seed maturation process. The importance of their role is due to their ability to maintain cell membrane structure, ion balance, and their action as molecular chaperones (Wu et al., 2008). LEA protein families have common structural features such as high hydrophilicity, low proportion of cysteine and tryptophan residues, and high content of arginine/lysine, glutamate, alanine, threonine, and glycine. The ubiquitous presence of LEA proteins in the plant kingdom have posed them as important targets of dictating desiccation stress tolerance. Researchers have identified LEA proteins in several plant species including wheat. Engineering of PMA1959 and PMA80 genes of wheat can induce drought-tolerant trait (Dat et al., 2000; Ried and Walker-Simmons, 1993; Cheng et al., 2002).

Recent research in bioinformatics suggests that LEA proteins might act as molecular chaperones. In a study, it is seen that recombinant forms of AavLEA1, a group 3 LEA protein from the anhydrobiotic nematode *Aphelenchus avenae*, and Em, a group 1 LEA protein from wheat, when subjected to functional analysis during a drought stress experiments with citrate synthase, which is susceptible to aggregation at high temperatures, suggest that LEA proteins do not behave as classical molecular chaperones; instead, they exhibited a protective, synergistic effect in the presence of the so-called chemical chaperone, trehalose (Goyal et al., 2005). In contrast, both LEA proteins can independently play a role in water stress tolerance.

4.2.4 Introduction of foreign genes

Drought-resistant genes are scattered in different plants. Genetic engineering and transgenic approaches can alleviate the adverse effects of heat stress by improving heat tolerance. It involves the incorporation of genes of interest into the chosen plants to improve heat stress tolerance in that particular plant (Akhter and Islam, 2017). However, the complexity of the genomic pattern makes it difficult to research for genetic modification in wheat. Heat stress for an extensive period increases protein synthesis elongation factor (EF-Tu) in chloroplast, which is associated with heat tolerance in wheat. The constitutive expression of EF-Tu in transgenic wheat protected leaf proteins against thermal aggregation, reduced thylakoid membranes disruption, enhanced photosynthetic capability, and resisted pathogenic microbial infection. The wheat genotypes accruing more EF-Tu showed better tolerance to heat stress than those exposed to less EF-Tu (Akter and Islam, 2017).

Recently, many TFs involved in various abiotic stresses have been found and engineered to improve stress tolerance in crops. Genome sequences of many plants are recently generated for improvement of stress tolerance. Relatively inexpensive sequencing technologies and approaches are being used by the researchers to sequence multiple wheat varieties. This will result in structural changes on a large scale that are known to play an important role in the adaptation of the wheat crop to different stressful environments (Akhter and Islam, 2017).

Furthermore, with the help of rDNA technology, specific genes can be introduced into the wheat to induce drought tolerance. HVA1 gene from barley is introduced in wheat, and it successfully induces drought tolerance (Wu et al., 2008; Xu et al., 1996; Nezhadahmadi et al., 2013). DREBs are a group of TFs involved in the expression of many genes that induce drought tolerance (Wu et al., 2008; Nezhadahmadi et al., 2013). Introduction of DREB1A into wheat under the control of rd29A promoter has resulted in better drought tolerance (Wu et al., 2008; Pellegrineschi et al., 2004).

Recently, a novel approach was employed where the scientists determined the genetic architecture during the drought tolerance in reproductive phase of wheat using a correlated trait and correlated marker effect model (Dolferus et al., 2019). The two main approaches used in this study included controlled environment phenotyping with help of surrogate osmotic stress tolerance trait and a novel QTL mapping approach. This led them to identify the novel genomic regions that aid in maintaining pollen fertility and spike grain number under reproductive stage drought conditions. It was revealed that a complex genetic network regulates the drought tolerance in wheat, which can be exploited in future to further improve the drought resistance in wheat and thereby yield better and improved versions.

5. Conclusion

Stress due to drought acts as a major constraint during the reproductive growth phase of the wheat plant. To induce drought tolerance in wheat, detection of genomic responses to water deficit is essential for multiple reasons. Firstly, it prepares intensive data regarding transcriptional reactions of plants to drought. Secondly, it elucidates the

role of genes, their expression, and functions during water stress conditions. Thirdly, it helps in distinguishing promoters that react to water-deficit stress and related *cis*-acting elements, which are both important for basic crop studies and transformation. Rapid improvements can be performed in drought resistance by engineering the genes that are responsible for the plant's growth proteins, antioxidants, regulators, and TFs. QTL analysis, omics studies, and molecular mapping are also established techniques used for qualitative and quantitative traits screening for understanding resistance or sensitivity and/or improvement of drought tolerance in wheat. Transcriptional regulation of genes is one of the important events in the molecular mechanism of drought tolerance; its mechanism is divided into two groups, i.e., ABA-dependent mechanism and ABA-independent mechanism (DREB-dependent mechanism). In addition, there are some limitations in this regard. For example, there is a challenge for QTL detection, for example, inconsistent repeatability, genotype and environmental interaction, numerous genes regulating crop yield, and use of improper populations for mapping. Moreover, there are other parameters also that limit the QTL efficiency for genetic development of an element; because of wrong interaction epistasis, it is difficult to carry the influences of an allele to extract substance. Therefore, the high variability in the nature of drought stress and inadequate information about its complicatedness has made it difficult to identify specific physiological traits needed for improved crop performance. Furthermore, latest advancements are being made in laboratory techniques and computational biology to identify genes associated with drought tolerance in wheat plant, and by implementation of the abovementioned techniques and factors involved in drought response mechanism through genetic engineering at molecular level and improved transgenic drought-tolerant crops of wheat varieties being produced, the scientific world is looking forward to it as a solution to the possible threat of food and nutrient shortage in near future due to exponentially increasing population of the world. So, there is an urgent need to have a deeper understanding of the complex regulatory molecular processes involved in drought response to deal with drought stress.

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CHAPTER

9

Cellular mechanisms of drought tolerance in wheat

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OUTLINE

1. Introduction

Wheat is a remarkable cereal crop of nutritional and economical significance throughout the world (Yadav et al., 2019). One-third of the world's population relies on wheat as their staple nutritional requirements (Ihsan et al., 2016). According to recent studies, wheat production is highly threatened by abiotic stresses. It is estimated to be affected from 4.1% to 6.4% yield loss upon per degree centigrade increment in environmental temperature (Liu et al., 2016). Similarly, salinity is also a major threat to wheat production worldwide (Mujeeb-Kazi et al., 2019). Another fatal abiotic stress is drought that is attaining global attention and poses serious concerns to wheat productivity (Jiangkang, 2016). It greatly reduces crop yield and productivity (Ludlow and Muchow, 1990). Other noticeable effects arise due to drought include deleterious impact upon vegetative and reproductive characteristics in the plants. In response to water deficiency, plants exhibit various changes in their molecular, biochemical, morphological, and physiological characteristics. The consequences arise from severe cases including loss of certain organs, functional damage and may also lead to death (Sangtarash, 2010).

Among global food security, the most acute threat is drought. Its severity depends on a lot of factors like rainfall distribution, soil's moisture storage capacity, and evaporation demand of the plant. Studies were carried out to investigate the exact mechanism of tolerance in plant against water scarcity at molecular levels. There are three

mechanisms that are involved in the reduction of crop yield by drought. These include (1) reduction in canopy absorption of radiations that are photosynthetically active, (2) reduction in harvest index, and (3) decrease in radiation use efficiency. The worldwide shortage of water has attracted concerns, which stimulated additional research input on fundamental science related to drought resistance and the applications of acquired knowledge for the development of drought-resistant verities (Fang and Xiong, 2015).

Competing with drought is a great challenge to breeders and agricultural researchers. According to estimate, approximately 1.8 billion people around the world will face water shortage, and 65% of the world's population will have to live under water-stressed conditions by 2025. Drought tolerance is a polygenic trait and helps the plants to cope with the water stress (Ingram and Bartels, 1996). The degree to which the plants adapt to water-deficient conditions varies among species of plants (Save et al., 1995).

According to their adaptation, drought plants can be categorized into three different types which include hydrophytes, mesophytes, and xerophytes. Mesophytes are one of the important types used as a model to study drought resistance. Drought resistance mechanism of plants is very complex. At their different developmental stages, plants possess different mechanisms for drought resistance, and at a particular developmental stage of plant series of events take place like photosynthesis, synthesis of protective macromolecules and antioxidants, stomatal movement, cell osmotic regulation, etc. Moreover, natural drought stress is unpredictable and dynamic. So, it is difficult to evaluate drought resistance of the given plant species. To determine drought resistance is the most difficult among other stress resistances (Fang and Xiong, 2015).

Furthermore, it is also dependent upon the occurrence of other biotic and abiotic stresses (Save et al., 1995). Some plants, like xerophytes, can adapt to the arid conditions naturally, but some plants like wheat exhibit drought tolerance by demonstrating several characteristics (Kramer and Boyer, 1995). Various tolerance mechanisms of plants like pigment content, stability, and high relative water content have been linked to drought by researchers (Clarke and McCaig, 1982). Membrane stability is also one of the criteria which are widely used to observe drought tolerance (Premachandra and Shimada, 1988). By understanding the physiological characteristics that help the plants to adapt to water-scarce environments could help in recognizing, screening, and selecting suitable genotypes of plants to be used in breeding programs (Zaharieva et al., 2001).

A good deal of signaling pathways and genes are involved in plants responsive to drought stress. Drought responsive genes are divided into three different classes:

1. Proteins that are involved in transcriptional regulation and signaling cascades like kinase, phosphatase, and the transcription factors.
2. Proteins that are associated with transportation and uptake of water, and ions like sugar transporters and aquaporins.
3. Functional proteins which protect cell membrane and proteins like osmotin and antioxidant (Bartels and Sunkar, 2005).

Genes that are responsible for drought stress are widely exploited and have been categorized through RNA sequencing and the Affymetrix GeneChip technology (Dugas et al., 2011). Reports suggested that various kinases such as CDPKs (calcium-dependent protein kinases), CIPK (CBL interacting protein kinase), and SnRK2 (sucrose nonfermenting protein-related kinase 2) and MAPKs (mitogen-activated protein kinases) are involved in the drought response (Malone and Oliver, 2011).

Drought tolerance correlates with the positive response of the plant's antioxidant system. According to a study, in drought conditions, reactive oxygen species (ROS) like OH (hydroxyls), H_2O_2 (hydrogen peroxide), SOD (superoxide), and oxygen that is singlet are created (Nezhadahmadi et al., 2013). In wheat, some studies exhibit that wheat genotypes with lower malondialdehyde (MDA) content and high osmotic regulator has enhanced tolerance against drought (Dhanda et al., 2004).

2. Drought tolerance in wheat

Among various types of stresses, drought stress is a kind having significant harm to the plant development and cause yield lose (Deepak et al., 2019). Water is a fundamental constituent of life, and 90% of the weight of plants which are physiologically active comprises water (Bradford and Hsiao, 1982). Thus, water stress is a major issue for wheat growing in almost all wheat growing areas. Ephemeral strategy, or called drought escape, is the mechanism wheat plants adopt owing to the shortage of water (Shavrukov et al., 2017). These phenomena are related to impaired growth as plants utilizing all of its energy for seed production and under the unfavorable environment,

the seed quality is negatively affected (Zampieri et al., 2017). In semiarid areas of high-temperature regions (North and South Africa, Argentina, and Mexico), drought stress occurs in combination with heat stress (Tricker et al., 2016). Drought is not only one of the factors that are responsible for agricultural loss, but it also contributes to soil erosion and ecological damage worldwide (Fang and Xiong, 2015). A large proportion of wheat is cultivated in rainfed areas which often gets a limited amount of rainfall leading to drought. So, during the vegetative and reproductive growth, wheat has to face water deficit. The degree of drought depends upon the amount of rainfall received and the moisture content of the soil. The major challenge for xerophytes as a result of drought is their survival, but in crop plants, the major concern accompanied by the stressed conditions is their yield and productivity. Drought greatly reduces the yield of wheat and has a very major impact on the economy of agriculture-dependent countries. It is estimated that drought accounts for economic loss of up to 50% wheat while it is 10%–20% due to pathogens (Kreps et al., 2002). In the coming years, because of rapid change in climate and increasing demands of food, it is important to develop such varieties of wheat that can use water efficiently and eventually can arise as drought-tolerant varieties (Trenberth et al., 2014). Metabolite-based marker technique is one of the most recent techniques used for the selection of crop varieties with improved water uptake mechanism in drought conditions (Degenkolbe et al., 2013).

The FAO has estimated that by the year 2025, 480 million people in Africa may be living in areas with significant water scarcity and the area which is approximately equal to 600,000 square km, that is currently classified as moderate water-limited, will face a severe level of water deficit (FAO, 2007). This is a particular challenge as wheat occupies a central position due to two major reasons: one reason being, it is a staple food in many countries around the world and the second reason being, farming practices and agricultural policies are mostly dependent upon the cultivation of wheat in many agricultural countries. The contribution of wheat to the world economy is significant. From 15 million hectares of arable land, wheat has a share of 15% that makes the total land utilized for wheat cultivation equal to 225 million hectares as per the figures of 2009 provided by FAO. The production of wheat needs to be doubled by the year 2025 (Highlights of Pakistan Economic Survey 2013–14). The contribution of wheat production to Pakistan's GDP is 4.44% as per the figures of 2013–14 (Fleury et al., 2010).

The *Triticum* species of wheat are important in the current situation, regarding the development of high-yielding cultivars even in water-limited conditions and are a leading source of human food (Tester and Langridge, 2010). An important aspect to consider for the crop plants is to keep them balanced with the increasing demands of human food consumption. In history, to keep pace with increasing demands for human food, high-yielding semidwarf mutants were bred under the revolution called "Green Revolution" (Ashraf et al., 2009). Thus, the main target for drought-related research is to recognize such genes and gene regions which can help in the development of new cultivars to be used in breeding programs and to be cultivated with the aim of a high productivity level. A future approach by (Caspar et al. 2019) is a good way to design drought tolerance. They include the natural progenitors of crops which have lost their drought tolerance, for instance, for the improvement of wheat (*Aegilops tauschii*), which is more drought tolerant than the wild emmer wheat, which has lost its drought tolerance ability with time. Fig. 9.1 highlights general approach to screen and identify tolerant mutant.

The development of crops that are high yielding seems to be an appropriate solution in the current environmental situations, but the nature of drought response and genomic complexity of wheat is a big challenge (Farooq, 2009). The current knowledge about drought-tolerant species and the utilization of biological, functional, molecular, and transgenic technologies have made the drought-related studies easy. In general, the breeding techniques to improve crops against drought tolerance focused on plant parts above the ground (Wachsman et al., 2015) and the information about the phenotype of root architecture in wheat during different seasons is very limited (Djanaguiraman et al., 2019). During drought stress, plants encounter a change in osmotic potential, turgor pressure, and cysteine proteases overexpression (Botha et al., 2017).

3. Cellular mechanisms of drought tolerance

Drought is considered as the major constraint for agricultural development. Plants have several mechanisms to cope with drought stress. They can be categorized into three different groups, which include drought avoidance, drought tolerance, and drought escape. During drought avoidance, plants maintain higher water potential despite the low moisture content in the soil. It is done by maintaining the turgor with roots, which are spread deep in the soil and by controlling transpiration through stomata. In the second one, which is drought tolerance mechanism, turgor is maintained by osmotic adjustment which results in increased elasticity of cell and reduction in its size. In drought escape, plant completes its cycle when there is sufficient supply of water before the drought (Fang and Xiong, 2015).

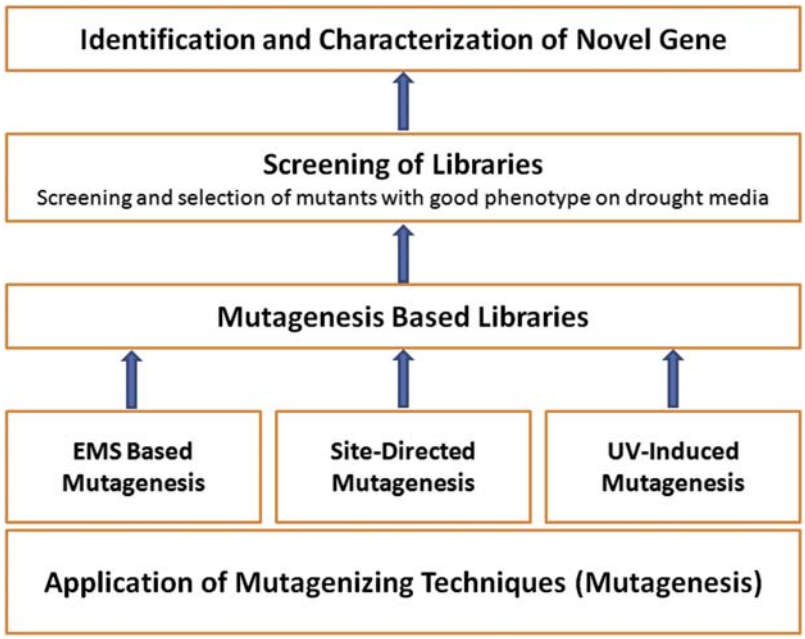

FIGURE 9.1 Strategy to identify drought responsive novel genes.

After sequencing whole wheat genome, remarkable opportunities arose for understanding multifarious architecture of water scarcity tolerance mechanism. Wheat has a complex and large allohexaploid genome (17 Gb) with ~80% of the repetitive elements and projected 124,201 annotated genes (Kulkarni et al., 2017). The study of the cellular mechanism can help in coping with the drought stress. The drought tolerance is a quantitative trait, and key genes can play an important role in mitigating the damage produced by the limitation of the water. Following are the genomic tools which can respond to the drought stress in the wheat; the study of these effects can help in improving the drought stress (Pessarakli, 2014).

It is further studied that various genes are known to be drought influenced and produce various kinds of drought stress–related enzymes and proteins, including the glutathione S-transferase, vacuolar acid invertase, and dehydrins. The production of the proteins like helicase, rubisco, etc. is the molecular basis for the drought tolerance (Fang and Xiong, 2015).

The previous discussion about the plant responses and the traits exhibited during drought by wheat show that drought tolerance is a very complex mechanism. By studying these mechanisms, researchers can pave the way for much advancement in the field of high yielding and economically beneficial agricultural strategies. In a water-limited environment, vessel structure plays an important role in conductance of water (Caringella et al., 2015; Kadam et al., 2015). Different tissues of plants have different hydraulic resistance that affects the transport of water in drought conditions (Bramley et al., 2015). Plants strategies against drought and high-temperature stress are described by (Zandalinas et al. 2018). The cellular mechanisms that wheat exhibits during water stress are enlisted in Table 9.1.

3.1 Leaf senescence

The rate of leaf senescence increases due to drought stress, which leads to remarkable reduction in the grain yield, especially if drought occurs during reproduction (Nawaz et al., 2013). Wheat faces the most deleterious effects of drought during its flowering and grain filling season due to which the yield is being affected significantly (Shamsi et al., 2010). When the functions of the leaves gradually deteriorate, changes in the color of the leaf are observed due to the breakdown of chlorophyll and membranes and water content also reduce with age—this stance is termed as leaf senescence. Chlorosis, leading to loss of photosynthesis, is a vivid sign of leaf senescence. In wheat, during grain development, flag leaf is a source of about 30%–50% assimilates. The genotypes of wheat which sustain flag leaf photosynthesis for prolonged periods produce a comparatively better yield. That is the reason, the advent and extent of senescence of flag leaves is another important indicator of drought and can be used to determine drought resistance in wheat crops. Extreme drought can cause senescence in the whole wheat plant, but it can also increase the

TABLE 9.1 Different geneses involved in response to drought stress.

Main target	Gene	Main effect	References
LEA protein	HVA-1	It has higher root and shoot biomass under the drought than improved and control recovery after the drought stress	(Sivamani et al. 2000)
Membrane protein	TaVAP	Increase in the mild drought stress response in the flag leaf	(Singh et al. 2007)
DREB	DREB1A	The study for 10 days has shown decrease wilting in the transgenic lines	(Pellegrineschi et al. 2004)
Mannitol	mtlD	The experiment was conducted for the time period of a month. The drought transgenic lines had enhanced tiller number, dry weight, and plant height than the control plants	(Abede et al. 2003)
Lipid transfer proteins	TaLTP1	Increasing by stresses of water, i.e., by NaCl treatment, hormone treatment, and PEG concentration	(Jang et al. 2004)

remobilization of stored carbohydrates during preanthesis from the stem and leaves to the developing grains. This can compensate for the loss in yield induced by senescence during drought (Farooq et al., 2014).

Hindrance of senescence is an important way to cope with drought stress. This is done by delaying the expression of senescence and giving the stay green (SG) genotypes, thereby facilitating normal photosynthesis. So, SG is an important adaptive physiological character that helps wheat during drought stress, although its effects on the crop yield are still being researched upon (Budak et al., 2013). (Nagy et al. 2013) carried out a study in which they studied the onset and stage of senescence during water deficit. They aimed to study the regulation of carbon and nitrogen metabolism during drought. The sensitive and tolerant wheat genotypes widely used in agriculture to drought were tested. The amount of total protein content, glutamine synthetase, and rubisco (ribulose bisphosphate carboxylase) was measured.

These were the distinctive traits to indicate the stage and onset of senescence in wheat. Senescence first appeared in older and then in younger leaves. In sensitive varieties, however, drought stress disturbed the sequence of senescence. In the drought-sensitive genotypes, it was observed that senescence first appeared in the flag leaves and then in the older leaves. It was detected that rubisco and protein content decreased while the amount of glutamine synthetase isoenzymes declined considerably in the younger leaves during drought. In drought-tolerant varieties, it was seen that these parameters did not change during drought, but the sequence of senescence was disrupted a little in them in comparison to the plants that possessed sufficient water. The results of their study indicated that glutamine synthetase isoenzymes are good indicators of water stress and can be applied for characterizing wheat cultivars for drought tolerance (Nagy et al., 2013). The study indicates that leaf senescence has a deep relation with water stress, and if carbon and nitrogen metabolism is monitored, progress can be made in the drought-sensitive genotypes of wheat to make them tolerant.

3.2 Photosynthetic response

Photosynthesis is one of the major and primary processes adversely affected by drought stress. Photosynthetic response to drought is a highly complex process which involves different limitations taking place at different sites

of the plant and stages of growth. Drought stress affects the key proteins that play a role in photosynthesis, especially, ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) that results in a reduction of photosynthesis (Perdomo et al., 2017). The rate, duration, and intensity of the stress determine the photosynthetic response. The reason being, these factors decide whether mitigation processes that are associated with acclimation would occur or not. Photosynthesis is either directly or indirectly affected by drought. The direct effect will be if CO_2 availability is decreased due to limited diffusion through stomata and mesophyll tissues or some changes in the photosynthetic metabolism. The indirect effect would be the oxidative stress that is a very major factor affecting the photosynthetic machinery. Acclimation is also an indirect factor affecting photosynthesis, and it includes the shedding of leaves or growth inhibition which will cause less water to be utilized helping the plant to maintain water status and promoting carbon assimilation (Chaves et al., 2009).

In the present day, the physiological traits that are linked to heat tolerance seem to be a superlative accessibility tool because they happen to exhibit the suitable allele combination for drought tolerance too. In a similar context to the effects of drought, photosynthesis can be linked to canopy architecture. An increase in temperature causes decrease in the duration of green area and leaf area index; so studying variations in rapid ground cover and leaf senescence can help in the manipulation of light interception traits. Rapid ground cover shows genotypic variations in simple and heritable breeding targets, for example, specific leaf area, the rate of seedling emergence, embryo size, and grain size. Optimization of the distribution of light can help improve the light interception traits and radiation use efficiency as wheat has a variety of canopy structures. In the modern varieties of wheat cultivars, leaves are smaller in size and more erect which shows that they have improved radiation use efficiency and light interception traits. Improved light interception traits would ensure better photosynthesis in the wheat cultivars and thereby increasing its yield and providing a better quality (Budak et al., 2013). Optimization of light interception traits will further pave the way to bring about improvements to the drought stress. In that case, radiation use efficiency can be manipulated, and phenomenon like photorespiration, dark respiration, and many other photosynthetic strategies can be explored.

In the previous research, it was established that temperature stress fighting traits have a link with the drought-tolerant traits too. So, in that respect, rubisco is an important enzyme that shows low affinity for CO_2 and higher for O_2. In drought-tolerant wheat, rubisco shows an excellent affinity for CO_2. Thus, this property can be utilized for the further development of drought-tolerant varieties (Cossani and Reynolds, 2012). Crops react to drought by closing their stomata, so that further loss of water can be avoided and plants can survive by the water already present in them. This happens due to the plants stress hormones, for instance, abscisic acid, which reduces water loss and makes water use efficiently. In the other condition, oxidative stress will result. Reactive oxygen species will start accumulating, eventually leading to death due to cellular mechanisms like enzyme inhibition, membrane lipid preoxidation, damage of RNA and DNA, and protein degradation (Ishikawa et al., 2010).

In drought-tolerant wheat cultivar; *Triticum durum* L. genotype, ear photosynthesis contributes more than 60% protein synthesis and crop accumulation. In another study, drought-tolerant wheat genotypes have an increased level of antioxidant enzymes. Not only various photosynthetic traits are important in the drought-tolerant genotypes but stress proteins and root system also have a great influence. There was found to be a relation between tolerant genotypes and overexpression of proteins from the thylakoid membranes. Glaidin and Glutenin contents were also observed to have increased in the drought-tolerant genotypes (Aliyev, 2012).

In another study conducted by (Huseynova 2012) certain drought-sensitive and drought-tolerant varieties of wheat were monitored for the changes in the efficiency of photosynthesis. Two durum varieties and two bread wheat cultivars were selected for the study. The durum cultivars were *Barakatli-95* and *Garagylchyg-2* while the bread cultivars were *Azamatli-95* and *Giymatli-2/17*. These were grown under different water availability conditions; normal water availability and water deficit. In the sensitive drought cultivars which were identified to be *Garagylchyg-2* and *Giymatli-2/17*, it was observed that drought inhibited the rate of photosynthesis severely while it was not much affected by the other two drought-tolerant cultivars. As a result of drought, a decline in chlorophyll content and relative water content was easily noticeable, most importantly during morphogenesis. This, as already established, shows that wheat is most affected by drought during the period of anthesis and grain filling. It was also observed that there was a significant increase in the activity of catalase during the drought in the drought-tolerant cultivars as compared to the control plants. Antioxidant enzyme activities were also increased in the drought-tolerant cultivars. Glutathione activity was found to have increased in the drought-tolerant cultivars too. This study shows that drought has a significant effect on the process of photosynthesis, but the drought-tolerant varieties of wheat can cope up with this stress by bringing up changes in their enzymes and their activities. This trait of the drought-tolerant varieties can be exploited to establish even more varieties by identifying the genes involved in the switching on of these mechanisms (Huseynova, 2012).

3.3 Osmotic adjustment

Osmotic adjustment is a very important phenomenon in drought-tolerant wheat genotypes. Plant cells maintain a balance of water, which is called Relative water content. Plants absorb water when the water potential is negative to maintain this balance. The water potential of cells can be decreased by the accumulation of different solutes, sugars, amino acids, proteins, and ions, especially K^+. Cellular enzymes are greatly influenced negatively by the presence of ions so they need to be stored in vacuoles. The solutes which do not cause damage to the cellular enzymes and stay in the cytosol are sugar alcohols (mannitol and sorbitol) and amino acids (glycine betaine and proline). These solutes are called compatible solutes. Due to the synthesis of these compounds, wheat and other crops show tolerance to drought. These solutes lower the water potential, facilitate water absorption, and maintain a balance between intracellular ions.

(Jalal-Ud-Din et al. 2009) accessed drought tolerance in different wheat genotypes and studied water relations with their tolerance mechanisms. They used five commercial varieties which were *Chakwal-97*, *NR-234*, *Inqilab-91*, *Wafaq-2001*, and *Margalla-99*. These were accessed at three cycles of drought in the stages of tillering, preanthesis, and milky growth stages. In their study, they observed that all the varieties showed higher levels of proline during drought stress with *Wafaq-2001* producing the highest amount. In many previous studies, it has been established and according to many researchers, it has been suggested that Proline might be involved in membrane stability during water deficit (Jalal-Ud-Din et al., 2009). The compatible solutes can make an osmotic adjustment and fight ROS which cause oxidative stress. They also make adaptive changes in the metabolic pathways protecting proteins and cellular enzymes. In a study carried out on *Triticum aestivum* leaves, it was observed that the major contributor toward osmotic adjustment was K^+ during the earlier stages of water deficit. The contributors in the later stage were identified to be glycine betaine, glucose, and proline (Nio et al., 2011). Compatible solutes were accessed in *T. aestivum* during the differing regime of irrigation. It was observed that drought decreases inorganic solutes in the plants but increases organic solutes (Loutfy et al., 2012).

(Chorfi and Taibi. 2011) studied the phenomenon of osmotic adjustment in two genotypes of wheat. The study's aim was to check the effect of water stress on different biochemical and physiological pathways in the two varying genotypes of wheat and by studying osmotic adjustment in them, identify their potential for survival and other adaptations during water stress. They observed proline, protein, and sugar accumulation and their transport to the roots and shoot and tried to find if there exists any discrimination between the two genotypes or not. The two genotypes observed were *Oued Zenati* and *Acsad 289*. There was not much difference between drought tolerance strategies, but there was a significant difference in the accumulation and osmoticum synthesis. It was observed that *Oued Zenati* had a higher accumulation of proline, but the other one was able to produce it too and utilize it in drought tolerance. Their research shows that if *Oued Zenati* is oppressed, it can prove as a selection tool of suitable varieties for arid and semiarid regions (Chorfi and Taïbi, 2011).

If polyethylene glycol (PEG) is applied in a hydroponic solution, it will cause osmotic stress (Natalie et al., 2011). (Izabela et al. 2013) carried out a study to determine the responses of different concentrations of PEG on a drought-tolerant *Chinese Spring* (CS) and drought-susceptible (SQ1) seedlings of wheat cultivars. The results of their study could be used in the QTL analysis of drought tolerance trait in the doubled haploid lines derived from these two cultivars. They also observed the biochemical and physiological characterization of traits in the drought-tolerant and drought-susceptible genotypes. The seedlings were grown for 21 days in normal conditions, and then the two genotypes were subjected to osmotic stress induced by varying concentrations of PEG 6000 for 7 days.

Along with other parameters of the leaf, osmotic potential and proline content were measured. The results showed significant differences between the two genotypes. There were increased proline and carbohydrate accumulations in the CS genotype which was drought tolerant. Gas exchange parameters, chlorophyll content, plant height, root length, seedling morphology and relative water content were also significantly affected due to osmotic stress (Izabela et al., 2013). Hence, proving that PEG is an important inducer of osmotic stress but proline accumulation in the drought-tolerant genotypes is an important adaptation and helps in the membrane stability and other factors important for the survival of the plants.

Relative water content, relative water potential, and cell membrane stability have great importance in osmotic adjustment. These were evaluated by Farshadfar (2012) when they studied drought tolerance in Iranian wheat. They found out that these physiological characteristics increase the drought-tolerant genotypes significantly (Hasheminasab et al., 2012). All these findings entail the significance of osmotic adjustment in the drought-tolerant genotypes of wheat and can be exploited to produce similar variations in the drought-sensitive genotypes to make them drought tolerant.

3.4 Antioxidant enzymes and signal transduction

During drought, crops also have to face oxidative stress due to the production of ROS mainly in the chloroplast, peroxisomes, and mitochondria. This is because of the closure of stomata that not only reduces net photosynthesis but also causes a limitation of CO_2. Many researchers found that an increased level of ROS and increased oxidative stress is observed during drought stress. ROS increase due to the decrease in CO_2 fixation, which causes a reduction in the regeneration of $NADP^+$. This causes an overreduction of the electron transport chain and leakage of electrons to oxygen by Mehler reaction. In water-stressed wheat cultivars, Mehler reaction causes 50% increase in ROS as compared to the wheat cultivars that were unstressed. Photorespiration also predominates during water stress, so it is also a very major contributor to ROS production. Photorespiration causes an increase of 70% in hydrogen peroxide accumulation during drought (Choudhury et al., 2013).

ROS induces different signaling pathways which involve hydrogen peroxides (as secondary messenger) like defense or acclimation mechanism. Calcium ions and sugar influx are involved in the downstream and upstream signaling pathways that are abscisic acid-dependent. This pathway is also linked with the origin of ROS. To cope with this oxidative stress, an antioxidant enzyme mechanism exists that fights off the ROS during drought stress. However, if drought stress is prolonged, it might overwhelm the system and lead to cellular damage or death (De Carvalho, 2008).

(Devi et al. 2012) carried out an experiment to study the potential of antioxidant enzymes in determining the drought-tolerance mechanisms in 10 genotypes of wheat cultivars. Out of these, five genotypes were drought-tolerant while five were drought susceptible. They were all grown in normal irrigation and water-deficit conditions induced by 6% mannitol solution. It was observed that the catalase activity was enhanced by 50% in the drought-tolerant genotypes in drought conditions as compared to the ones in a controlled environment. The water stress also caused an increased activity of glutathione reductase and peroxidase in the shoots and ascorbate peroxidase in the endosperms of the drought-tolerant genotypes of wheat seedlings. The activity of superoxide dismutase was not observed to be much affected. It was observed that out of these five enzymes if three were found to be present in some genotype during water deficit, it is likely to be drought-tolerant (Devi et al., 2012).

The study shows that the status of antioxidant enzymes is very helpful in determining the drought-tolerant/drought-susceptible nature of the wheat genotypes. The reason behind this is that superoxide dismutase level was not raised in the drought-tolerant plants, which might be attributed to the fact that superoxide is directly reduced by ascorbate oxidase (Noctor and Foyer, 1998). This research shows that drought-tolerant genotypes can tolerate oxidative stress very efficiently.

ROS are important inducers of stress tolerance during drought and initiate many signaling pathways to transcribe antioxidant enzymes, but they are only effective up to a certain limit. If drought stress increases to a certain limit, ROS will cause serious cellular damage. In contrast to the results mentioned above, (Jalal-Ud-Din et al. 2009) in their study found raised levels of superoxide dismutase (SOD) in the drought-tolerant genotypes. Cell membrane stability index, which is calculated with reference to the tissue damage caused by water stress is a significant source to identify drought-tolerant species. All of the genotypes that they examined had a decrease in the membrane stability index but it was found out that the genotype (Wafaq-2001) had raised levels of SOD and possessed higher membrane stability index as compared to other ones. This showed that SOD is also a very significant antioxidant enzyme which helps the drought-tolerant wheat cultivars to survive the water stress (Jalal-Ud-Din et al., 2009).

A similar study was carried out by (Wang et al. 2010) to find out the role of glycine betaine in drought tolerance. They subjected different genotypes of wheat cultivars to heat and drought stresses. They investigated the introduction of betaine aldehyde dehydrogenase gene into a wild cultivar "Shi4185" line. This gene was taken from garden orache plant. Their results showed that during drought stress, photosynthesis was improved in the transgenic variety of wheat. The reason for improved photosynthesis and water status can be attributed to the accumulation of glycine betaine during drought stress which helped the wheat cultivars to overcome oxidative stress (Wang et al., 2010).

Abscisic acid is also very important in modulating plant responses to drought stress. It regulates the relative water content by oscillations of stomata. It is also involved in inducing the expression of genes important for encoding the proteins that help in drought tolerance. (Bano et al. 2012) studied the role of abscisic acid and antioxidant enzymes in drought-tolerant wheat cultivars. They compared two wheat cultivars and found out the application of drought stress and abscisic acid. The activities were measured after 3 days of application. They observed that abscisic acid caused an increase in superoxide dismutase and peroxidase and also caused an increase in relative water content. Their research showed that abscisic acid is very much important in improving grain weight during a drought in drought-tolerant wheat cultivars (Bano et al., 2012).

3.5 Boiling soluble proteins

The total wheat genome has 0.2% of boiling soluble proteins, also known as BSPs. They play a very important role in coping with stress conditions like drought. These proteins remain soluble on boiling in the aqueous solution. BSPs act as a key component for the survival of the plant in environmental conditions that are not favorable for plants. They possess two distinctive properties that are higher thermal stability and high hydrophobicity (Sharma et al., 2019).

BSPs has an important role in drought tolerance as well. They are significant in helping wheat to cope with drought stress. In a study conducted by (Rakhra et al., 2014), the effect of drought on boiling soluble proteins was studied at two different stages of the wheat life cycle. It was studied at the vegetative phase and reproductive phase in drought-tolerant and drought-susceptible genotypes of *T. aestivum*. High levels of BSPs were observed in the drought-tolerant genotype, while no such rise in their level was observed in the drought-sensitive ones (Rakhra et al., 2014). Drought tolerance occurs through the transcription of certain genes and accumulation of specific proteins as already discussed. This happens through different transcriptional methods (MAP kinases and SOD Kinases) which have their roles in the signaling cascades. Some proteins transcribed have direct roles in the maintenance and protection of cell mechanisms and metabolism such as late embryogenesis, abundant proteins, chaperons, heat shock proteins, and some proteins that are involved in the water uptake and water transport systems including ion transporters and aquaporins. During drought stress, significant qualitative and quantitative changes are observed in all these important proteins. Some of these water stress-responsive proteins are hydrophilic. They remain soluble and highly stable even after a few minutes of boiling. That is why these are called boiling soluble proteins or hydrophilic. Their roles in the osmotic adjustment (already discussed), desiccation tolerance in seeds, membrane stability, stabilization of unfolded proteins, and accumulated ion binding capacity have been suggested (Rakhra et al., 2014).

Aquaporins are important proteins that have roles in the transport of water and other molecules across cell membranes. This is very important for plants to cope with drought stress. The complete role of aquaporins has not yet been quite established, but they have been found to have important roles in combating drought stress by maintaining relative water content, reduction of ROS accumulation, enhancing activities of antioxidant enzymes, and reduction of membrane damage (Zhou et al., 2012).

3.6 Stimulation of root growth

Plants obtain nutrients and water from soil with the help of their roots. Roots play an important role in plant's response toward drought stress. During primary stages of drought, plants tend to increase their root growth in order to absorb water that is deep in soil. Reports suggested that volume, length, density, and weight of roots are connected with resistance of water scarcity in crops (Hammer et al., 2009).

In arid areas, seedlings of woody plants develop vertical roots that are 10 times larger in size as compared to its above ground height. This widespread and deep rooting system enables plant to maintain higher potential of water in drought conditions. During drought conditions, plants adapt and modify their root architecture system. This is a diverse phenomenon that varies from specie to specie. Another factor that effect root growth is the nutrient status or water of aerial part of plant. Roots to shoots ratio is also detected under drought conditions. Previously, root/shoot ratio was used as a standard to describe the capacity of plant for the resistance against drought (Price et al., 2002).

The architecture of the root system is very important in combating drought stress. The root structure and root biomass define the pattern for water extraction from the soil (Prasad et al., 2018). The root system grows fast in the normal availability of water (Penny et al., 2018). Good root architecture makes sure that wheat extracts maximum soil water from soil under drought stress, improving the grain yield and quality (Dodd et al., 2011; Zhou et al., 2018). In maize crop, steep, cheap, and deep (SCD) ideotype is responsible for making it tolerant against the drought stress (Zhan et al., 2015). Many properties of this ideotype may also play a role in wheat against drought stress (Djanaguiraman et al., 2019). Although it has been well established that a deep and extended root system ensures that the wheat genotypes show tolerance to drought, but it may not always contribute toward an increased yield. (Palta et al. 2011) suggested that increased yield would depend upon the pattern of water stress in that specific environment (Paltaet al., 2011). However, wheat genotypes with an extended, deeper, dense, and high radial hydraulic conductivity show an increased yield and tolerance to drought stresses. (Wasson et al. 2011) also worked upon the same concept and came up with designing a breeding program in comparatively dry areas of India and Australia, although it could be used in other environments too. In that breeding program, genotypes with improved root systems could be used for increasing yield because they can make use of the deep-lying water which is more predictable as compared to variable seasonal rainfall (Wasson et al., 2011).

Even though improved root architecture is an important trait of drought-tolerant genotypes of wheat and it is a good indicator to select the drought-tolerant genotypes, there are no direct methods to identify it in the field. Much of the screening for tolerant genotypes is done in young seedlings or in vitro (in an artificial media) due to which there is a limitation to the inference of crops grown in the field (Nakhforoosh et al., 2013). Furthermore, the fibrous root system, which has fine and fragile lateral root network is not very detectable with commutated X-ray tomography imaging and cannot be recovered for measurement (Flavel et al., 2012). (Huang et al. 2013) suggested that these limitations could be overcome by doing measurements of root DNA, which will help in root phenotyping. This will have an advantage that there will be no need to extract leaves from the soil, and phenotyping could be done at a large scale (Huang et al., 2013).

4. Conclusion

Drought affects agronomic traits in wheat and rice crops differently (Zhang et al., 2018) because wheat adapts to water deficiency by osmotic adjustments and recovery after the stress in a better way (Daryanto et al., 2017). Drought tolerance is a quantitative trait with complex phenotyping (Fleury et al., 2010). Tolerant genotypes of wheat display some morphological, physiological, molecular, and biochemical pathways and traits. From recent studies, it is a widely shared opinion that breeding of crops tolerant to drought stress is not easy to achieve (Stanisław et al.,2019). Drought is also a reason for the reduction of total chlorophyll content (Hailemichael et al., 2016). Wheat is a very important cereal crop and is food for about 1/5th of the world population. The changes accompanied by a drought in the wheat cultivars and the mechanisms of coping with them can be manipulated and exploited to save losses in the yield and quality of wheat cultivars during wheat. There is much research going on in the area, and efforts are being made in developing new and improved genotypes. Cellular and physiological mechanisms in this regard occupy a very important spot. They are not only important indicators to identify drought-tolerant genotypes but are also being utilized in breeding programs to come up with strategies to screen drought-tolerant genotypes. Transgenic cultivars are another important option to make improvements in the current situation of agricultural practices which can prove as a revolution to fulfill the increasing food demands of the rapidly growing population of the world.

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CHAPTER

10

Drought-responsive ESTs in wheat

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OUTLINE

1. Introduction

Plants respond to various environmental pressures via adaptive approaches that are encoded by the genes in the plant genome (Isokpehi et al., 2011). The stimulation of a biotic or abiotic stress causes such genes to produce proteins in response to the strain (Isokpehi et al., 2011). Drought is an environmental stress that generates responses

toward water deficit (Isokpehi et al., 2011). Bioinformatics approaches serve as a great tool for identification of underlying molecular basis of universal stress proteins (USPs) (Isokpehi et al., 2011). Expressed sequence tags (ESTs) oblige as a new mode for the production of simple sequence repeats (SSRs) within the class of molecular markers (Kayesh et al., 2014). SSRs are the functional markers that fulfill the requirement of genetic mapping (Kayesh et al., 2014). Furthermore, the cDNA libraries also serve to be the source of ESTs and SSRs data integration having "CAG" as SSR sequence type has recognized drought-responsive ESTs in bread wheat (Isokpehi et al., 2011).

2. Wheat and drought stress

2.1 Introduction to drought stress

Drought is an abiotic, complex polygenic stress (Senapati et al., 2019), and it is the critical factor for arresting plant's growth and development specially of wheat cultivated in arid areas (Kilic and Yagbasanlar, 2010). Thus, in an arid and semiarid environment where a shortage of rainfall can lead to the scarcity of water if the duration lasts long it can result in drought stress causing severe yield losses (Senapati et al., 2019). The loss in the yield of plants due to drought is probably more than other roots; thus, affecting growth, development, and yield of the crop (Tietjen et al., 2017; Prasad et al., 2011). Moreover, the severity and time of stress are crucial (Farooq et al., 2009).

It is expected that drought stress will become the foremost issue for plant growth and yield reduction in the upcoming years because of global warming (Fahad et al., 2017; An and Liang, 2012). Zones that are under drought stress are severely affected by UV-B radiations of wavelength 280−315 nm (Bandurska et al., 2013). Also, various metabolic and physiological pathways are adapted by the plants to escape through drought stress (Budak et al., 2013). Drought responsiveness is a polygenic trait that is influenced by various ecological settings (Budak et al., 2013). Genetic identification and manipulation proceeds only when responses are acknowledged under highly stress circumstances (Budak et al., 2013; Nezhadahmadi et al., 2013). The fabrication of drought-tolerant genotypes entails numerous gene mapping and other molecular marker−associated approaches (Budak et al., 2013; Nezhadahmadi et al., 2013).

Under the condition of drought stress, wheat produces various enzymes through the activation of stress-tolerant genes (Budak et al., 2013). Drought stress impacts wheat crop through variations in response to water uptake (Budak et al., 2013). Stomatal closure leading to decrease in carbon dioxide diffusion to chloroplast results in the reduced rate of photosynthesis as you can see in Fig. 10.1. In addition to it, drought responses lead to increased aging of leaf; loss of chlorophyll; cell shrinkage due to solute loss; leaf yellowing; decreased size, number, and longevity of the leaf (Shah et al., 2018). Also, the rate of development increases with an increase in the rate of maturation of grains and ears. Membrane integrity is lost in the meantime, due to the production of reactive oxygen species during

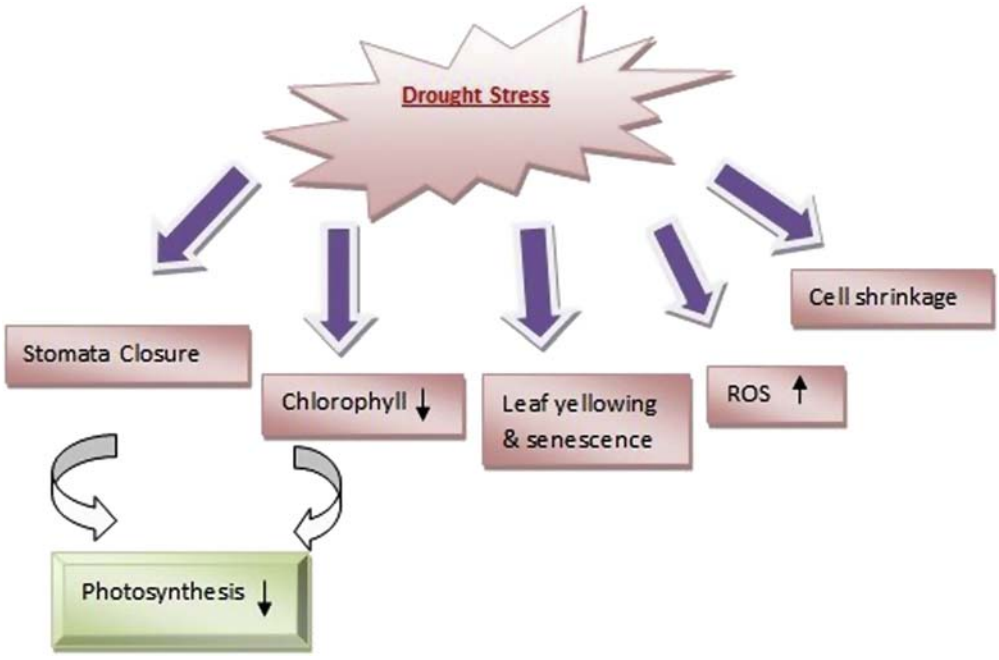

FIGURE 10.1 Effects produced by drought stress (Beltrano and Ronco, 2008; Valentovic et al., 2006; Siddique et al., 2000).

drought stress (Nagahatenna et al., 2015; Beltrano and Ronco, 2008; Valentovic et al., 2006). During or after the onset of anthesis, drought causes severe stress in comparison to that caused during vegetative growth (Beltrano and Ronco, 2008). Leaf water content and relative water content decrease resulting in increased canopy temperature, thus decreasing photosynthesis (Siddique et al., 2000).

The proceeding opted by scientists for drought tolerance measurement is membrane integration under water tension (Budak et al., 2013). This variation in reaction to drought stress corresponds to photosynthesis reticence, reduction in transpiration rate and chlorophyll, and an ultimate decrease in plant growth (Budak et al., 2013; Nezhadahmadi et al., 2013). Shoot and root elongation required for nutrient and water uptake is greatly disturbed under drought stress that results in plant growth reduction (Nezhadahmadi et al., 2013). Drought stress causes the plant endosperm to reduce its cellular number and metabolic activities through a decline in crop's sink force (Budak et al., 2013). Water stresses affect the growth of plants as well as alter the development of the wheat crop (Guttieri et al., 2001). The response of the plant to the drought stress is based on several factors like the genomic makeup of cultivar, the duration of stress, severity, and developmental stage (Beltrano and Ronco, 2008). The food consumption by increasing world population is estimated to double by 2025, but the loss of yield due to drought stress is likely to exacerbate in the coming future as world's water is a limiting factor (Somerville and Briscoe, 2001).

2.2 Mechanism of drought responsiveness in wheat

Hormonal concentration imbalance and alteration in pH is also an important consequence of drought stress on plants. During such stresses, concentration of abscisic acid rises and pH along with the conductivity of xylem decreases. Also, spikelet fertility, yield, and the number of grains decrease (Prasad et al., 2011).

Analysis has been performed on wheat seedlings for the identification of gene expression (Budak et al., 2013). This has provided with the conclusion that the junction period that is a connection point between the vegetative and reproductive phase of the wheat crop is actually drought vulnerable (Budak et al., 2013). The heat stress−tolerant enzymes include lea, Rab, rubisco, proline, GST, and helicase (Budak et al., 2013). The two important enzymes produced in response to drought stress are proline and rubisco designed in photosystem II and Calvin cycle, respectively (Budak et al., 2013). Overexpression of LEA proteins in answer to drought stress protects the vegetative tissues of the wheat crop (Budak et al., 2013). The size of LEA proteins in wheat significantly enlarges to cope with the drought stress (Budak et al., 2013). Dehydrin accumulates in the wheat plant under settings of drought stress to cause desiccation (Hassan et al., 2015). This capacity of dehydrin is attributed for triggering vital protective functions of the wheat plant (Hassan et al., 2015). One of the important roles performed by dehydrin is their antioxidative commotion (Hassan et al., 2015; Hu and Xiong, 2014).

2.3 Yield and drought responsiveness

The major factor responsible for the reduction of crop yield is drought (Hu and Xiong, 2014; Budak et al., 2013; Guo et al., 2013; Nezhadahmadi et al., 2013). The two main processes that contribute toward crop yield are growth and photosynthesis, both of which are badly affected by drought stress (Almeselmani et al., 2011). This feature of crop plants contributes toward the ultimate reduction of yield (Almeselmani et al., 2011). The only cure left with the plant breeders is the production of drought-tolerant plants (Mwadzingeni et al., 2016; Almeselmani et al., 2011). The two accepted drought-tolerant wheat varieties Zam-4 and Hashim-8 provided with good yield as compared to other non−drought-tolerant varieties (Khakwani et al., 2012). These two recognized varieties are recommended to be planted in rainfed areas in order to attain better yield (Khakwani et al., 2012).

3. ESTs introduction, their production, and uses

3.1 Introduction to ESTs

Single sequence reactions are responsible for the production of ESTs that are the fragments of mRNA retrieved from cDNA libraries via randomly selected replicas. ESTs are short fragments and represent only a portion or a small part of a gene, not the whole coding sequence. EST can be regarded as a small part of the active part of gene made from cDNA, thus making it possible to locate the useless or nontranscribing part of a gene. ESTs are short (200−800 nucleotide bases in length), unedited, randomly selected single-pass sequence reads derived from cDNA libraries (Nagaraj et al., 2007).

3.2 Method of their production

A messenger RNA is a representative of expressed genes (Nagaraj et al., 2007). However, RNA cannot be cloned directly. Therefore, it has to be converted into double-stranded cDNA by reverse transcription of RNA using the enzyme reverse transcriptase (Nagaraj et al., 2007). After this process, several copies of cDNA are developed to form libraries corresponding to the expressing parts of the relative gene, tissue, or organisms. Individual cloneshaving 5′ and 3′ ESTs associated with it are picked from the library; one sequence is generated from each end of the cDNA insert (Baxevanis and Ouellette, 2004) (Fig. 10.2).

3.3 Application of ESTs

ESTs have a wide range of applications. They provide an alternative to full-length cDNA sequencing. Also, ESTs are an inexpensive means of gene discovery. The randomly sequenced ESTs allow us to make gene discovery as they give information of the transcribed regions of the gene. After gene discovery, a scientist can make use of ESTs in allele identification, thus providing specific knowledge about the gene. They have applications in the fields of phylogenetics by allowing us to determine the evolutionary relationship between organisms with the help of various EST databases. ESTs are also applied in transcriptome profiling that is the collection of all the three types of RNAs along with the noncoding RNAs (Blackstock and Weir, 1999).

ESTs have major applications in proteomics that is the functional genomics where the proteome being expressed is the protein complement of a genome. So, once we have ESTs for a genome, we can know the proteins it is producing. Furthermore, they can also provide regions coding for potentially new proteins (Wu et al., 2002).

ESTs can be used to understand the details of a genome including chromosomal composition, organization, and structure (Wu et al., 2002). ESTs can also be used for the construction of genetic maps. Also, ESTs can be used as probes in several microarray experiments. They can also be employed in the study of single nucleotide polymorphism to detect variations in a specific population (Lindlof, 2003).

4. Wheat ESTs data

Wheat is one of the important staple food crops all around the globe. Wheat was cultivated approximately 8000 years ago by hybridizing tetraploid emmer wheat (*Triticum dicoccoides*) with diploid goat grass (*Aegilops tauschii*)

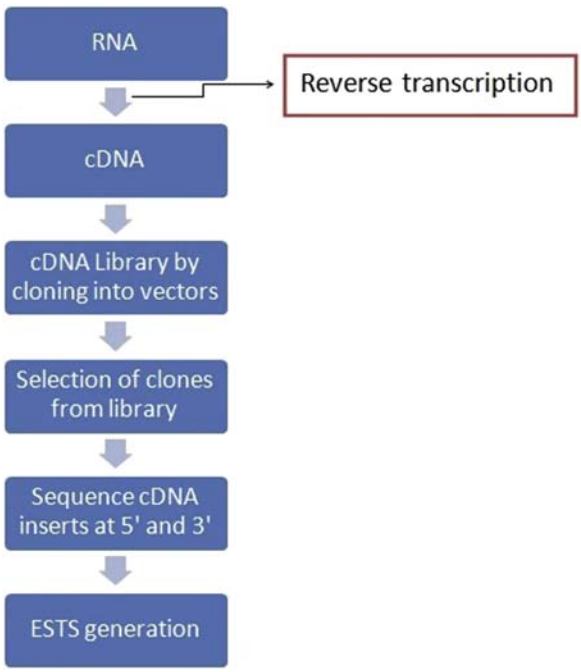

FIGURE 10.2 Production of expressed sequence tags.

(O'Neill and Jenner, 2012). The three wheat genomes originated many million years ago are named as A, B, and D genomes. A genome originates from *Triticum uratu* and D from *A. tauschii*, whereas the origin of B genome is not completely known (it may be from *Aegilops. speltoides*) (Dvorak et al., 2006; Salse et al., 2008). The B genome of wheat has gone rapid genetic rearrangements under polyploid conditions (Levy and Feldman, 2004).

4.1 Identifying ESTs in wheat

Identifying the EST data in wheat will give us knowledge about the improvement of this exceedingly important crop and the expressed component of the wheat genome. However, till date there is no method yet established for the identification of all the genes in the wheat genome even by using ESTs. It is estimated that an extensive EST program will hit approximately 30,000 to 50,000 genes in the wheat genome.

4.2 International Triticeae mapping initiative—ITEM and international Triticeae EST cooperative (ITEC)

ITEM was founded in 1989 to establish genetic maps for wheat and its relative plants. In the summer of 1998, ITEM created ITEC to initiate a global research on wheat ESTs. The success achieved can be evaluated by the statistic that we now have 1,858,577 ESTs for the Triticeae family with the highest number developed for wheat, i.e., 1,286,998 (January 1, 2013, data).

4.3 Wheat ESTs project

To achieve these goals and other long-term specific objectives, many projects have been initiated as you can see in Table 10.1. We review the findings of a very recent project (June 20, 2014) (Anderson et al., 2011) which assessed the genome of wheat on a large scale using ESTs.

4.4 Wheat ESTs specific to abiotic stress

278 ESTs in wheat have been identified as abiotic stress (salinity, drought, cold and heat) specific. ESTs from 811 loci were assigned to chromosome deletion bins among all the seven wheat chromosomes. The abiotic stress-specific

TABLE 10.1 Chronological development of wheat expressed sequence tags (ESTs) data.

Year	Achievement
2000	24,346 ESTs generated.
2001	300,000 ESTs were to be made publicly available, but the goal was not achieved.
2002	154,485 and 129,238 wheat ESTs were generated at DuPont and Japan, respectively.
2003	7000 wheat ESTs probes were mapped.
2004	1,00,000 Triticeae ESTs were developed. On wheat chromosome no 4; 1918 loci were detected by the hybridization of 938 ESTs. • 786 loci were mapped to chromosome 4A. • 529 to chromosome 4B. • 603 to chromosome 4D (Ross et al., 2004). Plan for developing Wheat Affymetrix chip was initiated. Genetic volume 168 described the mapping of ESTs to the wheat genome.
2005	A model system for the study of the wheat genome was developed. Corn takes the lead over wheat in dbEST count.
2006	Wheat achieves a notable increase in dbEST count (April 2006). Rice and maize get on the top of EST count having over 1,100,000 ESTs each, while wheat having 855,000 (September 2006).
2008	ESTs were submitted to Genbank by C. Tobias laboratory.
2009	EST libraries were constructed at Canada.
2012	ESTs were made available to the public. We now have 1,858,577 public ESTs for the Triticeae family with wheat having 1,286,998.

ESTs are not uniformly distributed in all the three genomes, e.g., the short and long arms of chromosome 4 have more loci in their distal regions. The number of loci mapped on different wheat genomes is as below (Ramalingam et al., 2006).

- Genome A has 258 mapped loci.
- Genome B has 281 mapped loci. (B genome also has the highest number of unique ESTs at seven loci.)
- Genome C has 272 mapped loci. (No unique EST loci were reported.)

Regarding chromosomes, homologous chromosome 2 had the highest number of EST loci (142 loci), and homologous chromosome 6 had the lowest number of EST loci (94 loci). The function of the mapped ESTs was linked to cell growth and metabolism, whereas most of the ESTs were associated to enzyme function (enzymes involved particularly in triggering response to abiotic stress such as beta-galactosidase, peroxidase, glutathione reductase, trehalose-6-phosphate synthase) and binding. There is a complex colinearity found between genomic sequences of rice and stress-responsive wheat ESTs.

5. Drought-responsive ESTs in wheat

5.1 Details about drought-responsive ESTs (genes) in wheat

ESTs are markers that can give an idea about the functionality of a gene too. So, details about the drought-responsive ESTs would correspond to the details of the genes, linked to these ESTs, whose functions or activity play a vital role in drought response in wheat (Nagaraj et al., 2007). As explained earlier, there are approximately 259 ESTs derived from 22 different cDNA libraries mapped to different abiotic stresses in wheat (Ramalingam et al., 2006). Out of this vast library of ESTs, some ESTs are linked to several genes that are somehow involved in drought response. Furthermore, these genes are believed to be linked with drought stress and produce several compounds under the conditions of drought tolerance. These include some enzymes and proteins like dehydrins (Close, 1996), vacuolar acid invertase (Trouverie et al., 2003), glutathione S-transferase (GST) (Anderson and Davis, 2004), and late embryo abundant (LEA) protein (Pnueli et al., 2002). Also, to that ESTs may also be used to count for the difference of drought tolerance in hexaploid wheat and tetraploid wheat. The difference is because of varying concentrations of nonhydraulic root signals (nHRSs) and hydraulic root signals (HRSs) (Engelbrecht and Kursar, 2003). Also, to that, over 13,000 ESTs have been obtained from two different genotypes of the wheat. Wild emmer wheat genotypes TR39477 (tolerant) and TTD-22 (sensitive) were obtained by the screening of 200 wild emmer wheat, and the ESTs obtained have shown that genotypes have a common share of elements of drought stress but with distinctly differential expression patterns, which explains their contrasting abilities to tolerate water stress (Ergen and Budak, 2009).

5.2 Mechanism of action of the genes linked to these ESTs

There are several genes that are involved in drought responses in wheat. Some of them are HVAI gene (Sivamani et al., 2000), PMA1959, and PMA80 (Cheng et al., 2002); these three genes encode for type 1, type 2, and type 3 types of LEA proteins, respectively. Also, to that, there is another gene that encodes for the production of proline (Gubiš et al., 2007). Another EST is linked to the gene V-PPase gene that codes for vacuolar H+ transporting pyrophosphatase enzyme. This enzyme has also been studied for development and abiotic stresses (Wang et al., 2009). The nHRS refers to an adaptive strategy to protect plants from damage under stress, and HRS involves the synthesis of chemical material by roots under droughtlike ABA. As the threshold of hexaploid wheat is greater as compared to that of tetraploid wheat, so in the case of hexaploid wheat, there is a more rapid and efficient production of nHRS and HRS, and so hexaploid wheat shows a better drought tolerance as compared to tetraploid wheat (Xiong et al., 2006).

5.3 Effects produced by their action

The plants respond to the drought stress by the initiation of signal transduction cascades that result in the reprogramming of transcription due to the release of various transcription factors and regulators. These transcriptional changes allow the plant to survive in drought condition (Bartels and Sunkar, 2005). These transcriptional changes activate the USPs, ubiquitination, and proteasome components because it leads to the production of new proteins

and degradation of existing ones that are not required in this new environment (Mahajan and Tuteja, 2005). Moreover, the genes discussed above have been studied for the effects they produce; the HVAI genes produce an enzyme belonging to type 3 LEA protein family that assists wheat growth under stress conditions (Sivamani et al., 2000). The PMA1959 and PMA80 produce proteins that have been shown to provide improved resistance to water deficiency (Cheng et al., 2002). Proline was also investigated as drought defense amino acid of wheat (Hong-Bo et al., 2006). The vacuolar H^+ transporting pyrophosphatase enzyme encoded by the V-PPase gene was linked with water stress in wheat (Kam et al., 2007).

6. Conclusion

Drought is recognized as a severe abiotic stress to crop plants. It can alter the metabolic pathways leading to critical changes. Wheat is a major crop and staple food in many countries, the yield of wheat decreases in moisture-deficit environment, so the phenomenon of drought tolerance in wheat is of considerable significance. Enzymes linked to stress tolerance in wheat include lea, Rab, Rubisco, proline, GST, and helicase. ESTs play a vital role in helping develop this understanding. To identify wheat ESTs, an extensive project by ITEM was started that lead to the discovery of 1,286,998 ESTs. Some particular drought-responsive genes in wheat identified through ESTs include HVA1 gene, PMA1959, PMA80, VPase. There still lies a great potential to discover EST-linked drought genes. The International Committee developed with this goal is constantly searching on new ways to accelerate the discovery; however, the large wheat genome is a challenge in this way. It is estimated that discovering all of the drought-responsive ESTs in wheat will take many more years.

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CHAPTER

11

Role of transcription factors in drought mediating pathways in wheat

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OUTLINE

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00011-X

1. Introduction

Homeostasis is one of the important biological processes in which the internal environmental conditions of the living organisms are maintained to a steady state. Disturbing homeostasis by any of the environmental factor turns a plant into a state of stressed and consequences into disrupting of various ongoing life-associated metabolic processes. Thus, stress is a perturbance during the normal growth behaviors of the plants and results in various triggered biological responses as a strategy known as survival of the fittest. Stress conditions are categorized into two groups: biotic stress and abiotic stress. Biotic stress is developed by certain biotic or living factors, while abiotic stress is caused by nonliving environmental factors.

Crops production in the world is hampered by significant and detrimental effects of both biotic and abiotic stress conditions. However, abiotic stress conditions are the major environmental constraints for the grain yield production of the cereal crops and are mostly concerned with various abiotic environmental factors such as temperature, light, and water. The balance of intensity and levels of such abiotic factors is adversely affected by global climate changes and leads to various stress conditions such as heat stress (high temperature), cold stress (low temperature), and drought stress (low precipitation). Furthermore, global climate changes and depletion of the ozone layer as a result of greenhouse gases and production of chlorofluorocarbons are drastic and alarming conditions for the existence of life on the earth and likely to increase in the future.

Wheat (*Triticum aestivum* L.) crop was cultivated on 218.3 million hectares of the world and yielded 761.9 million tons of the grains during 2017−18 (USDA, 2019). This crop is an excellent source of food and various health-promoting nutritional compounds such as proteins, dietary fibers, B-group vitamins, and minerals (Ahmad et al., 2018). Abiotic stresses such as drought, salinity, heat, cold, and waterlogging result into more than 50% of the grain yield losses among very important cereal crops (Wang et al., 2003). Such abiotic stress conditions are major threats to the wheat grain yield in various regions of the world (Zhang et al., 2016).

Several regions of the world are rainfed, where cultivation of food crops as a source of food for nutritional purposes is a major and critical issue due to drought conditions. Hence, drought is one of the major abiotic stresses that affect at least 32% wheat production in the low-income developing countries accounting 99 million hectares and up to 60% of wheat production in developed high-income countries (Chen et al., 2012). Latest estimates show that almost 820 million peoples of the world were exposed to the hunger accounting one in every nine peoples during 2018 (FAO, 2019). Meanwhile, population of the world is assumed to be doubled within the coming 50 years, hence grain yield increase of the agricultural commodities is one of the critical issues (Chaves and Davies, 2010). Developing the cereal crop varieties including wheat bestowed with tolerance against stress conditions including drought stress is one of the fundamental needs and prime objective of the plant breeding programs.

Plants exposed to water limited conditions, face extreme troubles in getting the moisture from rhizosphere to perform their normal biological processes. Besides, severity and duration of the drought are also correlated with other environmental factors such as heat and cold. Drought stress alters phenotypic, biochemical, and physiological behaviors of the plants and leads to severe grain yield losses (Maheswari et al., 2016) and tends to cease the primary metabolisms and other basic physiological processes necessary for plant's growth and survival, which ultimately results in yield losses; a major threat to plant productivity (Farooq et al., 2009).

Stress tolerance is a polygenic trait and controlled by the expression of the various stress responding genes. During inheritance, all the cells receive the complete set of the genes; however, cells differ due their genes expressions. Many genes are either turned on for expressions or turned off and remain inactive under specific internal and external environmental conditions. Activity of such gene expressions is controlled by various gene expression controlling mechanisms, which determines the type and ratio of the genes to be transcribed.

Transcriptional control is one of the gene expression controlling mechanisms, where, transcription of a certain gene is initiated in the presence of various types of transcriptional factors. Transcriptional factors are the proteins regulating the gene expression and attach to specific binding sites of the discrete DNA fragments called RNA polymerase II promoters during transcription and such a way mediate the essential life processes such as differentiation of cells, organization of tissues and organs, responses to the environmental factors and hormones, resistance to diseases and metabolic networks (Gonzalez, 2016). Fig. 11.1 shows the network of transcriptional factors, which are activated in the plants under drought stress conditions. There are two categories of genes, which respond under stress conditions: (1) group of regulatory genes that code for receptors, protein kinase, proteins, transcriptional factors; regulate degradation and detoxification of proteins; facilitate in the pathways for stress response signal transduction by altering the expression levels of stress-responsive genes along the downstream and (2) group of genes responsible

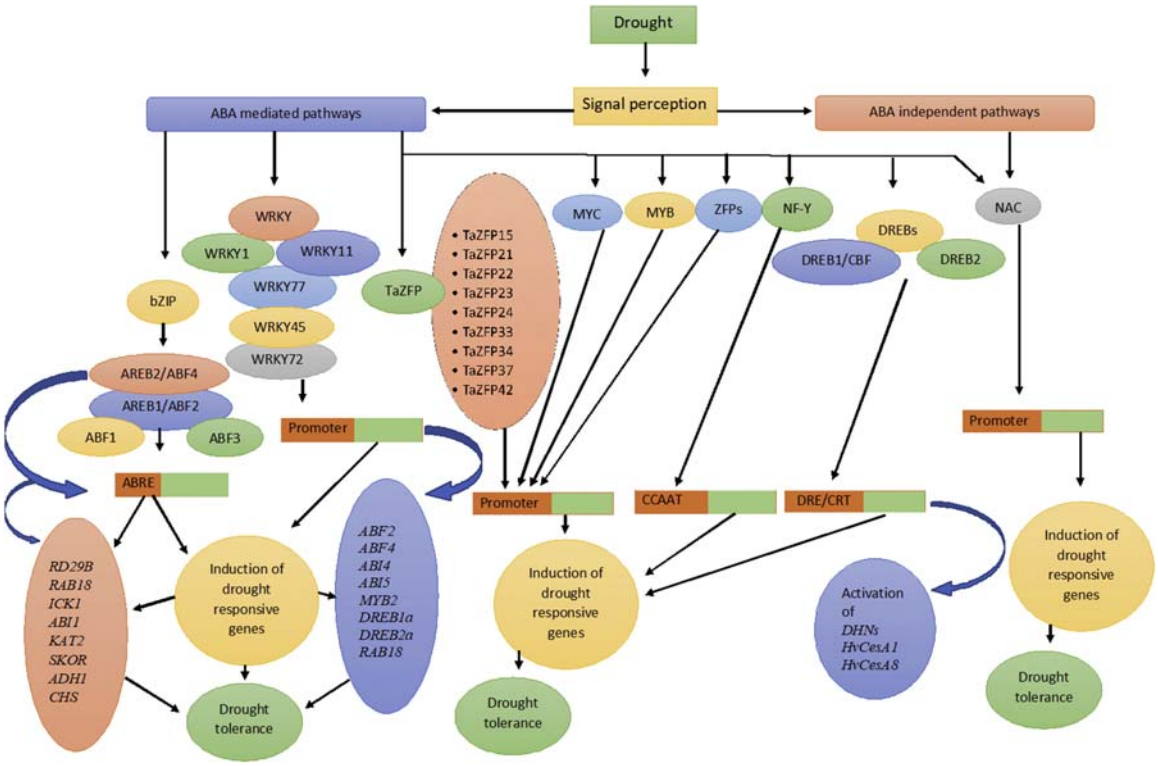


FIGURE 11.1 Network of transcriptional factors activated under drought stress conditions.

for plant recovery under stress conditions and coding for proteins involved in the functions such as redox regulation, osmolytes production, and ubiquitination (Herath, 2018).

In this chapter, variability, responses, and changes in the plants under drought stress conditions at biochemical, morphological, and molecular levels are discussed mainly focusing the transcriptional control network in the wheat plants.

2. Plant responses and drought effects

Drought confers divergent effects in the plant's normal metabolic and physiological functions. Several ways are adapted by the plants including wheat to circumvent the drought stress bottlenecks:

1. Impaired germination (Harris et al., 2002; Almaghrabi, 2012).
2. Reduced growth due to reduction in turgor pressure (Taiz and Zeiger, 2006)
3. Reduced height due to impaired cell elongation (Kaya et al., 2006; Hussain et al., 2008).
4. Decrease in water potential, relative water content, and transpiration rate of leaves (Siddique et al., 2001; Moayedi et al., 2010; Nawaz et al., 2014).
5. Lowered uptake of inorganic nutrients and reduced transpirational flow (Garg, 2003; Ahmad et al., 2018).
6. Reduction in photosynthesis due to decrease in leaf expansion, impaired physiology, premature leaf senescence, and less CO_2 uptake (Wahid and Rasul, 2005; Prasad et al., 2011; Fotovat et al., 2007; Mir et al., 2012).
7. Limited root respiration and biomass to improve growth and physiological activities of plant undergoing drought conditions (Huang and Fu, 2000).
8. Generation of reactive oxygen species (ROS), which include superoxide anion radicals, hydrogen peroxides, hydroxyl radicals, and singlet oxygen (Munné-Bosch and Penuelas, 2003). ROS reacts with lipids and proteins causing oxidative damage, thus impairing cell's normal physiological function (Foyer and Fletcher, 2001).
9. Shortening of the life cycle or growing season is a phenomenon known as drought escape. This approach enables the plant to reproduce before the environmental conditions become water deficit (Araus et al., 2002; Blum, 2010).
10. Control of transpiration through stomata and maintenance of water uptake by the extensive root system, this mechanism is called drought avoidance (Turner et al., 2001; Kavar et al., 2007).

11. Limitation of the number and area of leaves to cut down the water consumption. This is referred to as phenotypic flexibility (Schuppler et al., 1998).
12. Osmotic adjustment through osmoprotectants allows the plant cell to decrease the osmotic potential. As a result, the gradient for water influx increases to maintain turgor (Kramer and Boyer, 1995). Osmolytes also known as osmoprotectants, e.g., raffinose and galactinol, protect macromolecules by stabilizing their tertiary structures or by removing ROS produced as a response to drought (Mahajan and Narendra, 2005).
13. Maintenance and stability of plant's cell membrane, as the stability index of cell membrane is widely used for the evaluation of drought tolerance (Bajji et al., 2002).
14. Drought rhizogenesis, i.e., the formation of short, tuberized, hairless roots. These roots can withstand in a long drought period (Vartanian et al., 1994).
15. Plant produces abscisic acid (ABA) that tends the stomata to close to reduce water loss and plants protection. ABA is a growth inhibitor phytohormone (Morgan, 1990).
16. Synthesis of different types of stress proteins and TFs responsible for signaling of major pathways involved in drought stress, e.g., DREBs (Taiz and Zeiger, 2006).
17. Modulation of the activities of enzymes responsible for protection against oxidative damage caused by ROS (under drought condition). These enzymes include superoxide dismutase, peroxidase, ascorbate peroxidase, glutathione reductase, catalase, etc. (Liebler et al., 1986; Allen, 1995; Sairam and Saxena, 2000).
18. DREB1 and DREB2 are two important TFs that are responsible for ABA-independent drought-tolerant pathways. These cause the stress response genes to start expression under drought stress conditions. Their overexpression is being used in genetic engineering to obtain drought-tolerant plants.
19. Plants regulate genes that are involved in the perception of drought stress and then regulate mechanisms that protect plants from desiccation.

3. Osmoprotection

Osmotic adjustment in terms of water potential (Ψ_w) and solute or osmotic (Ψ_s) potential is essential for the survival of plants. Under drought stress conditions, water potential (Ψ_w) around rhizosphere drops below the water potential (Ψ_w) inside the cells. Consequently, plants increase their osmotic potential (Ψ_s) by synthesizing osmolytes and decrease the water potential (Ψ_w) inside their root hair cells as compared to the outside water potential (Ψ_w) in order to drive water from outside to the inside. The osmotic potential (Ψ_s) inside cells is lowered by the increased concentration of osmolytes in the cytoplasm. Osmolytes production confers tolerance to the cells against cellular dehydration and drought stress by adding membrane stability and dehydration management (Loutfy et al., 2012). The genes responsible for the synthesis of these molecules have been shown to be induced by water deficiency (Bray, 1993). Common osmolytes include proline, glycine betaine (GB), sucrose, pinitol, and aldolase. Studies have shown that proline and GB have a role in maintaining the stability of membrane and enzymes and provide the plant with adaptability during water deficit (Ashraf and Foolad, 2007).

4. Transcellular water transport

Osmotic balance through proper water conductance is critical to the plant during drought stress conditions (Ramanjulu and Bartels, 2002). Transportation of water across and inside the plants takes place in three different ways: apoplast (water moves along cell walls without entering the cytoplasm); symplast, water transport from cytoplasm of one cell to other through plasmodesmata; and transcellular path, water travels across the cell membrane (Steudle and Peterson, 1998). Intracellular water transport pathway is under the control of concentration and activity of aquaporins, which are major intrinsic channel proteins responsible for transporting water across membrane of the cells (Chaumont and Tyerman, 2014). Aquaporins can modify the water transportation potential of a membrane and increase water permeability by 10–20 folds (Maurel, 2001). Water uptake and hydraulic conductivity in wheat plant roots are highly affected by aquaporins (Bramley et al., 2007). Aquaporins are composed of six membrane-spanning α-helices joined by five (A–E) loops, where C and N terminals face toward the cytosol (Chaumont and Tyerman, 2014). Aquaporin genes are selectively expressed in response to external and internal stress signal perception (Kaldenhoff and Fischer, 2006). The expression level of genes that encode for aquaporins and the activity of these proteins depend upon the severity of dehydration.

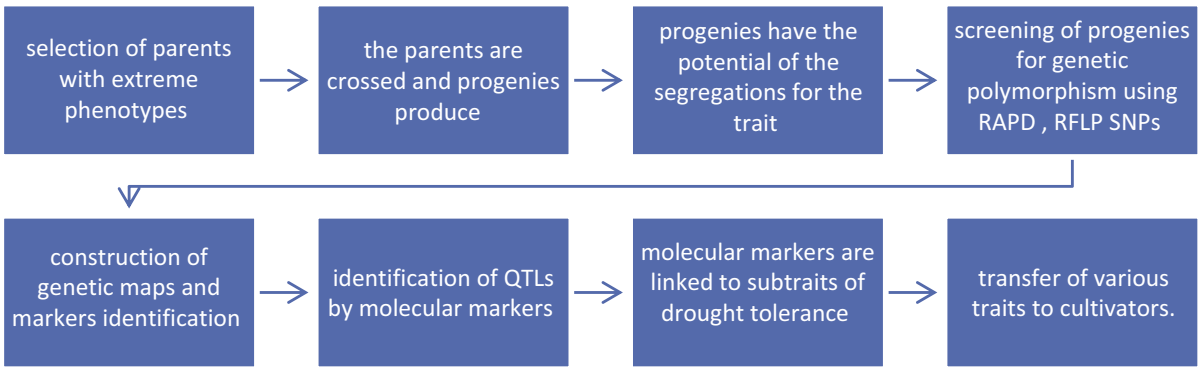
5. Lipid transfer proteins

Lipid transfer proteins (LTPs) make an important class of proteins performing the function of binding and transferring the lipids in the plants (Finkina et al., 2016). LTPs are involved in various processes such as synthesis of cuticular wax, lipid metabolism, and adaptations to environmental changes and stress conditions. Differential expression of LTP genes occurs as a strategy to induce a tolerance mechanism in the plants under both biotic and abiotic stress conditions (Garcia-Olmedo et al., 1995). Trevino (1998) reported the function of LTPs in conditions of water deficiency. The role of these proteins is suspected in cuticle biosynthesis. Most probably, the expression of genes encoding LTPs is upregulated in dehydration and provides an adaptive mechanism through which cuticle thickness can be increased to minimize water loss. Finkina et al. (2016) reported that a wide range of LTPs binds with a various type of ligands such as fatty acid chains with a length of C_{10}-C_{18}, galactolipids, phospholipids, sterols, organic solvent molecules, acyl derivatives of coenzyme A, few drugs, and prostaglandin B_2. They further described two subclasses of LTPs in the plants based on their structural arrangement as LTP1s (9−10 kDa) and LTP2s (7 kDa). Both mature LTP1s and LTP2s comprise unique polypeptide chain; however, LTP1s polypeptide chain contains 90−95 amino acid residues, while LTP2s polypeptide chain has 70 amino acid molecules (Kader, 1996).

6. Molecular breeding

Historically the selection of the elite germplasms was based on the morphological markers including vigor yield and associated traits, and such a technique is still widely used and useful. Nevertheless, this type of selection requires a long time even more than 6 years to evolve a crop variety of choice with stable genotype. To tackle these problems, new strategies such as selection and development of wheat varieties with desired traits using molecular techniques are now proved to be helpful and efficient. Molecular breeding is the application of molecular biology and a useful tool in developing plants against stress conditions. Molecular techniques are based on the selection of wheat genotypes using molecular markers and biotechnology (developing genetically modified organisms (GMOs)). Molecular markers may be either DNA or RNA segments; however, DNA markers due their potential value are widely used in the improvement of wheat crop (Koebner and Summers, 2003). Molecular markers are used to identify the genes on a locus associated with a phenotypic trait of interest. Different molecular techniques are used to enhance the tolerance of plant against drought and salinity. The loci that consist of the genes controlling the phenotype of the quantitatively inherited traits are termed as quantitative trait loci (QTL). QTL mapping can identify the crop variations (Nezhadahmadi et al., 2013). Various QTL drought tolerance inducing have been identified in barley and its close relative wheat by measuring yield and yield associated traits under water scarce conditions (Mathews et al., 2008).

Some of the traits are controlled and inherited through single genes like flowering time, osmotic adjustment, plant height, etc. Therefore, such traits can play an important role in adaptation to the drought-prone environment. A single OR gene is present on the short arm of 7A chromosome in wheat genome (Morgan and Tan, 1996). Thus, the breeding of this OR gene can improve the yield of the plant under water stress conditions (Morgan, 2000). Molecular breeding involves following steps:



Marker-assisted selection (MAS) is a one of the molecular technologies in which a marker is used as indirect selection of a genetic determinant or determinants of a trait of interest. MAS helps in identification of single genetic

components/genes of quantitative traits, thereby aiding the selection and breeding of drought-tolerant plants. This process is more efficient if the markers are tightly located to the loci of a gene that are related to stress. Since, the quantitatively inherited traits are controlled by many genes or QTLs, it is difficult to select all QTLs and incorporate them simultaneously in an organism genome. As the number of QTLs increases, the relative efficiency of MAS and their heritability decreases (Moreau et al., 1998).

Nowadays, the drought-induced genes are detected using molecular markers. Marker-assisted breeding (MAB) is intensively used for creating stress-tolerant lines in different crops. MAB is the selection of QTLs responsible for drought tolerance with the help of DNA markers (Ashraf, 2010). The AFLPs and SSR markers have helped in the mapping of senescence of flag leaf in normal and water stress environments. The QTL associated with the better performance under water stress conditions is detected on chromosome 2D of wheat (Verma et al., 2004). The DNA markers like RFLPs, SSR, AFLP are being used to tag the QTLs for drought stress in wheat. From the past few decades, the quantitative traits, especially for the drought tolerance are selected by the help of SDS proteins, isozymes, and DNA sequences (Davila et al., 1999). Molecular markers are useful to enhance drought tolerance in wheat under water stress conditions.

Marker-assisted backcrossing breeding is the simplest type of MABB, in which the aim is to incorporate a major gene from an agronomically inferior source (the donor parent) into a breeding line (the recurrent parent). The desired outcome is a breed containing only the major gene from the donor parent with the recurrent parent genotype present everywhere else in the genome. There is not any success evidence of MABB in the development of drought-tolerant wheat varieties. Regardless, MABB enables rapid transfer of a selected allele from the donor to the recipient's target locus within two or three backcrosses only (Hospital, 2003).

7. Transcription factors in wheat during drought

Various transcription factors regulated in drought are explained below.

7.1 C_2H_2 zinc finger proteins

C_2H_2 zinc finger proteins (ZFPs) construct very common DNA-binding motifs. It is a subfamily of eukaryotic TFs containing a QALGGH amino acid motif and is considered as plant specific (Bateman et al., 2004). C_2H_2 ZFPs are categorized by two cysteines (Cys_2) and two histidines (His_2). Cysteines and histidines are found in a zinc finger domain, and its purpose is to make the three-dimensional pattern, which comprises of two-stranded antiparallel beta-sheet and alpha-helix having a zinc ion in the center (Takatsuji, 1999).

The ZFP family plays a wide range of roles in biological processes and is a developmental parameter for various vegetative and floral organs in wheat and other plants (Takatsuji, 1999), especially under drought stress conditions (Price et al., 1997) such as flowering regulator, leaf senescence (Krichevsky et al., 2007), and initial shoot gravitropism (Morita et al., 2006). During drought stress conditions, the plant is stimulated to adapt through upregulation and accumulation of dry mass after perceiving specific signals from roots to shoots (Tardieu, 1996). So far, 47 C_2H_2 zinc finger genes have been recognized in bread wheat from the knowledge of present database (Sakamoto et al., 2004; Sekimata and Homma, 2004; Sugano et al., 2003; Englbrecht et al., 2004; Agarwal et al., 2007).

7.2 Family members of TaZFP

1. **TaZFP33**: A gene in TaZFP subfamily upregulated under drought conditions in early embryo and aleurone layer of the endosperm at grain maturation phase to protect the cell from dehydrin genes (Campbell and Close, 1997; Rorat, 2006)
2. **TaZFP42:** Potentially controlling the genes involved in the production of storage proteins in seed and amassing of starch (Kam et al., 2008).
3. **TaZFP15:** Plays a role in the drought by upregulating the starch accumulation in the leaves and sending the signals from root to shoot (Kam et al., 2008).
4. **TaZFP24:** It is downregulated in drought due to its role in growth and development, thus, giving suitable environment to plant for energy and food conservation to tackle the stress (Krichevsky et al., 2007).

5. **TaZFP21, TaZFP22, TaZFP23, TaZFP33, TZF34, and TaZFP37**: These all transcriptional factors are upregulated under drought, salt, and cold stress conditions. These are involved in ABA regulated pathway by stimulating the drought adapting genes for expression, a hallmark in plants under drought stress (Kam et al., 2008).

7.3 bZIP transcription factors

Basic leucine zipper is a family of TFs in plants, responsible for controlling many developmental and physiological mechanisms along with regulating responses toward stress. In angiosperms, 13 groups of bZIP homologs have been identified so far (Ying et al., 2011). These TFs are composed of a bZIP domain containing about 40–80 amino acids (Correa et al., 2008). The domain consists of two motifs: a leucine zipper (a-helical heptad repeat) involved in dimerization of the TF and a basic region (16 amino acids) that controls the specificity of the TF to its intended DNA. The connecting sequence of amino acids between the basic region and leucine zipper is called hinge.

Dimerization of the TF occurs when a helical coil is formed as a result of electrostatic interactions between two subunits. The new orientation exposes the basic region in a manner that allows interaction with DNA (Siberil et al., 2001; Rahaie et al., 2013). Studies revealed that some proteins bind DNA through preformed dimers, whereas others dimerize and still bound to their respective DNA (Kohler et al., 1999). Typically, bZIP TFs bind to DNA sequences harboring an ACTG core. bZIP containing proteins of plants reportedly bind to A-box, G-box, and C-box; however, interaction with nonpalindromic sequences has also been studied (Rahaie et al., 2013).

7.3.1 Mechanism of action in wheat during drought

ABA is a plant hormone having multiple roles in plant growth and tolerance toward abiotic stresses. ABA controls many, but not all genes that provide a suitable response to stress. All these genes have an appropriate cis-acting element known as ABA-responsive element (ABRE) on their promoter region that controls expression in response to ABA by binding to bZIP TFs (Ying et al., 2011). bZIP TFs control the expression of some genes under drought, which are responsible for changes like maintenance of root growth, inhibition of leaf growth, increased levels of chaperone proteins and stomatal closure (Hamanishi and Campbell, 2011).

ABF4/AREB2 bZIP TF is expressed and induced mainly under abiotic stress conditions including drought and ABA levels in vegetative tissues and controls the expression of various genes like *RD29B, RAB18, ICK1, ABI1, KAT2, SKOR, ADH1*, and *CHS*. ABF4 along with ABF3 increases the rate of plant survival and stomatal closure under water scarce conditions. Knockout phenotypes show hypersensitivity toward drought and salinity (Kim, 2005). ABA-responsive element binding protein 1 (AREB1), also known as ABF2, is a bZIP TF that is a regulator of ABA-dependent and drought-inducible genes in a vegetative tissue. LEA genes are controlled by this TF and are responsible for the alleviation of dehydration stress, mainly by their chaperone functions (Fujita, 2005; Wang et al., 2003). Similarly, *Wlip19* gene encoded by bZIP TF has increased expression in water deficiency and high ABA levels.

7.4 WRKY

WRKY TFs are among the 10 largest families of plant TFs. More than a 100 of such TFs have been identified in different species (Ulker and Imre, 2004). WRKY TFs play very important and diversified role in the web like signal networking in the plants. They act both as repressor as well as activator of different genes. WRKYs play an important role in plant defense mechanisms and phenomena like germination, senescence, and abiotic stress. The unique characteristic of WRKY TFs is their DNA binding domain, which consists of invariant amino acid sequence, "WRKY" at their N-terminus. Many WRKY TFs have been identified at this specific domain and are conserved in all of them, which gives the family its name (Eulgem et al., 2000; Rushton et al., 1996). Besides, WRKY TFs also contain a signature, zinc finger at their C-terminus.

7.4.1 Mechanism of action in wheat during drought

Plants face the deficiency of water during the drought spells, hence conservation of the plant water is necessary by reducing the water loss through transpiration (Qiu and Yu, 2009). WRKY TFs play an important role in such strategic processes by upregulating or downregulating certain genes by interacting with MAP kinases, calmodulin proteins, histone deacetylase, and resistance proteins. WRKY TFs can play an antagonistic role to salicylic acid, jasmonic acid, ethylene and control via auxin and cytokine as well (Agarwal et al., 2011; Antoni et al., 2011; Rushton et al., 2012). WRKY TFs help plant survive the drought conditions by reducing rate of transpiration, reducing size of stomatal

opening (Babitha et al., 2012) and production of osmoprotectants (Qiu and Yu, 2009; Rushton et al., 2010). Osmoprotectants are the special molecules that surround and stabilize plant proteins during desiccation conditions.

Experimental data suggest that drought conditions imposed on many plants, led to the activation of many WRKY TFs, like WRKY1, WRKY72, WRKY77, WRKY11, WRKY45, by ABA signaling pathway, which ultimately led to the production of galactinol (osmoprotectant) by the activation of Gols1 gene (Qiu and Yu, 2009; Xie et al., 2005; Wu et al., 2009; Rushton et al., 2010). WRKYs have also been reported to play a regulatory role for ABA-responsive elements binding factors (AREBs). In vivo and in vitro promoter-binding studies showed that the target genes of WRKYs, which are involved in ABA signaling, include well-known ABA-responsive genes, such as *ABF2*, *ABF4*, *ABI4*, *ABI5*, *MYB2*, *DREB1a*, *DREB2a*, *RAB18* (Rushton et al., 2012).

7.5 NAC

NAC TFs belong to one of the largest TF families found in plants only. Until now, 100 transcriptional factors have been identified and categorized into six groups (Rahaie et al., 2013). The transcriptional activation of some biological processes takes place by the formation of helix-turn-helix that binds to the target DNA (Aida et al., 1997). The three different NAC genes, including NAM (no apical meristem), ATAF (Arabidopsis transcription activation factor), and CUC (cup-shaped cotyledon), have conserved NAC domain (from first letters of each gene).

NAC family proteins consist of a huge number of genes (135) that are extremely important in plant development (Aida et al., 1997). These TFs are involved in various processes for the plant development as a response under abiotic stress. NAC TFs regulated processes such as lateral root development, shoot apical meristem formation, cell wall development, secondary metabolism, and senescence (Nakashima et al., 2012). The NAC protein consists of the N-terminal and a C-terminal. The C-terminal is a highly conserved region and operates as a functional domain. The C-terminal acts as the transcriptional activator or repressor along with the protein binding activity (Hu et al., 2006).

The overexpression of stress-responsive NAC genes exhibits improved drought tolerance (Rahaie et al., 2013). NAC TFs recognize cis-element NACRS, which is a drought responsive element (Tran et al., 2004). However, the N-terminal is a conserved region and consists of the DNA-binding NAC domains and consists about 150−160 amino acids and subdivided into five subdomains (A−E) (Ooka et al., 2003). NAC domain forms the homo and the hetero dimers with other NAC containing proteins, nuclear localization and DNA binding (Olsen et al., 2005).

7.5.1 NAC TFs of wheat

TaNAC 8 TF acts as a transcriptional activator and is involved in defense responses against both biotic and abiotic factors (Xia et al., 2010). TaNAC TFs overexpression enhance tolerance to drought, salinity, and freezing stresses (Rahaie et al., 2013). TaNAC 4 is a transcriptional activator during biotic and abiotic stress responses (Xia et al., 2010). TaNAC 69 genes are upregulated during drought conditions and are involved in normal cellular activities of roots. Overexpression leads to enhanced drought tolerance and improved water use efficiency.

7.6 NF-Y

Nuclear Factor Y (NF-Y) is also known as heme-activated protein or CCAAT binding factor. It is a heterotrimeric TF which is present in eukaryotic organisms. It regulates the activation of many genes by binding to cis elements, which contain a highly conserved core sequence CCAAT. Plants possess gene families code an NF-Y subunit instead of a single gene. Wheat (*Triticum aestivum*) genome has at least 36 and 37 NF-Y subunits and Dr1 gene. NF-Y is composed of three proteins, namely NF-YA, NF-YB, and NF-YC. Each mature NF-Y TF is made up of one subunit derived from each family. NF-Y and Dr1 families play important function in wheat drought adaptation.

TaDr1 along with a member of each subunit family, including one TaNF-YA, five TaNF-YB, three TaNF-YC, and TaDr1 gene are involved in response to drought stress. During drought, eight genes are downregulated and three genes are upregulated. TaNF-YA1 shows significant upregulation during drought. TaDr1A, TaNF-YB, and TaDr1B are upregulated by twofold. The evolution of many NF-Y gene families in wheat has many flexible regulatory mechanisms. The expression of TaNF-Y produces drought response, which suggests that NF-Y has physiological roles, besides, regulation of gene expression in wheat adaptation to stress. Overexpression of TaNF-Y B2 could produce drought-tolerant wheat.

7.6.1 Mechanism or action of NF-Y

NF-Y TF is made up of three subunits NF-YA, NF-YB, NF-YC. These join to form the activated TF. NF-YB and NF-YC join in the cytoplasm and translocate toward the nucleus and bind to the third subunit NF-YA, which on

attachment to dimer creates a heterotrimer. This heterotrimer is the mature NF-Y TF. Resulted mature TF binds to the promoter consisting of a pentamer nucleotide sequence, i.e., CCAAT in its core. This can result in either positive or negative transcriptional regulation. NF-Y leads to enhanced drought resistance, although the mechanism is somewhat still unclear. Overexpression of NF-YA5 reduces the susceptibility to drought. The miRNA169 precursors, miRNA169a, and miRNA169c are downregulated in a drought if treated with ABA-dependent manner.

7.7 DREBs

Dehydration-responsive element binding factors (DREBs) are one of the most important TFs that activate the genes responsible for drought tolerance in plants (Naruska et al., 2003). DREBs are among the first families of TFs that were discovered for their function in regulating genes of drought tolerance under water-deficit conditions (Sarah et al., 2011). DREBs are classified under AB2/ERF family of TFs (Sazegari and Ali, 2012). This family is named after AB2 family because all proteins of this family share a conserved domain of amino acids (the AP2 domain). This domain is responsible for binding to DNA motif in the promoters of target genes (Andeani et al., 2009). This family further consists of two subclasses known as DREB1/CBF (CBF; C-repeat binding proteins) and DREB2 that are activated by cold and dehydration, respectively (Agarwal et al., 2006).

DREBs undergo immediate response to abiotic stress situations and activate the expression of functional downstream genes that have a role in abiotic stress (Sakuma et al., 2006). Their binding to the promoters on their target genes is very specific as they bind to a distinct region known as DRE/CRT sequence. This DRE (dehydration-responsive element) sequence consists of conserved sequence of five base pair CCCAG known as C-repeat sequence (Shinozaki and Yamaguchi-Shinozaki, 2000).

ABA production is enhanced under the conditions of water shortage (Xiong et al., 2002; Ashraf, 2010). DREB genes show a response to exogenous ABA such as the wheat TaDREB2 (Xue and Loveridge, 2004; Xu et al., 2008). ABA promotes the regulation of DREB and enhanced promoter activity (Kizis and Pages, 2002). Thus, we can say that ABA is responsible for inducing some important signal transduction pathways via DREB proteins for drought tolerance, such as the suppression of seed germination, minimizing transpiration by the stomatal closure, and increasing senescence and abscission (Wasilewska et al., 2008). Wheat DREB2 TF known as WDREB2 is a DRE/CRT binding protein that plays a significant role in abiotic stress responses, and its expression is enhanced by cold, drought, salt, and exogenous ABA treatment (Nakashima et al., 2000). WDREB2 gene produces different isoforms of this TF as a result of alternative splicing mechanism (Egawa et al., 2006).

7.7.1 Mechanism of action in wheat during drought

Conditions of drought stress lead to consequences that favor increased expression of DREB genes. Overexpression of DREBs have following physiological effects:

1. Activation of genes that encode late embryogenesis abundant (LEA) proteins, also called as dehydrins (DHNs) (Caramelo and Lusem, 2009; Lee et al., 2005; Kobayashi et al., 2008). These proteins are quite hydrophobic and protect the cells from stress by increasing membrane stability, preventing false folding, and processing of proteins (Tunnacliffe and Michael, 2007).
2. Activation of two cellulase synthase enzymes, HvCesA1 and HvCesA8. The function of these enzymes is the biosynthesis of primary and secondary cell wall. Thus, they have a role in the wound recovery (Sarah et al., 2011).
3. Stunned growth, dwarfism, delay in flowering time, and slower development. These effects allow the plant to reduce water consumption in drought conditions (Kim et al., 2004; Oh et al., 2007).
4. Proline content in leaves increases due to enhanced expression of DREBs. Proline is an osmosis regulating substance and has a role in moisture absorption and dehydration resistance.

7.8 MYB

MYB proteins are a superfamily of TFs that play a vital role in the developmental processes, as well as defense mechanisms in the plant. In Arabidopsis gene family, MYB has the largest number of members (Riechmann and Ratcliffe, 2000). MYB genes have been discovered in various species such as V MYB gene of avian myeloblastosis virus (AMV), first MYB identified gene (Klempnauer et al., 1982), insects, fungi, and slime molds (Lipsick, 1996) and in 1987, the first plant MYB gene, C1 identified in *Zea mays* (pea plant). Comparatively, plants have higher number of MYB genes than fungi or animals (Riechmann and Ratcliffe, 2000). The evidence of MYB genes presence in eukaryotes suggests that these genes are very ancient evolutionally. A domain of MYB is made up of one of the three

imperfect repeats, each of them containing approximately 52 amino acid residues that take up a helix-turn-helix-conformation that weaves itself in the DNA's major groove. Plant MYB genes were classified into three major groups including R2R3-MYB with two adjacent repeats, R1R2R3-MYB having three adjacent repeats and heterogeneous group collectively referred as MYB-related proteins, which usually but not always contain a single MYB repeat (Rosinski and Atchley, 1998; Jin and Martin, 1999; Stracke et al., 2001).

R2R3-MYB genes have been extensively studied in the past. They are involved in various physiological and biochemical processes, i.e., regulation of secondary metabolites (Nesi et al., 2001; Baudry et al., 2004). R2R3-MYB genes have also shown their involvement in the control of cell morphogenesis (Lee and Schiefelbein, 1999, 2001; Higginson et al., 2003); the regulation in the formation of meristem, floral, and seed development (Shin et al., 2002; Steiner-Lange et al., 2003); and cell cycle control (Ito et al., 2001; Araki et al., 2004). Some genes were also involved in various defense and stress responses (Abe et al., 2003; Denekamp and Smeekens, 2003; Nagaoka and Takano, 2003). MYB gene in a plant is also responsible for phenylalanine metabolism.

7.8.1 Mechanism of action in wheat during drought

In wheat (*T. aestivum*), MYB TFs are named as TaMYB and are classified into different families. Abiotic stress adversely affects the growth of the plant and their productivity. MYB TFs show responses in these stresses. MYB TFs play crucial roles in response to the abiotic stress in plants, but their function and characteristics in wheat (*T. aestivum*) have not been fully investigated. However, certain studies show changes in MYB TFs during abiotic stress specifically in drought conditions. MYB2 functions in response to the ABA-mediated drought stress. Overexpression of AtMYB44 can decrease the rate of water loss and enhance drought and salinity tolerance. Engineered drought-tolerant wheat is not fully synthesized yet; however, different experiments are performed on Arabidopsis lines. Over-expression of AtMYB96 in engineered Arabidopsis lines can make wild type somewhat drought tolerant. Also, AtMYB15 accounts for drought and salt stresses tolerance. It has been observed through experiments that MYB gene is involved in the opening and closing of stomata. As MYB gene can regulate stomatal movements, it is inadvertently involved in plant drought tolerance. AtMYB60 and R2R3-MYB genes in Arabidopsis are involved in stomatal movement regulation. In guard cells, AtMYB60 is specifically expressed and its expression is negatively modulated during drought. Studies also show TaMYBsdu1 is an important regulator involved in the adaptation of wheat to salt and drought tolerance. Overexpression of TaMYB33 is engineered in Arabidopsis to enhance the ability for osmotic pressure, balance reconstruction, and ROS scavenging. TaMYB33 promotes salt and drought tolerance partially through detoxification of ROS. It possesses the superior ability for osmotic balance reconstruction. Through these studies, it has been observed that MYB plays pivotal role in the production of drought-tolerant wheat species.

7.9 Ethylene response factor

Ethylene response factor (ERF) TFs are a large multigene family of TFs that regulate the expression of ethylene-dependent genes. They direct the specific plant responses to ethylene signals and are significant key players in biotic stress only. The recent studies have investigated that they play an important role in abiotic stress as well, depending on the conditions. In addition to functioning as both activator and repressor elements, ERFs can also act as an integrative node and is a common TF of different signaling pathways. The ERF proteins possess a highly conserved set of sequences termed as the ERF domain which provides an affinity of ERF to GCC box that is present in the promoter region of ethylene responsive genes. In addition to GCC box, the ERF proteins also bind to the DRE/CRT motif located at stress-responsive gene's promoter region known as the cis-acting element that responds to stress, mainly drought and cold.

7.9.1 Mechanism of action in wheat during drought

ERF gene was isolated in wheat (*T. aestivum*) by screening a drought-induced cDNA library method. The transcription factor was named as TaERF1 (T. festival ethylene responsive factor 1), which is positioned on the TaERF gene on the 7A chromosome. TaERF1 encodes a 355-amino acid putative protein with a conserved DNA-binding domain and a conserved N-terminal motif (MCCGAIL). Protein interaction assays indicated that the putative phosphorylation site (TPDITIS) in the C-terminal region was a potential phosphorylation substrate for TaMAPK1 protein kinase. MAPK cascade plays an important role in environmental and nonenvironmental stress. TaERF1 overexpression activates the stress-related genes, including PR and COR/RD genes that regulate the stress tolerance mechanisms under abiotic stress. TaERF1 gene encodes a GCC-box and CDT/DRE binding factor involved in multiple signal stress transduction pathways.

8. Changes in TFs and molecular makeup during protective mechanism in wheat under drought

Genetic diversity of wheat has been severely affected by domestication and a low tolerance to abiotic stresses has resulted from various breeding programs. Water shortage results in crop loss and yield reduction (Krasensky and Jonak, 2012). A plant under stress can adopt one of the two strategies: stress avoidance and stress tolerance (Levitt, 1972). The former involves the implementation of protective mechanisms that delay or remove the negative effects of stress. Stress tolerance, on the other hand, encompasses all the mechanisms employed by a plant to acclimatize itself to a stressful environment. The response against stress like the drought is dynamic, entails various changes in regulatory mechanisms and includes alterations in metabolic pathways and expression of genes, which ultimately result in physiological and morphological stability (Krasensky and Jonak, 2012).

8.1 Regulation by transcription factors

Interaction of TFs occurs with cis-elements present in the promoters of stress-responsive genes. The expression is upregulated, and the plant is provided tolerance against abiotic stress specifically (Agarwal et al., 2006). Many families of TFs play a crucial role in determining wheat plant responses under water deficiency. Members of the NAC, bZIP, C_2H_2 zinc finger, APC, and WRKY families have been shown to play a major role in generating stress responses. In wheat, some TFs are induced by ABA synthesis, which is increased during dehydration. ABA-dependent protein synthesis involves the genes of MYC/MYB and bZIP/ABRE systems, whereas DREB genes are ABA-independent (Agarwal et al., 2006).

Lea genes are expressed both by ABA-independent and ABA-dependent mechanisms (Egawa et al., 2006). Their expression is enhanced after activation with MYB, bZIP, or DREB TFs and their product, LEA proteins, are involved in relieving dehydration stress by various mechanisms, including membrane protection against dehydration. Rahaie et al. (2013) studied 10 MYB TF genes from *T. aestivum* and found that *TaMYBsdul* was upregulated in both leaves and roots of plants exposed to water-deficient conditions. *TaMYB1* expression also amplifies, particularly in the root, when the plant is subjected to dehydration. Studies have also shown that an increase in the expression of *TaMYB33* induces drought tolerance mainly by increasing the efficiency of detoxifying ROS and adjustment of osmotic balance. Similarly, another MYB gene, *TaMYB3R1*, is involved in generating responses to drought at certain conditions including low temperatures and salinity. TaNAC 69 is an NAC TF protein in wheat, and its overexpression is induced by water deficiency (Xue et al., 2006). Evidence also suggests that TaNAC 8 might be involved in wheat responses toward drought (Rahaie et al., 2013).

8.2 Changes in metabolism and molecular makeup

Changes in water potential causes disturbance in cellular homeostasis and various mechanisms are employed to prevent cellular damage and death by desiccation.

8.2.1 Detoxification

Water scarcity leads to the disruption of photosynthesis and an increase in the rate of photorespiration, resulting in an unbalanced homeostasis. Reduced carbon dioxide fixation and excessive reduction of ETC cause the transfer of high-energy electrons to molecular oxygen leading to the formation of ROS. These molecules are highly destructive to cellular components like proteins, lipids, and DNA (Miller et al., 2010). In such conditions, plants deploy ROS scavenging mechanisms including production of antioxidants like glutathione (GSH), ascorbic acid (AsA) and enzymes such as ascorbate peroxidase (APX), glutathione peroxidase (GPX), peroxiredoxin (PrxR), and superoxide dismutase (SOD) to detoxify ROS and maintain cell survival (Mittler et al., 2004).

PrxR and GPX are involved in clearing hydrogen peroxide from the stroma, whereas SOD detoxifies ROS produced in peroxisomes, stroma, and mitochondria (Miller et al., 2010). CATs are the major detoxifiers of peroxisomes, whereas mitochondrial detoxification is carried out by AOX (alternate oxidase) and SOD. During drought, mitochondrial ROS are produced due to an increase in respiration rate caused by a shortage of chloroplast ATP synthesis. Antioxidants like ascorbic acid, tocopherol, and glutathione are also produced in excess to detoxify ROS. AsA acts as electron donor, whereas GSH is a maintainer of redox equilibrium (Foyer, 2005). Alpha tocopherol (Vit E) has a crucial role in protecting lipids from the destructive effects of ROS (Miller et al., 2010).

8.2.2 Chaperone functions

Overexpression of genes to produce protective proteins like LEA, rubisco, and proteases under drought stress is one of the adaptions in plants (Demirevska et al., 2008).

1. Rubisco is involved in carbon dioxide fixation and photorespiration (Jensen and Bahr, 1977) and is efficiently mobilized under stress.
2. Water deficit in wheat causes an increase in proteolytic activity particularly cysteine protease, and their reorganization of metabolism plays an important role in relieving stress (Demirevska et al., 2008). Proteases are responsible for the efficient removal of damaged or unnecessary proteins, adjustment of metabolic pathways, and remobilization of nutrients under stressful conditions (Simova-Stoilova et al., 2006).
3. It is assumed that LEA proteins are induced by cold or osmotic stress while their exact mechanism of action is unknown. It is also concluded that LEA proteins protect molecular and cellular structures by processes like sequestering ions, hydration buffering, and membrane protection. They can also protect other proteins and instigate reactivation of denatured proteins (Goyal et al., 2005). Dehydrins are a class of LEA proteins and are accumulated during dehydrative stress and high ABA levels (Hassan et al., 2015). They are mainly distributed in the nucleus, cytosol, and plasma membranes. WCOR410 is a dehydrin that is present in peripheral region and is responsible for preventing destabilization of membranes during water scarcity (Danyluk, 1998).

9. Conclusion

Climate change is an inevitable threat against the cereal crop production in the world; meanwhile, population is expected to reach 9.8 billion by 2050 and 11.2 billion in 2100. Food security for elevating population requires crop varieties endowed with adaptations against harsh environmental conditions, especially drought is a challenging task. Drought tolerance is a polygenic trait and involves induction of various tolerance-inducing genes and various drought tolerance mechanisms. Besides, wheat genome is very complicated, five times larger than human genome and consists of 85% of the repetitive DNA sequences making insurmountable to accomplish whole wheat genome sequencing. Wheat breeders are striving to produce elite wheat varieties with better quality and yield traits adapted to drought stress conditions using available molecular level information associated with various drought adaptive mechanisms. They own success in such endeavors by introducing molecular techniques, developing transgenic plants (GMOs) using biotechnological techniques, discovering transcriptional factors (TFs) inducing the genes for drought tolerance, detecting LTPs, aquaporins detection responsible for transcellular water movement pathways that regulate osmotic adjustment under drought, recognizing osmotic adjustment in plants through osmoprotectants, and elaborating phenotypic and physiological drought adaptive changes. However, the progress is limited as compared to the coming population peril, and progressive efforts are needed leading to identification and understanding of drought tolerance mechanisms at the molecular and genes expression levels using biotechnological techniques to make a breakthrough in the improvement of the wheat grain yield and ensuring the global food security.

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CHAPTER

12

LEA proteins and drought stress in wheat

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OUTLINE

1. Introduction

Wheat cultivation reaches more than any other crop of the world. For the first time, wheat was found to be originated in South Asian area of the globe. One archeological study proved wheat to be grown in Nile Valley. Regarding domestication of food crops, wheat is found to be the first that was used as a staple food since some 8000 years ago. It was cultivated in Europe, North Africa, as well as West Asia. When we look into present statistics, we analyze that wheat is that commercial crop which is grown on maximum land as it is a great source of carbohydrates and provides good nourishment. Wheat is leading all food and cash crops including maize, rice, cotton, etc. (Curtis, 2008).

In July 2014, a draft sequence of bread wheat was published in *International Journal of Science*. According to that published paper, the genome of wheat in comparison to corn was found to be seven times larger and approximately 35–40 times larger than rice. Moreover, when it was compared with the human genome, it was exactly five times larger (International Wheat Genome Sequencing, 2014). Recently, International Wheat Genome Sequencing Consortium (IWGSC) provided the newest version of wheat reference genome (Appels et al., 2018) with the best

assembly quality, containing 14.5 Gb sequences with 94% genome coverage which was assembled using POPSEQ data and HiC map (chromosome conformation capture) (https://wheat-urgi.versailles.inra.fr/Seq-Repository/Assemblies).

The optimum growing temperature is about 25°C. Maximum growth of wheat crops has been observed at a temperature ranging from 20 to 37°C. Wheat can be grown in almost all the environmental conditions which include xerophytic as well as littoral. This accounts for the worldwide distribution of wheat crop and excessive human consumption among other vegetables (Curtis, 2008; Monneveux et al., 2012).

Wheat provides maximum nourishment to human body as compared to any other crop of the world. It is considered as best of the cereal foods. Wheat plant is the leading source of protein among all vegetables and has the greatest nutritional value as compared to other cereal crops like maize and rice. Wheat can be easily converted into flour as well as it has ease of storage, interesting as food tastes good. All these properties make wheat plant a major component of human diet (Curtis, 2008; FAOSTAT, 2017). According to a research, wheat is a source of carbohydrates in most of the Asian and European countries. Wheat has multiple nutritional elements present in its composition such as vitamins, fatty acids, amino acids, and also a minute amount of legume protein. With estimation wheat provides more than 20% of the food protein to almost half of the world. Wheat is one of those few crops which are used as staple food in both developing and underdeveloped countries, which proves it to be economically excellent for countries all around the world (Curtis, 2008; Šramková et al., 2009).

1.1 Drought stress

The major types of stress or tolerance that a crop confronts are of two types including drought avoidance and dehydration tolerance or stress. Drought is an important challenge to agricultural scientists and plant breeders. Approximately four-tenths of the agricultural land is within the arid or maybe semiarid conditions around the world. A general assumption is that by the year 2025, approximately 1.8 billion people will pass through a phase which will be a complete water shortage period (Nezhadahmadi et al., 2013).

One of the main factors that limit the growth of crops worldwide is drought, which is a polygenic stress (Kilic and Yağbasanlar, 2010). It is a common and most important limitation to agricultural progress, affecting expressions of different genes, plant yield, and quality. Recently, research has been done regarding the effect of drought and dehydration stress on the photosynthetic and the metabolic plant attributes. Plants have developed a number of methods to overcome drought stress constituting avoidance of drought and dehydration tolerance. Molecular, biochemical, anatomical, and physiological changes are the basis of these adaptive mechanisms (Guo et al., 2013).

Water stress activates many biochemical and physiological responses in plants including the closure of stomata, respiration activation, and repression of photosynthesis, and cell growth. With the accumulation of osmolytes and stress-tolerance proteins, a plant adapts itself to drought stress at both cellular and molecular level. Abscisic acid (ABA) is a phytohormone produced under drought stress conditions. This hormone causes stomatal closure and expression of stress-tolerance genes. In some cases, exogenous ABA stimulus is required for stress-inducible genes. However, research has proved that for the gene expression of drought tolerance, both ABA-dependent and independent regulation systems are required in order to bring about complete tolerance (Shinozaki and Yamaguchi-Shinozaki, 2007; Liu et al., 2018).

Most plants face a decrease in water during their lifetime, and most plants exhibit stress-tolerant structural components, e.g., seed, pollen, and spores (Ingram and Bartels, 1996). The molecular and genomic analysis helped in the identification of many drought-tolerance genes in *Arabidopsis*, rice, and other plants, also many transcription factors has also been identified which helps in regulation of stress-inducible gene expression. These genes provide the initial response to stress and aid in the development of stress tolerance (Shinozaki and Yamaguchi-Shinozaki, 2007; Liu et al., 2018).

During some stage, every living organism confronts water limitation which affects the organism's growth and development. If the plant is unable to overcome these limitations, they may die and become extinct in the later course of time. Naturally and as a result of various evolutionary processes, to overcome it, organisms have developed different strategies. One of the best solutions to this problem is LEA protein which plays a crucial role in the early seedling stage (Nezhadahmadi et al., 2013).

Wheat is a diverse crop that has multiple genes present and is associated with drought stress. One of these genes is *LEA* gene which encodes the LEA protein. Conformational changes of transcription factors occur when a wheat plant is subjected to water loss or water scarcity. LEA protein responds to helicase, carbohydrate, or rubisco when it confronts a drought stress. In this chapter, major emphasis will be on wheat crop under stress condition with respect

to LEA protein mechanism with the future aspects to overcome this phenomenon (Nezhadahmadi et al., 2013; Gao et al., 2014).

1.2 Effects of drought stress on wheat

Wheat growth is strongly inhibited during drought stress conditions, specifically the seedlings of the wheat crop. Water is regulated in the roots of crop or either in the apoplast of root and certain circumstances both in the apoplast and outside the root. Soluble sugar content increases to a high content of drought stress such as proline or betaine. This can be used as a key factor for wheat seedlings to sense water stress (Guo et al., 2018).

Drought stress is the most common water stress caused by water deficiency. Low water content disturbs the bilayer structure of the membrane and makes it extremely porous. Stress in the lipid bilayer also disrupts proteins of the membrane which results in the cellular organelles disruption, deceased integrity of membrane, and changes in enzymatic activity. Dehydration of protoplasm increases the concentration of electrolytes and disturbs cellular metabolism (Liu and Zhu, 1998).

Additionally, from among other detrimental effects, drought also impairs the vegetative growth of plants, specifically the shoot growth (Shih et al., 2008).

1.3 The LEA protein groups

LEAs were discovered by Leon Dure (Dure and Chlan, 1981). He identified several families of proteins accumulating rapidly at late seed developing stage in wheat (*Triticum aestivum* L.) and cotton (*Gossypium hirsutum* L.) during the embryonic stage. After this, LEA proteins were discovered within the vegetative parts of the plant tissues, undergoing stress conditions as well as in the invertebrates and certain bacteria which have desiccation tolerance property. These proteins are mostly confined to the mitochondrial matrix of the plant seed mitochondria, protecting against cold, high salinity, and also desiccation (Magwanga et al., 2018; Chen et al., 2019). Their biochemical and physiological characteristics are still unknown. Its gene expression suggests a very strong role against dehydration. The protein was found to be an intrinsically unorganized kind of a protein localized in the matrix of mitochondria, which folds upon dehydration into a class A alpha-helical form that inserts laterally in the inner membrane to provide protection in the dry state (Stupnikova et al., 2006).

LEA genes belong to the gene family which plays a role in drought tolerance. LEA proteins are the Late Embryogenesis Abundant proteins present within the embryos of plants and enhance their tolerance for drought conditions (Magwanga et al., 2018; Dang et al., 2014; Liang et al., 2016). The role of the LEA proteins in drought tolerance is present predominantly in wheat, barley, and tomato plants. It is important to investigate the regulatory mechanism which is followed by LEA genes. Drought, ABA, and salinity regulate LEA genes expression. Extensive research has been done on identifying the elements controlling the ABA-induced gene expression. ABA-responsive element (ABRE) is one of the best characterized cis elements regulating water stress. ABRE contains CACGTC palindromic motif. Dehydration-responsive element (DRE) A9 base pair conserved sequence TACGACAT is recognized to be present within the drought-inducible gene's promoter region (Wang et al., 2007).

Most of the LEA proteins possess low molecular weight (10−30 kDa). These proteins are formed during a late period of development of the seed. Dure and Chlan (1981) first discovered the LEA proteins in cotton seeds. Extensive research has been carried out henceforth, with LEA protein being also detected in wheat, maize, soybean, barley, rice, sunflower, *Arabidopsis*, and *Brassica napus* (Liang et al., 2016; Wang et al., 2007; Hundertmark and Hincha, 2008; Amara et al., 2011; Choi et al., 1999; Sasaki et al., 2013; Prieto-Dapena et al., 1999). These proteins have been shown to be present in cytoplasm and nucleus. Also, in higher plant seeds, the proteins are encapsulated within seedlings root and other organs (Hong-Bo et al., 2005).

A bioinformatics study suggests in building a computational database, i.e., LEAPdb with the function of in silico analysis of LEA proteins. LEAPdb database currently covers about 710 nonredundant and guardian sequences of LEA proteins from organisms. This systemic analysis led to the discovery of in-depth physiochemical properties (Shih et al., 2008).

LEA proteins comprise seven different families or groups (Table 12.1). All groups from 1 to 7, with the exception of group 5, are hydrophilic or the typical LEA protein groups (Dure, 1993a; Finn et al., 2009). However, the group 5 LEA protein members are characterized as the "atypical" or hydrophobic proteins (Battaglia et al., 2008).

The first three groups are actually within the range of plant tissues and different kinds of plants (Table 12.1). Certain group 1 and 3 homologues are also found to be existing in certain bacteria and some invertebrates (Browne et al., 2002). Amino acid sequence and RNA homology form the basis of this classification system which is classified in the cytoplasm and nuclear region. Traditionally, the LEA group of proteins is classified on two bases (Guo et al., 2013):

TABLE 12.1 Species distribution of different groups of LEA proteins.

Group	Subdivision	Organism
Group 1	2 superfamilies	Wheat, cotton
Group 2	3 superfamilies	Angiosperms, gymnosperms, bryophytes, fungi, algae, cyanobacteria
Group 3	2 superfamilies	Plants, fungi, microbes, animal kingdom
Group 4	4 superfamilies	Sunflower, *Arabidopsis*, soybean, etc.
Group 5	4 superfamilies	Maize, carrot, *Arabidopsis*, tomato, hot pepper, etc.
Group 6	Diverse	Barley, *Arabidopsis*, rice, wheat, etc.
Group 7	Diverse	Fruits of tomato, melon, apricot, and grape (Battaglia et al., 2008)

- Amino acid sequence or conserved motifs.
- Protein or oligonucleotide probability profile (POPP) (Guo et al., 2013).

1.3.1 Group 1 LEA proteins (D-19)

LEA proteins of group 1 were identified by internal 20-mer sequence. They have high hydrophilicity due to high charged residue content. Group 1 LEA proteins are accumulated during the embryo development, particularly in dry seeds within the plants. Organs undergoing dehydration also seem to accumulate group 1 LEA proteins such as the pollen grains. Group 1 protein-characterized genes are responsive to ABA and water-deficient conditions.

In vitro experiments employing recombinant wheat (*T. aestivum* L.) Em proteins have shown their ability in protecting citrate synthase (CS) or lactate dehydrogenase (LDH) from aggregation or inactivation because of freezing. Wheat TaEm proteins expressed in *Saccharomyces cerevisiae* tend to attenuate growth inhibition in yeast growth mediums with high osmolarity (Battaglia et al., 2008).

The first identified proteins of this group were the developing cotton seed D-19 and D-132 LEA proteins. Due to the high glycine (Gly) residues (approximately 18%), these proteins have random coil-like unstructured forms within aqueous solutions. The structural analysis predicted through circular dichroism (CD) suggests a few proteins having a left-handed extended helical PII conformation (or poly (L-Pro)). The unstable and flexible structural form of this group of proteins was also confirmed by nuclear magnetic resonance (NMR) spectroscopy. The hydrophilic 20-mer conserved sequence is the reason for most of the homology between the group 1 and other taxa of the LEA proteins. Tandem repeats of this sequence might be present in multiple copies. Some other conserved motifs are also present in the group 1 plant LEA proteins, such as N-terminal (TVVPGGTGGKSLEAQE[H/N]LAE) and C-terminal (D[K/E]SGGERA[A/E][E/R]EGI[E/D]IDESK[F/Y]) sequences. A unique representation of group 1 LEA is seen across most taxonomic domains (bacteria, archaea, and eukarya). This has been concluded because of the identification of homologous (20-mer containing) group 1 LEA proteins in various species like *Bacillus subtilis* (bacteria), *Artemia franciscana* (crustacean), and methanogenic archaea (Battaglia et al., 2008). The bacterial group 1 LEA proteins have the ability to block enzyme inactivation upon freeze−thaw treatments in vitro, and it has analogous functions to plant LEA proteins (Campos et al., 2013).

1.3.2 Group 2 LEA proteins (D-11)

Dehydrins (DHNs) is a term commonly referred to the group 2 LEA proteins. These were initially identified in the embryos of seeds of cotton. This group is the most characterized one from among all other LEA protein groups. As a result of high charged amino acid proportion, the dehydrins tend to show high hydrophilicity. This hydrophility is further enhanced because of the low nonpolar hydrophobic contents, and decreased tryptophan (Trp) and cysteine (Cys) residues percentage. The proteins included in this group have a distinctive conserved K-segment, which is a 15-residues Lysine-rich motif (EKKGIMDKIKEKLPG). K-segment may be in 1−11 copies on a polypeptide. An additional conserved Y-segment is also found to be present in 1−35 tandem repeats in this group of LEA proteins. A Ser-rich S-segment is also present along with some other conserved polar and hydrophilic sequences in between the K-segment. Based on the presence and assembly of these multiple conserved segments, the group 2 LEA proteins are further classified into mainly five subgroups. K-subgroup proteins contain the K-segment while those inclusive of an additional S-segment are grouped in the SK subgroup. Likewise, YSK, YK, and KS subgroups have also been classified. CD spectra and NMR analysis demonstrate that group 2 LEA proteins have unadorned hydrophilic unstructured configurations in the aqueous form. Key factors responsible for group 2 LEA protein induction are seed desiccation and water-deficit conditions. During optimal growth conditions, these proteins are distributed

throughout vegetative tissues of the plants. The primary protective mechanism of the membranes involves the α-helical amphipathic structures formed by the K-segment of group 2 LEA proteins. High ionic content and high solute concentration in the dehydration state induce the adoption of a more structured form of group 2 LEA proteins thereby playing a physiological role in water-deficit plant responses. The ability of certain plants to tolerate freeze stress at temperatures as low as −196°C is due to the formation of buds which reassume growth once favorable conditions return. Group 2 LEA proteins develop in the extreme wintertime dehydration state during which desiccation of the buds is maximum. Because of the expression of these proteins in response to cold stress, they are also referred to as the COR (the cold-responsive) proteins. The stress-responsive pathway adapted by this particular group of LEA proteins may be ABA-dependent or ABA-independent one. These proteins are majorly accumulated in the nucleus or the cytoplasm. The phosphorylated S-segment in the SK2 proteins is postulated to be the possible nuclear localization signal (NLS). However, phosphorylated state is not the utmost requirement in other NLS. Although there are no metal-binding pockets in the group 2 LEA proteins, some His-rich dehydrins have the ability to bind metals like Cu^{+2} and Ni^{+2}, whereas acid dehydrins tend to bind Ca^{+2} metals. The acidic dehydrins act as calcium buffers or calcium-dependent chaperon-like molecules. On the flip side, the metal-binding ability may be attributed to the detoxification potential under stress conditions, where ROS production is associated with metal toxicity. Thus, these proteins act as scavengers under the oxidative stress conditions induced by drought or other forms of physiological stress (Battaglia et al., 2008).

1.3.3 Group 3 LEA proteins (D-7/D-29)

An 11-amino acid-repeating motif is present in this group of LEA proteins. The difference in the molecular mass of these proteins is due to the number of this particular 11-mer motif. Additionally, some other conserved sequences have been found in these proteins which are rarely repeated and their sequence is different from that of the 11-mer motif. The group 3 LEA proteins are the most diverse group of proteins in comparison to the other LEA protein groups. This is due to the alterations present in the conserved 11-mer motif of amino acid in the wide variety of plant and bacterial species, as well as the different strains of the same plant species. This 11-mer motif variability leads to the subclassification of the group 3 LEA proteins into 3A (D-7 LEA) and 3B (D-29 LEA) subgroups, respectively. The 3A subgroup is highly conserved as it possesses the same 11-mer motif with minimum variability. However, the 3B group is more heterogeneous with the vast variability of the 11-mer motif. The secondary structure of the group 3 LEA proteins is mostly an amphipathic α-helical right-handed coiled-coil dimer. CD and infrared (IR) spectrums of group 3 proteins suggest the absence of this secondary structure in the aqueous form. However, the exposure by glycerol, glycol, ethylene, methanol, or fast drying induces the secondary coiled-coil structure. The structure of group 3 LEA proteins depends on the dehydration or drying rate. When the dehydration rate is slow, a β plated sheet conformation along with the α-sheets is acquired. Upon rehydration, the random coiled structure is regained, indicating the potential of reversal of the structural transitions. The reducing sugars form a cytoplasmic glass in association with the LEA proteins (by changing their conformation and molecular mass) which prevents the cellular organelles from dehydration stress in association with the membranes. Aside from plants, certain organisms also possess the group 3 LEA proteins, such as the *Deinococcus radiodurans*, *Haemophilus influenzae*, and *Caenorhabditis elegans*. AavLEA1 is the best characterized group 3 LEA protein outside the plant kingdom. This protein is unstructured and less compact in aqueous form due to a high degree of hydration; however, upon dehydration, a reversible α-helical form was observed. During specific developmental stages, the group 3 LEA protein expression is controlled by ABA-dependent or stress-regulated pathways, in comparison to other LEA protein groups. These proteins are so far discovered and are widely distributed in most plants, algae, nonvascular and seedless vascular plants. This diversity indicates that this group protein might have a range of intracellular localization and different targets. The research so far indicates the role of group 3 LEA proteins in their contribution to overcome the adverse effects of drought stress in most of the plant species including wheat (Battaglia et al., 2008).

1.3.4 Group 4 LEA proteins (D-113)

The wide distribution of the group 4 LEA proteins is seen in the vascular (angiosperms or gymnosperms) and the nonvascular (bryophytes) group of plants. The N-terminal of the LEA proteins is conserved in this family. This is usually 70−80 residues in length. The C-terminal in group 4 LEA proteins is less conserved and is variable in size. The motif 1 (AQEKAEKMTA[R/H] DPXKEMAHERK [E/K] [A/E][K/R]) in the N-terminus is conserved in group 4 LEA proteins and is characterized by the consensus sequence, while four other motifs are also found in group 4 LEA proteins. The presence or absence of motif 4 and 5 classifies two subgroups within the group 4. Group 4A has three motifs (1, 2, and 3) in the N-terminus; whereas group 4B possesses all five motifs with motif 4 and 5 in the C-terminal region. Group 4A has small proteins (80−124 residues in length) while that of 4B are

comparatively longer (108–180 residues in length). The initial 70–80 residues of group 4 LEA proteins adopt an α-helical conformation while the rest of the residues remain in a random uncoiled conformation. Similar to the group 3 LEA proteins, the group 4 LEA proteins have also been found to be associated with the crystal glass formation in cold stress dehydration state. These proteins were originally discovered in the dry embryo accumulations. Group 4 LEA protein transcripts were identified in the coleorhizae of developing wheat seeds. However, the same seeds under abiotic stress seem to accumulate group 4 LEA proteins in the coleoptiles. In other plant seeds, the group 4 LEA proteins are found scattered among different tissues and may or may not be induced by stress or ABA pathways. D-113 LEA protein is homogeneously distributed in all of the tissues of the embryo. These protein transcripts show response to drought, salinity, or temperature stresses. Histone deacetylation leads to the repression of group 4 LEA protein transcript formation during germination, as predicted by gene analysis. Group 4 LEA proteins seem to prevent LDH inactivation even when 99% water is lost to dehydration, thus helping the plant to cope with the drought stress (Battaglia et al., 2008).

1.3.5 Group 5 (atypical LEA proteins)

All those LEA proteins which lack the usual hydrophilic properties and possess hydrophobic contents in high quantity are characterized in this group of proteins. So most of the members of this group are nonhomologous. Therefore, the hydrophobic proteins related structurally are divided into further subgroups. The subgroups include the 5A (D-34), 5B (D-73), and 5C (D-95) groups, respectively. A little is known about this group of LEA proteins. During the later stages of seed development, the transcripts of these proteins start to accumulate. Stress environments such as that of UV light, cold, drought, salinity, and wounds also initiate the development of these proteins. They adopt a globular-like confirmation in stress state which is because of their insolubility after boiling (Battaglia et al., 2008).

1.3.6 Group 6 LEA proteins (PvLEA-18)

The first protein identified from this group is the PvLEA-18 protein of bean. So far this family has almost 36 members identified, most of which are from the vascular plants. Small-sized proteins are present in this group (7–14 kDa). The prominent feature of this group of LEA proteins is that their structure is conserved to a great extent. Total four distinguishing motifs are present in this group, out of which motifs 1 and 2 are highly conserved. LEDYK sequence in motif 1 and the "Thr" and "Pro" residues on position 7 and 6, respectively, are 100% conserved. The group 6 LEA proteins are inherently unstructured. These proteins are highly hydrophilic and lack the "Trp" and "Cys" residues. One important feature of group 6 LEA proteins is that they do not show coagulation at high temperature. They migrate at a higher molecular mass than predicted from their amino acid sequence during SDS-PAGE. The embryo radical accumulates high concentration of the PvLEA-18 proteins during the earlier seed germination phase and pollen grain formation. Additionally, their level also tends to rise after ABA treatment and water stress conditions, predicting their possible protective role as well. In contrast to the other groups of LEA proteins, dehydration inactivation of the enzymes is not prevented by the PvLEA-18 proteins. The molecular targets of this protein are different as compared to that of other LEA proteins. This indicates that these proteins owe their protective role to factors other than their hydrophilicity (Battaglia et al., 2008).

1.3.7 Group 7 LEA proteins (ASR1)

This group also contains a large number of hydrophilic residues and is further subdivided into multiple subfamilies. ASR1 proteins are small in size, heat stable, and unstructured intrinsically. These proteins possess three consensus sequences (motifs 1, 2, and 3). Motif 3 contains an NLS and is localized in the C-terminal region. Only the N-terminus of ASR1 proteins contains the Motif 5. Another conserved sequence of motif 4 is also found in these proteins. All of these motifs are His-rich regions. The physiochemical properties of proteins of this group are correlated to that of other LEA protein groups. Like the other LEA proteins, these group proteins also accumulate during late embryogenesis phase and in water-deficit stress conditions. Gene expression of these proteins is variable among different species of plants. Transcripts of group 7 LEA proteins may accumulate during fruit ripening, seed and pollen maturation, senescence, or environmental stresses such as drought, salinity, cold, or limited light. Sugar level may also alter their gene expression and so will the ABA conditions. The tissue and organ specificity of the group 7 LEA proteins is diverse. Tomato, grape, melon, and apricot seeds possess the transcripts of group 7 LEA proteins. As is the case with other LEA protein groups, group 7 LEA proteins also show a random uncoiled aqueous structure, but Zn ion binding or desiccation stress resulted in the ordered conformation of these proteins (Battaglia et al., 2008).

2. Molecular structure of LEA proteins

The LEA proteins have a molecular weight of approximately 10–30 kDa. The molecular and structural properties of the proteins are determined using CD spectrum or Fourier transform infrared (FTIR) spectrum. Artificial lipid granules or vesicles are used to study the mode of action with the membrane. Also, we use genetic approaches such as RNA interference, overexpression, or green fluorescent protein (GFP) tagging to study the function and localization of the proteins in plants. There is an extensive study indicating the correlation between the expression on LEA proteins or their genes with stress resistance (Shih et al., 2008; Hand et al., 2011; Tunnacliffe et al., 2010). Many transgenic approaches have shown that overexpression of LEA proteins from different species into wheat, rice, *Arabidopsis*, tobacco, and lettuce provides higher abiotic stress-resistant phenotypes (Leprince and Buitink, 2010). However, the precise molecular function of LEA proteins is still unclear and so far LEA proteins have been suggested to act as stabilizers, hydration buffers, membrane protectants, antioxidants, organic glass formers, and/or ion chelators (see Amara, 2012, for references). Recent research on LEA protein also have shown that these proteins act as chaperones (Kovacs et al., 2008; Hincha and Thalhammer, 2012; Cuevas-Velazquez et al., 2017). To test this proposed mechanism or hypothesis, a recombinant wheat protein was observed. This protein belongs to group 1 LEA protein. An experiment with CS in heat-stress condition where the enzyme is likely to aggregate at high temperature shows that LEA proteins do not behave like molecular chaperones classically. A model is proposed which proves that LEA protein act just like a "molecular shield" which helps the protein to escape damage during dehydration (Shih et al., 2008; Hatanaka et al., 2013).

2.1 Three-dimensional structure of LEA proteins

2.1.1 Solution status

The secondary structure of LEA protein is characterized by techniques such as NMR or FTIR spectroscopy. Biophysical properties are determined using the Em proteins of wheat embryos. When observed under UV spectrum, it was found that the Em proteins in KC1-HEPES buffer have about 70% of random coils with only minor spiral symmetry. Hydrodynamic techniques showed that Em proteins are globular proteins (Shih et al., 2008). Em proteins still contain over 50% random coiled conformations in the presence of trifluoroethanol (TFE), a common α-helical-promoting cosolvent. Far-UV CD spectra of various temperatures revealed that the soybean GmD-19 proteins were highly disordered in solution state and underwent the temperature-induced unfolding process. In the presence of TFE or sodium dodecylsulfate (SDS), both being α-helix-promoting agents, the spectra indicated that the proteins adopted restricted α-helical conformations. Although SDS micelles might induce the conformational change, incubation of GmD-19 proteins with phospholipids had no effect on protein structures (see Shih et al., 2008, for references).

2.1.2 Dry status

Protein function can be determined easily as the LEA proteins accumulate during late embryogenesis where the water content is severely low. Knowledge of the structure of LEA proteins in the dry state is of great importance. The first ever protein that was used to determine the structure in dehydrated state was "*Typha latifolia* D-7 LEA protein." FTIR spectrum showed that these proteins possess secondary structures, i.e., sheet and helix-like structures (Shih et al., 2008). As water is removed, the protein assumes progressively a more folded conformation. At 84.5 wt%, LEA protein is completely solvated. At 50% water between 83.5% and 50.4%, the protein is unstructured. In this range and below this point, water molecules no longer are sufficient to fully solvate the protein. At less than 20% water, the protein becomes more dehydrated and begins to adopt a significant amount of secondary structure. By decreasing water, α-helical structure is apparent, and hairpin-like structures are formed (Amara, 2012).

3. Recombinant LEA proteins

Wheat LEA genes have been manipulated to prevent drought resistance in most of the plants. For instance, *DHN-5*, a wheat desiccant that was overexpressed in *Arabidopsis*, displayed better growth, water retention, and more negative water potential under drought stress conditions. Another gene, *TaLEA3* from wheat, enhances leaf water potential, as well as the average rate of growth of the recombinant plant (Jewell et al., 2010). Overexpressing wheat TaLEA3 and TaLEA2 in yeast also improved transgenic yeast tolerance to hyperosmotic, salt, and freezing

stresses (Yu et al., 2005). The synthetic peptide PvLEA-22 has the ability to preserve liposomes in the dry state (Furuki and Sakurai, 2014). *AavLEA1* is a recombinant LEA protein, which is prepared by the following protocol:

Group 1 LEA protein Em cDNA sequence is amplified by PCR using synthetic oligonucleotide-sequenced primers. The sequence is cloned into pCR2, cut using enzymes, and ligated. The plasmid is transformed into *Escherichia coli* strain. Expression of the protein with N-terminal His-tag, production and purification of AavLEA1 recombinant protein are quite important (Goyal et al., 2003).

4. LEA proteins and drought stress in wheat

The two most common natural factors having a negative impact on the yield of wheat are high temperature and water stress (Aprile et al., 2013). The LEA proteins are abundant in the seeds of higher plants and are known to occur in the seedlings of all plants. Their main function is the induction of drought tolerance in plants including wheat (Hong-Bo et al., 2005). The proteins activate when there is extreme water loss. Nature has adopted a safety mechanism in the plants which help them to overcome the different kinds of stress a plant is made to face in the environment, which for the wheat plant is in the form of LEA proteins. Drought is a single largest abiotic stress factor causing a remarkable reduction in yield of wheat crops worldwide (Budak et al., 2013). Plants mainly respond to stress environments by altering the gene expression and modification of gene products, i.e., proteins. Some of the genes of wheat are known to express at a great pace when facing drought stress, resulting in the production of beneficial proteins and enzymes including dehydrins (Close, 1996), vacuolar acid invertase (Trouverie et al., 2003), glutathione S-transferase (GST) (Anderson and Davis, 2004), and LEA protein (Pnueli et al., 2002); expression of ABA genes and production of proteins like RAB, rubisco, helicase, proline, and carbohydrates are molecular basis of drought tolerance in wheat (Nezhadahmadi et al., 2013).

During drought stress, some proteins are overexpressed including the LEA proteins. These proteins occur in the vegetative tissues during the desiccation of seeds under drought stress (Dure, 1993b).

Among all, three conserved domains have been identified in all group 2 LEA proteins, which are the K, Y, and S segments; the presence of the K-segment allows wheat dehydrin DHN-5 to protect the activities of LDH and β-glucosidase in vitro (Drira et al., 2013). The expression of both DHN-5 is induced by ABA and by several stress conditions like salt and dehydration (Brini et al., 2007; Yang et al., 2012; Arumingtyas et al., 2013; Liu et al., 2015).

The LEA proteins undergo an increase in size modification, and their size may rise as high as 200 kDa as compared to 10−30 kDa normal weight (Ouellet et al., 1993). The LEA proteins also assist in the recovery of other proteins that have been denatured as a result of water stress and can be recognized by their specific sequence of amino acids (Dure, 1993b). Research has been carried out on this category of proteins, and the main focus of the scientists is the genetic engineering of these proteins for enhanced resistance to water stress in the wheat plant.

5. Stress signaling pathways

The drought stress is first recognized by the membrane receptors of the plant cells, and then the signal is transuded downstream resulting in the generation of second messengers including calcium, reactive oxygen species (ROS), and inositol phosphates (Fig. 12.1). These second messengers regulate the intracellular calcium level with the help of Ca^{2+} sensors, i.e., calcium-binding proteins. These proteins then interact with appropriate partners and initiate a phosphorylation cascade to target the major stress-responsive genes or the transcription factors controlling these genes. Overexpression of transcription factor gene activates several downstream stress-responsive genes to amplify stress tolerance. These stress gene products direct plant adaptation and plant survival, consequently beating unfavorable conditions. Hence, the plant responds to stresses as an individual cell or as an organism. Stress alters gene expression and may be involved in the production of different hormones like ABA. Moreover, these molecules then amplify the initial signals and may initiate a second round of signaling which can carry out the same or different signaling pathways (Mahajan and Tuteja, 2005).

The stress-responsive genes are mainly classified as early- and late-induced genes. Early genes respond to stress within minutes. These transcription factors do not synthesize new proteins, and the signaling molecules are already present. However, late-induced genes respond slowly to stress, i.e., within hours after stress. Their expressions are often sustained. These genes comprise the major stress-responsive genes such as RD (responsive to dehydration) which encodes and modulates the proteins needed for synthesis, for example, LEA proteins, membrane-stabilizing proteins, and osmolytes.

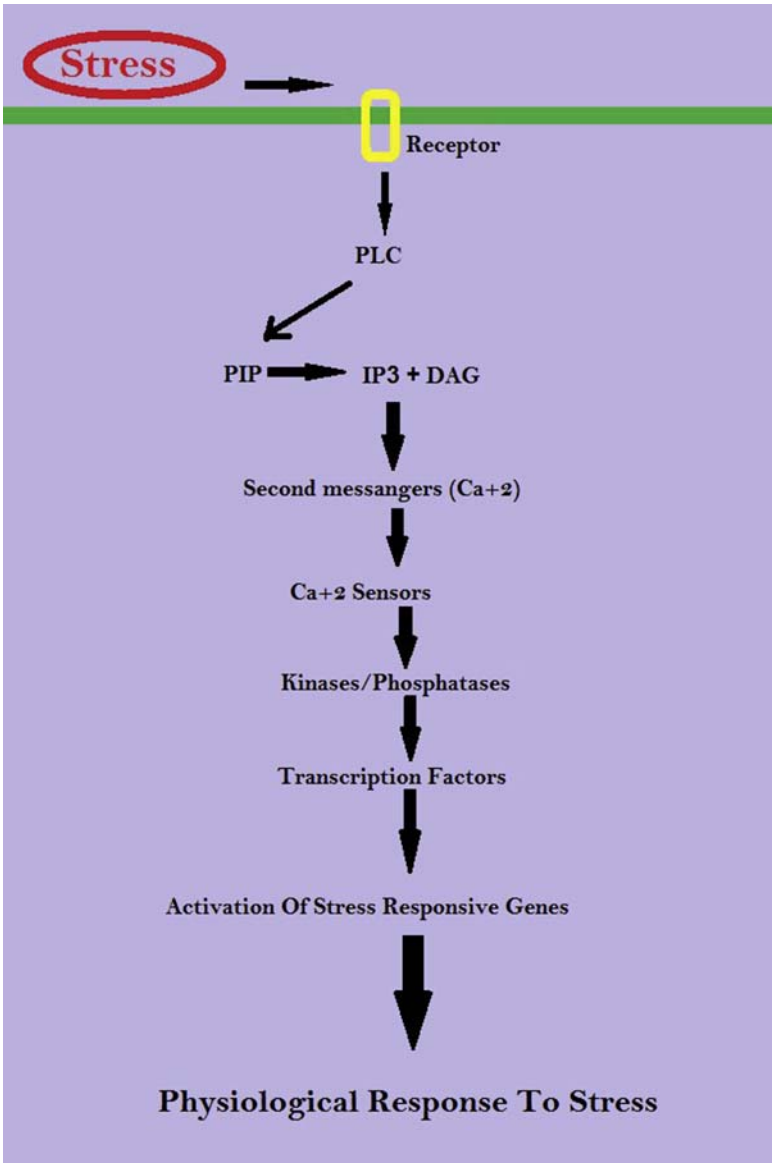

FIGURE 12.1 General signal transduction pathway under stress.

Drought stress causes various changes in cells including alteration in the expression of LEA genes, molecular chaperones synthesis, which assists the protection of associated protein from proteinases and degradation and removal of denatured proteins (Zhu et al., 2007).

RD genes that are responsive to desiccation are modulated by drought gene (Zhu et al., 2007; Seki et al., 2001). RD genes are divided into two main groups. RD group 1 includes the regulatory, gene expression and the signal transduction during the response to the stress of the crops, and the RD group 2 contains those proteins whose function is protection against stress directly (Seki et al., 2001).

Water-deficit conditions during late embryogenesis stages induce the LEA protein accumulation. LEA proteins showing specific amino acid composition and expression are highly hydrophilic. These characteristics make them important in desiccation tolerance. Under desiccation stress, the random structure of LEA turns to a coiled α-helix structure (Fig. 12.2) (Hand et al., 2011).

On the basis of biochemical properties and sequence alignments, LEA proteins are divided into different groups. Group 1–3 LEA proteins are most frequently identified in the wheat plant. The group 1 LEA proteins are classified by their 20-mer motif. The Em wheat protein characterizes this group. Dehydrins (group 2) of LEA proteins accumulate in response to dehydration. One LEA protein, RAB or D-11, induces a response to different stress conditions (Bray, 1997).

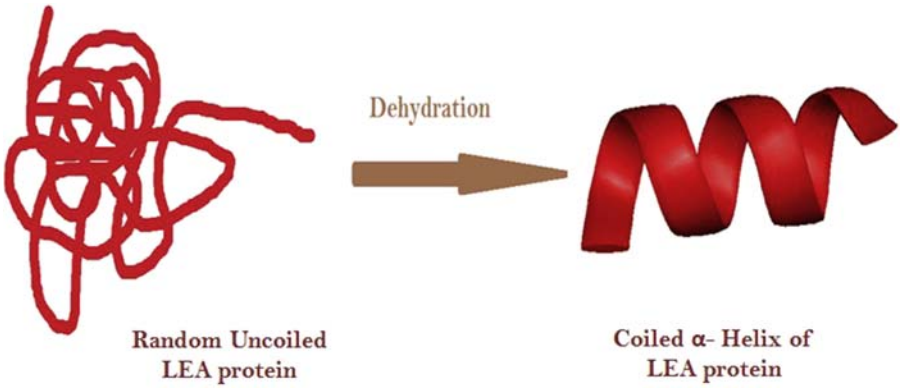

FIGURE 12.2 In the process of dehydration, LEA proteins form the coil structure of α-helix.

Extensive studies in wheat seedling stage indicate that *HVA1* gene facilitates increased wheat growth under drought. Overexpression of *HVA1* gene group 3 LEA proteins within the roots and leaves of wheat tends to retain tolerance to drought stress (Browne et al., 2002). *HVA1* gene has 11 amino acid motifs in nine repeats. In wheat, the size of LEA proteins reaches to 200 kDa in response to drought stress. Therefore, these proteins survive even after denaturation (Hand et al., 2011).

Sequence analysis of *pMA2005* shows that gene contains 11 amino acid tandem repeats. *pMA2005* codes mRNA of wheat group 3 LEA proteins. Expression of the *pMA2005* gene is considered to be a significant player in drought tolerance induction within the wheat plants (Curry et al., 1991).

In developing seeds of wheat, LEA transcripts of group 4 accumulate in coleoptiles during stress. However, in normal conditions, quantitative reverse transcription of developing seeds showed a high content of the LEA transcripts in coleorhizae (Battaglia et al., 2008). Group 4 LEA proteins contain conserved N-terminus, which forms α-helix and a diverse C-terminal to form random coil structure (Sivamani et al., 2000). Group 5 LEA proteins mostly adopt a globular structure and contain several hydrophobic residues (Ramanjulu and Bartels, 2002).

6. Future prospects

The tendency of wheat plants to tolerate drought can be enhanced by the incorporation of drought-related QTLs to the modern forms of wheat cultivars. For this strategy, identifying candidate loci related to drought tolerance is a major task, which can be successfully undertaken by the modern QTL mapping techniques and Omics studies (Budak et al., 2013).

Wild varieties of wheat such as *Triticum dicoccoides* can be exploited for this purpose because of their great stress-tolerant properties. Molecular level characterization of drought-tolerant LEA proteins and others is to be carried out first, after which, the development of transgenics shall identify their proper role in the cells. Once the tolerance loci integration is confirmed, field trials in special environments are to be carried out which give a detailed view of morphological and physiological characteristics of the newly developed cultivars. This is very helpful in determining their performance when exposed to drought stress or the possible yield enhancement (Budak et al., 2013).

Several breeding methods have been performed to produce drought-tolerant wheat. At ICARDA (International Center for Agriculture Research in Dry Areas), germplasm, produced by crossbreeding of wild wheat species, increases high yield under drought. To enhance the yield, the priority is to improve drought tolerance of the wheat plant. Water stress condition is applied at various stages of crop growth and development to identify water stress–tolerant wheat genotypes. Root system size of wheat can be a selection target for drought tolerance. Crop root extends to deeper soil regions and alters their morphology and gene expression, thus increasing the water uptake by wheat. Wheat genotypes with good water management can bear high yields in drought conditions (Manschadi et al., 2006). Wheat genotypes with good water management and recombinant LEA protein could be used to generate new breeding cultivars to increase yield in drought.

Drought management strategies are very important in which crop establishment, maximum growth of crop, and increasing seed yield are considered. Many agronomical ways are practiced to control drought stress, such as field irrigation control and drought resistance gene identification through screening. Preservation of water source is the aim in drought conditions. Therefore, crop rotation can limit the water needs by irrigation.

It is important to detect the plant's genomic responses to drought stress as it provides intensive information about transcriptional reactions and helps in distinguishing reactive stress promoters and associated elements. Drought resistance can be improved by manipulating the genes and transcriptional factors that regulate plant growth. QTL analysis and molecular mapping have been also performed for both qualitative and quantitative characteristics including drought resistance stress. Due to some limitations, QTL does not give distinct impact and tends to cease in various groundwork (Sahebi et al., 2018). It is difficult to identify specific trait or gene needed for improvement to increase yield because of the high variability of water stress in nature.

Manipulation of functional gene and genes involved in signal transduction has been successfully performed in various plants including wheat that resulted in enhanced desiccation tolerance. Transcriptional factors are also modified and altered, overexpression of TFS in model plant *Arabidopsis* and wheat also showed better survivability (Carver, 2009).

Field performance of multiple transgenic crops has been evaluated recently. The results indicated that the LEA proteins increased the yield gain in the water-stressed environment (Carver, 2009; Cho and Hong, 2006).

7. Conclusion

The major concern associated with the enhancing world population is the decline in food yield due to many stress factors (Mahajan and Tuteja, 2005). One of the main stress factors is drought, limiting food production in the agricultural fields. Wheat is grown on arid agricultural fields (Kilic and Yağbasanlar, 2010). Common wheat possesses a genome which is complex and has a size of 16 Gbp, comprising 90% repeated sequences (Hassan et al., 2015). Drought causes serious threats in wheat production areas. It is now understood that any signal of stress is recognized at membrane level by different receptors and after that it is transferred to different cells to activate genes involved in introducing drought tolerance (Mahajan and Tuteja, 2005). Drought regulates many protein kinases. One of them is mitogen-activated kinase which regulates osmotic homeostasis. Different systems of phospholipids are activated by drought stress, which form different molecules of the messenger (Zhu, 2016). Dehydration-responsive element-binding proteins (DREBs) comprise a diverse group of TF's that initiate many functional gene expression and stress tolerance induction (Jan et al., 2017). Drought stress causes regulation of expression of different genes, including induction of DHN gene (LEA gene group) (Zhu, 2002). Dehydrins (DHNs), responsible for protective functions, are produced in response to ABA. DREB controls the expression of cold-regulated (COR) gene. LEA proteins are also known as dehydrins or cold-responsive protein. Several research studies predict that the expression of LEA-inducing gene is increased by raised level of DREB expression (Hassan et al., 2015). LEA protein has many functions in stress control. It maintains the metabolism of many plants under the influence of stress factors. It also has a role in dehydration tolerance where it protects the cytoplasm from adverse effects of dehydration. These proteins are expressed during all developmental stages with nonspecific tissue affinity (Hong-Bo et al., 2005). Additionally, the protein helps in protecting different cellular structures because of its unique structure which helps in binding water, thus helping in maintaining minimum cellular requirement. These genes are not identified in plants with sufficient water availability but in plants experiencing water-deficient conditions, thus predicting their role in drought tolerance (Zhu, 2002).

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CHAPTER

13

Role of osmoprotectants and drought tolerance in wheat

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OUTLINE

1. Introduction

1.1 Drought

An extensive period in a particular region that deprives the plants or land of the water supply or provides it in the minimal quantities is commonly referred to as drought. A low level of precipitation in the environment can lead to the ramification of drought which may last for days, weeks, months, or even years in case of extreme circumstances. Drought can also be defined as a prolonged period in which excessive dryness prevails leading to all sorts of economic as well as agricultural loss. It is a commonly accepted concept that a particular region under high-pressure conditions for a long time period causes the drought to occur. The cloudless and completely clear sky which is formed because of such prevailing weather conditions initially leads to lesser precipitation in the environment and ultimately drought (Sheffield and Wood, 2008).

1.1.1 Types of drought

There are different types of drought, some of which are as follows (Fig. 13.1):

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00013-3

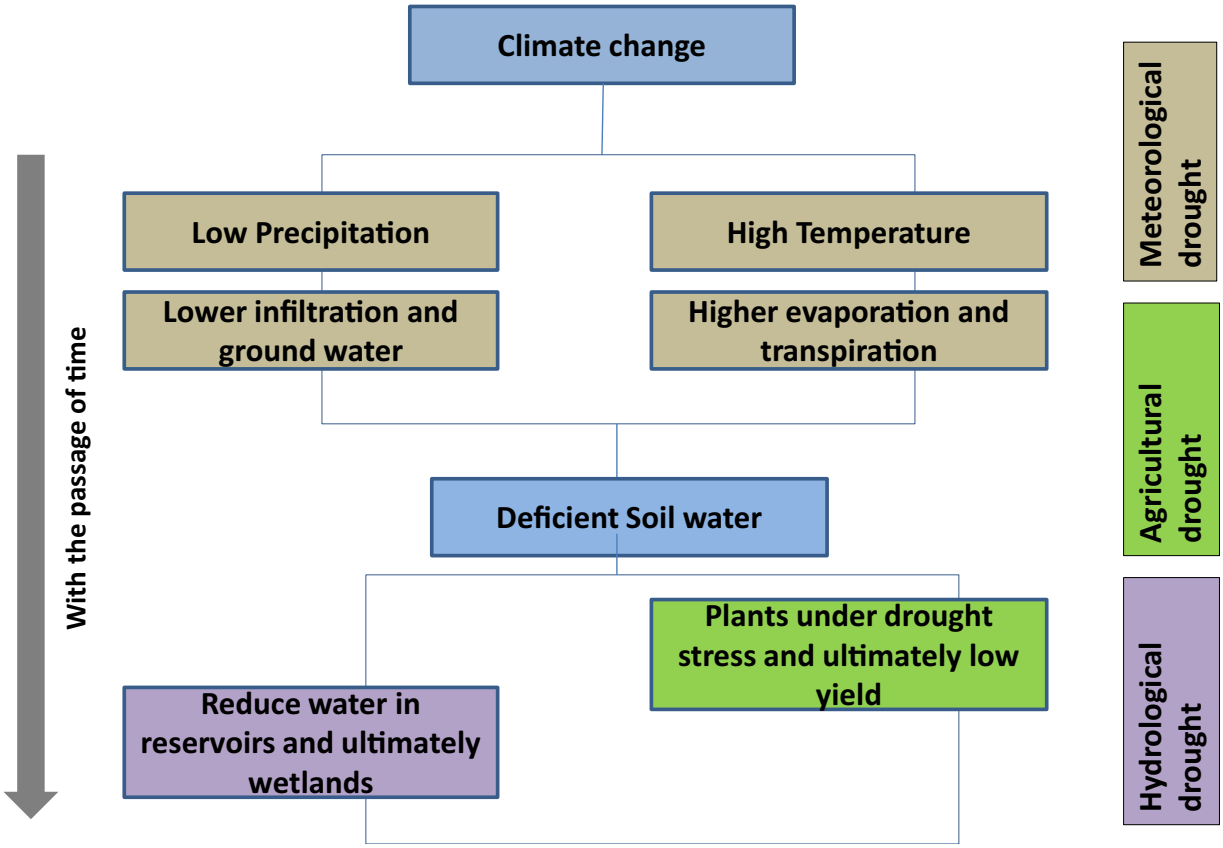

FIGURE 13.1 Drought, its types, and a few impacts due to drought stress.

1.1.1 Meteorological drought: This kind of drought is caused primarily because of weather and leads to a shortage of water in a particular region naturally (Quiring, 2009).

1.1.2 Agricultural drought: A considerable decrease in the average moisture that enables the crops to grow in the fields or promote the production of grass over a range of land is referred to as agricultural drought. The majority of the cases of agricultural droughts premise on a below average precipitation in the environment; it may as well occur during normal precipitation states provided that the agricultural techniques are being employed, or the condition of the soil call for an excessive amount of water (Quiring, 2009).

1.1.3 Hydrological drought: Instability in the maintenance of water in lakes, aquifers, and reservoirs may lead to a particular condition of drought which is termed as hydrological drought. Since it premises on a rarely high human demand of water, it may or may not occur during the lower precipitation states of the environment (Quiring, 2009).

Although the air, temperature, and wind conditions play a major role in defining the meteorological conditions which might lead to drought, the role of pedology (study of soil in its natural environment) and vegetation conditions cannot be ignored. Therefore, it goes without saying that soils with an enhanced capacity of storing water for a long span might remarkably be better as well as resistant to different types of drought. Not only the ground water but its depth determines the resistance of a soil against drought. To disable the soil to dry up and be jeopardized, a dense vegetation cover might be put to use. It is indispensable to mention here that droughts are commonly found in the arid and the semiarid areas. Also, the high mountain regions, where the precipitation in the environment is commonly lower than average and rainfalls are not too frequent, represent equal incidence (Quiring, 2009).

1.1.2 Hazards and risks associated with drought

Enumerating the whole list of such hazards might be beyond the scope of this chapter, therefore the focus has been drawn to a few of conspicuous hazards, but the list is exhaustive:

1. Prolonged periods of droughts lead to dehydration in plants
2. Symptoms may include stalled growth, abrupt leaf and fruit shedding, and ultimately withering
3. Pastures as well as harvest yields are severely affected by drought conditions

4. Shortage of food might also occur in addition to the shortage of water
5. In the worst case scenario, famine may also originate as a consequence of a prolonged period of drought
6. Not only the effect of wind but also the flooding during the drought conditions might lead to soil erosion
7. Another extreme consequence of prolonged periods of droughts may be subsidence which is quite hazardous for the entire land
8. If a particular region is brought under the conditions of drought over and over again, it might lead to a permanent damage to the soil, from which it would not be able to recover
9. Desertification is premised on the conditions of drought
10. Drought may also lead to excessive forest fires since dried up vegetation is remarkably more vulnerable to catch fire
11. Environmental changes which are brought about by drought include lack of biodiversity in the species, changes in the migration patterns, increased soil erosion but decreased quality of air (Cook et al., 2007; Namias, 1983; Schubert et al., 2004; Trenberth and Branstator, 1992).

In a nutshell, droughts occur due to a whole range of reasons which drastically disturbs the water cycle of the environment. One of such reasons is a considerable decrease in the rainfalls which may lead to a lower level of water in the soil, lakes, reservoirs, aquifers, etc. Whenever the human demand of water is not sufficient to meet the agricultural requirements, a period of drought is destined to occur (Lockwood, 1986). Drought can cause huge loss at the economic as well as the agricultural level.

1.2 Osmoprotectants

Osmoprotectants are the extremely soluble, nontoxic, and electrically neutral small molecules or compounds that facilitate in achieving the osmotic balance between cytosol and the cell surrounding, thus helping cells to adapt and survive in severe environmental situations. They are also called compatible solutes or osmolytes (McNeil et al., 1999). Osmoprotectants can be found inside all the organisms ranging from bacteria to plants, animals, and in humans as well. They protect cell constituents like proteins against denaturing, enzymes and membranes against detrimental effects of destabilizing ions. They also help to ensure the balance of osmotic pressure so as to retain cell volume. They also possess cryoprotectant and heat-protectant properties (McNeil et al., 1999; Rathinasabapathi, 2000; Rontein et al., 2002).

1.2.1 Types of osmoprotectants

Chemically there are three types of osmoprotectants:

1. Betaines and allied compounds
2. Polyols and sugars (e.g., mannitol and trehalose)
3. Amino acids such as proline (Pro)

1.2.1.1 Betaines

Betaines are the derivatives of completely N (nitrogen)-methylated amino acids, distributed in plants, animals, and microorganisms. These are quaternary ammonium compounds, Fig. 13.2 represents the chemical structures of the three distinguished betaines from plants: glycine (Gly) betaine, proline (Pro) betaine (stachydrine), and beta alanine (β-Ala) betaine, as well as choline sulfate (choline-*O*-sulfate) and dimethylsulfoniopropionate (DMSP). The latter two compounds are osmolytes; however, these are not included in betaines since DMSP contains a tertiary sulfonium replacement for quaternary ammonium group, and choline-*O*-sulfate carries ester of a sulfate instead of a carboxyl group—but structurally these are nearly close analogs of betaines and therefore exhibit similar chemical and physiological characteristics.

Typically, the concentration of betaines and some other osmoprotectants increase during dealing with stresses such as saline soil, water scarcity, and chilling (low temperature) since the biosynthetic enzymes are stress-related. Osmoprotectants are chiefly confined to the cell cytoplasm together with cell organelles while nearly absent in the vacuoles that occupy around 90% of the plant cell volume. For instance, *Atriplex gmelini* (halophyte) was observed to contain 320 mM betaine in its cytoplasm, but only 0.24 mM in its vacuole. On the other hand, isolated plastids from several plants have also been found with high level of betaine or DMSP, particularly when separated from plant exposed with salt-stressed (McNeil et al., 1999).

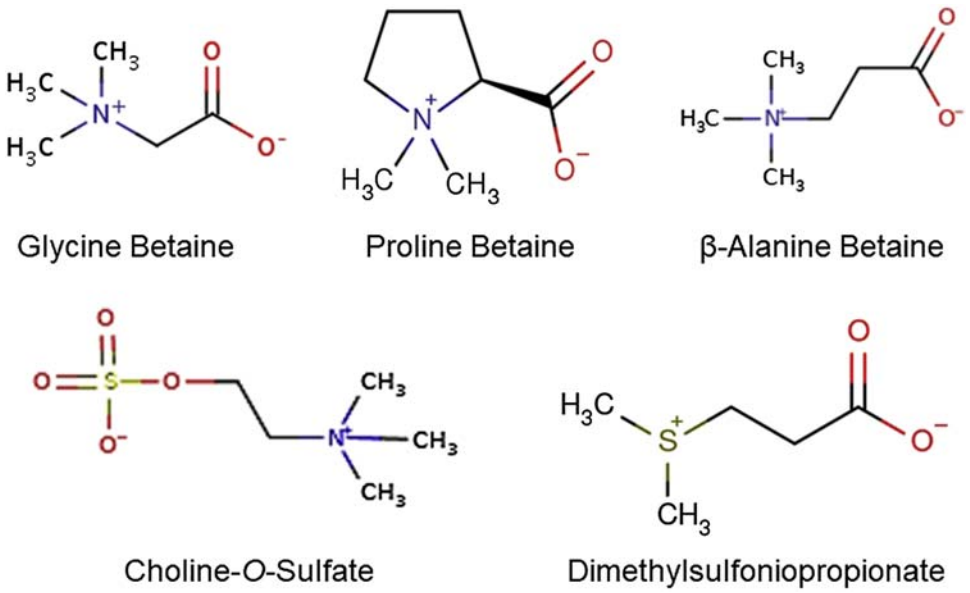

FIGURE 13.2 Structure of different types of osmoprotectants.

1.2.1.2 Glycine betaine

Gly betaine (N, N, N-trimethylglycine) is the quaternary ammonium compound largely occurred in wheat (*Triticum aestivum*) in response to dehydration stress. This compound is chemically neutral and therefore amphoteric over a wide range of pH scale. Additionally, this compound is highly soluble in water, but contains a nonpolar hydrocarbon moiety that exhibits three methyl groups. The molecular properties of Gly betaine allow this compound to interact with domains of both hydrophilic and hydrophobic macromolecules such as enzymes and protein complexes. Gly betaine performs its function by accumulating at a high level on tissue water basis in plants under drought. It acts as a protein stabilizer as mediating activity of chaperone to prevent folding of undesirable protein while maintaining cellular homeostasis and also enhances the tolerance against high temperature (Khan et al., 2009), drought, oxidative and salinity stresses (Roychoudhury and Banerjee, 2016).

Natural reserve of Gly betaine is not enough to ameliorate the deleterious effects of dehydration. None of all varieties of wheat can generate Gly betaine naturally under stress. In some crops the exogenous application of Gly betaine has been performed. This externally applied Gly betaine can be immediately penetrated into the leaves and transported to the plant's other organs, where it may contribute to improve in stress conditions. However, the efficacy of penetration can be enhanced by using different surfactants, for instance, kinetic, lus-50 and sito+ (Sakamoto and Murata, 2002).

1.2.1.3 Polyols and sugars

A firm correlation has been reported between the accumulations of different sugars, viz. galactinol, raffinose family of oligosaccharides (RFO), trehalose and fructan, and polyols (sugar alcohols) like mannitol and D-inositol with the drought stress tolerance. In wheat specifically, mannitol has been reported to improve the growth and resistance to drought and salinity significantly. It is assumed that mannitol acquires this tolerance either by scavenging hydroxyl group or by stabilizing structure of the macromolecule. Furthermore, the D-inositol level accumulates under drought stress and is believed to protect cell membranes and enzymes from deteriorate effects of hydroxyl radicals (Ashraf and Foolad, 2007; Sairam et al., 2002). Moreover, amounts of organic osmolytes like total soluble sugar and free amino acids were increased during salinity stress in studied genotypes of tomato (Balal et al., 2016).

1.2.1.4 Proline

Proline is an abundantly occurred amino acid in higher plants and is known to accumulate in excessive quantity under stress conditions. It is the major reservoir of nitrogen and energy during dry spell. In addition to its prime role of maintaining the osmotic balance as being an osmolyte, it also functions to (1) stabilize the subcellular structures such as proteins and membranes, (2) scavenging uncharged molecules (free radicals), and (3) buffering cellular

redox (oxidation/reduction) potential under the dehydration condition. Rapid disintegration of proline molecule upon relief of stress state may produce sufficient reducing agents which promote mitochondrial oxidative phosphorylation and for recovery and repairing from stress, ATP may be generated. This compatible solute protects the cell components during dehydration. The osmotic adjustment done by it helps to maintain the turgor pressure of the cell that allows the cell expansion and plant growth during water scarcity. It further allows stomata to remain almost partially open, and assimilation of CO_2 continues at water potentials which otherwise may be inhibitory. The high level of proline is due to either its enhanced synthesis from glutamate and ornithine or its decreased oxidative degradation (Allard et al., 1998; Eivazi, 2012).

1.2.2 Functions of osmoprotectants

Abiotic stress factors like droughts, salinity, and extreme weather conditions are the known reasons for the damage to crop productivity. Organisms that exist in a habitat with these predominate limitations have adapted themselves to survive in unfavorable conditions through the use of osmoprotectants like polyols, ectoine, betaines, proline, and trehalose in the cytoplasm of the cells. Some plants have low levels of these compatible solutes while others do not have any. Metabolic engineering aims at rising the levels of these solutes to provide better tolerance to these crops against severe environmental conditions.

1.2.2.1 Protection of proteins

In sodium chloride (NaCl)-sensitive plants, severe environmental situations such as drought and salty soils can diminish a variety of activities crucial for processes of respiration and photosynthesis. Excess NaCl or inadequate water has a number of cellular targets, unlike various toxins and herbicides. The harmful effects of the resulting stresses might be due to dehydration and ion displacement. NaCl-stressed rice accumulates polyamines and proline (Pro). These accumulated molecules have been observed in protecting plants from several damages, caused by dry spell or excessive salinity. Some plants were found to store common saccharides, polyols, and/or, in some cases, accumulate less common saccharides like trehalose. It is assumed that Pro, polyols, and saccharides help as physiologically well-suited solutes that rise according to the requirement in order to maintain a suitable osmotic pressure between the cells and their surroundings. Another evidence is that higher concentrations of these molecules serve as stabilizer for some macromolecules and/or molecular assemblies, thereby reducing either the loss of enzyme activity or integrity of membrane which is observed in water scarcity condition. Within the cell, each osmoprotectant is structurally distinct particularly based on its size, shape, and charge on it and could be assumed to benefit various classes of osmotically sensitive molecules or structures (Garcia et al., 1997).

1.2.2.2 Osmotic balance

Due to severe environmental conditions, a sudden change in the level of solute in the cell disturbs the balance. To restore this balance, the water starts moving from inner side of the cell to the outer side by osmosis, if the concentration of the salt, substrate, or any solute is high outside. Similarly, drought stress in wheat plant causes imbalance in transportation of ions, which ultimately leads to low transpiration rate and reduced growth (Iqbal, 2018). Moreover, as a result, the transportation of substrates and cofactors stops, and the cell goes into a shock. This state is referred to as osmotic shock or osmotic stress. Conversely, if the concentrations of salts become low in the surrounding of the cells, the water will start entering the cells making them swell up, and in extreme conditions, the cells will either burst or undergo apoptosis. Usually unicellular organisms are more likely to be affected by osmotic shock, but mammals also suffer from this in certain conditions. Osmoprotectants help to restore the osmotic balance. When a cell turgid, due to external osmotic potential, opens membrane channels, it permits efflux of osmolytes that transport along with water and restores normal fluid concentration.

1.2.2.3 Cell volume regulation

The cell volume is particularly regulated by osmolytes in animals and bacterial cells. Survival of human and animal cells involves prevention of excessive variations to the cell volume. Instability in the regulation of cell volume contributes significantly to the pathophysiology of numerous disorders, for instance, liver failure, hypercatabolism, sickle cell anemia, diabetic ketoacidosis, fibrosing disease and infection (Lang, 2007). Therefore, osmoprotectant compounds are released in order to restore the cell volume that holds water with them. The shrunken cells accumulate organic osmolytes either by altered metabolism (sorbitol and glycerophosphocholine, and monomeric amino acids) or by $Na+$ coupled transport (myoinositol (inositol), betaine, taurine, and amino acids) (Lang, 2007; Wijayasinghe et al., 2017).

1.2.3 Mechanism of osmoprotectants

The physicochemical basis for this remarkable osmoprotective effect is challenging to understand. However, there is suitable confirmation that in osmoprotective effect, osmoprotectant molecules are excluded from the layer of water that is in contact with protein surfaces. In this situation, native protein structures (folded) are favorable thermodynamically since these involved minimal surface area to the water layer. On the other hand, most of the solutes, for instance, NaCl or $MgSO_4$ directly interact with protein surfaces, moreover favor unfolding structure of proteins that resulted to denaturation (McNeil et al., 1999). There is an alternative perspective that can be proposed based on the evidence that osmoprotectants such as sucrose and trehalose both develop glasses in the dry form (process known as vitrification). It has been recommended that glass formation itself is sufficient in order to stabilize dry biomaterials (Crowe et al., 1998). Tolerance to the abiotic stresses is a complicated mechanism, although mechanism of stress tolerance may vary from species to species. However, the basic cellular responses against abiotic stresses at different developmental stages are conserved among most of the species. Among which, the overproduction of the various types of organic compatible solutes is the common stress responses. Therefore, osmolyte accumulation plays a foremost role in sustaining the activities of the cells and tissues during water-deficient conditions and has been suggested as a powerful tolerance approach for water deficits.

Plants have stress-tolerance mechanisms that may include polyamines, carbon metabolism, apoptosis, but specifically referring to drought, osmoprotectants are very important for the plants in case of water deficiency as drought intolerance can be a major reason for death in plants. These were initially observed in yeast. Ongoing studies in plants show that these have an effective role in plants too when it comes to the drought tolerance. These proteins that express osmoprotectants mainly act as antioxidants. Osmoprotectants can provide an effective feedback to reactive oxygen species (ROS). Genetic engineering/modifications in these proteins can be produced to enhance the resistance of plants drought. Osmoprotectants come from the class of the adaptive traits that are expressed only under the stress conditions (Kolbe et al., 2005; Silva et al., 2011; Chen and Murata, 2008).

In the structure of the osmoprotectants, these are mainly composed of amino acids, polyols, tertiary and quaternary ammonium, and tertiary sulfonium compounds. These are nontoxic in nature at a proper molar concentration of the cell; these maintain the structure of different membranes of the cell. The hydrophilic and hydrophobic interactions of these compounds with the lipid membrane are very important in this phenomenon. At times, the concentration of these compounds in the plants, to stabilize the integrity of plant in drought conditions, is the reason why scientists use the biotechnological/genetic engineering approach to improve the production of osmoprotectants in the plants (Cattivelli et al., 2008; Umezawa et al., 2006).

There are many known osmoprotectants such as mannitol, proline, but considering the latest research and the reviews published, there is still no known mechanism of action of osmoprotectants known. Most recent research studies show that these osmolytes (osmoprotectants) accumulate in the membrane to reduce the osmotic potential of the cell thus actively helping the cell to maintain a constant turgor pressure. Given are some osmoprotectants and their role and action in different plants after genetic engineering. As osmoprotectants are mainly the type of solutes called the "compatible solutes," they are not harmful to the plants in high concentrations. These accumulate in the halotolerant plants in high concentration, causing the stability of many proteins and enzymes, etc., but interestingly these are never accumulated in the plants under normal condition even if the affinity for production of these is increased in the plants in a balanced amount (Serraj and Sinclair, 2002; Rontein et al., 2002; Loescher et al., 1992). Apart from the accumulation in the plants, these compounds also help in hunting the ROS. There is an outbreak of ROS in the plants under the stress condition, thus these compounds act as a scavenger to the ROS hunting them down. This is done as osmoprotectants activating the ROS scavenging enzymes or using other unknown mechanisms for the repression of the ROS (Cattivelli et al., 2008; Shen et al., 1997).

Furthermore, the osmoprotectants are also involved in the changes in the activity of the ion channel proteins via direct or indirect mechanisms. The introduction of certain tissue-specific promoters, for example, in rice, is an important development toward the role of osmoprotectants. In this way, only specific areas are targeted in plants that cause the activation of specific tissues, preventing the overexpression in the plants that many be toxic for the plants.

Mannitol is recognized to be one of the most important osmoprotectants. Its effect on the plant and their drought tolerances seem to be divergent on different plants. For example, when the mt1D gene was engineered in some plants and they showed considerable improvement of the drought and salt stresses in the plants but in contrast, when it was engineered in the tobacco plant it caused salt tolerance and failed to show any drought tolerance. So, the behavior of mannitol varies from plant to plant, i.e., the accumulation of mannitol in the membrane of the cell has different effects on different plants. In addition to mannitol, glycine betaine, which is another important osmoprotectant, is considered as a most important osmoprotectant in the latest research studies. Extensive research has been conducted on the mode of action and working with this compound in the plants and its enhancement via

genetic engineering in plants. This as mentioned above can also be injected via roots and shoots or proper release through modifications in the plant tissues. The accumulation of Gly betaine in the nonstress conditions can be an effective reason for the increased yield under the nonstress conditions. Gly betaine also has a role in the defense of the reproductive organs of the plants in which it is expressed. Proline is another important type of the mainly known osmoprotectants. Recent studies have shown that researchers on the *AtP5CS* gene from *Arabidopsis* and the *OsP5CS* gene from rice showed the expression of proline in all these plants is a major contributor to tolerance in these plants.

Trehalose, one of the most commonly known osmoprotectant, was first found in yeast. The trials that have been carried out on the plants show that the *AtTPS1* enzyme expressed by trehalose is one of the most significant and important enzymes in the drought tolerance of the plant. Several trials also showed its effect on the plants as the enzyme expression causes the production of trehalose-6-phosphate that can affect the morphology of the plants. Also, it causes the production of important carbohydrates that will accumulate in the membrane. Another, *TPS* gene is also involved in the production of the osmoprotectants, a controlled expression of which in rice can cause a stress-inducible and tissue-specific effect in the rice plants. The mechanism of action of almost all the osmoprotectants is almost the same, there might be a few differences in the mode of action, but the overall procedure of action of these is quite similar. Extensive research is being carried out on the genetic modification and the actual mode/mechanism of action of these, but yet the complete information about them is unknown. This is because the plant life and generation time are longer than that of animals, and the field of osmoprotectants is quite new to us (Avonce et al., 2004; Ashraf, 2010; Vinocur and Altman, 2005; Wahid et al., 2007).

1.2.4 Role of osmoprotectants under drought conditions

The drought which affects a significantly large proportion of land annually is one of the most damaging environmental factors and abiotic stress experienced by the crops, limiting both the growth and productivity of the plants. An estimate suggests that >45% of the global agricultural land is subjected to either constant or frequent drought. Under such reduced water content and drying conditions, crops like wheat acclimatize themselves through the assemblage of certain low-molecular-weight organic compounds, collectively known as osmoprotectants, such as sorbitol, trehalose, sucrose, RFO including in sugars, mannitol including in sugar alcohols, proline in amino acids and glycine betaine and polyamines work under amines (Bohnert and Jensen, 1996; Eivazi, 2012) that accumulate under drought state and function as osmolytes in order to maintain plant cell turgor, stabilize cell proteins and structures (Ebeed et al., 2017).

"Osmoregulation" or "osmotic adjustment," commonly known as the accumulation of osmolytes is seen as a potent solution to overcome the drastic effects brought by drought to wheat (Allard et al., 1998). It is an adaptive mechanism which decreases the cell osmotic potential and hence the stability of water absorption and the turgor pressure of the cell. This in turn helps in sustaining the physiological responses, i.e., opening/closing of stomata, photosynthesis process, and ultimately plant growth expansion. Compatible solutes are also involved in detoxification of ROS. Furthermore, certain solutes are also involved in maintenance of cellular components from injury through dehydration. These compatible solutes are also found in the cytoplasm of the wheat cells. During reduced water potential, the accumulation of osmoprotectants requires surplus water to be taken up from the surrounding environment, leading to immediate buffering effect of water shortage within the organism (Agboma et al., 2008; Ashraf and Foolad, 2007). Moreover, by the exogenous application of different osmoprotectants, the temperature of canopy of wheat crop has also been reduced (Suryavanshi and Buttar, 2018). Further, application of certain osmoregulators, particularly Gly betaine and proline provided a significant role on several plant growth and ultimately seed yield under normal or stress states (Dawood, 2016). Additionally, the accumulation of these osmoprotectants is helpful in modulating the phytohormones (salicylic acid, abscisic acid, jasmonates, cytokinins, ethylene, brassinosteroids) that mediated the stimulation of osmolytes under abiotic stress (Sharma et al., 2019).

1.2.4.1 Role of glycine betaine

Glycine betaine is an organic compound, mainly localized within plastid (chloroplasts), and performs an essential role in osmotic adjustment of chloroplast and protection of thylakoid membranes, thus retaining efficacy of photosynthesis (Wang et al., 2010; Gupta and Thind, 2015). In general, Gly betaine plays roles in plant cells protection against adverse effects under stress through (1) stabilizing the osmotic balance, (2) preserving the chemical structure of macromolecules and sustaining membrane permeability, (3) protecting the organelle involved in photosynthesis and promoting the capacity of photosynthesis, and (4) improving antioxidant activities of the enzyme and acting as scavengers against free oxygen radicals. Gly betaine can be applied by exogenously, therefore plays a dynamic role

in chloroplast osmotic adjustment and enhanced drought tolerance (Dawood and Sadak, 2014) besides other resistances, in both Gly betaine accumulated and nonaccumulated plants.

Under drought condition, application of 100 mM of Gly betaine on corn/maize cultivars improved kernels weight, leaves area, plant/grains yield (20%), and harvest index by 5% (Anjum et al., 2012), whereas by the exogenous application of Gly betaine under water stress condition, the endogenous proline amount has been enhanced which in response maintained photosynthesis process in rice plants (Cha-um et al., 2013). The 50 mM amount of Gly betaine has been observed the most effective on foliar, improving several growth attributes and yield of grains in wheat cultivars (Shahbaz et al., 2011), while 100 mM Gly betaine with 1.5% potassium proved to be the best combination for high grain yield of wheat cultivars (Raza et al., 2014) under drought. Therefore, it has been noticed that different plants have altered threshold levels of Gly betaine (Dawood, 2016).

1.2.4.2 Role of proline

Proline is a highly vital proteinogenic amino acid for various essential metabolic processes occurred within the plant tissues. Proline can play as a signaling molecule to (1) control mitochondrial functions, (2) govern cell proliferation, (3) activate specific expression of gene, which can be helpful for plant under stress (Hayat et al., 2012), and (4) help in seed germination and flowering during developmental stages (Singh et al., 2017). Besides, proline act as an osmoprotectant, it also serves in production of turgor, storage of carbon (C) and nitrogen (N), required for preservation of proteins structure, cytosolic pH, redox status, and acting as an antioxidant for ROS in plants at optimum level during stress conditions (Ashraf and Foolad, 2007; Hayat et al., 2012). Under abiotic stress conditions, there is endogenous accumulation of proline indicated in plant tissues; however, external application of proline also increases its level in plant tissue which helps to induce tolerance in plants (Ashraf and Foolad, 2007). However, how effective is this application depends on plant species as well as on plant developmental stage and concentrations of proline being applied. Meanwhile, under certain conditions and the amount being applied, proline can be injurious, since it has been investigated that plants inhibit cell division and growth can be inhibited (Maggio et al., 2002).

It has been examined that by the external application of proline @ 30 mM on maize plants during water stress condition, the photosynthetic factors inclusion of transpiration rate enhanced (Ali et al., 2007). On the other hand, proline reduces harmful effects during water stress on uptaking of nutrients since it also promotes up take of essential nutrients in maize plants (Ali et al., 2008).

1.2.4.3 Role of trehalose

Trehalose is a well-known nonreducing disaccharide, made by two glucose molecules. Generally, plants comprise trace quantities of it. Trehalose plays an important role in various developmental stages of plants, for instance, (1) embryo and flower formation, (2) involved in maintenance of carbon metabolism and regulation of photosynthesis, (3) storage body for carbohydrate, and (4) source of energy besides performing as osmolyte during abiotic stresses (Lunn et al., 2014). The trehalose treatment has been provided under drought condition which in return enhanced the photosynthetic pigmentations in the rice plant (Abdelgawad et al., 2014). Further, role of trehalose is investigated in wheat crop which showed an effective growth under stress due to increase in osmoprotectant compounds (Sadak, 2019). The external application of trehalose is also beneficial in deteriorating oxidative stress. The exogenous utilization of trehalose has been examined on sunflower (Kosar et al., 2018) and wheat (Ibrahim and Abdellatif, 2016) plants which showed enhanced gaseous exchange and improvement as osmoprotectant under drought stress. There has been found a positive correlation between concentration of osmolytes (like proline, total soluble sugar, ions, total soluble nitrogen) with osmotic pressure which increased during drought stress in wheat plants by the exogenous application of trehalose (Aldesuquy et al., 2018). In general, trehalose improves production of all the plant species, however, with different responses under drought stress.

2. Conclusion

In the light of the abovementioned information, it is only fair to conclude that the role of osmoprotectants cannot be overemphasized as far as the drought tolerance in wheat is concerned. There are some different kinds of osmoprotectants which are being utilized to serve the purpose above with the environmental conditions, particular crop under discussions and a few other factors determining the type of osmoprotectants which is going to be the most suitable for use.

However, it is indispensable to state that the role of osmoprotectants in the conditions of drought is an area of extensive research. With a widespread use of the osmoprotectants, the exact outcome has not yet been achieved. There still is a long way to go to the research of osmoprotectants and the possible outcomes and rather benefits which they can provide under the conditions of drought. With the current pace, the technique may enable the farmers and scientists to rule out the negative impacts of drought altogether. Efforts are being put to induce permanent tolerance against drought in wheat which may enable us to get rid of famines, as well as the economic and agricultural losses which are a consequence of drought and are mentioned in the former part of the chapter.

It is of prime importance to mention here that all of the measures which are being utilized against drought are applicable on the short-term basis. Let it be the use of osmoprotectants for the temporary water conservation to enhance the efficiency. However, the need for long-term measures against drought in wheat is not to be condoned. This is exactly why osmoprotectants is an area of extensive research and are being played with to enhance their capacity to induce a permanent resistance against drought in wheat. This is what can be anticipated as an achievement of the near future.

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Further reading

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CHAPTER

14

Spot blotch in bread wheat: virulence, resistance, and breeding perspectives

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OUTLINE

1. Spot blotch: an exigent reality

Among the foliar blights, spot blotch (SB) caused by *Cochliobolus sativus* anamorph:*Bipolaris sorokiniana* poses a major threat to the warmer wheat-producing regions of the world (Wiese, 1987; Mathur and Cunfer, 1993; Zhu et al., 2014). The disease significantly reduces grain yield and quality and has long been identified as a serious concern, particularly for the developing world where food shortages are already prevalent (Duveiller, 2004; Kumar et al., 2010). SB is also referred to as *Helminthosporium* leaf blight or foliar blight, possessing extremely variable pathogenicity with a wide range of host within wild and cultivated *Triticeae* species (Singh and Dhaliwal, 1993; Chaurasia et al., 1999; Zhu et al., 2014).

The disease poses serious constraints to wheat grown on rice–wheat cropping system, and the use of conservation tillage practices furthers the incidence of SB (Duveiller and Sharma, 2009). Furthermore, the increasing threat of SB in the previous decade has compelled crop breeders to acquire such varieties that can resist pathogen invasion. Progress in this regard remained slow, and the reason might be the identification of reliable levels of resistance and unique sources of genetic diversity. Similarly, the role of environmental effects on disease expression cannot be ignored. Therefore, conclusions can only be drawn when resistance evaluations are expanded over several years (Chaurasia et al., 1999). SB is, although, critical for hot and humid climates; still incidence of the pathogen on wheats

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00014-5

grown in the North-western Russia indicates the likelihood of fungal virulence in European conditions (reviewed in Chowdhury et al., 2013). Nonetheless, the recent shifts in global climate, particularly, the rise of temperature, has necessitated urgency to identify resistance sources and develop SB-resistant wheat varieties (Joshi et al., 2007; McMullen, 2009; Lillemo et al., 2013).

2. Symptoms of the spot blotch and life cycle of the pathogen

The fungus is a saprophyte and produces thick-walled conidia for survival. Furthermore, the inoculum overwinters on rice stubbles, wheat seeds, soil, and weeds may provide additional shelter (Murray et al., 1998; Acharya et al., 2011). Primary infection is usually initiated on the coleoptile or primary roots. Healthy plant tissues are pierced by the pathogen, and conidiophore germination completes in 4 h; appressoria appear at the point of intact of epidermal cell wall after 8 h, and hyphae from preinfected cells enter the neighboring cells in 24 h. Infected tissue disintegrates as the infection creeps through the epidermis into the cortex region and takes over the endodermis (Bisen and Channy, 1983; Arabi and Jawhar, 2003). SB detection becomes possible in the form of lesions with dark brown color after 3 weeks of plant emergence. Yellowing if present might be due to toxin production, and the numbers of lesion are directly proportional to the quantity of viable spores in soil (Lillemo et al., 2013). In susceptible genotypes, the lesion spreads vigorously, and lesions may attain a size up to several centimeters causing leaf death. Fruiting bodies are easily observed on old spots at the time of development under humid conditions. Infected spikes have shrunken grains with characteristic black points toward the embryo (Duveiller and Sharma, 2009; Chowdhury et al., 2013).

Warm temperatures favor growth of pathogen, whereas the optimal soil temperatures are 28−32°C. Spread of the inoculum within the region requires movement of soil either through wind or water, whereas long-distance dissemination of the pathogen is achieved through seed dispersal (Murray et al., 1998; Acharya et al., 2011). Lower leaves are often more severely damaged because SB is a seed-transmitted disease and progression of the disease is from lower to upper plant parts. Under favorable conditions, disease epidemics are observed when infestation is during the heading time (Han et al., 2010; Acharya et al., 2011). In older lesions, often conidia formation is observed during humid conditions. Symptoms caused by coinfection of SB and tan spot (caused by *Pyrenophora tritici-repentis*) are sometimes difficult to differentiate unless laboratory support is provided (Duveiller et al., 2005; Joshi et al., 2007; Lillemo et al., 2013).

3. Yield losses due to spot blotch

Wheat is the staple food crop cultivated on extensive scale throughout the world for its high nutritional value. Approximately 35% of the world's population relies on wheat, and this dependence on wheat crop is likely to rise rapidly than for any other crop (Sharma et al., 2002; Joshi et al., 2007). Sustainable wheat production in the past three decades has played a key role in ensuring food security in the most populous parts of the world such as India, Pakistan, and Bangladesh (Joshi et al., 2007). However, SB has emerged as a major wheat production constraint in warm, humid wheat-growing areas, posing threats to sustainable food production (Dubin et al., 1998). The disease causes serious yield losses to wheat crops in South East Asia (Saari, 1998), North and Latin America, Africa (Duczek and Jones-Flory, 1993), India (Joshi et al., 2004), China, and Brazil (Naitao and Yousan, 1998). More recently, SB has also expanded into the cooler, nontraditional irrigated rice−wheat production areas (Lillemo et al., 2013).

The pathogen can destroy seedlings, roots, leaves, nodes, spikes, and grains during various stages of plant development (Gilchrist and Pfeiffer, 1991). However, disease becomes severe during the grain-filling stage and causes significant yield loss and deteriorates grain quality (Saari, 1998). According to an earlier estimation, about 25 million ha of wheat land is ruined by SB (Dubin and Ginkel, 1991; Duveiller and Gilchrist, 1994; Ginkel and Rajaram, 1998). SB accounts for 85% of wheat yield losses in Zambia (Raemakers, 1988) and 40% in Philippines (Lapis, 1985). Grain quality was severely affected during an experiment at Londrina, Brazil, with highly susceptible cultivars. The losses ranged from 79% to 87% (Hetzler et al., 1991). Similarly, yield losses of 38% were reported using African wheat cultivars during growth chamber studies in Netherlands. Indian subcontinent on-farm wheat trial studies have revealed that Nepal faced 16% crop losses and Bangladesh about 15% due to SB (Saari, 1998).

In Pakistan, Iftikhar et al. (2010) reported rise of disease severity (DS) and incidence during the year 2005. Maximum severity of 2.5 with incidence 84% was noted in the central Punjab province. Atiq-ur-Rehman et al. (2011)

stated that there prevailed a massive cataclysm on the wheat variety Bhakkar-2001, followed by Inqilab-91, Faisalabad-08, Lasani-2008, and Seher-2006 in southern Punjab. The disease index of SB was 24.8%. Nearly, each variety grown on farmer's field was found susceptible to SB.

Villareal et al. (1995) assessed losses of SB at Poza Rica (Mexico) using important agromorphological parameters, i.e., number of grains/m^2, 1000-grain weight, number of grains per spike, harvest index, spikes/m^2, and biomass above ground. Correlation coefficient between these mentioned parameters was calculated. Foliar fungicides were applied to determine the percentage of yield reduction. Their results indicated that the reduction due to SB in 1000-grain weight was 30.05%, number of grains per spike was 24.6%, and number of grains per m^2 was 32.8%. The data also revealed that Chinese germplasm increased the grain yield and may be used as a resistance source in breeding. The following important aspects were noted:

i) Change in biomass was due to change in spikes per m^2 and 1000-grain weight.
ii) Reduction in harvest index showed significantly positive correlation with grains per m^2, grains per spike, 1000-grain weight, and test weight.
iii) Percent reduction in grains per spike was linked with 1000-grain weight.
iv) Changes in 1000-grain weight might be due to changes in test weight.

4. Epidemiology of spot blotch

Epstein and Nicholson (1997) studied the composition of extracellular matrix (ECM) of fungi. ECM comprises glycoproteins, which are helpful in the attachment of the fungi to host surface. These fungal glycoproteins are insoluble in water and withstand chemical response offered by the host to dissolve and break down it for further molecular actions. ECM is vital to concentrate and localize the enzymes required for host infection. ECM also prevents fungus from dehydration and secures it from toxic metabolites released by the plants in response to infection. Geimba and Brandelli (2002) reported on the details of extracellular enzymatic activity shown by *B. sorokiniana* isolates. Six isolates were studied from different areas of Brazil; the isolates differed with respect to composition and enzyme activity, showing diverse genetic makeup of the *B. sorokiniana* isolates.

Disease spread is positively correlated with optimal conditions. In favorable climates, pathogenicity is more prolific in the field, and it is inevitable to be aware of the conditions facilitating disease establishment. Air dispersal remains dormant until February, as mean temperatures are usually below 20°C. Third and fourth week of the March is the season to see the highest number of conidia (Duveiller et al. 2005). Gurung et al. (2012) compared the severity, incidence, and area under disease progress curve (AUDPC) in early- and late-sowing wheat in South Asia. Field studies were planned to assess the potential and development of the disease. Air samplers revealed highest aerial density of conidia and disease incidence in susceptible (Sonalika, BL1472) and resistant (NL750, Milan/Shanghai-7) varieties during first 3 weeks of March. It was also concluded that wheat cultivars were more severely affected when planted late, i.e., between December 11 and 26 as compared with optimally sown genotypes on November 26. Moreover, incidence of airborne conidia was in accordance with results of the studies performed by Duveiller et al. (2005). Few of the most important environmental factors influencing SB include the following:

v) Prolong leaf wetness and high temperatures are correlated with foliar blight (Sentelhas et al., 1993).
vi) High temperature and relative humidity for long periods (>12 h) accelerate the chances of foliar blight epidemics in the Indo-Gangetic plains where wheat-growing season is November through April (Duveiller, 2004).
vii) Reis (1990) in Brazil described that foliar blight occurs when wheat leaves remain wet >18 h at an average temperature of 18°C.
viii) Nema and Joshi (1973) and Singh et al. (1998) stated that *Cochliobolus* infection was much severe at 28°C and higher, i.e., between late February and March.
ix) Higher foliar blight may also occur due to late planting or low soil fertility Duveiller and Sharma (2009).

5. Disease assessment

Double digit rating scale is used to measure the foliar infection (Saari and Prescott, 1975) since infection starts from the basal leaf and advances toward the flag leaf. Therefore, to assess the disease, focus is made on the height of the infected plant and infection severity of the disease plant. Percentage DS is calculated as:

$$\% \text{ severity} = \{D_1/9 \times D_2/9\} \times 100$$

where D_1 = first digit; disease progress in height, D_2 = second digit.

Area under disease progression curve is to be noted for estimating disease epidemiology over a particular time interval (Roelfs et al., 1992).

$$\text{AUDPC} = \sum_{i=1}^{n}\left[\left\{\left(Y_i + Y_{(i+1)}\right)/2\right\} \times \left(t_{(i+1)} - t_i\right)\right]$$

where Y_i = disease level at time t_i, $t_{(i+1)} - t_i$ = time (days) between two disease scores, n = number of dates on which SB was recorded, time includes three different growth stages (GS63, GS69, and GS 77) as on Zadoks scale (Zadoks et al., 1974).

For disease prevalence and disease index, the following formulae were applied by Iftikhar et al. (2010).

$$\text{Prevalence \%} = \text{Locations showing foliar spots/total locations} \times 100.$$

$$\text{Incidence \%} = \text{Number of samples showing foliar spots/total number of samples} \times 100.$$

6. Host–pathogen interaction

Biotrophic and necrotrophic growth phases are exhibited by the hemibiotrophic pathogen *B. sorokiniana*. During the biotrophic phase, the pathogen attacks living epidermal host cells and produces hyphae by penetration through cuticle and cell wall, respectively. As the hyphae approach to the mesophyll layer, they cause epidermal and mesophyll cell death, termed as the necrotrophic phase. Wtsniewska et al. (1998) explained that the host cell destruction during necrotrophic phase is due to an electrolyte is emitted by the host cell, which is exceeded with pathogen severity. Cell devastation is carried out without intact fungal hyphae due to a mycotoxin. Association of fungal development with oxidative damage in epidermal and mesophyll cells is revealed by reactive oxygen intermediate hydrogen peroxide (H_2O_2) (Leng and Zhong, 2012). During these histochemical studies, a compound 3,3-diaminobenzidine (DAB) to visualize hydrogen peroxide was used (Kumar et al., 2001). Positive correlation was found between host establishment, and the amount of H_2O_2 produced in the leaf lesion reveals the correspondence of hydrogen peroxide for successful infection. Seed infection occurs in two ways:

i) Direct infection of the outer layer of cell wall of the pericarp.
ii) Through entrance into the stigma and then the pericarp cells.

Host cell walls produce hydrolytic enzymes at the tip of the hyphae, facilitating fungal spread. Host response to fungal infection may cause development of appositions between cell walls and the plasma membrane in cells adjacent to the fungal cells (Han et al., 2010).

As a response to pathogen attack, plants produce a wide range of secondary metabolites that may hinder the pathogenic activity. Nicholson and Hammerschmidt (1992) reported that phenolic compounds such as phytoalexins, phytoanticipins, or lignins (physical barrier) can perform an important role in disease resistance. Matern and Kneusel (1988) highlighted that the swift deposition of phenols at the place of infection decelerates the growth of pathogen and triggers assembly of phytoalexins or other stress-attributed contents. Decrease in total rate of translation, emission of ethylene, and formation of fade glycoproteins were also reviewed by Matern and Kneusel (1988). Mishra et al. (2011) reported that higher phenolic contents were observed in resistant rather than in susceptible wheat varieties.

Bakri et al. (2010) correlated the pathogenicity of *C. sativus* with the production and activity of xylanase. Xylanases are assumed to be important in interaction between hosts and pathogens of germinating plants and are usually required for efficient maceration of grasses (Braun and Rodrigues, 1993). Bakri et al. (2010) showed higher xylanase production in strongly aggressive rather than in weakly aggressive isolates. However, the authors found no correlation between origin of isolates and production of the enzyme. So it is deduced that xylanase affects the aggressiveness of the isolates of *C. sativus*. Total phenolic contents, phenylalanine ammonia lyase activity, and lignin accumulation are correlated to DS and AUDPC in SB-resistant (Yangmai 6) and SB-susceptible (Sonalika) wheat varieties. In resistant variety, DS, AUDPC, and lesion size were minimum and concentration of phenolic contents increased. On the contrary, mean phenolic content, phenylalanine ammonia lyase amount, and lignin concentration were found significantly low in the presence of high DS, AUDPC, and lesion size in susceptible parents (Eisa et al., 2013).

Different wheat varieties respond differently to infection. Negative correlation existed between DS and soluble proteins. High regression values along low disease incidence have been monitored (Mishra et al., 2011). The systematic shotgun proteomics approach was used to check the early response to *C. sativus* infection. In this regard, NBS-LRR protein was found as one of the major plant disease resistance proteins (Al-Daoude et al., 2013). Using mass spectrometry, Carlson et al. (1991) reported that the most active and abundant phytotoxin produced by fungus parasitizing plants is prehelminthosporol ($C_{15}H_{22}O_2$) produced by *B. sorokiniana*. Phytotoxin helminthosporol adversely affected the plant cell membranes with respect to their permeability, besides affecting the functioning of H^+-ATPase, Ca^{+2}-ATPase, and 1,3-beta-glucan synthase in barley roots. The enzyme 1,3-beta-glucan synthase is involved in the defense mechanism of plant cells against biotic stress; its activity is greatly inhibited by the toxin (Michel Briqet et al., 1998). By using two-phase portioning, plasma membrane was isolated by aqueous polymer. It was examined that the proton ATPase pumping activity hazardously affected or was completely inhibited when toxin dose was increased up to 500 μmol. At the same toxin concentration, ATP hydrolysis remained less harmful along with 35% inhibition while Ca^{+2} uptakes were inhibited 60%. 1,3-Beta-glucan was stimulated at lesser quantities of toxin, and higher toxin quantities were inhibitory. Moreover, this toxin is reported to be playing a major role to kill or weaken the host cells and initiate pathogenesis (Liljeroth et al., 1994; Mishra et al., 2011).

7. Genetic diversity in *Cochliobolus sativus*

Fungal genomes have the remarkable ability to undergo mutation and generate new virulence types for invading important crops (Zhong et al., 2002). The SB pathogen can be characterized on the basis of culture, colony color, texture, conidial morphology, and pathogenic nature. Using these parameters, Asad et al. (2009) made four classes of pathogens where no differences were observed between different isolates during pathogenicity test; however, variation was observed in their aggressiveness. Similarly, characterization of genetic diversity in globally collected isolates of *C. sativus* was carried out using eight sets of primer combinations. A total of 577 amplified fragment length polymorphic (AFLP) markers were recorded for 70 isolates of four *Cochliobolus* species. However, cluster analysis revealed low correlation between pathotypes and AFLP groups. This low correlation shows that there might be the role of para-sexuality causing genetic exchanges in the fungal population (Zhong and Steffenson, 2001).

Three pathotypes, 0, 1, and 2 have been reported from 33 isolates in North Dakota based on the infection responses of three host genotypes following the nomenclature by Valjavec-Gratian and Steffenson (1997). Four pathotypes (pts 1−4) were claimed by Arabi and Jawhar (2003) on the basis of lesion form and infection response of the genotypes with mean disease rating from 1.76 to 7.46. According to them, Pt1 exhibited low virulence on all used genotypes. Pts 2 and 3 were moderately virulent and Pt4 was highly virulent. The two most common pathotypes they identified were Pt3 (35%) and Pt4 (42%) (Arabi and Jawhar, 2003). Eleven unique haplotypes depicting the variability of isolates were detected using random amplified polymorphic DNA (RAPD) markers. Nine haplotypes of three phylogenetic origins within *C. sativus* isolates were sorted out using ITS-RFLP markers (Arabi and Jawhar, 2007). Six pathotypes among 34 isolates were reported using 20 lines in Australia by Meldrum et al. (2004). Karyotype analysis using counterclamped homogeneous electric field (CHEF) electrophoresis of 16 isolates of *C. sativus* from diverse regions of the world revealed that VHv 1 is the unique locus in Pt2 isolate that causes virulence. This information about genome structure and divergence is a prerequisite for advancing the awareness about genetics and pathology of *C. sativus* (Zhong et al., 2002). Aggarwal et al. (2010) investigated the molecular diversity in *B. sorokiniana* isolates sampled from different regions, and among the 40 isolates, variability in degree of pathogenicity was evident.

C. sativus has 15 chromosomes ($n = 15$), and genome size of approximately 33 Mbp with chromosomal sizes ranging from 1.25 to 3.8 Mbp has been estimated (Tsuchiya and Taga, 2001). Molecular genetic maps and an electrophoretic karyotype have been developed for *C. sativus*. The linkage map contained 27 linkage groups. Virulence-specific locus VHv 1 from isolate ND9OPr in the CHEF gel was localized on a chromosome of 2.8 Mbp. The total map length of the fungus was estimated 1329 cM based on the map distance covered by linked markers. Physical to genetic ratio was calibrated as 25 kb/cM (Zhong et al., 2002).

8. Control measures for spot blotch

SB is a threat to wheat production; it badly affects small farmers due to severe yield penalties. In susceptible cultivars, the yield losses of 20% and 52% have been reported (Sharma and Duveiller, 2004; Sharma et al., 2006).

Maximum yield losses are observed whenever the flag leaf and the leaf immediately below are infested by SB prior to spike formation (Acharya et al., 2011). Sowing date adjustment may also play a role to control the foliar infection by the *C. sativus*. Early seeding is suggested as a preventative measure of SB. This practice of early sowing can show fruitful results in the areas where rainfall raises when wheat is about to be harvested (Singh et al., 1998). Wheat is exposed to severe foliar blight pressure if sown late, i.e., December 30, and if optimally sown on November 30, the chances of foliar infection are minimum. Several other abiotic factors are also reported to be interrelated with foliar infection (Sharma et al., 2003). The available control measures for SB are summarized in the following section.

8.1 Chemical control

Mehta and Igarashi (1985) reported that in many tropical areas where more than one disease appears simultaneously, chemical measures become indispensable to suppress the virulence. For this purpose, suitable spraying schedule of specific fungicides with predetermined amounts is necessary. Time of the first spray, number of sprayings, and their interval should be taken into consideration. Maneb or mancozeb application is a common practice. Results have shown that SB was well controlled by 3–4 applications of mancozeb or three applications of propiconazole. Viedma and Kohli (1998) reported that black point in grain caused by *B. sorokiniana* can be controlled by using iprodione, guazatine, or triadimenol fungicide at a rate of 200 g/100 kg seed. Systematic foliar fungicides application can also be performed, such as tebuconazole, flutriafol, cyproconazole, flusilazole, epoxiconazole, and metconazole. For optimum results, spraying should be done between heading and grain-filling stages. When the DS is high, fungicide application can be doubled, and this may reduce the yield losses to 38%–61%. Sharma-Poudyal et al. (2005) argued that chemical control of the *C. sativus* by seed treatment and foliar fungicides could enhance crop production. Successive use of Vitavax 200B for 2 years proved effective for the increase in germination up to 43% and inhibited seedling infection by *C. sativus* in 2003. Only seed treatment may not be effective, and foliar spray was necessary to reduce severity and to increase grain yield. Sharma et al. (2006) claimed that in scarcity of high SB-resistant wheat cultivars, the use of fungicide Opus (epoxiconazole) could minimize DS to below 10%. Domiciano et al. (2010) reported on the role of silicon (Si), in resistance to SB. Different levels of diseases were found linked with changed concentrations of Si. The AUDPC, number of lesions per cm^2 of leaf area, and DS substantially lowered by 62%, 36%, and 43.5% in +Si treatments. No reasonable effect of Si on lesion size was noted. The experiment inferred that Si application to wheat could enhance resistance against SB.

8.2 Biological control

Bailey and Lazarovits (2003) focused on the control of SB through management of the crop residue and organic amendments. Soil structure changes with agricultural practices are the major causes of soilborne plant diseases. Tillage rotation and burning can add organic matter back to the soil. Furthermore, risks of pathogen exposure may be reduced by exercising organic amendments, manures, and composts, which may abridge soil-borne diseases. Aggarwal et al. (2004) studied the role of a fungus *Chaetomium globosum* that parasitizes *C. sativus*. The authors examined both *in vivo* and *in vitro* that the antifungal compound produced by the *C. globosum* could inhibit the activity of *C. sativus* causing SB of wheat. Isolates of *C. sativus* and *C. globosum* (Cg1 and Cg6) fungi showed mycoparasitism during interaction. Cg2, Cg3, Cg4, and Cg5 isolates of *C. globosum* exhibited antibiosis with *C. sativus*. A culture obtained from the isolate Cg2 totally blocked the mycelial growth of *C. sativus* in liquid broth. Significant differences between fungal isolates were detected during in vitro studies. The authors also concluded that there was a considerable positive correlation between antifungal compounds extracted from the abovementioned isolates in antagonism to *C. sativus* on seedlings in glasshouse. Moreover, it became clear that Cg2 had the antifungal metabolites equipped with maximum bioefficiency under laboratory and glasshouse environments.

Aggarwal et al. (2010) studied microbial detoxification of the pathotoxin of *B. sorokiniana* in wheat. The BS toxin produced is a compound of the eremophilane family. Its detoxification has been evaluated with the help of isolates of *Trichoderma* spp., *C. globosum* and *Pseudomonas fluorescens*. Detoxification of BS toxin has been done in the semisynthetic medium of different concentrations. Reduced mycelial growth was observed in this modified medium (BS toxin + semisynthetic medium). The growth of detoxifying agent was reduced by increasing the concentration of BS toxin proving the antagonistic potential. High-performance liquid chromatography revealed almost complete degradation of BS toxin in *C. globosum* samples. Ondrackova et al. (2013) claimed that mycoparasites can reduce the intensity of *B. sorokiniana* pathogenicity. Fungi *Clonostachys* f. *rosea* and *Clonostachys rosea* f. *catenulata* were found efficient against the pathogenicity of the *B. sorokiniana*. Activity of *B. sorokiniana* was proved by the antagonistic

against the strains of *C. rosea* with low and medium efficiency; both colonies arose around an inhibitory region. It was noteworthy that strains with high efficiency degraded *B. sorokiniana* colonies and overgrew without formation of any inhibitory zone. Development of *B. sorokiniana* was found reduced on the seeds treated with a mixture of *C. rosea* f. *rosea*, *Trichoderma* sp., and *B. sorokiniana*. Moreover, seeds treated with *Clonostachys* and *Trichoderma* showed positive results with respect to germination and seedling length.

8.3 Resistance through breeding

After the limited success through chemical (Sharma-Poudyal et al., 2005; Domiciano et al., 2010) and biological controls (Duveiller and Sharma, 2009; Aggarwal et al., 2010; Ondrackova et al., 2013), here comes the need to control this biotic stress through breeding. Different filial (F) progenies were selected to achieve the desired trait. The advancement in breeding for resistance can be examined by comparing disease scores, grain yield potential, and other yield-related traits of elite lines with their resistance and susceptible controls (Mujeeb-Kazi et al., 1996).

It was concluded by Villareal et al. (1995) that *Thinopyrum curvifolium* derivatives showed better resistance to *C. sativus* in Poza Rica, Mexico. Increased grain yield and test weights were compared with other breeding materials, and the germplasm under study was found as a genetic resource for establishing better SB-resistant breeding material. Immature embryos of two spring wheat varieties HUW-206 and HUW-234 were used by Arun et al. (2003) to raise the somaclones as R_2, R_3, and R_4 generations. Few of the somaclones exhibited enhanced disease resistance along with increase in yield more than their parents. This performance of the somaclonal variants got stabilized in R_4 generation. Hence, the study proved the chances of wheat improvement through somaclonal variation. About 116 commercial spring wheat cultivars and advanced breeding lines were chosen during the experiment in Nepal by Mahto et al. (2011). Wheat cultivars and lines were evaluated by maintaining artificial epiphytotic conditions at the two-leaf stage. Disease reaction was observed during 6–10 days after infection. Results showed that 30%, 31%, 19%, and 10% of the estimated wheat cultivars and lines were found resistant to SB. Using resistant parent and further backcrossing enabled breeders to incorporate the genetic resistance (Zhang et al. 1998).

SB resistance was controlled by two genes (Srivastava et al., 1971; Adhalka et al., 1984); later on, three genes were found responsible (Joshi et al., 2004; Sharma et al., 2007). Some other researchers are of the opinion that recessive genes are responsible for SB resistance (Singh et al., 1998, 2000; Ragiba et al., 2004). Sharma et al. (1997) had a different view that SB resistance in wheat was quantitatively inherited with intermediate- to high-heritability estimates. The sources of simple inheritance for SB resistance can be Milan/Shanghai #7 containing a single dominant gene for resistance (Neupane et al., 2007). Sonalika, BL 1473, and Nepal 297 were susceptible (Duveiller et al., 2005). Mujeeb-Kazi et al. (2007) highlighted *Aegilops tauschii* as a resistant source against SB (*C. sativus*). The authors succeeded in intergeneric cross-product "Mayoor," a unique germplasm that had two sources of resistance pyramided from, i.e., *T. curvifolium* and *A. tauschii* accession 222. Synthetic hexaploid wheats obtained from crosses of *Triticum turgidum* × *A. tauschii* exhibited remarkable resistance to *C. sativus*.

9. Molecular diagnostics for spot blotch

With the progression of techniques used to uncover the disease aspects in plants, diagnostics for SB at molecular as well as genetic level have surfaced. Efforts have been made to determine the genes or quantitative trait loci (QTLs) involved with SB. QTLs responsible for resistance to SB in wheat genome have been detected and mapped. RAPD markers were used to evaluate the genetic diversity of the *B. sorokiniana* isolates (Muller et al. 2005; Jaiswal et al., 2007; Pandey et al., 2008) as well as to understand the genetic resistance of SB (Patil and Hanchinal, 2011). Sequence characterized amplified region (SCAR) markers as $SCARBS_{600}$ were developed by Aggarwal et al. (2011) capable to differentiate *B. sorokiniana* from other fungal parasites. On the other hand, 15 simple sequence repeats (SSRs) were also found associated with SB resistance (Sharma et al., 2007). Recently, three SSRs, *Xwgm570*, *Xgwm544*, and *Xgwm437*, have been validated for SB resistance on chromosomes 6A, 5B, and 7D, respectively (Tembo et al., 2017).

9.1 *Quantitative trait loci* associated with spot blotch resistance

QTLs responsible for SB resistance in wheat have been identified (Kumar et al., 2009). Four QTLs (*Qsb.bhu-2A*, *Qsb.bhu-2B*, *Qsb.bhu-5B and QSb.bhu-6D*) on chromosomes 2AL, 2BS, 5BL, and 6DL were predicted. Moreover, Kumar et al. (2010) validated these QTLs in wheat lines "Ning 8201" and "Chirya 3." SB resistance QTLs were found

colocated with *Lr34* and *Lr36* by Lillemo et al. (2013). In this study, minor QTLs on 7DS flanked by *wPt-7654* and *gdm88*, and this locus has been designated as a gene *Sb1*. Two more SB resistance genes *Sb2* at a 0.62 cM interval between markers *Xgwm639-Xgwm1034* on 5BL (Kumar et al., 2015) and *Sb3* at 0.15 cM between Xbarc133-Xbarc147 with genetic interval of 602-kb physical genomic region on Chinese spring chromosome 3BS have been identified and mapped (Lu et al., 2016). Examining 19,460 wheat accessions, QTLs conferring multiple biotic resistance including SB have also been identified (Kumar et al., 2016) (see also Table 14.1).

9.2 Recent genotyping approaches for genetic dissection of spot blotch

Gurung et al. (2014) used illumina Infinium 9K wheat single nucleotide polymorphisms (SNPs) for genome-wide association mapping of multiple leaf spot diseases including SB. Kompetitive allele-specific PCR (KASP) is another approach of genotyping that can be applied in crop improvement (Semagn et al., 2014). Most recently, Rasheed et al. (2016) validated KASP assays for genes of economically important agronomic traits in bread wheat. A large number of functional genes in a single tool kit are now available for high-throughput screening. Genotyping-by-sequencing (GBS) has also been used to dissect the genetic basis of plant diseases. Nested association mapping for stem rust resistance in wheat using GBS technique has also been reported by Bajgain et al. (2016). Li et al. (2015) reported a high-density GBS map of bread wheat and its application to dissect complex diseases. Using anchoring GBS tags on chromosome was used for wheat genetic improvement, and a consensus map was constructed using 28,644 GBS markers (Li et al., 2015). Genome-wide association mapping of *Fusarium* head blight (FHB) resistance in wheat using GBS has been performed with the help of 19,992 identified SNPs (Arruda et al., 2016). GBS approach can be cost-effective, accurate, and high throughput in advanced next-generation technologies (Elshire et al., 2011; Poland et al., 2012).

Relatively less attention has been paid yet to evaluate the genetic and molecular interactions of *C. sativus* with crops harboring and hosting this pathogen. It seems vital in the future to isolate and characterize the gene/s responsible for virulence in the pathogen and genes for resistance in the host. Map-based cloning is a technique being used to isolate virulence or avirulence loci from fungi (Orbach et al., 2000). Transcription factor (TF) TaPIMP1 of type R2R3-MYB was found to be involved in the regulation of defense and stress-related genes for host resistance to *B. sorokiniana* and drought stress (Zhang et al., 2012). Dubos et al. (2010) also noticed TFs and the MYB family involved in biotic and abiotic stresses. Gene silencing in *C. sativus* was performed by Leng et al. (2011). RNA-mediated gene silencing system was established for *C. sativus*. The polyketide synthase gene (CsPkS1) was involved

TABLE 14.1 QTL information for spot blotch resistance in bread wheat.

Chromosome	QTLs	Marker interval	Interval size (cM)	LOD PVE%	Reference
1B	QSb.cim-1B	Xwmc128-Xgwm374	0.4	8.5 8%	Zhu et al. (2014)
3B	QSb.cim-3B	990937|F|0-1123330|F|0	2.7	6.7 17.6%	
5A	QSb.cim-5A	1086218|F|0-982608|F|0	12.1	4 12.3	
2AL	QSb.bhu-2A	Barc353-gwm445	37.4	2.8	Kumar et al. (2009)
2BS	QSb.bhu-2B	Gwm148-374	15	2.6	
5BL	QSb.bhu-5B	Gwm067-gwm371	13.2	11.5	
6DL	QSb.bhu-6D	Xbarc 175-gwm732	30	3.3	
2A	QSb.bhu-2A	Xgwm425-Xbarc159	8	2.9	Kumar et al. (2010)
2B	QSb.bhu-2B	Xgwm149-Xbarc91	21.2	4.3	
5B	QSb.bhu-5B	Xgwm067-Xgwm213	9	2.5	
7D	QSb.bhu-7D	Xgwm111-Xgwm1168	3	6.6	
7D		wPt-7654-gdm88	42	5.81	Lillemo et al. (2013)

LOD: logarithm of the odds, PVE: Percent variance explained.

in melanin biosynthesis pathways in *C. sativus*. In addition to identification of resistant loci, this silencing mechanism could increase our arsenals to tackle SB in ways that are economically and environmentally sustainable.

10. Summary and way forward

Association mapping technique makes it easy to determine the resistance of multiple genes with quantitative effects. Results of the technique can impart new trends in breeding programs. Association mapping of QTLs in spring wheat land races for the resistance of SB and bacterial leaf streaks has been performed by Adhikari et al. (2012). Polymorphic 832 diversity arrays technology markers revealed five genomic regions for SB resistance on chromosomes 1A, 3B, 5B, 7B, and 7D. Genome-wide association mapping of SB can be done with the help of GBS approach using a high number of markers. This next-generation genotyping technique can reduce representation sequencing for targeted portions of the genomes. Barcoded adapters are used to sequence multiplex libraries in parallel. There are multiple methods, but GBS is one for genotyping using next-generation sequences of multiplex DNA-barcoded reduced-representation libraries. GBS with two enzymes (*Pst1* and *Mse1*) with fragment size < 350 bp and having multiplex level 48 up to 384 using TASSEL tools has been reported by Poland et al. (2012) and might be used for association mapping analysis of SB resistance. Under all circumstances, demographic changes causing population increase may be considered by wheat breeders to fulfill the needs of nutritionally vulnerable populations. Moreover, finding out suitable nonhost crops as well as improving SB resistance with single or pyramided genes in wheat cultivars may control the severity of the pathogen. In South Asia, wheat production is threatened by biotic stresses such as foliar blight, and with global climatic changes, SB may add to the concerns of mankind; therefore, the challenge of SB needs to be well integrated with future food security and climate change concerns.

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CHAPTER

15

Karnal bunt (*Tilletia indica*) in wheat

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OUTLINE

Wheat is grown yearly on 215 million hectares, an area equivalent to that of Greenland, and it also occupies 30.3% of all land devoted to cereals. In the year 2017, the harvested surface area of wheat was 281.543.071 ha, and world production of wheat was 771.718.579 tons (CGIAR, 2018). Top four wheat-producing countries are China, India, the Russian Federation, and the United States, respectively. A worldwide average of wheat is 2.04 metric tons per hectare. Today, nearly US $50 billion worth of wheat is traded each year globally and in the next decade. It is expected to pass rice as the world's most important food crop. Production of wheat must continue to increase annually by 2% to meet future demands imposed by population and prosperity growth (CGIAR, 2018; FAO, 2019).

Many factors affect the yield, quality, and the increase in wheat demand. One of the most important ones is plant disease arisen from infectious organisms and environmental factors such as drought, soil fertility, and quality. According to FAO estimates, diseases and pests in cereals have caused yearly 23 million ton loss, which is an amount that can feed 150 million people. Despite intensive crop protection practices, actual grain yield losses due to pathogens in global wheat production between the years of 2001 and 2003 were about 10%, while only 2% of losses were due to viruses (Oerke, 2006). The most important diseases affecting wheat are rusts, powdery mildew, loose smut, leaf blight, and bunt diseases.

Wheat bunt is known to be one of the most important fungal plant pathogens. It has been the focus of the publications in early plant pathology, such as M. Mathieu du Tillet (Tillet, 1755) who indicated that wheat bunt caused from the seed contamination by the greasy and blackish powder contained in infected seed. This contribution has later reflected in the generic name as "*Tilletia* Tul. and C. Tul.," published in 1847 (Tulasne and Tulasne, 1847).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00015-7

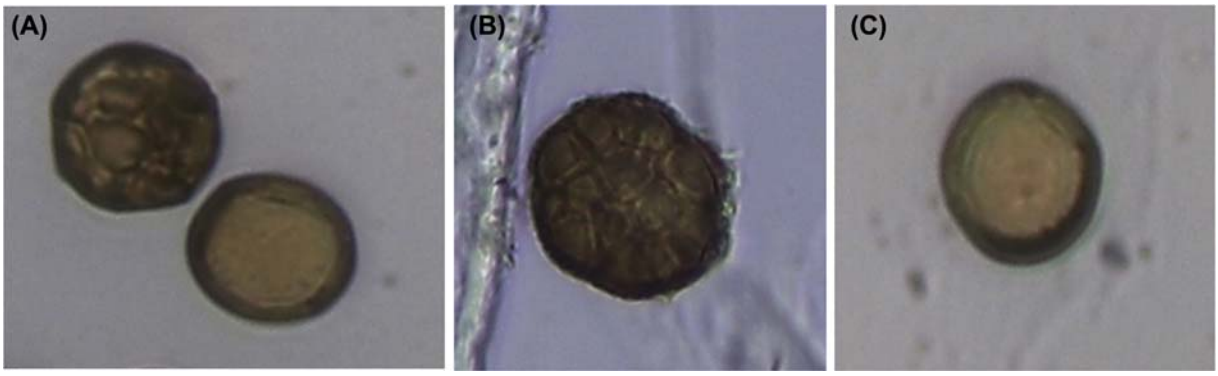

FIGURE 15.1 (A) *Tilletia caries* and *Tilletia foetida* spores. (B) *Tilletia caries* spore. (C) *Tilletia foetida* spore.

1. *Tilletia* species

The genus *Tilletia* is a grass disease fungus infecting cereal crops either locally or systemically. Smut fungi take place in the class of Ustilaginomycetes, subphylum Ustilaginomycotina, phylum Basidiomycota. As a result of the infection, symptoms of the plant appear blackened, because of this appearance; the name of the class is derived from the term "ustulatus" meaning burned (Carris, 2001a). The cereal-infecting *Tilletia* species forms teliospores in the ovaries of their hosts defined as bunt fungi. It is also considered to be the origin of the word "burned" (Duran and Fisher, 1961; Carris, 2001b).

Three important genera are causing *Tilletia* infection in the wheat. The most common one is common bunt, also known as stinking smut or covered smut, which causes disease both in spring and winter wheat. *Tilletia* infection has resulted from two very closely related fungi, *Tilletia caries* (DC.) Tul. [= *Tilletia tritici* (Bjerk.) Wint.] and *Tilletia laevis* Kühn. [= *Tilletia foetida* (Wallr.) Liro., *Tilletia foetons* (Berk & Curt)]. The two pathogens differ mostly in their spore wall structure. *T. laevis* has a smooth surface; *T. tritici* has a reticulated surface (Fig. 15.1). These fungi survive on the surface of the seed and in soil. The most important source of infection is contaminated seed, and pathogen infects wheat at the seedling stage (Mathre, 2000).

The other is dwarf bunt, caused by the fungus *Tilletia controversa* Kühn, which is a quarantine pest in many countries (Zhou et al., 2018). It occurs on autumn-planted wheat, and it has never reported on spring-planted wheat. The symptoms and life cycle of *T. tritici* and *T. controversa* are very similar, and the difference of teliospore structures can distinguish them. *T. controversa* teliospores cover with a conspicuous hyaline gelatinous sheath with a thickness of 1.5–5.5 μm (Duran and Fischer, 1961).

Although its limited geographic distribution and lower yield impact, the third one, Karnal bunt (KB), is the most crucial smut fungi infecting wheat. It is also called with other scientific names such as Indian bunt of wheat, new bunt, partial bunt of wheat, and carie de Karnal (Fig. 15.2).

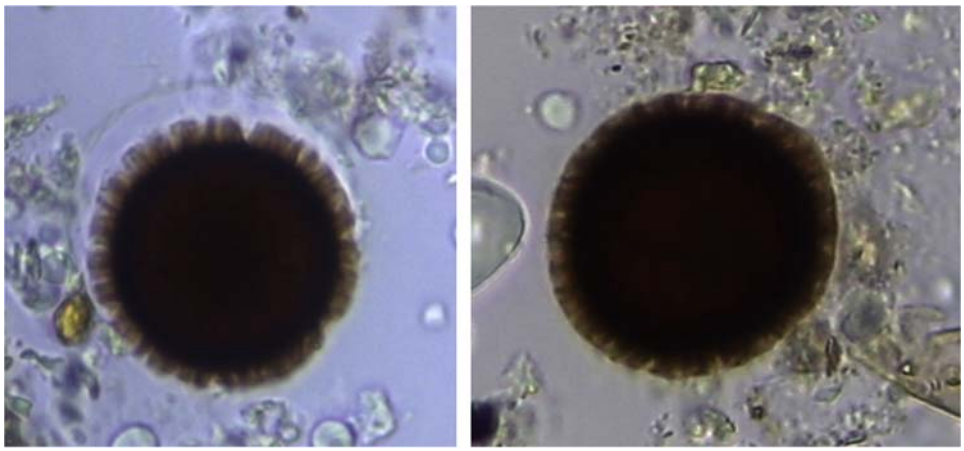

FIGURE 15.2 *Tilletia indica* spores.

TABLE 15.1 Differences of teliospore morphology of *Tilletia walkeri*, *Tilletia horrida*, *Tilletia ehrhartae*, and *Tilletia indica*.

	Mean spore size (μm)	Max spore size (μm)	Color and shape of spore	Spore ornamentation and median profile
T. indica	35–41	45–50+	Orange, generally dark reddish-brown to opaque black Globose to subglobose	Densely echinulate or finely cerebriform, truncate, sometimes curved and smoother appearance
T. walkeri	30–31	36–45	Pale yellow to dark reddish-brown, generally reddish-brown Globose	Coarse, cerebriform, and irregular with gaps between spines obvious in profile after bleaching
T. horrida	24–28	<36	Pale yellow—dark chestnut brown, generally dark or light chestnut-brown Globose to subglobose	Echinulate, sometimes cerebriform ridges. Generally curved and polygonal scales
T. ehrhartae	24–28	<28	Very dark olivaceous brown (mature spore). Opaque (melanization of the scales) Globose to subglobose	Cylindrical to slightly tapered spines and rarely cerebriform; broadly truncated to slightly rounded at apex

**T. indica* and *T. walkeri* (Milbrath et al. (1998); Castlebury (1998); Castlebury and Carris (1999); Cunfer and Castlebury (1999)). **Tilletia barclayana* and T. *horrida* (Duran and Fischer (1961); CMI description no. 75 (1965); Khanna and Payak (1968); Durán (1987); Aggarwal et al. (1990); Castlebury and Carris (1999); Castlebury (1998)). **T. ehrhartae* (Pascoe et al. (2005)).
Modified from IPPC, 2016.

Three *Tilletia* species other than *T. caries*, *T. laevis*, and *T. controversa* can be confused with *Tilletia indica*, because of their morphological similarity. One of these species is *Tilletia walkeri* that infects *Lolium perenne* and *Lolium multiflorum*. *Tilletia horrida* is the other one *Tilletia* species that is a pathogen of *Oryza* spp., and the last one is *Tilletia ehrhartae that is* a pathogen of *Ehrharta calycina*. Briefly, these species infected Poaceae species. They also have been detected in harvested wheat (*Triticum aestivum*) or seed in Australia and America (Castlebury, 1998; Castlebury and Carris, 1999; Pascoe et al., 2005). Therefore, accuracy of identification of these species is essential.

Tilletia barclayana (smut of various Poaceae, e.g., *Panicum* and *Paspalum*), *Tilletia eragrostidis* (on *Eragrostis*), *Tilletia inolens* (on *Lachnagrostis filiformis*), *Tilletia rugispora* (on *Paspalum*), and *Tilletia boutelouae* (on *Bouteloua gracilis*) have similar morphological characteristics with *T. indica*. However, these species have been shown not to infect *T. aestivum* (EPPO, 2008). The morphological differences among *T. indica*, *T. walkeri*, *T. horrida*, and *T. ehrhartae* are the size, range, mean, ornamentation, and color of their teliospore (Table 15.1).

2. Morphology of *Tilletia indica*

Teliospore of *T. indica* is globose to subglobose. Generally, immature or rarely mature teliospores have a small hyphal fragment. The diameter of the teliospores usually ranges between 22 and 47 μm. This size of teliospores sometimes is larger up to 35–41 μm (Fig. 15.3). Colors of immature teliospores are rather different and change between pale orange-brown to dark, reddish-brown, whereas those mature teliospores can be black or opaque color. According to Carris et al. (2006), mature teliospore densely ornamented with sharply pointed to truncate spines, occasionally with curved tips, 1.4–5.0 (–7.0) μm high, which may appear as either individual spines or closely spaced, narrow ridges in surface view. A thin hyaline membrane covers the spines (Carris et al., 2006; CMI, 1983). Sterile cells of *T. indica* can be spherical, spheroidal, or tear-shaped, yellowish-brown, 10–28 × 48 μm, with or without

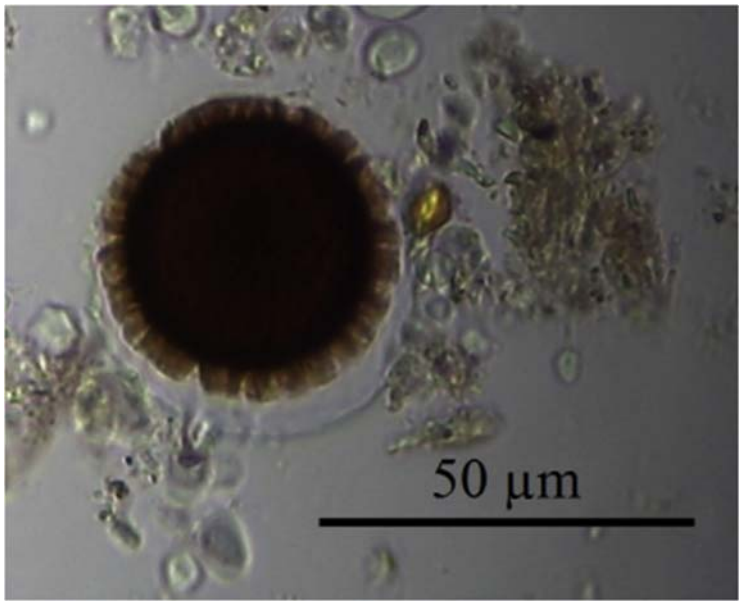

FIGURE 15.3 Teliospore of *Tilletia indica*.

an apiculus, with smooth walls up to 7 µm thick and laminated. Sterile cells are probably uncommon in sieved washings (Carris et al., 2006; CMI, 1983).

3. Distribution of *Tilletia indica*

T. indica (synonym = *Neovossia indica*) causes KB disease in wheat. Although the first detection of KB was made from the region Faisalabad in Pakistan in 1909 (Anonymous, 1992), it was first formally recorded from a small city, Karnal, in the Indo-Gangetic plain, and it was identified by Mitra (1931). The pathogen is now a widespread problem in India (Delhi, Uttar Pradesh, Haryana, Punjab, Himachal Pradesh, Rajasthan, Madhya Pradesh, Jammu and Kashmir, West Bengal, and Gujarat). It has also become established in other parts of Asia including Pakistan (Punjab, Northwest Frontier Province), Afghanistan, Nepal, Iran, and Iraq. It was first confirmed outside Asia in 1972, in the state of Sonora in Mexico. In 1996, KB was detected in limited areas of Arizona, USA. KB disease has not been recognized in Turkey and the EPPO region (Crous et al., 2001; Fuentes-Davila, 1996; EPPO, 2007) (Fig. 15.4).

4. Hosts of *Tilletia indica*

The major host of the KB is *T. aestivum* whereas rare hosts are *Triticum durum* × *Triticosecale* sp., *Secale cereale*. Although *Secale* spp. have been shown to have the potential to be a host (Sansford et al., 2008), *Aegilops geniculate*, *Bromus* spp. *Lolium* spp., *Triticum dicoccon*, and *Oloptum miliaceum* have been found to infect in *T. indica* in the greenhouse but has not been observed in the field (Inman et al., 2003).

5. Teliospores and life cycle of *Tilletia indica*

KB life cycle is based on information available of smut fungi even though biology and genetics of *T. indica* and cellular and molecular biology of KB disease are poorly understood. KB has three different morphological types of teliospore in the life cycle. The first morphological form is a nonpathogenic haploid phase. It grows like unicellular yeast (sporidial form). The primary sporidia or the macro (filiform) conidia are splash dispersed.

FIGURE 15.4 Distribution of *Tilletia indica* in the world.

It germinates to give rise to interconvertible allantoid (infective entity) and filiform (reproductive) secondary sporidia. Being allantoid- and filiform-like sporidia, there are two types of secondary sporidia. Second is filamentous dikaryon. It occurs as a result of fusion of two compatible haploid cells. It colonizes and infects plant tissues and cells. Only allantoid sporidia can infect and cause the disease. Filiform sporidia increase the inoculum by division on host/soil surface (Dhaliwal and Singh, 1989a). When the wheat leaf begins to dry, an enormous amount of the secondary sporidia infecting wheat ear head is released (Dhaliwal and Singh, 1988, 1989b). This phase occurs due to sporogenous mycelium within host tissue (Kumar et al., 2000), and it is defined as teliospore.

While Mitra (1931) reported KB disease as a soilborne, now it is also known as an airborne and seedborne (CSL, 2004; Sharma et al., 2017). But it is not directly transmitted from the seed to the plant. The pathogen is airborne in the form of sporidia or teliospores. Primary sources of inoculum of diseases are soil or seeds (CSL, 2004; Sharma et al., 2017). Equipment, tool, or man moving from milling places, wheat straw, and farmyard manure move the spores of diseases (Sharma et al., 2017). Development of diseases is directly affected by environmental conditions. Suitable temperatures of germination of teliospores range from 15 to 25°C. While the disease progression also depends on moisture (water holding capacity) in the soil, the soil type would not have a significant effect on germination during the cropping season (Peterson et al., 2017). Period of these conditions is varied from country to country. For example, these conditions of North Indian plains progress from February to March (Dumalasová and Bartoš, 2009; Rush et al., 2005).

KB has a monocycle of its life cycle. The teliospores begin to germinate in the soil around the flowering period of wheat and form a promycelium carrying many sickle-shaped primary sporidia. Primary sporidia germinate to form mycelium on plant surfaces, and this stage is followed by the production of secondary sporidia resulting in the infection of wheat leaf due to dispersion effect of wind or rain splash. Secondary sporidia create germ tubes and grow toward stomatal openings of the glume, lemma, or palea where they enter the plant. The intercellular hyphae progress through the glume, lemma, palea, and possibly rachis and enter the ovary base from these tissues. The most favorable conditions for the infection of wheat ears during flowering periods are cloudy weather and increasing humidity after light rain showers (EPPO, 2008). These factors cause too rapid infection of the grains in the ear (Goates, 1988). At harvest, teliospores usually scatter locally from bunted grain and can stick to the surface of healthy grains as an external contaminant (CSL, 2004). Both bunted grains and teliospores in the soil are the primary sources of the infection.

6. Symptoms of *Tilletia indica*

Due to the initially small number of grains in the wheat head that is infected by *T. indica*, it is quite challenging to recognize these few grains. Initially, it is difficult to distinguish the appearance of the infected wheat head from healthy. For these reasons, there may be difficulties in detecting *T. indica* until after harvest. In the period after

FIGURE 15.5 Grain samples contaminated with *Tilletia indica*.

the harvest, freshly infected grains contain an unwanted odor owing to the presence of triethylamine. Symptom indicates the presence of the disease. However, other criteria should be taken into consideration in the diagnosis of KB because it is a mutual feature with other smut diseases (common and dwarf bunt).

The symptoms of the disease depend on climate characteristics. The symptoms are most clearly during the flowering period of wheat in humid and warm weather. As a result of infection, the number of spikelets and the length of ears are reduced as well as an infected plant of height may be shorter than healthy wheat. Infected grains are generally empty. Inside the infested grains is filled with rectangular or oval sori dusty brown or black sports masses of 1−3 mm in diameter (Fig. 15.5).

Infection of grains starts from hilum and running along to suture. As a result, the endosperm remains intact, but the seed coat becomes partially or completely ruptured. When the infection is not severe, the symptom of the disease is only a black point just below the embryo toward the suture. When the infection is severe, spores are replaced by tissues throughout the suture and along with the adjacent endosperm. Infected grains are separated from their glumes, and such grains and both glumes and grains may fall to the ground. As a result of KB infection of whole or a part of the wheat, grains filled with a black powder pile consist of millions of teliospores. Grain quality is reduced, because of the color, smell, and taste of the products produced from such grains.

7. Climatic requirements of *Tilletia indica*

There have been many studies on the origin, life cycle, and epidemiology of *T. indica* (Smith et al., 1996; Bonde et al., 1997; Nagarajan et al., 1997; Stein et al., 2005; Mansoori, 2015). Moreover, the relationships between survival and growth of *T. indica* teliospore and surrounding environmental conditions have been densely investigated in situ and in vitro studies (Smilanick et al., 1989, 1985; Peterson et al., 2017; Kaur and Kaur, 2008). The growth, survival, and control of propagules of *T. indica* were investigated in several aspects in control conditions by Smilanick in 1989. The germination ability of *T. indica* secondary sporidia at 25°C was investigated at different relative humidity. Sporidial survival was found to decrease at the lowest relative humidity. The germination of teliospores was evaluated in two different locations. In both places, after 7 months of germination increased a little; however, after 22 months, the germination of teliospores, which were only buried in dry soil, was found to remain high. During the dry and hot summer months, when the maximum temperature exceeds 45°C, teliospores ensure the survival of the pathogen. Dormancy fresh teliospores may break their dormancy when exposed to 40−43°C in direct sunlight for 18 days or longer (Krishna and Singh, 1982). The disease of teliospores survives in the soil for several years (Bonde et al., 2004). *T. indica* teliospores can resist in harsh environments and sometimes can remain viable for

2–5 years in contaminated soils (Mathur and Cunfer, 1993). The spores germinating within 2 mm of the soil surface are the source of sporidia spreading to leaves (Smilanick et al., 1985). *T. indica* has three types of teliospore dormancy. The first of the dormancy is postharvest in that germination of long-term stored seeds with teliospores is abundant compared with the freshly harvested seeds (Bansal et al., 1983; Mitra, 1935; Rattan and Aujla, 1990; Smilanick et al., 1985; Thinggaard and Leth, 2003). The long-term (second type) dormancy stimulates survival of teliospores in the field conditions. The third type of dormancy can be induced by cold temperatures (Carris et al., 2006) and has been recorded even 4–8 days of frozen conditions at 0°C (Sidhartha et al., 1995).

KB is a disease of arid or semiarid regions with warm summers and cold/mild winters (Jones, 2009). Microclimatic conditions in the plant canopy are more effective on the KB diseases than macroclimatic ones (Singh et al., 1996; Coakley, 1983). However, macroclimatic conditions produce the microclimate, and there is a limit to which the latter can facilitate disease development under microclimatic conditions unfavorable to diseases. The relationship between the average disease infection (%) and meteorological parameters has been demonstrated by the studies conducted during the most sensitive growth periods of wheat (Singh et al., 1996; Aujla et al., 1989). After rainy days, the increase of relative humidity and the occurrence of cloudy weather provide the creation of favorable conditions for the development and spread of the disease. Such weather also helps to increase disease infection. During the ninth SMW, increased relative humidity after morning and evening rains is the most favorable conditions for the multiplication of secondary sporidia. Rainfall and rainy days during 10th, 11th, and 12th meteorological weeks helped in the multiplication of KB in wheat (Singh et al., 1996). A study showed that 35 days passed around wheat anthesis were critical for infection in the United States (Goates and Jackson, 1996).

Climate models have been developed to simulate the spread and development of the disease in the suitable meteorological condition in its country of origin, India (Jhorar et al., 1992; Mavi et al., 1992; Kaur et al., 2007). In many countries, some of these meteorological models have been used to predict the potential establishment and spread of KB, and many studies have been carried out to adapt these meteorological methods (Stansbury and McKirdy, 2002; Sansford, 1998; Murray and Brennan, 1998; Smiley, 1997; Holmes et al., 1996). Despite the high number of methods to predict the occurrence of *T. indica* such as Humid Thermal Index, the majority of these methods have limited to specific local conditions (DumalaSoVá and BarToš, 2009).

8. The thresholds of inoculum of *Tilletia indica*

Teliospores germinate on the topsoil and form promycelia, developing primary and secondary sporidia in turn. Secondary allantoid sporidia of *T. indica* released from mycelial colonies germinate and reproduce on the soil. The proliferations of sporidia on soil, leaves, and spikes indicate that the inoculum from soilborne teliospores can have an only starting role in KB epidemics (Jones, 2009). Running cycles of production sporidial in the ears ensure an adequate inoculum of *T. indica* to cause KB epidemics (Dhaliwal, 1989). Although the amount of teliospores is adequate during the postwintering period, this amount may sometimes be reduced due to the early germination of the present inoculum and cannot reach the necessary amount for the critical infection period. Factors that add to the dormancy of teliospores play a vital role in this issue. The evidence indicated that *T. indica*–contaminated seed samples (provided by CIMMYT Mexico where *T. indica* occurs) showed no formation of KB when sown in Europe. The teliospores cannot survive probably long enough on the soil surface conditions of Europe. As a result, for *T. indica*, a typical pathogen sample for the warm climatic region, there is much trap for the reasons for predicting pathogen risk from temperate zones. Even for areas where only the mean temperature rise is expected, the timing of warm and rainy periods with increasing temperature is vital for the location and spread of the disease.

9. Detection of *Tilletia indica*

The procedure of detection of teliospore of *T. indica* describes in the diagnostic scheme (Fig. 15.6). This diagnostic scheme contains the following steps:

1. Application of a size-selective sieving wash test, which is a quarantine method, is imported seeds or grain.
2. To detect morphological identification of teliospores, sieving wash test is used.
3. For the molecular confirmation, isolation and/or germination of teliospores are made.

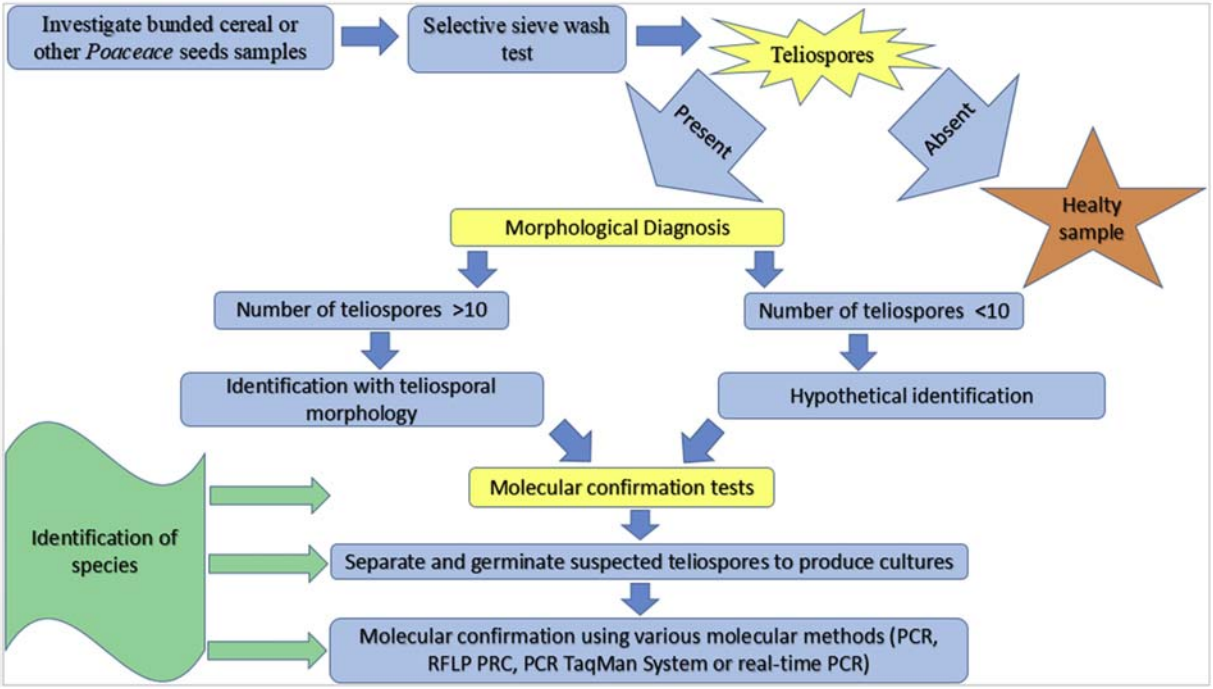

FIGURE 15.6 Diagnostic schemes for the detection of *Tilletia indica* in the grain samples (Anonymous, 2017).

EPPO published a quarantine method for detecting *T. indica* in *Triticum* spp. in 1991 (OEPP/EPPO, 1991). *T. indica* is A1 quarantine list for the European Union (EU). It means that EU is not present, it is forbidden to enter, and it is a potentially harmful organism. According to this protocol, field inspections should be carried out during the growing season between heading and harvest. The bunted seed detected during these observations should be examined under microscopy for the proper characterization of teliospores of *T. indica*. For quarantine purposes, seeds infected should be tested by the washing test to check with the presence of the fungus as recommended by OEPP/EPPO (1991).

Direct visual observation for KB generally may not be adequate for quarantine purposes since low levels of infection may not be detected by only dry seed inspection (Agrawal et al., 1986), and even low seed infections can substantially contaminate healthy seed lots (Aujla et al., 1987). For these reasons, when a sample is detected contaminated with *T. indica*, the final decision needs to be confirmation tests. Therefore, to produce cultures for molecular confirmation tests, suspected spores are isolated, and it is germinated. Afterward, germinated individual teliospores remove to the culture for confirmation techniques that it is performed using advanced molecular methods based on PCR.

10. The social and economic impact

The yield loss of *T. indica* was found to be 0.3%–0.5% even in the highest epidemic years in India (Singh, 1994). Current yield losses are low in percentage. However, its financial impact is high in wheat production areas (Jones, 2007). The main economic losses due to *T. indica* are not related to the yield losses caused by the disease in the product.

Even though KB was determined first in the United States in 1996 and then in South Africa in 2000, it has long been known to occur in India, Afghanistan, Iraq, Mexico, and Pakistan. As a result of the concerns about its appearance in European countries, through agricultural trade activities, it has been included in the EC Plant Health Directive list of quarantine organisms, since 1997. Quarantine measures, losses in the export markets (seed and food) in the control, and treatment of infected cereals are mainly economic losses of the KB. After KB disease has been implemented to quarantine regulation in America, many countries in the world have created similar quarantine regulations (Bonde et al., 1997; Fuentis-Davila, 1998). The implementation of quarantine regulations harmed wheat grain trade and wheat research program. It is very costly to perform these regulations against KB disease. Strong expertise and a significant amount of funding are needed for these applications. This zero tolerance policy applied to the disease adversely affects grain trade. This negative situation increases wheat costs and affects consumers negatively.

Quarantine measure has also restricted the development of control measures to be taken against the KB disease and research on the development of resistant varieties. For example, in the United States, Washington State University studied intensively before the KB disease was quarantined in 1984. However, researches on KB have limited to the studies conducted in the containment facilities of America in Ft. Detrick, MD, since 1984, and the zero tolerance regulation has interfered with other researches on wheat by restricting access to germplasm and use of off-season nurseries in Mexico. Economic results are assessed by considering the disease levels of the countries affected by KB disease (Jones, 2007).

Vast fields of wheat in the Mediterranean and European region are at a high risk of infection by *T. indica* (Sansford et al., 2008). Although there is no KB in the European Union countries, the socioeconomic impact of the disease in an outbreak situation has been made with a detailed pest risk analysis (PRA) (Brennan et al., 2004a, 2004b). The first PRA conducted in 1996 before 2004 was based on the available literature records. It stated that the loss in quality caused by *T. indica* would be more than the yield. It said that the potential damage, export control, and seed certification costs would be increased due to the quarantine effect of the pathogen. In 1996, Kehlenbeck et al. carried out a PRA for Germany in 1997, following a PRA in the United Kingdom. Considering the best scenario, only in terms of yield damage in this PRA, Germany estimated that there would be a 0.5% loss in wheat production and 5 million euros in economic damage.

In Australia, the semiarid region of growing wheat is also assumed to be at risk (Stansbury and McKirdy, 2002). It stated that the economic loss to occur when *T. indica* entered in Australia was 55 ADB dollars per ton. In this case, it is noted that the smallest share in financial loss will be caused by the loss of yield (Murray et al., 1996).In the detailed PRA of the United Kingdom carried out in 2004, the policies and regulations applied in the countries where the KB exists are examined. Outbreaks of KB and its components that may be associated with its formation are identified. These components are direct costs, reaction costs, and control costs (Brennan et al., 2004a, 2004b). It was estimated that reaction and control costs would constitute 99.5% of the total economic cost of the outbreak of KB in the United Kingdom. The values and their reasons are summarized below. The direct prices are the quality and yield losses (downgrading affected milling wheat to feed) in crops affected by KB. Reaction expenditures include the measures to be taken in the product infected with the disease, their costs, and the expenses for their management, for example, price and export effects, cost for the seed and the livestock industry, cost of quarantine and management diseases, machinery cleaning and facility cleaning, additional fungicide inputs as well as treatment of mill by-products (Sansford et al., 2008).

When a single outbreak occurs in an area of 50,000 ha, it is estimated that the total cost will be 454 million euros in 10 years due to the costs mentioned above and phytosanitary controls. If plant health official controls are less implemented and national spread, it is expected to cost 548 million euros. In such a case, if the disease spreads across the EU, then it is foreseen that the cost should be increased by 10 times for 10 years. As a result, the cost is estimated to be 4540 million euros. As stated, due to high control costs, it may be worthwhile in cases where controls prevent *T. indica* spreading nationally or spreading into the EU. Nevertheless, the least costless way is to keep the pathogen out through phytosanitary measures.

The value of damaged grain due to KB and the demand for products produced from infectious grain may vary depending on the color disorder and the content of triethylamine, the level of the disease, and the requirements of the market (Warham, 1986). The most important feature of this pathogen is that when more than 3% of grains are affected, the grain is no longer accepted for processing and is declared unfit for human consumption (Warham, 1986; Ullah et al., 2012). Disease incidence was 2%–28% (Mansoori, 2015). In India, experiments show that when the susceptible cultivars of wheat are cultivated in areas suitable for KB disease development, the level of infection is generally above 3% and affects the quality of the grains seriously (Gill et al., 1993; Sharma et al., 2004; Sansford et al., 2006). Studies on susceptible European wheat cultivars developed disease levels exceeding 3% (Riccioni et al., 2008). In countries such as India, wheat quality criteria are different from those of European countries. Quality assurance schemes in Europe, such as those in the United Kingdom, are zero tolerance of *T. indica*–affected or *T. indica*–contaminated grains. Such a situation in Europe will result in loss of income in the process from downgrading milling to animal feed. This will also affect product costs (Sansford et al., 2008).

11. Effect of climate change on *Tilletia indica*

Climate change has been the most significant threat of this century. It contributes to the death of approximately 400,000 people in a year, and the loss is more than 1.2 trillion dollars in the world (Anonymous, 2007). Plant diseases are directly affected by climate change and global agricultural productivity. As a result of effective management

strategy against diseases and pests, it has reached twice as much as food production; however, approximately 10%−16% of the global harvest is still threatened by pathogens (Chakraborty and Newton, 2011).

Due to climate change, it is valid on temperature, carbon dioxide, and humidity. It is thought that the temperature increase will lead to geographic expansion of pathogen and vector distributions in many cases. Thus, it is estimated that the pathogen will interact with more hosts and provide new opportunities for pathogen hybridization (Baker et al., 2000; Brasier et al., 1999).

Other characteristics such as the number of generations that the pathogen creates in the reproduction per time interval and the degree of participation affect the rate of evolution of a pathogen (Garrett et al., 2006). Temperature affects the rate of reproduction of many pathogens. Due to the increase in temperature, more time will be provided for pathogen development. Increased overwintering and oversummering rates will be contributed to pathogen evolution through existing large pathogen populations. Climate change may also affect sexually or asexual reproduction of pathogen populations. Changing temperatures in some cases contribute to the increase of sexual propagules and therefore may accelerate the evolutionary process of the pathogen population (Pfender and Vollmer, 1999). The crops, alternative hosts' biomass, and amount of inoculum of necrotrophic pathogens will be increased under the influence of climate change. This change will cause the pathogen to lose the advantage of a subsequent partially resistant variety that will reduce the density of inoculum (Melloyet et al., 2010).

Temperature changes will provide better opportunities for the overwintering of the sexual stages. This situation will accelerate the development of gene recombination and the development of more aggressive pathogen species (McElrone et al., 2005). Since soil is a highly complex ecosystem, different climate change parameters will be useful in various soil microorganisms and related biological processes. These changes depend on particular soil conditions. Therefore, the few generalizations of climate change interpretation can be made (Pritchard, 2011).

Due to the climate changes, many conditions such as warming, precipitation, and generation of polycyclic pathogens may also affect the geographic distribution of pathogens (Juroszek and Tiedemann, 2013). Short-life cycle pathogens adapt to climatic changes more rapidly due to high reproductive speeds and effective distribution mechanisms in the presence of host plants (Coakley et al., 1999). The survival of pathogens, the acceleration of the life cycle of vectors and fungi, and the increase in sporulation and infection are facilitated in winters with high night temperatures (Harvell et al., 2002).

In the past 30 years, analysis of weather data from different locations of Punjab, India, has determined that early warming came in February. Temperature changes affect the growth of crops and host−pathogen interaction. Hence, it is thought that the diseases such as yellow rust, KB, *Fusarium* head blight and root rust spread rapidly, if temperature and humidity increase in the absence of resistant wheat cultivars. As a result, this change is predicted to affect wheat production, which is an essential product of India, as it may cause changes in the profile of pathogens (Kaur et al., 2008).

Climate change has a vital role in geographic distribution (Mina and Sinha, 2008). Temperature changes can trigger the development of a pathogen in the dormant stage, inducing an epidemic. For example, an increase in temperature with adequate soil moisture may increase evapotranspiration, resulting in humid microclimate in crops. This situation may lead to the incidence of diseases favored under these conditions (Mcelrone et al., 2005). Diseases such as common bunt (*T. caries*) and KB may be important because of changes in soil moisture and temperature due to climate change in regions where the appropriate seed treatment is not applied (Oerke, 2006). Besides, the difference in the geographic distribution of *T. indica* due to climate change is stated in the studies of PRA in Europe (Baker et al., 2000; West et al., 2012).

As a result, a limited number of studies have been conducted on the impact of climate change on plant diseases in field conditions or on disease management under climate change. To overcome this lack of information and to have a broader perspective about the impact of climate change on plant diseases, (1) effectiveness of present physical−chemical and biological control methods, including disease-resistant varieties under the influence of climate change, should be carefully evaluated; (2) climate change scenarios should be included in all studies developing new tools and strategies; (3) disease risk analyses based on host−pathogen interactions should be implemented; and (4) the number of the studies questioning how slight differences in climate characteristics may affect host and pathogen adaptation should be increased.

12. Conclusions

Although the economic loss is not very high, KB is considered to be a significant threat. KB of wheat has a different life cycle than the other smut (dwarf and common smut) diseases known in the world. The morphology and climate

requirements of teliospores play a significant role in the development of the disease. *T. indica* is soil and airborne pathogen that may remain viable in the soil for 2–5 years depending on surrounding environmental conditions.

Although *T. aestivum* is host to various *Tilletia* species such as *T. walkeri*, *T. ehrhartae*, *T. indica*, and *T. horrida*, *T. barclayana*, *T. eragrostidis*, *T. inolens*, and *T. boutelouae* are known not to infect *T. aestivum*. However, *T. walkeri*, *T. ehrhartae*, and *T. horrida* species have infected with *T. aestivum* that has similar morphological characteristics with *T. indica*. The size, range, mean, ornamentation, and color of their teliospores of *T. walkeri*, *T. ehrhartae*, and *T. horrida* are different from those of *T. indica*.

KB is usually evaluated morphologically, but sieve wash test is often used in case of doubt. PCR-based molecular techniques are preferred if doubt is still not resolved. Wheat yield losses due to KB are negligible, but the disease has economic importance due to the quarantine measures and their effective cost. The zero tolerance quarantine established to prevent the spread of the disease is a costly approach and may not be able to prevent the spread of the disease effectively. Although wheat yield losses caused by KB disease are regarded as less important, it is costly due to quarantine practices, and KB has a serious threat to international wheat industry in the world trade. Further studies are needed to determine the effects of climate change on the disease because our current data and information level would not be able to estimate actual yield loss/grain potential related to the changes in environmental conditions.

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CHAPTER

16

Wheat–*Thinopyrum intermedium* introgression lines enhancing wheat streak mosaic virus (WSMV) resistance

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OUTLINE

1. Introduction

Since the dawn of human civilization, plant pathogens have been posing serious constraints to food production and will continue to intensify economic losses (Baker et al., 1997; Chakraborty and Newton, 2011). Future food security and avoiding widespread hunger is a complex interplay of increased crop productivity and better management of plant diseases. Conversely, availability of less appropriate germplasm and emerging virulence in plant pathogens is undermining our efforts of increasing crops productivity in an environmentally and socially sustainable way (Schwarzacher et al., 1992; Tanksley and McCouch, 1997; Rasheed et al., 2018).

More recently, crops productivity has been stagnant, and the progress on anticipated annual increases of our major crops is sluggish (Shiferaw et al., 2013). On the other hand, population growth and climatic changes are expected to rise, and this will modify plants interaction in both wild and managed ecosystems (McCouch et al., 2013; Mujeeb-Kazi et al., 2017). Plant diseases could depress yields by as 82% in cotton and 50% in other major crops. About 10%

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00016-9

−16% of the annual global harvest (US$220 billion) is lost to plant diseases; this excludes postharvest losses that are particularly high in developing countries (Chakraborty and Newton, 2011). Thus, protecting food crops from diseases seems to be the strategy that can substantially increase food supply and may address sustainable agriculture (Ali et al., 2016; Tariq et al., 2018).

Alarmingly, recent studies have revealed that climate change is inevitable, and over the past 100 years, the earth's natural climate and ecosystem services have got modified in response to human activities. Studies have indicated that climate change will modify the rate of evolution in pathogens and the recent climatic shifts will redefine the overall complexity of host−pathogen interactions (Mujeeb-Kazi et al., 2013; Rasheed et al., 2018). Furthermore, with the mean global temperature risen by 0.74°C, CO_2 levels altered in the past 100 years; this will have serious implications in plant diseases control and may push the limits of human endurance (for details, see Chakraborty and Newton, 2011).

Increasing genetic diversity of our major food crops is a potent mean of mitigating the impacts of climate change (Schwarzacher et al., 2011); this may outsmart our crops to stay ahead of the evolving virulence in pathogens (Masood et al., 2016; Rasheed et al., 2017). Thus, breeding-resistant cultivars with wider genetic base offer an applied strategy to safeguard staple food crops such as wheat against diseases as well as extreme weather events (Tanksley and McCouch, 1997; McCough et al., 2013; Divis et al., 2006; Mujeeb-Kazi et al., 2019).

2. Role of bread wheat in global food security and sustainable agriculture

Acknowledging that human is facing one of the greatest challenges of his entire civilization; how to feed the massive human population of 9 billion under a changing climate and in the context of growing competition for land and natural resources (Schwarzacher et al., 2011; Mujeeb-Kazi et al., 2019). With an annual production exceeding 749 million tons bread wheat contributing nearly 35% of the human calories (FAO, 2018). Emergence of agricultural practices and their subsequent spread around the Mediterranean region some 10,000 years ago were responsible for the rise of human civilization. *Triticum* spp. were included in the early domesticated taxa that marked the foundation of modern farming system (Zeder, 2008; Charmet, 2011). For wheat species, Fertile Crescent was recognized as the center of origin (Feldman and Sears, 1981) where the ancestral species are still widespread (Feldman and Levy, 2009).

The evolution of bread wheat involved two independent polyploidization events (Fig. 16.1). The latter event took place ~10,000 years ago and resulted in bread wheat landraces (Feldman and Levy, 2009; Mujeeb-Kazi et al., 2019). In

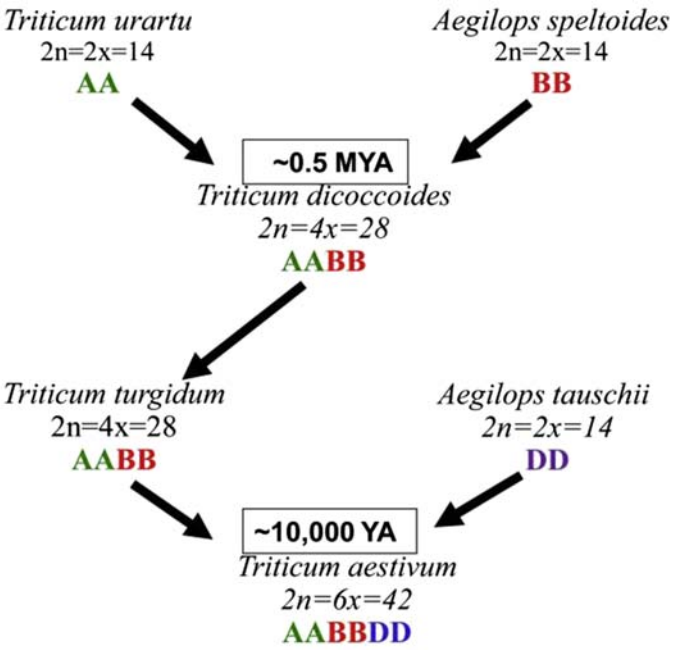

FIGURE 16.1 Origin and evolution of hexaploid wheat. *Modified from Dubcovsky and Dvorak (2007).*

wheat like other cereals, domestication relied on traits related to yield potential as well as those that facilitated harvesting (Zohary and Hopf, 2000; Vaughan et al., 2007). Following domestication, extensive backcrossing and selection of the elite lines has produced high-yielding pure wheat varieties. The due process also resulted in loss of useful variation particularly that of resistance to stresses, which existed and is ample in ancestral species even today (Sears, 1973, 1977; Tanksley and McCouch, 1997; Mujeeb-Kazi et al., 2013; Ali et al., 2016; Rasheed et al., 2018; Alemandri et al., 2019).

In this connection, alien genes derived from various *Triticeae* species have emerged as important resources for enhancing wheat genetic base. *Wheat streak mosaic virus* (WSMV) is an important disease of bread wheat with growing magnitude of yield constraints. *Thinopyrum intermedium* (JJJ^SJ^SSS, $2n = 6x = 42$) carries *Wsm1* locus conferring resistance to WSMV. Hybrids of wheat and *Th. intermedium* are associated with WSMV resistance and yield returns in the presence of viral pressure, and no linkage drag has been associated with this alien chromatin. These wheat–*T. intermedium* lines carrying *Wsm1* gene along with details of their successful utilization for wheat improvement are described in this chapter.

3. Wheat streak mosaic virus

WSMV is an emerging virus that threatens cereal production and could trigger significant losses to wheat (Tatineni et al., 2011; Alemandri et al., 2019; Gupta and Tatineni, 2019). WSMV was initially reported from the United States (Mckinney, 1937); since then, the disease has spread widely within the wheat-growing world (Byamukama et al., 2013; Bennypaul et al., 2019; Gupta et al., 2019). The disease may affect both winter and spring wheat; the disease spread by wheat curl mite (WCM) (Singh et al., 2018; Alemandri et al., 2019). Yield penalties vary from 2.5% to 5%, but in some cases, losses may reach as high as 100% (Divis et al., 2006; Graybosch et al., 2009). Volunteer wheat, timing of infectivity, genetic background of wheat cultivars, and temperature are some of the critical factors determining disease severity (Ali et al., 2016; Bennypaul et al., 2019).

4. Salient features of wheat streak mosaic virus genome

WSMV of the family Potyviridae is a rod-shaped virus (size = ~700 nm long and ~15 nm wide) under electron microscope (Singh et al., 2018; Bennypaul et al., 2019). The largest numbers of plant RNA viruses are grouped in this family and are illustrated by mono- or bipartite positive-sense RNA genome (Gupta and Tatineni, 2019). The virus has single-stranded 9,384-bp genome. The genome is translated into a single transcript; posttranslational cleavage of this polyprotein results into at least 10 functional proteins (Gupta and Tatineni, 2019). These include P1, helper component-protease (HC-Pro), P3, 6K1, 6K2, cylindrical inclusion (CI), nuclear inclusion "a" (NIa-VPg), nuclear inclusion "b" (NIb), capsid protein (CP), and encapsidation proteins (Fig. 16.2). Each protein plays an important role in establishing pathogenesis to cell to cell movement and RNA genome replication of the virus (Tatineni et al., 2011; Singh et al., 2018; Gupta and Tatineni, 2019). Comprehensive details of the genes are mentioned in Tatineni and Hein (2018) and Singh et al. (2018). Recently, it has been shown the WSMV results in modification of the transcriptional profile of viruliferous mites in such a way that it enhances viral–host association and population growth of WCM to further viral transmission (Gupta et al., 2019).

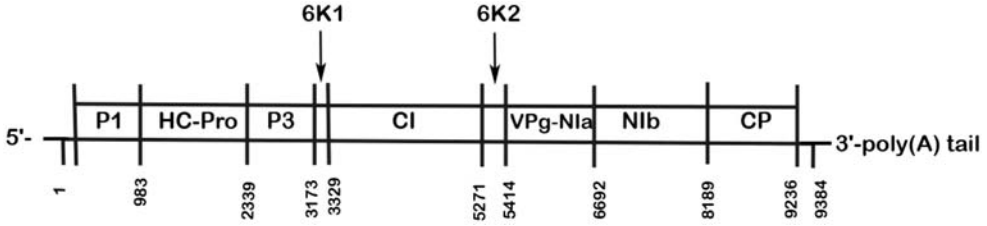

FIGURE 16.2 Genomic map showing the organization of wheat streak mosaic virus. The RNA genome is represented by bar with nucleotide sequence positions below. The translated polyprotein is processed by viral proteinases into mature proteins. The names of each protein are given inside or above the boxes and include P1, HC-Pro, P3, 6K1, CI, 6K2, NIa, Nib, and CP. *Modified from Stenger, D.C., Hall, J.S., Choi, I.R., French, R., 1998. Phylogenetic relationships within the family Potyviridae: wheat streak mosaic virus and Brome streak mosaic virus are not members of the genus Rymovirus. Phytopathology 88, 782–787 and Fahim, M., Ayala-Navarrete, L., Millar, A.A., Larkin, P.J., 2010. Hairpin RNA derived from viral NIa gene confers immunity to Wheat streak mosaic virus infection in transgenic wheat plants. Plant Biotechnology Journal 8, 821–834.*

5. Symptoms and transmission of wheat streak mosaic virus

WSMV-infected wheat plants are stunted and exhibit a variety of symptoms including appearances of greenish-yellow streaks running parallel along the leaf axis; leaf margins are rolled (Singh et al., 2018; Alemandri et al., 2019). These symptoms are often easily confused with other diseases associated with environmental stresses, nutritional disorders, or chemical damage to the leaf tissues (Singh et al., 2018). The infected plants may remain vegetative and would produce fewer tillers with low-quality seeds. In some cases, host plants die away, and yield penalties are maximum in such cases (Lanoiselet et al., 2008; Velandia et al., 2010; Bennypaul et al., 2019). In addition to wheat, WSMV may infect a broad range of hosts within the family Poaceae. WSMV and WCM persist on the "green bridges" (Singh et al., 2019). WSMV can infect *Secale cereale*, *Lolium rigidum*, *Hordeum* sp., *Avena fatua*, *Tragus australianus*, *Eragrostis cilianensis*, and *Panicum capillare* as alternative hosts (Ali et al., 2016; Tatineni and Hein, 2018; Singh et al., 2018).

Effective transmission of WSMV is achieved via WCM as well as infested seeds (Lanoiselet et al., 2008). When primary host, e.g., wheat, is not available, both mites and WSMV carry over on other grasses (Gupta et al., 2019). Environmental factors that could positively or negatively influence plant growth, and/or multiplication of the WCM benefits disease epidemics. Temperature, light, and soil fertility affect plant growth, whereas plant growth stage during pathogenesis, wind speed and direction, timing of infection, and genotype used influence WCM population load (see Singh et al., 2018; Bennypaul et al., 2019). Infections set in early winter are more devastating than those established later in spring, as mites get ample time to reproduce and spread into the adjoining areas (Thomas and Hein, 2003; Gupta and Tatineni, 2019).

WCMs are remarkably successful in colonizing new host plants; the aggressiveness of WCM population may be perceived from the fact that WCM once reached to a new host plant completes two generations in just 14 days and establishes a population density significantly higher than the initial source from where it originates (Singh et al., 2018). In certain outbreaks of WSMV, more than one type of infectious particle take place, i.e., WSMV can interact with High Plains virus (HPV) and *Triticum* mosaic virus (TriMV) to coinfect a single host, and WCM can vector both these viruses (Singh et al., 2018; Gupta and Tatineni, 2019).

6. Management and control of wheat streak mosaic virus

So far only one gene of WSMV resistance within the primary gene pool of wheat has been exploited and, WSMV remains a major threat to global wheat production (Graybosch et al., 2009; Mutti et al., 2011; Schwarzacher et al., 2011; Tatineni and Hein, 2018). WSMV infects both winter and spring wheats, and among the viral diseases of cereals and in terms of losses inflected, WSMV ranks second after Barley yellow dwarf virus (Ellis et al., 2003; Gupta and Tatineni, 2019).

In general, WSMV infections are detected on leaves and stunting of the plants. However, symptomatic identification is not a reliable method for the confirmation of WSMV. Recently, ELISA methods have been established for monitoring WSMV. In addition, cDNA amplification and RT-PCR as well as quantitative RTPCR (RT-qPCR) methods have been developed to identify the virus (Schubert et al., 2015). Recently, studies have indicated that WSMV lowers root biomass and thereby reduces water use efficiency of infected plants, making WSMV as serious concern for arid regions and future water scarcity associated with climate change scenarios (Price et al., 2010; Singh et al., 2018). Of the few available WSMV control options, important ones are discussed in the following sections.

6.1 Cultural practices for the control of wheat streak mosaic virus

Epidemics of WSMV are largely attributable to the occurrence of volunteer wheats and related grasses where WSMV and WCM overwinter the harsh weathers (Thomas et al., 2004). Both preharvest and postharvest green bridges, especially wheat as leftover from previous seasons as a result of a hailstorm needs special attention, as these are the preferred choices of WCM colonisation (Gupta et al., 2019).

Eliminating these potential hosts may prevent the probabilities of WSMV infection. Delayed plantation is seen with success, and this reduces the losses to WSMV (Divis et al., 2006; Singh et al., 2018). However, regions where wheat is grown for both feed and grain purposes remain at a higher risk of WSMV infection, which could ultimately serve as a means of WCM and WSMV spread in the region (Alemandri et al., 2019). Removal of volunteer wheat or

other grasses in such cases is only helpful in curtailing magnitude and diversity infection but may not reduce the possibilities of WSMV outbreaks (Hunger et al., 1992; Gupta and Tatineni, 2019)

Visual symptoms of WSMV on leave result in adjustments of the cell biomolecules and overall makeup; these modifications altogether change the leaf reflection spectra (West et al., 2003). Remote-sensing monitor changes in the reflected light from wheat crop canopy have been used to assess WSMV alerts (Mirik et al., 2006). However, satellite and remote sensing provides a robust and inexpensive means of identifying WSMV infection and warning systems (Mirik et al., 2006). Still, it is barely a monitoring tool for crops and cannot be used to control WSMV (Richardson et al., 2004).

More recently, seed transmission of WMSV has also been reported. Although seed transmission frequency is not very high, it is extremely important for the dispersal of WSMV to new destinations. Like all viral diseases, reducing the intensity and magnitude of losses caused by WSMV relies upon prevention. A major management strategy to limit WSMV or WCM includes cultural practices and the use of resistant or tolerant cultivars (Ali et al., 2016; Gupta and Tatineni, 2019). To restrict seed transmission of WSMV rigorous plant, quarantines are helpful to minimize the spread of WSMV (Lanoiselet et al., 2008).

6.2 Chemical control measures for controlling wheat streak mosaic virus

Application of chemical substances (as pesticides) offers one of the most efficient and widespread approaches for controlling plant diseases. For example, some of the deadliest plant pathogens are of fungal nature, and fungicide applications have immense success rate in reducing the incidence of such infections. However, viral diseases cannot be controlled by agrochemicals, and agronomic conditions must be improved for limiting viral infections (Perring et al., 1999; Singh et al., 2018). Herbicides are applied before wheat-growing season to eliminate the alternate host plants. Some miticides are reported to be efficient in curtailing WCM, but the habitats of mites (shelters mainly in the rolled leaves of infected plants) and optimum timing and conditions for chemical application reduce the efficiency of miticides (Velandia et al., 2010; Singh et al., 2018). Furthermore, their cost and environmentally hazardous nature of pesticides are the major concerns for plant biologists, and the use of chemicals is discouraged (Lu et al., 2011; Alemandri et al., 2019).

6.3 Engineered resistance to wheat streak mosaic virus

Although agronomic management and the application of pesticides have potential to reduce crop losses to diseases, the time and cost-effectiveness coupled with potential environmental hazards and increased tolerance of the pathogens through selective pressure are the rising concerns (Curtis et al., 2002; Chen, 2005; Gupta et al., 2019). Recently, transgenic avenues have also been searched for WSMV control. Among transgenic wheat lines, viral resistance is derived from the regulation or interfering of viral genes (Tatineni and Hein, 2018; Gupta and Tatineni, 2019). Among transgenic WSMV-resistant wheat varieties, immunity or complete resistance to WSMV has been reported, where either important life cycle genes of the virus were interfered or expression of viral coat protein, replicase gene, or RNA interference was exploited to limit replication of WSMV (Fahim et al., 2010; Gupta and Tatineni, 2019). Although transgenic wheat confers nontransient WSMV resistance in laboratory as well as greenhouse conditions, field examinations have shown yield disadvantages as well as breakdown of transgenic wheat to defy WSMV (Tatineni and Hein, 2018; Singh et al., 2018; Gupta et al., 2019; Guptaand Tatineni, 2019). Nevertheless, emerging research is associated with raising concerns about the environmental impacts and crossing of transgenic lines with native plants populations; such cultural sensitivity and undetermined future are the concerns that may be debated (Altieri, 2000; Mall et al., 2018).

6.4 Natural resistance to wheat streak mosaic virus

Most wheat cultivars lack resistance to WSMV, and where resistance is reported, it breaks and tends to remain ineffective at elevated temperatures (Seifers et al., 2007; Fahim et al., 2010; Singh et al., 2018). Therefore, attempts were made to explore natural resistance against WSMV in both cultivated and wild *Triticeae* (Friebe et al., 1996; Cox et al., 2002). Perennial wheat grasses, *T. intermedium* syn. *Agropyron intermedium* (Host) Barkworth and Dewey ($2n = 6x = 42$, JJJ^sJ^sSS) and *Thinopyrum ponticum* (Podp.) Barkworth and Dewey ($2n = 10x = 70$, $JJJJJJ^sJ^sJ^sJ^s$), were the first reported species that displayed effective resistance to WSMV (Wells et al., 1973, 1982; Ali et al., 2016; Gupta et al., 2019). Both species contain genes that show elevated resistance to WSMV and may limit the WCM population

(Schwarzacher et al., 2011; Ali et al., 2016). These perennial wheat grasses of the tertiary genome pool have been selected and used as potent means of increasing the genetic diversity of wheat (Li and Wang, 2009; Ali et al., 2016).

Among the alien WSMV-resistant sources, *T. intermedium* resistance is fundamentally derived from three chromosomal regions. Few sources that carry *T. intermedium* chromatin were formerly believed to be a group 4 recombinant, and later corrected and reconfirmed as it was the homoeologous group 7 long arm (Friebe et al., 2009). The second source of WSMV resistance is carried by wheat—*T. intermedium* amphiploids in the popular Zhong series developed in China (Chen et al., 2003). Although both confer tolerance/resistance, neither of the two have been used commercially. Previously, compensating Robertsonian translocations were not recovered in both sources (Friebe et al., 2009). However, very recently, group 7 compensating translocation lines have been recovered (Liu et al., 2011). The widely applied source of WSMV resistance (*Wsm1* gene) is mapped to the short arm of the group 4 of *T. intermedium* designated as 4Ai#2S chromosome (Ali et al., 2016; Singh et al., 2018). Examples of wheat—*Thinopyrum* recombinants given in this chapter also carried the *Wsm1* resistance (Figs. 16.4—16.6); details on bread making quality attributes of these lines are given in Divis et al. (2006), whereas field screening for WSMV resistance and molecular aspects of *T. intermedium* chromatin in different breeding populations are covered in Ali et al. (2016).

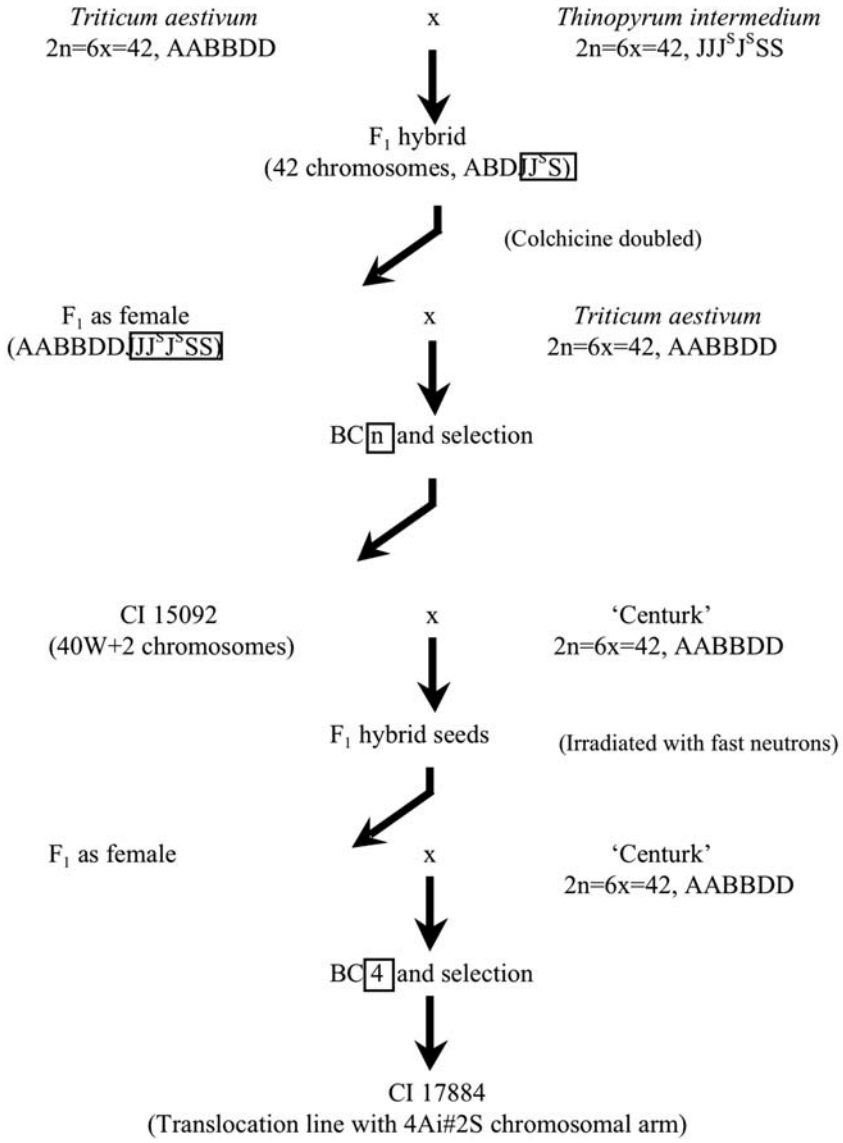

FIGURE 16.3 Schematic representation of wide hybridization and alien gene transfer from *Thinopyrum intermedium* (JJJ^SJ^SSS genome) to *Triticum aestivum* (AABBDD genome). CI 17884 is a *wheat streak mosaic virus* (WSMV)—resistant line. BC represents back cross, W represents wheat chromosomes, and "Centurk" is a wheat cultivar. *Based on Wells et al., 1973, 1982; Divis, L.A., Graybosch, R.A., Peterson, C.J., Baenziger, P.S., Hein, G.L., Beecher, B.B., Martin, T.J., 2006. Agronomic and quality effects in winter wheat of a gene conditioning resistance to wheat streak mosaic virus. Euphytica 152 (1), 41—49.*

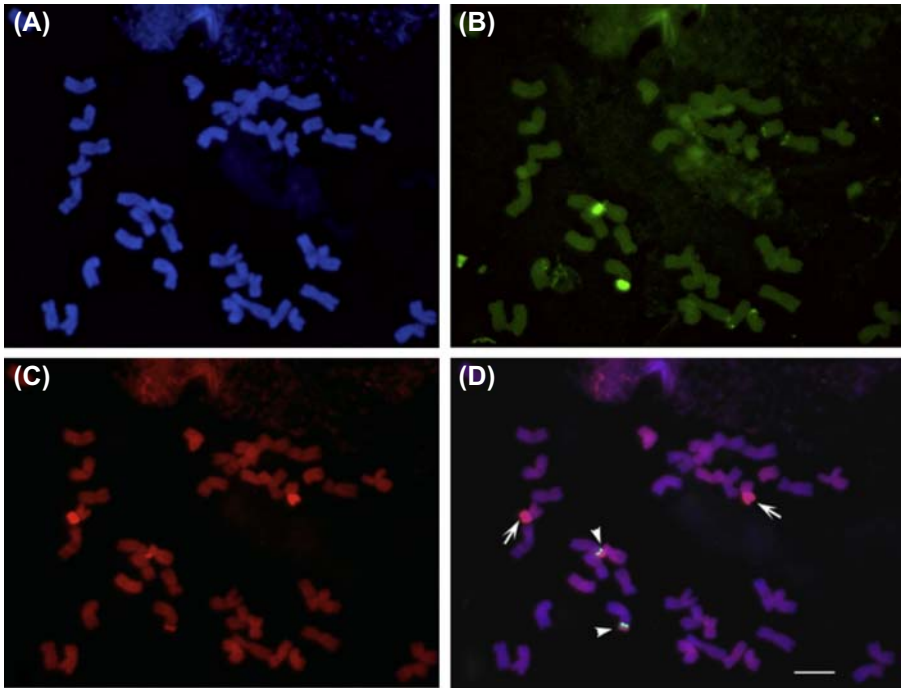

FIGURE 16.4 Root-tip metaphase chromosomes of the wheat streak mosaic virus—resistant line N02Y5018 (2n = 42) after fluorescent in situ hybridization (FISH). (A) Wheat chromosomes fluoresce blue with DAPI. (B) Hybridization pattern of the pTa794 clone labeled with digoxygenin 11-dUTP (detected in green) showing the physical location of 5S rDNA sites in wheat. (C) In situ hybridization of the total genomic DNA from *Thinopyrum intermedium* labeled with biotin 16-dUTP (detected in red). The genomic in situ hybridization allows the detection of *T. intermedium*—origin chromosome segments. (D) Overlay of A, B, and C images, indicating alien chromosomal arm (arrows) and small secondary segments (arrows head) present above the 5S rDNA sites. Bar represents 10 μm.

6.5 Natural resources of wheat streak mosaic virus resistance used for bread wheat improvement

Two genes, i.e., the *Wsm1* and *Wsm2* conferring WSMV resistance, have been used in wheat improvement programs (Friebe et al., 2009; Graybosch et al., 2009; Lu et al., 2011). The *Wsm1* resistance is of *T. intermedium* origin; successful transfer of this resistance is traced back to Wells et al. (1973) where the authors transferred this gene into wheat germplasm CI 17884 (Fig. 16.3). This resistance is mapped on the short arm of *T. intermedium* delivering efficient resistance against WSMV (Singh et al., 2018). The first commercial WSMV-resistant cultivar "Mace" also harbored this resistance (Graybosch et al., 2009). Similarly, mapping studies in CO960293-2 wheat line have indicated *Wsm2* gene to be residing on chromosome 3BS (Lu et al., 2011). To date, the origin of how this resistance has emerged is not clear, as its pedigree or parents comprise WSMV-susceptible lines (Haley et al., 2002). Perhaps, epigenetic phenomenon and chromatin remodeling via DNA methylation may explain the origin of this resistance. However, there are no such data available to support the origin of *Wsm2* resistance. Recently, *Wsm2* selection has been introgressed into wheat cultivars "RonL", "Snowmass" and "Oakley CL" (Haley et al., 2011; Zhang et al., 2015; Singh et al., 2018). Another *T. intermedium*—derived gene, the *Wsm3,* has been identified and mapped to T7BS·7S#3L (Liu et al., 2011). Importantly, lines carrying this resistance have been reported effective against WSMV at much higher temperature (see below); however, this source is yet to be used in wheat improvement commercially.

Although *Wsm1* offers resistance and this selection has been known for almost five decades (Wells et al., 1973), the first commercial cultivar Mace was released lately (Graybosch et al., 2009). Reason for this very slow success toward the release of WSMV-resistant cultivar was the original lines that carried *Wsm1* and that were frequently associated with disadvantageous attributes (Seifers et al., 1995). A number of studies indicated that wheat lines with *Wsm1* carrying *T. intermedium* chromatin (Fig. 16.4) had significantly lower yield when viral pressure was not available (Divis et al., 2006). Therefore, interest resided in lines that offer resistance but do not compromise on yield or other essential bread making quality. Examples mentioned here or earlier in Ali et al. (2016) were evaluated for potential linkage drag (Divis et al., 2006). In the presence of disease pressure (i.e., WSMV), grains or yield differences have been reported between resistant and susceptible lines, i.e. in the presence of virus, lines with *Wsm1* or *T. intermedium* chromatin had much higher yield than lines missing this alien chromatin (Figs. 16.4 and 16.5).

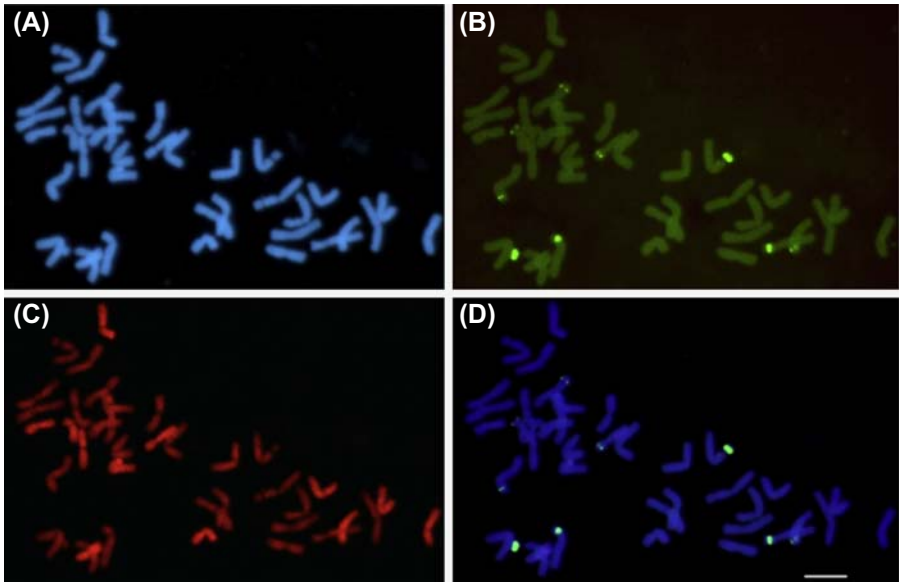

FIGURE 16.5 Root-tip metaphase chromosomes of the wheat streak mosaic virus—susceptible line N02Y5082 (2n = 42) after fluorescent in situ hybridization (FISH). (A) Wheat chromosomes fluoresce blue with DAPI. (B) Hybridization pattern of the pTa794 clone labeled with digoxygenin 11-dUTP (detected in green) showing the physical location of 5S rDNA sites in wheat. (C) In situ hybridization of the total genomic DNA from *Thinopyrum intermedium* labeled with biotin 16-dUTP (detected in red). The genomic in situ hybridization could not detect any *T. intermedium*—origin chromosome segments. (D) Overlay of A, B, and C images. Bar represents 10 μm.

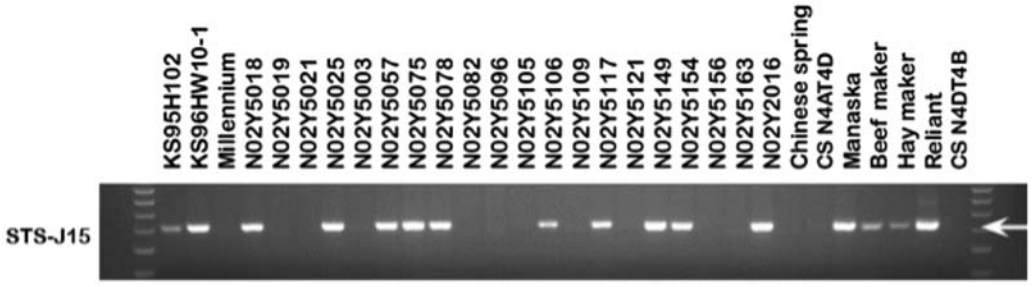

FIGURE 16.6 PCR amplification pattern of STS-J15 markers from wheat—*T. intermedium* hybrid lines. *Arrows* indicate to the 420 bp product linked to Wsm1 gene.

Since it is likely to be durable solution, it has been pursued from times when WSMV resistance was first reported (McKinney and Sando, 1951). In fact, the most promising WSMV resistance known today in commercial cultivars has its origin in wheat—*T. intermedium* hybrids. These lines contain *T. intermedium* chromatin on the homoeologous group 4, i.e., on 4DS or 4AS chromosomal translocations (Haber et al., 2007; Schwarzacher et al., 2011; Ali et al., 2016). Moreover, size of the known *T. intermedium* fragments associated with resistance varies considerably among different wheat germplasm and lines that carry WSMV gene as terminal alien fragments have been produced through *ph* gene manipulation (see Friebe et al., 2009).

Thinopyrum group confers extraordinary levels of resistance to WSMV as well as other leaf mosaic viruses such as HPV or TMV (Tatineni and Hein, 2018; Gupta and Tatineni, 2019), whereas rye is susceptible to WSMV and can resist both green bug and WCM colonization (Divis et al., 2006; Ali et al., 2016). Wheat cultivar Mace derived from this study is the only known cultivar that offers resistance against the two Argentinian WSMV isolates (Alemandri et al., 2019). Several genes for WCM resistance from the wild-related *Triticeae* species have been transferred into wheat backgrounds, but reports suggest that some biotypes of WCM have overcome this resistance (Friebe et al., 1996; Chen et al., 2003; Hein et al., 2012; Byamukama et al., 2013; Ali et al., 2016).

7. Temperature sensitivity of wheat streak mosaic virus resistance selection

All three WSMV-resistant genes, i.e., *Wsm1*, *Wsm2*, and *Wsm3*, show temperature dependency above 18°C (Divis et al., 2006; Seifers et al., 2006; Graybosch et al., 2009; Liu et al., 2011). The *Wsm1* selection is effective at 20°C, and with rising the temperature up to 25°C, the characteristic symptoms of WSMV appear. Furthermore, the *Wsm1* gene could not resist WSMV at higher temperature, and lines become susceptible at 28°C (Fahim et al., 2012). On the other hand, the *Wsm2* resistance was originally ineffective above 18°C, but subsequent exposure of this selection to virus over several generations has resulted in line "c2652" that protects wheat lines against WSMV up to of 28°C (Fahim et al., 2012; Singh et al., 2018). Nonetheless, Liu et al. (2011) have shown that *Wsm3* derivatives are effective sources of resistance up to 24°C. All known sources that carry *Wsm1* alone exhibit characteristic symptoms of WSMV at 27°C, but wheat—*T. intermedium* substitution lines that carried entire chromosomes 4Ai#2 were stable at 27°C, suggesting the presence of further resistance genes in *T. intermedium* (Fahim et al., 2012). It has also been shown that the winter wheat cultivar "Mace" with *Wsm1* gene resists the coinfection of WSMV and other related *Triticum mosaic virus* (TriMV) up to 19°C, but neither the *Wsm2* nor the *Wsm3* derivatives could not resist TriMV above 18°C, indicating the effectiveness of *Wsm1* selection (Graybosch et al., 2009; Liu et al., 2011).

WSMV may interact with related viruses such as HPV and TriMV to coinfect a single host, due to synergistic interaction; such infections cause severe damages (Singh et al., 2018; Tatineni and Hein, 2018). It is revealed that "Mace," the first WSMV-resistant winter wheat cultivar (carrier of *Wsm1* gene), resists coinfection or disease synergism of WSMV and TriMV up to 19°C (Gupta and Tatineni, 2019).

Presence of alien material (4D recombinant chromosome) in these wheat-breeding lines always correlated with WSMV resistance in the field and was ascertained using fluorescent in situ hybridization (FISH; for details, see Schwarzacher et al., 1992). In contrast, lines without alien chromatin do not show resistance to WSMV. FISH is a powerful technique that could identify and physically map alien genes, chromosomal segments as well as genome in case of polyploid species (Schwarzacher et al., 2011). However, it is expensive and requires immense expertise. Therefore, previously known tightly linked PCR marker was used (Fig. 16.6) to see the presence of *Wsm1* gene (resistance). The PCR molecule allowed determination of *T. intermedium* chromatin and discriminated resistant and susceptible lines with 100% accuracy (Ali et al., 2016). The PCR-based marker will ensure maximum exploitation of the WSMV resistance and their earliest availability to wheat growers and will facilitate marker-assisted selection breeding approaches.

Introgression of suitable genes for traits of interests and development of crops with robust resistance represent the fundamental goals of plant breeding (see Friebe et al., 2009; Ali et al., 2016). WSMV resistance lines involving small alien fragments of *T. intermedium* translocations are preferred due to diminishing probability of linkage drag (Friebe et al., 2009; Schwarzacher et al., 2011; Ali et al., 2016). However, all larger alien fragments are not detrimental; they may possibly introduce more valuable variation. The short arm of *T. intermedium* chromosome 4Ai#2 has no or unknown negative effects, and under field conditions, it provides benefits against WSMV. Chromosomal arm 4Ai#2S (harboring *Wsm1* and WCM resistance) also carries *Tapesia yallundae*—resistant gene(s) (Chen et al., 2003; Divis et al., 2006; Li and Wang, 2009). Recently, the *Lr19/Lr25*- and *Lr24/Lr26*-resistant sources have also been mapped to *T. ponticum* chromosomes 7 and 3 long arms; those are also transferred as blocks and have added potential (Li and Wang, 2009). In either case, if reduction in size of alien chromatin is required, it is possible via *phph* manipulation (Qi et al., 2007; Mujeeb-Kazi et al., 2017).

8. Gene pyramiding approaches: increasing genetic diversity and addressing sustainable agriculture

Breeding wheat cultivars with durable resistance to multiple stresses is holding immense promise for wheat improvement and climatic resilience. Pyramiding of diverse stress-tolerant genes into a single genotype, i.e., combining more than one gene, may provide more durable resistance than sequential releases for single genes. For example, three powdery mildew (Pm) resistance genes were stacked into an elite wheat cultivar "Yang047," and it displayed excellent Pm resistance (Liu et al., 2000). Likewise, Wang et al. (2001) studied wheat lines derived from crosses of elite parents possessing Pm resistance genes, *Pm2*, *Pm4a*, *Pm8*, and *Pm21*. Different Pm gene combinations were recovered; results indicated that plants with combination of pyramided genes had better response than lines carrying only one gene. Furthermore, wheat line with Pm2 and Pm4a combination showed immunity to Pm, suggesting that pyramiding different Pm genes provides sustainable means of utilizing resistance genes (Wang et al., 2001). Nine genes conferring resistance to cereal cyst nematodes are found within the cultivated and wild *Triticeae*

species. So far, two resistance genes have been pyramided in a wheat background that displayed significantly higher resistance than that of CreX and CreY single introgression lines (Barloy et al., 2007).

Koller et al. (2018) have analyzed transgenic lines with two pyramided *Pm3* alleles generated by crossbreeding of lines with transgenic Pm3 alleles. All four allele-pyramided lines showed improved Pm resistance compared with their parental lines. Similarly, herbicides-resistant lines produced through conventional breeding when they had combined traits by pyramiding gene approaches conferred 18- and 19-folds more resistance compared with susceptible lines (Domínguez-Mendez et al., 2019). Similarly, pyramiding gene may also interact with one another in a common background, and combination or stacking of resistance genes against green bug biotypes revealed contradictory results. It was found that pyramided genes provided no additional protection compared with the resistance conferred by the single resistance gene (Porter et al., 2000). Furthermore, detection of the Ug99 race TTKSK is virulent to *Sr31* and most other stem rust resistance genes in wheat. These races present threat to global wheat production. More durable resistance to TTKSK race, as well as to leaf rust and Fusarium head blight (FHB), has been produced. These lines with pyramided genes offer resistance to leaf rust, FHB as well as to race TTKSK (Zhang et al., 2019).

Although there are numerous examples where multiple resistance genes have been stacked in wheat genotype and these genes in combination have displayed superior resistance, there is no single report available where the known WSMV resistance genes were combined in one genotype. It is proposed with high confidence that all the known genes of WMSV resistance, i.e., *Wsm1*, *Wsm2*, and *Wsm3*, may be stacked in one genotype, which will safeguard the future wheat cultivars against WSMV epidemics.

9. Summary and way forward

Recognizing that the world today faces one of the biggest challenges of all times: how to feed 9 billion people by 2050 in ways that are sustainable and are not detrimental to the planet Earth. Bread wheat is a mainstay of food security; most of the wheat in the developing world will continue to be consumed as food, whereas in developed world, the diversified resources of food and income have resulted in using more animal products (Pingali, 2007). Previously, crops failure and high bread prices have been associated with unrest, and this highlights the immense significance of wheat (Trego, 2011).

Fungal and viral strains are evolving and better adapting to changing climates than their hosts do (Hovmøller et al., 2011). Genomic information of WSMV is encoded in its single-stranded RNA genome lacking proofreading activity, and RNA viruses tend have high mutation rate (Elena and Sanjuán, 2005). Similarly, the aggressiveness of fungi may be inferred from their power to generate additional spores than they would produce previously. Plant breeders have achieved remarkable achievements in handling novel variations needed for bestowing resistance and yield outputs (Borlaug, 1983). Certainly, utilization of high-yielding varieties has significantly improved crop productivity, but it is associated with narrowing down the genetic base of crops such as wheat, and the process may still be continued (Tariq et al., 2018; Mujeeb-Kazi et al., 2019). The emergence of *Ug99* group of stem rust races has raised the alarm and importance to search and deploy diverse sources of resistance. The *Ug99* races are virulent to almost all resistance genes deployed in most of the wheat varieties under cultivation (Singh et al., 2008). Likewise, mutations in WSMV may potentially put all deployed sources of WSMV resistance at risk or even render them ineffective.

The resistance as wheat—*Thinopyrum* hybrid lines exemplified above is attributed to *Wsm1* gene; more successful approach is to have varieties that possess durable resistance contributed by minor genes. Therefore, the best means to improve resistance would be to stack *Wsm1, Wsm2,* and *Wsm3* genes following pyramided gene approach to "stack" all genes in one genotype. This on one hand will reduce the probability of simultaneous mutation events in the pathogen as well as in the resistant genes. Such gene pyramiding approaches have wider application, although these genes may not be as effective as the durable resistance from minor genes but still, for surely, provide a cushion to impart sustainable productivity.

Domestication has played an enormous role in setting human civilization; our understanding of the adaptation under domestication is still very limited. Green Revolution and modern plant breeding have dramatically transformed world wheat production and agriculture at large. Due to the advent and application of high-throughput and robust genetic mapping techniques, major alleles for almost all stresses have been identified, which has benefitted both producers and consumers because of the low production costs and affordable food prices (Shiferaw et al., 2013). Furthermore, we have been able to keep feeding the ever-growing human population, and since the reference genome sequence of wheat (IWGSC, 2018), diploid wild progenitors and other wild resources have been completed (Rasheed

et al., 2018). It will reveal some more details of the *Triticeae* genomics and alleles that had played important roles in plant domestication. Findings of such results will be of great importance and may be translated into improvement of wheat cultivars, enhancement of their genetic diversity, and conservation of the wheat germplasm.

Acknowledgments

The author thanks Hazara University, Mansehra, Pakistan, and University of Leicester, UK, for financial support and PhD fellowship, and R.A. Graybosch (USDA-ARS and Department of Agronomy & Horticulture, University of Nebraska, Lincoln, NE, US) for providing seeds of wheat—*Thinopyrum intermedium* hybrid lines.

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CHAPTER

17

Climate change leading to postharvest losses in bread wheat

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OUTLINE

1. Preface, bread wheat, postharvest chain and facilities

Bread wheat (*Triticum aestivum*) postharvest chain has three major steps including grain storage, transportation, and milling. Depending on the production and destination area, wheat grain may be stored at different levels in the supply chain (farmer, distributor, and miller) using various infrastructures such as in silos, warehouses, bags, containers, traditional storage structures, or in other defined units. Transportation of bulk or packaged wheat is done by different vehicles (trucks, rails, and ships) (Table 17.1). Both storage and transportation steps can have diverted duration, and the postharvest life of wheat grain can range from a few days to many months.

A wheat grain storage system is an artificial ecosystem in which deterioration of the stored product results from the effects of abiotic physical (e.g., temperature, moisture, storage structure) and chemical (e.g., carbon dioxide, oxygen) factors as well as biotic factors including grain attributes, microorganisms, insects, mites, rodents, birds (Jayas, 1995; Magan et al., 2011; Moses et al., 2015). Each factor can act independently on the stored wheat ecosystem or interacting with other factors (Fig. 17.1).

This chapter summarizes the factors affecting postharvest life of wheat grains and analyzes the impact of climate change to postharvest losses of the product.

2. Wheat grain required attributes

According to legislative standards, for both wheat (*T. aestivum* L.) and durum wheat (*Triticum durum* Desf.) grains intended for processing for human consumption—specific criteria must be met related with moisture content,

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00017-0

TABLE 17.1 Summary of postharvest handling of wheat grain at different levels of supply chain.

Level of supply chain	Postharvest handling	Facility/vehicle
Farms	Storage	Bulk; bin, silo bag, warehouse
	Transportation	Bagged, bulk; trucks, rails, and ships
Distributor	Storage	Bagged, bulk; bin
	Transportation	Bagged, bulk; trucks, rails, and ships
Wheat mills	Storage	Bagged, bulk; bin
	Milling	

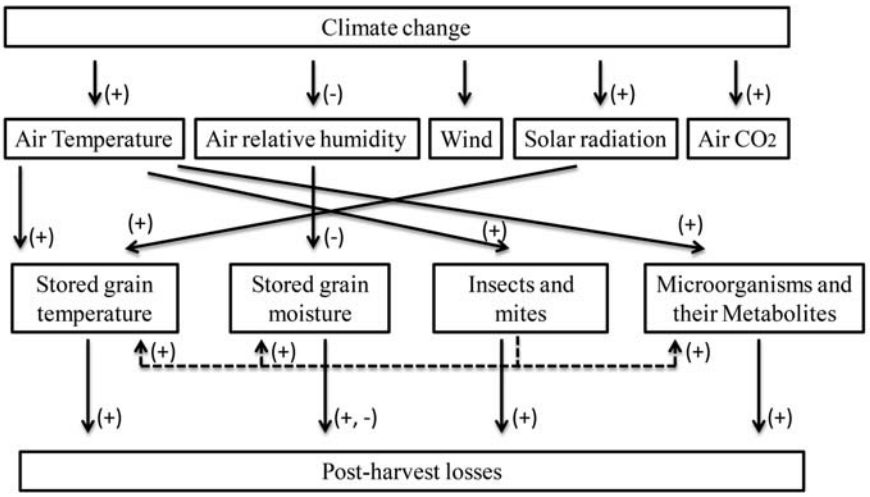

FIGURE 17.1 Factors affecting bread wheat postharvest losses and their interactions. In each arrow the symbols + or − correspond to increase or decrease, respectively, in the value of the affected parameter.

extraneous matter, toxic or noxious seeds, filth, contaminants, and hygiene (Alimentarius, 1995). Some of these factors are only affected by preharvest management (i.e., toxic seeds), whereas others (i.e., moisture, filth, hygiene) are dynamically changing at postharvest level in a wheat grain storage system. The maximum moisture content of both wheat and durum wheat grains must be below 14.5% (w/w), but lower moisture levels should be required depended on the climate, duration of transport and storage. Grains visibly bored or tunneled by insects must not exceed 1.5% and 2.5% (w/w) for wheat and durum wheat, respectively, and the maximum level of impurities of animal origin (including dead insects) is at 0.1% (w/w). The ergot alkaloid should be below 0.05% (w/w) in wheat and 0.5% (w/w) in durum wheat, and the levels of deoxynivalenol (DON) at 300−2000 μg/kg depending on the regulations of different countries (Alimentarius, 1995; van Egmond et al., 2007). Wheat grain must fulfill all standards during the whole postharvest chain.

3. Effect of abiotic factors on wheat grain storage artificial ecosystem

Temperature is a major factor affecting wheat grain postharvest behavior acting directly and/or indirectly through interactions with other factors. The safe storage duration of wheat at standard grain moisture (<14% w/w) decreases as storage temperature increases. For example, below 15°C, the wheat may be stored for more than 9 months, whereas at 30°C the storage duration may be only for 1−4 months (Table 17.2). The temperature and its distribution in a stored wheat grain system are affected by many factors such as ambient air temperature, air convection, local wind velocity, solar radiation, and storage facility structure and size (Chang et al., 1993; Gastón et al., 2009; Jia et al., 2001).

TABLE 17.2 Indicative storage duration of wheat grain depending on grain moisture and temperature.

	Grain moisture (% w/w)								
Grain temperature (°C)	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**22**	**24**
30	*1–4*[a]	<1	<0.5	–	–	–	–	–	–
27	**4–5**	*1–2*	<1	<0.5	–	–	–	–	–
25	**6–8**	*1.5–3*	<2	<1	<0.5	–	–	–	–
20	**7–9**	*2–5*	*1–4*	*1–2*	<1	<0.5	–	–	–
15	**>0 9**	**5–8**	*2–5*	*2–4*	*1–2*	<1	<0.5	<0.5	–
10	**>0 9**	**6–9**	**5–8**	**3–5**	*2–4*	*1–3*	*1–2*	<1	<0.5
5	**>0 9**	**7–9**	**6–8**	**4–8**	**4–7**	*2–4*	*2–3*	*1–2*	<1

[a]*Numbers correspond to the storage duration in months. Numbers in bold correspond to a safe storage duration. Numbers in italics correspond to a marginal safe storage duration.*

In a conventional wheat storage system, both heat and mass are continuously exchanged between the stored grain and the environment resulting in simultaneous heat and mass exchanges at the exposed surfaces of the grain by means of "convection" in the longitudinal direction and heat exchange through the storage facility barrier (e.g., wall) by means of heat conduction in the radical direction (Lo et al., 1975).

In conventional wheat storage systems, where temperature may be only regulated via aeration, the increased environmental temperature due to climate change will directly result in increased storage temperature enhancing postharvest losses. Except for direct effect from external heat sources, the temperature of a wheat grain system is affected by internal heat sources (respiration of the biotic components such as grain itself and insects). Areas with increased temperature can be formed (hot spots) within stored bulk grain by metabolic heat production of the respired insects. High rates of insect reproduction under favorable environmental conditions and the low thermal diffusivity of the grain are two important factors that can enhance the formation of hot spots (Cofie-Agblor et al., 1995). An indirect additive increase in postharvest losses related with temperature factor is expected by the synergistic effect of climate change and biotic components of stored grain.

Grain moisture is a major factor affecting storage duration and postharvest losses of wheat (Table 17.2), and moisture must be below 14.5% (w/w). High moisture levels enhance activity of biotic factors (insects, mites, fungi) resulting in increased postharvest losses. Increased grain moisture corresponds to high water activity (a_w), and fungi can infest grain at values of $a_w > 0.7$. There is a close relationship between grain a_w and relative humidity (RH) of air, and there is a trend for equilibrium of RH with a_w. In stored wheat system, the initial grain moisture can be dynamically changed depending on the size and structure of the facility and the storage temperature (Chang et al., 1994; Gastón et al., 2009; Jamali et al., 2016). Moisture has the trend to migrate from high temperature to low temperature areas of wheat grain bulk. Increased ambient temperature, size of grain bulk, and initial grain moisture enhance the migration of moisture resulting in the formation of high moisture spots within the wheat storage system that can be favorable for infestations and infections. Storage factors/conditions related with moisture may be improved with the changing climate, resulting in reduced postharvest losses, due to low moisture of harvested grain, in some areas such as Africa and Asia (Miraglia et al., 2009; Moses et al., 2015; Paterson and Lima, 2011). However, immediate storage of harvested grain in warm conditions can result in threats due to moisture condensation at postharvest level (Moses et al., 2015). Extreme weather events (i.e., high precipitation levels, storms, floods), predicted for some areas (i.e., Europe) due to climate change may result in high moisture of harvested wheat grain that contributes on either enhanced postharvest losses or on higher cost for proper grain drying.

4. Effect of biotic factors on wheat grain storage artificial ecosystem

4.1 Climate change effect on postharvest losses through effects on insects

Insects are considered one of the major biotic factors resulting in quantitative and qualitative losses in a stored wheat grain system. Many insect species can infest stored wheat grain (Table 17.3). Quantitative losses in a stored wheat grain system by insect infestation have an increasing trend during storage duration since insects consume grains and increase their population. Also insect-related quantitative losses can occur at milling level of supply chain

TABLE 17.3 Insects and mite species that infest stored wheat grain.

Species	Minimum temperature to complete life cycle (°C)	Optimum temperature (°C)
Insects		
Ahasverus advena	18	30–32
Callosobruchus spp.	19–22	28–35
Corcyra cephalonica (stainton)	18	28–32
Cryptolestes spp.	18–23	27–37
Cynaeus angustus	–	20–30
Dermestes lardarius (L.)	15	25–30
Ephestia cautella (Walker)	15	25–30
Lasioderma serricorne (F.)	22	32–35
Oryzaephilus surinamensis (L.)	21	31–34
Plodia interpunctella (Hubner)	18	28–32
Rhyzopertha dominica (F.)	23	33–35
Sitophilus granarius (L.)	15	26–30
Sitophilus oryzae (L.)	17	27–31
Sitotroga cerealella (Oliver)	16	26–30
Stegobium paniceum (L.)	17	25–28
Tenebrio molitor	15	25–30
Tribolium confusum (du val)	21	30–33
Tribolium castaneum (Herbst)	22	32–35
Trogoderma granarium (Everts)	24	33–37
Typhaea stercorea	15	25–30
Mites		
Acarus siro (Oudemans)	7	21–27
Tyrophagus putrescentiae (Schrank)	11	28–32

Compiled from Allen et al. (2012), Bailey (1955), Barak and Harein (1981), Barker (1967), Bell (1975), Benhalima et al. (2004), Cofie-Agblor et al. (1995), Coombs (1978), Hagstrum et al. (1994), Howe (1965), Jacob (1996), Mason and McDonough (2012), Moses et al. (2015), Sinha et al. (1962, 1969), Throne and Cline (1994).

which is associated with lower flour yields when insect-infested wheat grain is used in milling process (Sánchez-Mariñez et al., 1997). Insects contaminate stored wheat grain with their cast skins, excrement, fragments of immature insects, and other by-products resulting in quality losses (Sánchez-Mariñez et al., 1997; Smith et al., 1971). Insect infestations can result in organoleptic quality deterioration of the final products and in technological quality defects due to changes in gluten, nonreducing sugars, sedimentation value, and protein quality (Girish et al., 1975; Jood and Kapoor, 1992a, 1992b; Jood et al., 1993; Sánchez-Mariñez et al., 1997; Sharma et al., 1979). Poor overall sensory acceptability due to taste defects of bread produced by wheat grain infested by insects has been reported (Jood et al., 1993). Bread prepared from flour infested with *Tribolium castaneum* and *Tribolium confmum* showed many changes advanced by longer infestation periods including a progressive darkening of the crumb, reduction in slice size, and a distinct offensive taste and odor (Smith et al., 1971). Flour from insect-infested wheat exhibited changes in rheological properties such as dough stability, dough development times, water absorption, and mixing stability, while bread had an offensive odor and volume, and loaf characteristics were negatively affected (Sánchez-Mariñez et al., 1997).

Global warming has the dominant effect related to postharvest losses of stored wheat grain resulted by insects infestation. Temperature increase, based on current climate change scenarios, is identified as the dominant

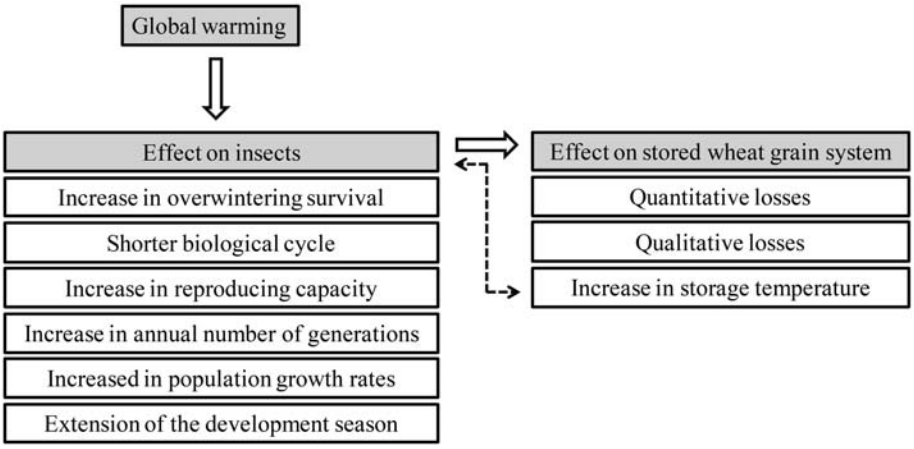

FIGURE 17.2 Global warming effect on stored wheat grain through effects on insects.

abiotic factor directly affecting insects (Bale et al., 2002). Temperature increase can affect insect geographical distribution and infestation levels in a stored wheat system. Higher temperatures result to increased overwintering survival, shorter biological cycle, increased reproducing capacity and annual number of generations, increased population growth rates, and extension of the development season of the insects (Bale et al., 2002; Porter et al., 1991) (Fig. 17.2). These parameters can act additively resulting in extreme high insect infestation and high losses of stored product. The insect metabolic activity also contributes to a further warming of a stored wheat system enhancing the postharvest losses (Fig. 17.2). In a stored wheat grain system, the metabolic heating of grain and the formation of hot spot is highly depended on storage temperature. Depending on insect species (*Sitophilus granarius*, *Sitophilus oryzae*, *Rhyzopertha dominica*, *Tribolium castaneum*, and *T. confusum*), the heat production is found to be increased by more than twofolds in 30°C storage temperature than those in 20°C, and storage at 30°C initial temperature of infested wheat caused a temperature increase within 10 h by about 2.5–6°C (Cofie-Agblor et al., 1995).

There is little evidence of any effect on insects by direct CO_2 increases at the levels of 540–970 ppm due to climate change (Porter et al., 1991). However, in specific wheat grain storage systems (i.e., air-tight storage), indirect atmosphere composition modification can occur by respiration of both insects and grain. Wheat storage atmosphere composition can affect insect reproduction and mortality but in much higher CO_2 and lower O_2 concentrations than those in natural conditions. In wheat grain air-tight storage system, levels of CO_2 above 40% (v/v) or O_2 below 2% (v/v) are required for 100% mortality of all stages of *Sitophilus granarium* L. with immature stages being more susceptible (Bailey, 1955). Studies on insect respiration based on respiratory quotient of the species *S. granarium* L. in a stored wheat grain system has shown depletion of O_2 caused by the respiration of the insects, and the grain is a more crucial factor affecting insect mortality than CO_2 accumulation (Bailey, 1955).

TABLE 17.4 Fungus species and related mycotoxins affecting wheat grain.

Infection level	Fungi	Mycotoxin
Preharvest	*Fusarium* spp.	Deoxynivalenol (DON) Nivalenol (NIV)
	Claviceps spp.	Ergot alkaloids Zearalenone (ZEN)
Postharvest	*Penicillium* spp.	Ochratoxin A (OTA) Citrinin
	Aspergillus	Aflatoxin B1 Tenuazonic acid

Compiled from Andersen et al. (2015), Debegnach et al. (2019), Giray et al. (2007), Hwang and Lee (2006), Iqbal et al. (2006), Jennings et al. (2004), Limay-Rios et al. (2017), Neme and Mohammed (2017), Pitt et al. (2013), Tittlemier et al. (2015), Tralamazza et al. (2016), Yoshizawa and Jin (1995).

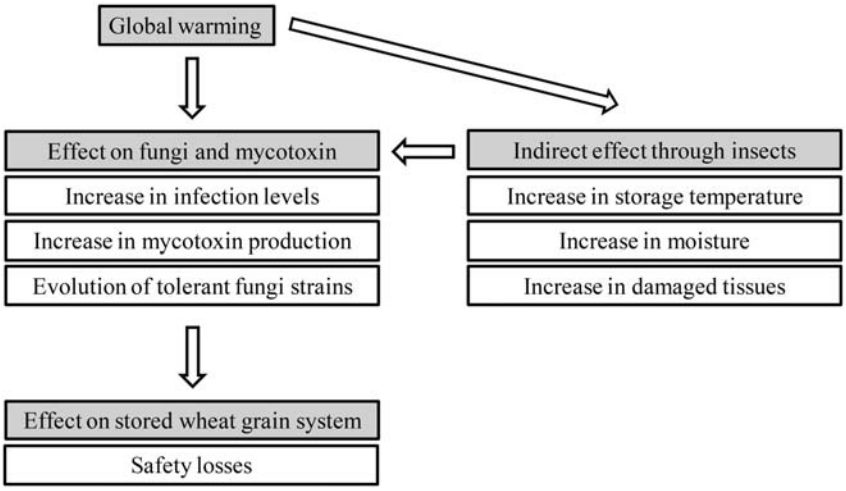

FIGURE 17.3 Global warming effect on stored wheat grain through effects on microorganisms and their metabolites.

4.2 Climate change effect on postharvest losses through effects on microorganisms and their metabolites

Wheat grain is naturally colonized by eukaryotic (fungi) and prokaryotic (bacteria) organisms, and fungi are the major biotic microbial factors affecting postharvest losses. Under specific conditions, there are fungi species that can produce a wide range of secondary metabolites classified as mycotoxins that are toxic low-molecular weight compounds. Wheat grain postharvest losses due to fungi infections and mycotoxins production are related with food safety issues since foodstuff contaminated by mycotoxins has human and animal health risks (D'mello et al., 1999; da Rocha et al., 2014; Duarte et al., 2010; Pinotti et al., 2016). Wheat grain is a commodity prone to infections by mycotoxigenic fungi at both pre- and postharvest levels (Table 17.4). The preharvest fungi infestations and mycotoxin contamination of wheat can be enhanced at postharvest level under favorable conditions.

In a stored wheat system, temperature and moisture are the most important factors that enhance fungi infestations and mycotoxin production. Depending on fungus species, the optimal temperature for the production of mycotoxins is within the range of 15–33°C (Sanchis and Magan, 2004). Temperature in a stored wheat system is greatly affected by the external atmospheric temperature because wheat grain storage capacities are not equipped with refrigeration. Temperature increase by climate change may increase or decrease mycotoxin levels depending on cultivation and storage region. In cold regions (e.g., parts of Northern Europe and Northern America), the postharvest losses may be increased by the extension of the duration at optimal temperature during storage for mycotoxin production, whereas in some hot regions (e.g., Africa, Southern Asia), the extended duration of temperatures above the upper thresholds for mycotoxin production could result in reduced losses. Temperature increase may have an indirect negative effect, through moisture modification, on the enhanced stored wheat spoilage and mycotoxin production. At higher storage temperatures, there is an increased production of metabolic water through increased grain and/or insects respiration rates. The resultant increase in condensation and wet pockets can initiate spoilage mold activity with the possibility for increased contamination with mycotoxins (Magan et al., 2011). Postharvest losses due to fungi infections and mycotoxin production may be increased indirectly through the enhancement of insect activity within the stored wheat system resulting in increase in both temperature and moisture, and damaging grain tissues that are favorable factors for infections. A brief description of global warming effect on postharvest losses of bread wheat through effects on microorganisms is presented in Fig. 17.3.

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CHAPTER

18

Investigation of the effects of environmental stresses on the development and yield of wheat seedlings with physiological and biochemical parameters and some gene expressions

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1. Introduction

Global warming has caused climate changes, especially problems such as reduction in water resources, fires, drought, and desertification. Turkey is one of the risky countries in terms of environmental hazards due to the global warming. Given the average precipitation in Turkey, a significant decline in precipitations was detected over the years. In 2000, the average precipitation decreased by 7%, which adversely affects the agricultural production (Öztürk, 2002). It has been stated that if the conditions causing drought persist, bigger problems may occur in the next time (Türkes, 1999).

In the wheat production during 2017–2018, the United States is in the first place with a share of 20%, whereas Turkey is in the ninth rank with a share of 3%, so that Turkey is among the important wheat manufacturers in the world. Also, Turkey takes place near the top among the durum wheat manufacturers in the world with a share of 10% (http://www.tmo.gov.tr/Upload/Document/hububatsektorraporu2017.pdf).

The amount of water that the wheat plant needs during the growing season varies depending on the development cycles. Accordingly, the amount of precipitation in our country affects the yield, and in the wheat yield, the amount of wheat produced changes by years. A factor that has the most important effect on the wheat yield is the amount of precipitation and the distribution of precipitation throughout the year. Accordingly, the wheat is grown in the large areas and is produced mostly in the agricultural lands that are lack of irrigation in a precipitation-dependent manner (http://www.tgdf.org.tr/wp-content/uploads/2017/10/iklim-degisikligi-rapor-elma.compressed.pdf). It has been stated that the development of wheat is also affected by the temperature (Muslu and Ergün, 2013; Ergün et al., 2014) and the production of wheat is sensitive to the climatic conditions.

2. Effects of environmental stresses on the development of wheat seedlings with physiological and biochemical parameters and some gene expressions

Floods significantly restrict agricultural production in many parts of the world. Areas of about 10 million hectares are affected by floods every year (Sayre et al., 1994). Flood occurs due to the rise of groundwater to the level of soil surface due to factors such as excessive rain and irrigation. Özçubukçu et al. (2014) found that catalase activity in waterlogging conditions was higher in Ducula-4 cultivars than in Doğankent cultivars. In the study, Myb2 expression increased in both types in the early hours of application. Waterlogging conditions caused inhibition on chlorophyll and carotenoid content on wheat (*Triticum aestivum* L. cv Doğankent and Ducula-4) seedlings (Ozcubukcu and Ergun, 2013).

Drought is one of the abiotic stress factors that have the most important effect on the cultivated areas and the crops. Yayık (2017) examined the effects of drought and drought−NO (nitric oxide) interactions on wheat seedlings (*T. aestivum* L. cv. Sultan, Yüreğir, İkizce). The researchers found that the drought application decreased the shoot height in all three varieties and that the dry weight of the shoot decreased in Sultan and İkizce varieties and increased in Yüreğir variety. Drought application causes chlorophyll amount decrease in seedlings. Antioxidant enzyme activities (catalase [CAT], glutathione reductase [GR], and ascorbate peroxidase [APX]) increased in all three wheat varieties with drought application. The amount of proline has been shown to be increased in the wheat seedlings exposed to drought. It was determined that NAC and TaLTP1 gene expressions increased in all three varieties as compared with the control. It was determined that this increase in gene expressions was higher in Sultan variety of wheat seedlings, which is a sensitive type of wheat.

Many stress factors damage cell homeostasis by increasing free radicals (Polle, 2001). These stresses produce reactive oxygen intermediates in the organelles. The activity of the antioxidant enzymes is associated with the stress tolerance (Chaitanya et al., 2002). Increased amounts of antioxidants in the cell can protect the cell from damage, which may be associated with the stress tolerance (Van Der Mescht et al., 1998). Flood stress in plants affects numerous metabolic events. Antioxidant enzymes such as CAT, GR, APX, and superoxide dismutase (SOD) protect the cell by breaking down the harmful oxygen species in the cells (Ahmed et al., 2002).

One of the important factors affecting the growth and development of plants is temperature. Ergün et al. (2014) applied temperature and heavy metal to *T. aestivum* L. cv Ç1252 and Gün 91 varieties of wheat seedlings. As a result of the study, it was determined that total chlorophyll levels decreased due to the increase in temperature, whereas carotenoid levels increased slightly. It was stated that catalase activity was increased in Gün 91 variety of wheat seedlings under the stress conditions and decreased in Ç1252. Consequently, it was determined that Gün 91 variety of wheat seedlings was more resistant to temperature−heavy metal stress than Ç 1252 variety. In the study, it was determined that the expression level of TaMYB73, TaERF1, and TaSRG transcription factors increased under Cr-temperature stress conditions. The researchers stated that the relevant transcription factors could regulate the genes responsible for Cr and temperature stress.

Muslu and Ergün (2013) found by SDS-PAGE that soluble proteins were increased in the shoots exposed to temperature−heavy metal interactions in bread wheat (*T. aestivum* L.cv Dağdas) seedlings.

It is known that the climate changes caused by increasingly global warming in our world and Turkey adversely affect the agricultural production and productivity. Wheat is known to be one of the most important cereals for the nutrition of human beings. Turkey is among the leading wheat manufacturers in the world. As a result, it is obvious that more detailed research on the physiological, biochemical, and molecular mechanisms of environmental stresses such as flood, drought, and salinity due to climate changes is evident. Therefore, we believe that it is possible to increase wheat yield by selecting stress-tolerant species.

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CHAPTER

19

Potentially toxic trace elements in wheat and their effects on the plant development and concentration of essential nutrients

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1. Introduction

The information on concentrations of trace elements in wheat is quite extensive. However, most of the data are limited to few elements, so-called heavy metals, such as As, Cd, Cr, Cu, Hg, Ni, Pb, Se, and U. Until recently, information about other trace elements is scarce. This may be due to insufficient quality of analytical techniques used for determination of some trace elements since, in biological material, many elements are present at rather low concentrations. Unfortunately, this has led to a commonly accepted opinion about the elements as unnecessary impurities that do not play any essential role in the biochemical processes in plants. Meanwhile, one may assume that such a situation was caused by lack of more detailed information on biogeochemistry of the trace elements. As a consequence, sometimes, researchers try to predict environmental behavior of one trace element based on available experimental data on another element that has similar chemical characteristics, and its biochemistry is more fully studied.

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00019-4

In this chapter, we will discuss recent experimental findings on several rare earth elements (REEs) and one metalloid, antimony. There is still little information about the elements in wheat.

2. Rare earth elements

The REEs comprise Sc, Y, and the lanthanides (La to Lu). The elements have very similar chemical and physical properties. Despite the name, REEs are not rare in the environment. The concentration of Ce in soil is almost equal to that of Cu and Zn. The concentration of the rarest REEs, Lu and Tm, in the most soils is comparable with that of Cd and Se. While REEs are abundant in soil, their concentrations in plants are usually very low (Brioshi et al., 2013; Khan et al., 2017).

The behavior of REEs in the soil−plant system is not fully understood. Until recently, REEs have not been characterized as essential plant nutrients or environmentally hazardous metals. Although REEs have previously been considered to be nontoxic, recent experimental studies demonstrated toxicity of REEs for bacteria (Challaraj Emmanuel et al., 2011), plants (Thomas et al., 2014), and humans (Gwenzi et al., 2018).

REEs have been used in agriculture since the 1970s. In China, the REE-based fertilizers are widely used to increase the yield and quality of crops. Many experiments have been performed to demonstrate the beneficial influence of REEs on the plant growth. However, the beneficial effects have been reported mainly by the Chinese researchers. It was found that REEs stimulate the synthesis of chlorophyll (Chen et al., 2015) and promote seedling development (Xu et al., 2016). Notice that data of the experiments are sometimes contradictory and inconsistent. For example, it was reported that treatment of seedlings with REEs led to up to 25% reduction of the seedling biomass (Thomas et al., 2014). The application of REEs also inhibited the plant growth (Ruíz-Herrera et al., 2012). Therefore, it seems that the reported beneficial effects hardly could result from direct influence of the REEs on the growth processes of plants. This action might be caused by certain indirect effects influencing the development of the crop plants. The contradictory observations may also be explained by different levels of applied REEs. It looks that positive response is possible when concentration of available REEs in soil is rather low, less than 10 mg/kg (Maheswaran et al., 2001; Diatloff et al., 2008).

The distribution of REEs in different cereal crops was described in many publications (Ding et al., 2006; Fang et al., 2007; Challaraj Emmanuel et al., 2011; Wiche and Heilmeier, 2016; Martinez et al., 2018). There is also information on distribution of REEs in wheat (Zhang and Shan, 2001; Tian et al., 2003; Shtangeeva and Ayrault, 2007; d'Aquino et al., 2009).

2.1 Europium

Europium (Eu) is a very interesting trace element. Under different environmental conditions, Eu can change its valence state and thus serve as an indicator of biogeochemical processes. There have been few reports on distribution of Eu in different plants and beneficial or toxic effects of the trace element (Tian et al., 2003; Shtangeeva and Ayrault, 2007; d'Aquino et al., 2009; Vijayaraghavan et al., 2010; Shtangeeva, 2014).

2.2 Cerium

Cerium (Ce) is the most abundant of the REEs. It was shown that uptake of K, Mg, Ca, Na, Fe, Mn, Zn, Cu, and Mo by plants may be affected as a result of exposure to Ce^{3+}, thus indicating that Ce^{3+} is able to influence the nutritional status of plants and further affect the plant growth (Diatloff et al., 2008; Liu et al., 2012). On the other hand, it was found that addition of Ce to soil may promote N and C assimilation, increase PSII activities, and improve the plant development (Zhao et al., 2012; Ramírez-Olvera et al., 2018). Probably, the different conclusions on effects of Ce on plants may be due to different approaches used for the experimental design.

2.3 Model experiments on effects of rare earth elements on wheat and rye

Results of model greenhouse experiments showed that even insignificant increase of concentration of Eu and Ce in soil can lead to accumulation of the REEs in wheat and rye. When the plants were grown in the REE-free soil

(control), rye seedlings could accumulate a bit more Eu and Ce as compared with wheat seedlings. When wheat seedlings were grown in the Eu-spiked soil, concentration of Eu in roots of the plants was 150 times higher than Eu concentration in roots of control wheat seedlings. Concentration of Eu in roots of rye seedlings grown in the Eu-spiked soil increased only nine times in comparison with control.

Numerous studies reported that many metals have an inhibitory effect on the fluxes of essential nutrients in a plant (Adriano, 2001; Ahsan et al., 2009; Khan et al., 2015). We may suggest similar effects for REEs too. For example, it was shown that REEs can affect membrane stability of cells (Hu et al., 2004). Therefore, REEs could also influence the ionic interactions with the cell. In particular, La was able to affect an uptake of K, Sc, Mn, Se, and Rb either increasing or decreasing the uptake rates (Wang et al., 2008).

In our experiment, we observed a statistically significant ($P < .05$) decrease of leaf La concentration resulting from growth of wheat seedlings in the Eu-spiked soil. Concentration of Sc decreased statistically significantly in leaves of the rye seedlings grown in the soil spiked with Ce. In roots of the wheat seedlings grown in the Eu-spiked soil, a statistically significant increase of Ca was found. In roots of the rye seedlings grown in the Ce-spiked soil, concentration of K was statistically significantly higher compared with K concentration in roots of the rye seedlings grown in the Ce-free soil. It looks there was no marked effects of bioaccumulation of Eu or Ce on concentration of essential nutrients as well as other REEs in the both plant species. Moreover, our experiments with germination of wheat seeds in the medium spiked with 0.01 mg/L Eu showed that the treatment was favorable for a following growth of the seedlings in soil (Shtangeeva and Ayrault, 2007).

2.4 Relationships between rare earth elements in the rhizosphere soil and in different parts of wheat

The behavior of REEs in soil and in plants may be characterized by relationships between different REEs and also trace elements that are chemically similar with the REEs.

It may be expected that correlation between these elements will be statistically significant and positive. However, our calculations showed that although this statement was sound, it is not universally true. For example, correlation between La and Sc was statistically significant ($P < .05$) and positive in both soil and wheat grown in the soil (Fig. 19.1). Correlation between La and Sm was statistically significant only in soil and in roots of wheat; there was no correlation between these REEs in leaves (Fig. 19.2). Moreover, a statistically significant positive correlation between Eu and Ce was observed only in soil; no correlation between these elements in roots and leaves was found (Fig. 19.3). One may assume that behavior of trace elements, including REEs, in different media may differ. In plants, REEs may be a part of organic molecules; in soil, they may be mainly components of inorganic compounds.

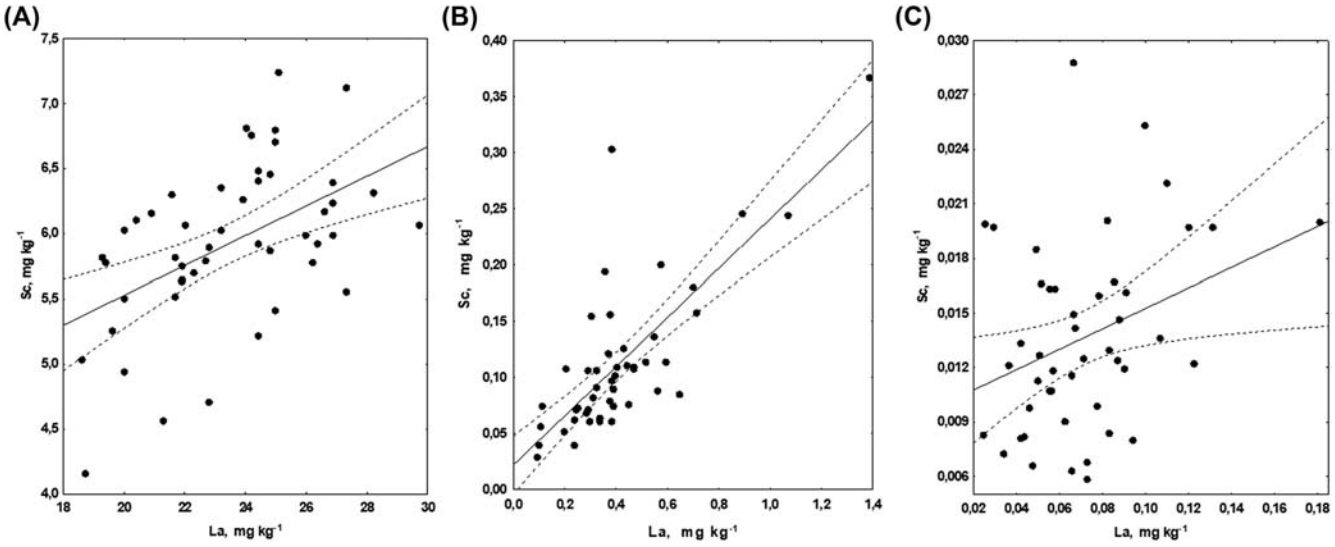

FIGURE 19.1 Correlation between La and Sc in soil (A), roots (B), and leaves (C) of wheat seedlings.

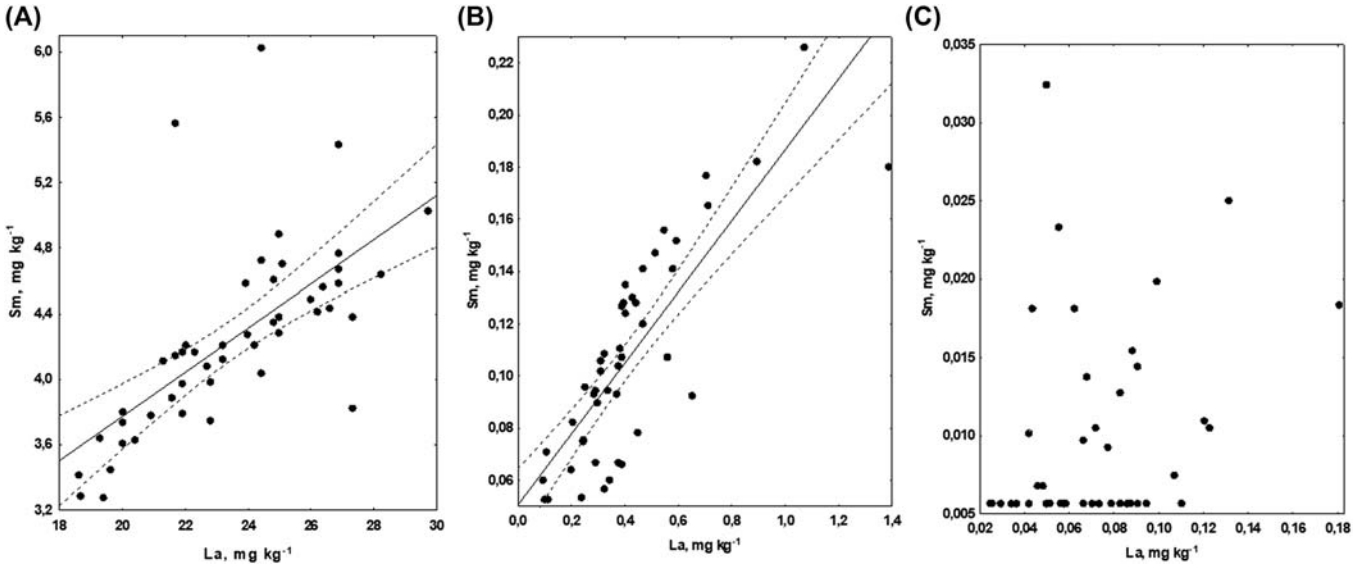

FIGURE 19.2 Correlation between Sm and La in soil (A), roots (B), and leaves (C) of wheat seedlings.

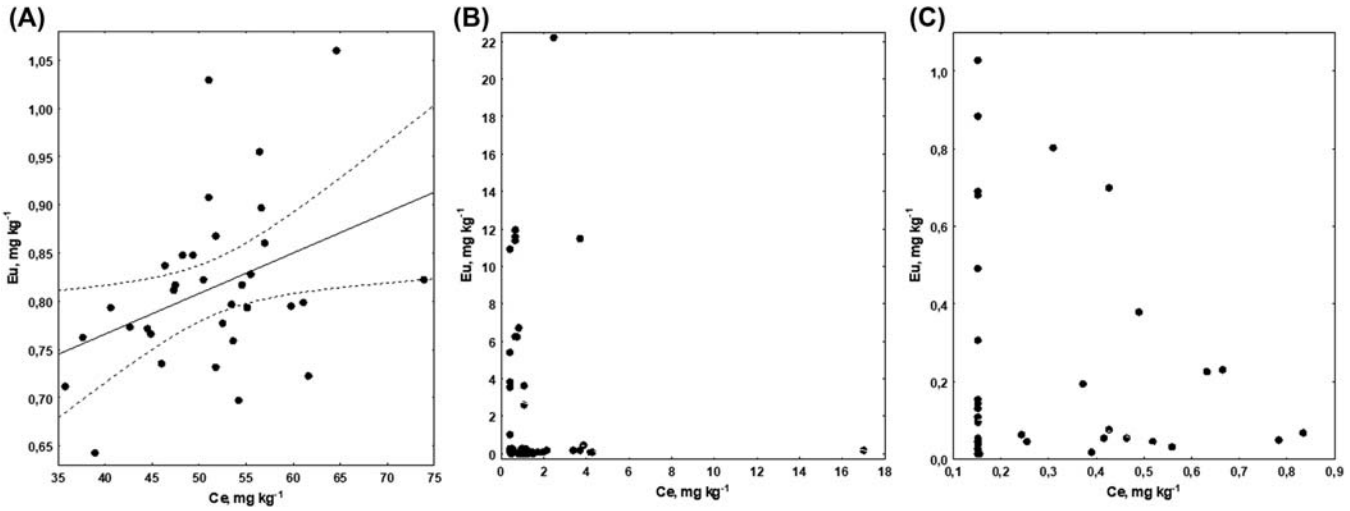

FIGURE 19.3 Correlation between Eu and Ce in soil (A), roots (B), and leaves (C) of wheat seedlings.

3. Antimony

Antimony (Sb) has partially metallic and partially nonmetallic properties. Antimony is a naturally occurring mineral component that was found in various environmental samples, generally, at low concentrations. In noncontaminated soils, Sb occurs in the range of <0.3–8.4 mg/kg (He, 2007; Wilson et al., 2010; Cheng et al., 2014). Concentrations of Sb in terrestrial plants from uncontaminated sites range from 0.2 to 50 mg/kg (Tschan et al., 2009; Conesa et al., 2011; Wang et al., 2017).

Antimony and many of its compounds are toxic. It was suggested that effects of Sb poisoning are similar to As poisoning (Gebel, 1997). Some researchers consider Sb as being less toxic than As (Duester et al., 2011), but others suggest that it is more toxic (Pawlak et al., 2010). Little is known about mechanisms of Sb uptake by plants (Tschan et al., 2009). Since Sb is a nonessential trace element, the transport systems hardly may be evolved for its uptake. It was speculated (Filella et al., 2009) that Sb is taken up by transporters for vital elements or biological molecules.

Chemical similarities between Sb and As suggest similar behavior of the elements in the environment (Wilson et al., 2010). Although there is no any experimental evidence, the common practice has been to extend the observed

behavior of As to Sb solely on the basis of the similarity between these elements (Filella et al., 2009). Till now, however, there is no consensus on this point. On the one hand, there are some evidences showing that the biogeochemistry of Sb and As is similar (Skordas, 2007; Oprea et al., 2010). On the other hand, some researchers argue that the environmental chemistry of Sb does not closely parallel to that of As (Fu et al., 2016; Rajabpoor et al., 2019). Therefore, the available experimental data on As biogeochemistry should be used with caution to predict environmental behavior of Sb.

Recently, contamination of the environment by Sb has become a growing concern. Like many other metals and metalloids, Sb at elevated concentrations may be toxic and potentially carcinogenic (Zhang et al., 2018). The toxicity and environmental cycling of elements depend on their oxidation state. The Sb(III) and Sb(V) are the most common valence states of Sb under ordinary environmental conditions. The trivalent form occurs under moderately oxidizing conditions. The pentavalent form predominates in highly oxidizing environments (Tschan et al., 2008). In soil, Sb(III) is oxidized within hours to Sb(V) (Krachler et al., 2001). However, even under oxidizing conditions, substantial fractions of Sb may be present as Sb(III) (Belzile et al., 2001). At present, there is no enough information on Sb phytotoxicity to make general conclusions. It may only be speculated that different Sb forms may have different bioavailability. Some experimental results partially confirm this assumption (Tschan et al., 2010).

Here, we will describe our experimental data on Sb uptake by wheat and effects of Sb bioaccumulation on the plant development and nutrition.

Although uptake of elements by vascular plants growing in soil may differ compared with bioaccumulation of the elements from aqueous solutions, given the limited knowledge on biogeochemistry of Sb and the mechanisms of its bioaccumulation, we will start from hydroponic experiments to exclude the influence of various factors that affect elemental uptake when plants grow in soil.

The aims of the experiments were to study how the chemical form of Sb presented in growth medium can influence the uptake of the element by plants and to estimate effects of different Sb forms on wheat and rye.

Seeds of wheat *Triticum aestivum* L. and rye *Secale cereale* L. were divided into three groups. Seeds from first and second groups were germinated in the media spiked with either Sb(III) as $SbCl_3$ or Sb(V) as $SbCl_5$. Last group of seeds served as a control. Concentration of Sb in the germination media was 75 mg/L. After 4 days, first portion of seedlings from all groups was taken for analysis. The rest of the seedlings were transferred to vessels filled with water. At this stage, the following treatments were applied: seedlings germinated in the Sb-free medium were transferred to vessels spiked with either Sb(III) or Sb(V). Seedlings germinated in the water spiked with Sb(III) or Sb(V) and seedlings germinated in the Sb-free medium were transferred to vessels filled with clean water. Then, plants were collected within 1, 3, and 5 days after transplanting.

3.1 Antimony uptake by wheat and rye seedlings

The distribution of Sb in the seedlings germinated during 4 days in Sb-free medium and in the media spiked with Sb(III) or Sb(V) is shown in Fig. 19.4. When seedlings were germinated in the media spiked with Sb, its concentration increased in all plant parts. There were certain differences between uptake of Sb by wheat and rye as well as differences in the ability of the plants to accumulate different Sb forms. In most cases, rye was capable of accumulating larger amounts of Sb than wheat.

Although wheat and rye are botanically similar, concentrations of many organic compounds in the plants are different (Pomeranz, 1988). Concentrations of macro- and trace elements in the plants can be different too (Shtangeeva et al., 2011; Jākobsone et al., 2015). Rye and wheat also differ in the ability to uptake Sb(III) and Sb(V) (Fig. 19.4). When rye seeds are germinated in the medium spiked with Sb(V), concentration of Sb in the seedlings is higher than that in the rye seedlings germinated in the medium spiked with Sb(III). In wheat, concentration of Sb is higher in the seedlings germinated in the medium spiked with Sb(III) as compared with Sb content in the seedlings geminated in the medium spiked with Sb(V). Probably, different plant species are capable of identifying Sb(III) and Sb(V) and can take up the preferred form selectively.

The experiments with sunflower and maize grown in the soil spiked with Sb(III) and Sb(V) showed that accumulation of Sb in sunflower was higher after the Sb(V) treatment. In maize, no difference in the Sb uptake between the two Sb treatments was found (Tschan et al., 2010). However, it is difficult to compare uptake of elements by plants grown in so different media as soil and water.

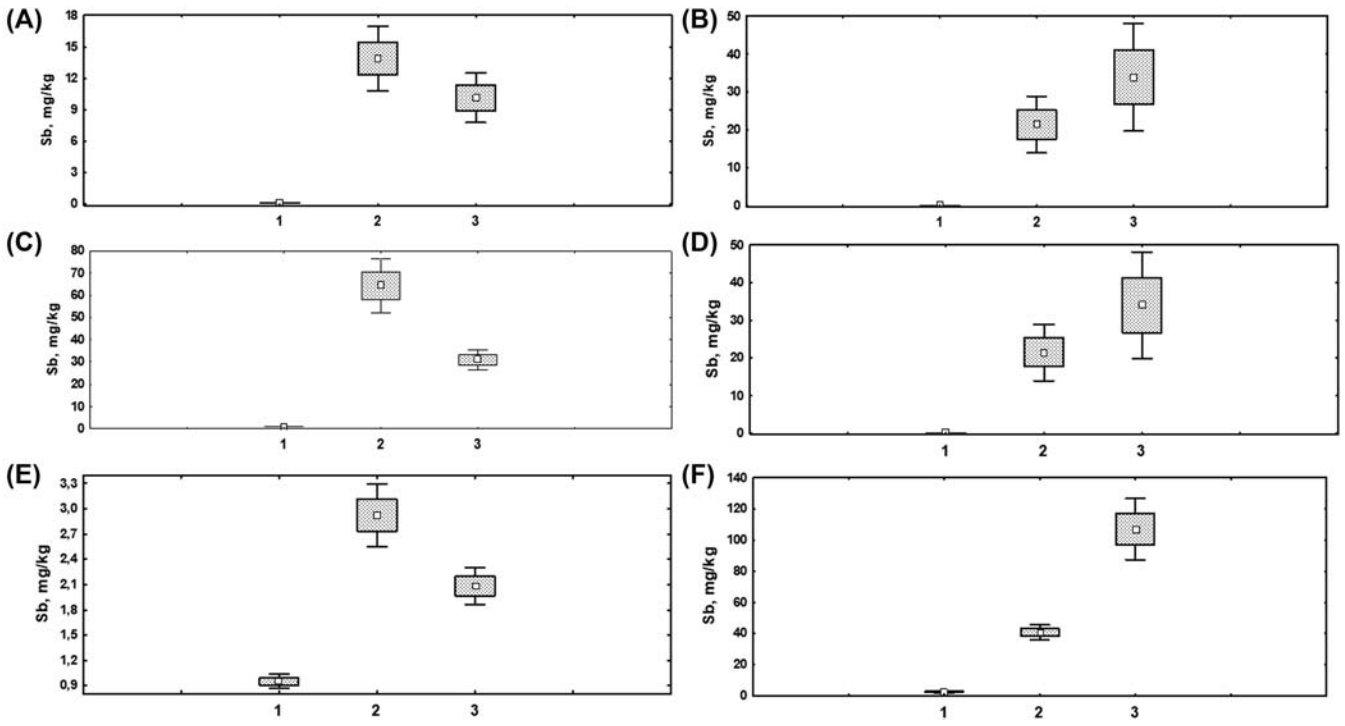

FIGURE 19.4 Mean concentrations ± SD of Sb in seeds of wheat (A) and rye (B), in roots of wheat (C) and rye (D), and in leaves of wheat (E) and rye (I). 1—seeds were germinated in the Sb-free water, 2 and 3—in the medium spiked with Sb(III) and Sb(V), respectively.

3.2 Effects of Sb accumulation on concentrations of nutrients in wheat and rye seedlings

The accumulation of Sb caused variations in the concentrations of several macro- and trace elements in the wheat and rye seedlings. In roots of the plants, concentrations of Mg, Ti, and K decreased compared with those in roots of control plants. Besides, concentration of Co in roots of wheat and concentration of Rb in roots of rye were lower than those in roots of control plants. In seeds of wheat, we found a decrease of K and increase of Mn. In seeds of rye, the accumulation of Sb led to increase of Li and Al and decrease of Mo. In leaves of the two plant species, the bioaccumulation of Sb did not result in marked variations in concentrations of different elements.

The variations in the concentrations of different elements in the seedlings could affect the physiological state of the plants. In fact, we observed a necrosis of the rye leaves resulted from bioaccumulation of Sb. In wheat seedlings, however, no visible symptoms of phytotoxicity were found. The different sensitivity of the two plant species to Sb might be due to physiological differences between wheat and rye in the Sb tolerance.

The variations in the leaf biomass of wheat seedlings are shown in Fig. 19.5. With time, the biomass of control seedlings increased. When control seedlings were transferred to water spiked with Sb, the plant development was suppressed (Fig. 19.5A). The development of leaf biomass of the wheat seedlings grown in the water spiked with Sb(V) was in fact stopped. The biomass of the seedlings grown in the Sb(III)-spiked water increased with time, but the increase was less than in control plants. When seedlings germinated in the Sb-spiked water were transferred to Sb-free medium and grown there for 5 days, biomass of the seedlings constantly increased with time. In this case, leaf biomass of the seedlings germinated in the Sb(V)-spiked medium increased even more than the biomass of control seedlings (Fig. 19.5B).

3.3 Dependence of Sb uptake on Sb form in the growth medium and plant species

When wheat seedlings germinated during 4 days in the Sb-spiked medium were transferred to vessels filled with clean water, concentration of Sb in the plants decreased with time (Fig. 19.6). It may be suggested that Sb was easily taken by a plant and was also easily removed from it when the plant was transferred to a medium with no Sb. Probably, after such a fast bioaccumulation of Sb, it was not bound tightly to organic molecules of the plant cells.

Plants have various mechanisms preventing negative effects from toxic metals, including reduction of metal uptake by changes in the kinetic properties of transporters and exudation of complexing agents (Singh et al., 2011). Metal

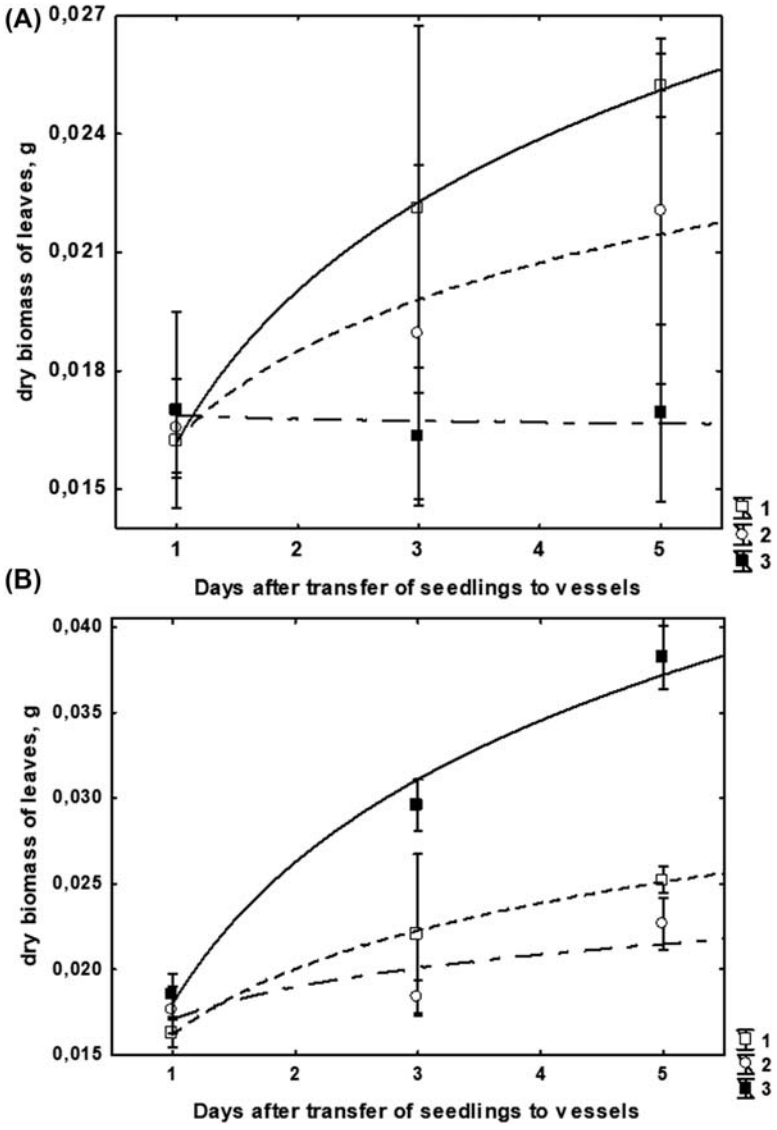

FIGURE 19.5 Variations in biomass of leaves of wheat seedlings. (A) Seedlings germinated during 4 days in the Sb-free medium were transferred to vessels filled with clean water (1), water spiked with Sb(III) (2), and water spiked with Sb(V) (3); (B) seedlings germinated in the Sb-free medium (1) and in the media spiked with Sb(III) (2) and Sb(V) (3) were transferred to vessels filled with clean water. *Reproduced with permission from Shtangeeva et al., 2012. Uptake of different forms of antimony by wheat and rye seedlings. Environmental Science and Pollution Research 19 (2), 502–509.*

influxes and effluxes are controlled by plants considering the needs of the plant to maintain metal–ion homeostasis. The toxic effects of different Sb forms may be different for different plant species. For example, the treatment with Sb(V) was more toxic for rye seedlings because they all died before end of experiment. More significant impact on wheat leaf biomass was also observed after treatment with Sb(V) compared with treatment with Sb(III) (Fig. 19.5A).

In Fig. 19.7 are shown variations of Sb in the wheat seedlings germinated in the Sb-free medium and then grown in the water spiked with either Sb(III) or Sb(V). With time, concentration of Sb in roots of the seedlings grown in the medium spiked with this trace element increased. On the other hand, the increase of Sb in leaves was followed by a subsequent saturation with Sb.

3.4 Correlation between As and Sb

Arsenic and Sb are chemical analogues. However, only in roots of the wheat grown in the Sb-spiked medium, the correlation between these elements was statistically significant and positive. Probably, the transfer of As and Sb within a plant occurs differently. Positive correlation between these elements in roots may be explained by similar mechanisms of their uptake by roots. The absence of correlation between As and Sb in seeds and leaves suggests that the biochemistry of the two metalloids may be different. Other researchers also came to the same conclusion (Xia, 2011; Vaculík et al., 2013).

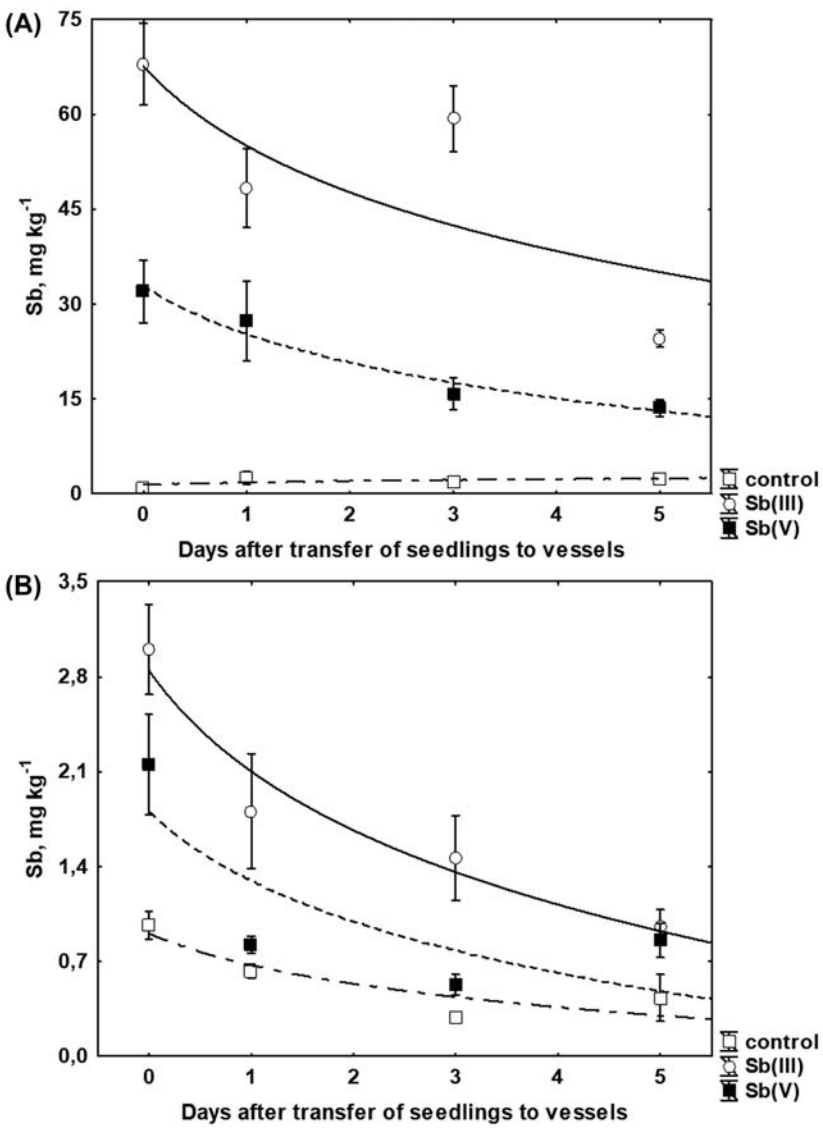

FIGURE 19.6 Variations in Sb concentrations in roots (A) and leaves (B) of the wheat seedlings transferred to vessels filled with clean water after germination in the media spiked with Sb(III) and Sb(V) during 4 days. *Reproduced with permission from Shtangeeva et al., 2012. Uptake of different forms of antimony by wheat and rye seedlings. Environmental Science and Pollution Research 19 (2), 502–509.*

4. Growth of wheat in highly contaminated with Sb media

The goal of the following experiments was to estimate the effects of Sb on the development of wheat seedlings and distribution of macronutrients and trace elements in the plants germinated or grown in highly contaminated with Sb water or soil. For this experiment, we used Sb(V).

4.1 Effects of Sb on germination of wheat seeds and concentrations of nutrients in wheat seedlings

Germination of wheat seeds in a highly contaminated by Sb medium during 7 days resulted in suppression of development of leaves and especially roots of the seedlings. The decrease of the plant biomass correlated with increase of Sb concentration in a plant. In Fig. 19.8 are shown concentrations of Sb in roots of the 7-day-old seedlings and biomass of the roots. The concentration of Sb in roots of the seedlings exposed to 150 mg/L Sb was less than concentration of Sb in roots of the seedlings germinated at lower Sb concentration (100 mg/L). Probably, when

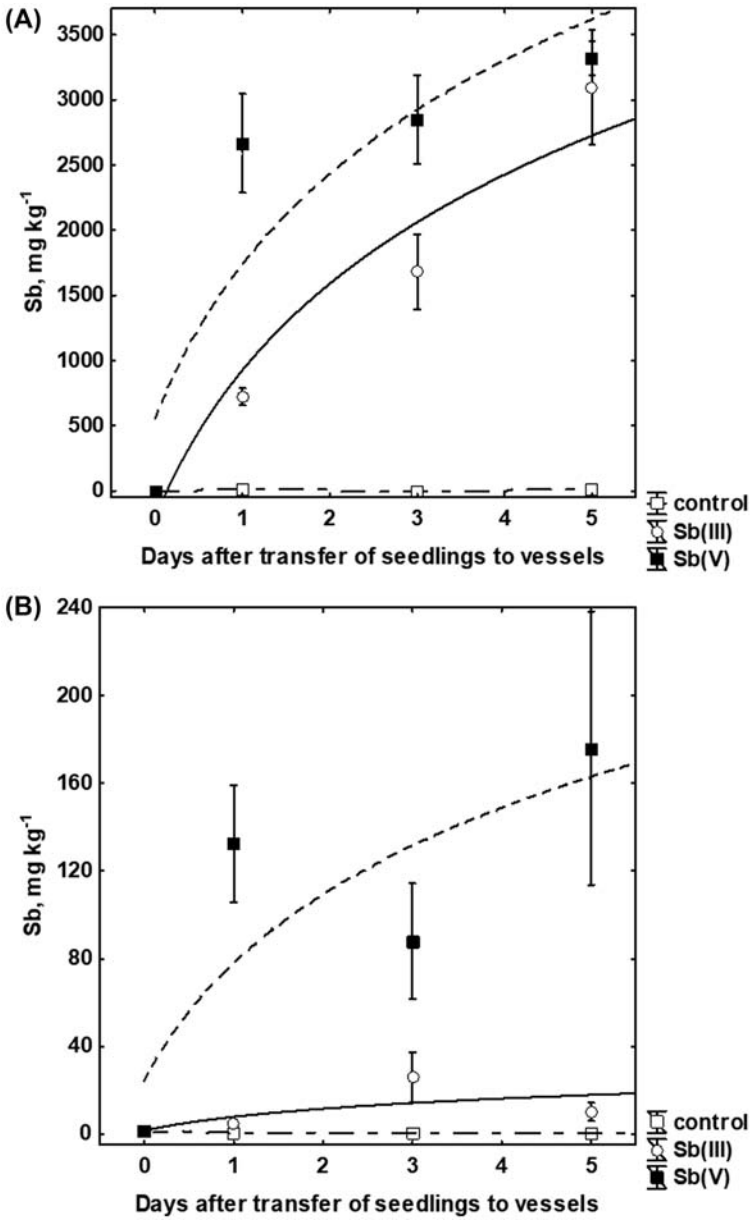

FIGURE 19.7 Variations in Sb concentrations in roots (A) and leaves (B) of the wheat seedlings transferred after germination in the Sb-free medium to vessels filled with water spiked with Sb(III) and Sb(V). *Reproduced with permission from Shtangeeva et al., 2012. Uptake of different forms of antimony by wheat and rye seedlings. Environmental Science and Pollution Research 19 (2), 502–509.*

the seedlings were germinated in the medium with higher Sb concentration (150 mg/L), the translocation of Sb from roots to leaves was enhanced.

The concentration of Sb in leaves was lower than that in roots. It is known that roots can serve as an effective barrier preventing transfer of toxic elements to upper plant parts (Shtangeeva et al., 2009; Boussen et al., 2013). Once Sb concentration in the growth medium does not exceed a certain level, the transfer of Sb from roots to leaves may be limited. However, when roots are saturated with Sb, the excess of Sb may more easily be transferred to upper plant parts.

The accumulation of Sb in the 7-day-old wheat seedlings resulted in a decrease of Ca in the plants. In seeds, the amount of Ca was reduced 2 times. In roots, concentration of Ca decreased from 2.5% to 0.5%. Calcium is an important plant nutrient. The decrease of its concentration can pose threats to the plants. In leaves of the 7-day-old seedlings germinated in the Sb-spiked medium, we also found a decrease of K from 7.1% to 4.0%, and in roots, we found a decrease of Na from 2.2% to 0.3%. The decrease of the concentrations of essential plant nutrients could affect the development of the seedlings.

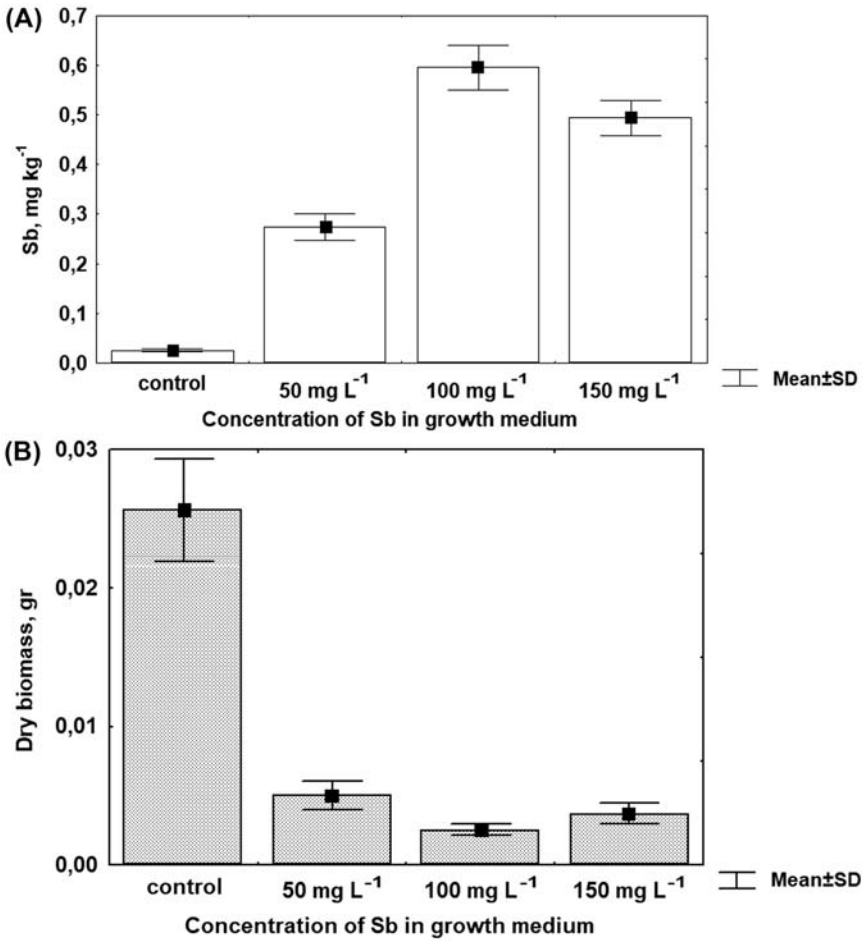

FIGURE 19.8 Variations of Sb concentration in roots (A) and in dry biomass of roots (B) of 7-day-old wheat seedlings germinated in water spiked with Sb. *Reproduced with permission from Shtangeeva et al., 2011. Bioavailability and toxicity of antimony. Journal of Geochemical Exploration 110, 40–45.*

4.2 Effects of Sb on the plants grown in water

There were marked variations in the biomass of the wheat seedlings grown in the water spiked with Sb. During first 24 h of exposure to Sb, the distinction between leaves of control plants and plants grown in the Sb-spiked medium was no means sharp. Growth of the seedlings in the Sb-contaminated water during the following 5 days resulted in suppression of the leaf development. The most significant decrease of the leaf biomass was found when the seedlings were grown in the medium spiked with 150 mg/L Sb.

The effects of Sb on roots differed depending on Sb concentration in the growth medium. The development of roots slightly decreased during first hours of exposure to 50 mg/L Sb and significantly decreased during the following 5 days. The same was observed as a result of exposure of wheat seedlings to 100 and 150 mg/L Sb. In this case, however, the root development in fact was stopped by the end of the experiment.

It was reported that growth of maize and sunflower seedlings in the water containing 24 mg/L Sb for a week did not produce toxicity symptoms (Tschan et al., 2008). On the other hand, the authors found that development of roots of wheat seedlings was inhibited when Sb concentration in the water was 30 mg/L.

In Table 19.1 are shown concentrations of macro- and trace elements in the 13-day-old wheat seedlings grown in the Sb-spiked water. The wheat seedlings were capable of accumulating large amounts of Sb. The Sb bioaccumulation correlated with Sb concentration in the growth medium. This indicates that Sb can easily be absorbed from water by roots and large quantities of the trace element may be transferred to upper plant parts.

4.3 Effects of Sb on the plants grown in soil

The development of the wheat seedlings grown in control (Sb-free) soil and in the soil spiked with Sb was distinct. The biomass of the control seedlings increased constantly with time. The biomass of the seedlings grown in the soil

TABLE 19.1 Mean concentrations of elements (μg/g of dry matter) in different parts of wheat seedlings grown for 5 days in water spiked with Sb.

Treatments	Ca%	Co	Cu	K%	Na%	Pb	Sb
Seeds							
1	2.79 ± 1.07	0.003 ± 0.004	0.03 ± 0.02	0.93 ± 0.56	1.2 ± 0.3	0.14 ± 0.011	0.02 ± 0.02
2	2.26 ± 0.68	0.008 ± 0.006	0.03 ± 0.02	1.23 ± 0.85	1.09 ± 0.21	0.03 ± 0.04	0.90 ± 1.08[a]
3	2.42 ± 0.49	0.004 ± 0.005	0.03 ± 0.025	1.31 ± 1.03	1.08 ± 0.19	0.02 ± 0.01	1.36 ± 1.18[a]
4	1.80 ± 0.89[a]	0.001 ± 0.001	0.02 ± 0.02	0.72 ± 0.62	0.87 ± 0.39[a]	0.04 ± 0.07	1.50 ± 1.73[a]
Leaves							
1	1.11 ± 0.34	0.003 ± 0.004	0.03 ± 0.02	6.47 ± 2.41	1.62 ± 0.20	0.01 ± 0.01	0.02 ± 0.02
2	1.13 ± 0.16	0.007 ± 0.006	0.02 ± 0.01	5.37 ± 1.83	2.01 ± 0.73	0.01 ± 0.01	0.15 ± 0.16[a]
3	1.09 ± 0.36	0.004 ± 0.004	0.02 ± 0.02	4.69 ± 1.97[a]	1.69 ± 0.43	0.01 ± 0.01	0.31 ± 0.32[a]
4	0.86 ± 0.42	0.002 ± 0.002	0.01 ± 0.01	4.57 ± 0.72[a]	1.47 ± 0.33	0.03 ± 0.04	0.16 ± 0.15[a]
Roots							
1	1.51 ± 0.61	0.004 ± 0.006	0.21 ± 0.08	3.55 ± 1.07	3.40 ± 0.72	0.03 ± 0.04	0.02 ± 0.01
2	1.37 ± 0.34	0.007 ± 0.006	0.03 ± 0.001[a]	0.85 ± 0.31[a]	2.95 ± 0.37	0.01 ± 0.01[a]	2.76 ± 4.23[a]
3	1.14 ± 0.47[a]	0.004 ± 0.005	0.02 ± 0.01[a]	0.42 ± 0.24[a]	2.04 ± 0.90[a]	0.01 ± 0.01[a]	3.72 ± 1.29[a]
4	1.33 ± 0.52[a]	0.002 ± 0.02	0.02 ± 0.02[a]	0.41 ± 0.15[a]	1.78 ± 0.38[a]	0.01 ± 0.01[a]	5.01 ± 2.39[a]

1—control, 2, 3, and 4—concentrations of Sb in the growth media were 50 mg/L, 100 mg/L, and 150 mg/L, respectively.
[a]*Differences between control and plants grown in the Sb-spiked water were statistically significant* ($P < .05$).
Reproduced with permission from Shtangeeva et al., 2011. Bioavailability and toxicity of antimony. Journal of Geochemical Exploration 110, 40–45.

contaminated with Sb was less than the biomass of the control seedlings. Moreover, in this case, the development of the seedlings was significantly inhibited by the end of the experiment.

4.4 Accumulation of Sb in wheat grown in contaminated soil and water

Comparison of Sb concentrations in the wheat seedlings grown in soil and water spiked with 50 mg/L Sb showed that after 5 days of exposure to Sb, its concentration in leaves and especially in roots of the seedlings grown in water was higher than concentration of Sb in the seedlings grown in the Sb-spiked soil during 7 days. In water, Sb is present in soluble form. The solubility of Sb in soil is controlled by various soil–metal interactions. In particular, part of Sb can retain on the surface of the soil particles and, as a consequence, its mobility and bioavailability may be reduced.

Antimony concentration in wheat seedlings increased with time. These changes were more marked in roots than in leaves. The level of uptake and transfer of Sb from roots to upper plant parts was higher in the wheat seedlings grown in water than in the wheat grown in soil. During 3 weeks, concentration of Sb in the soil-grown plants increased slowly. Then, the Sb bioaccumulation increased significantly. It was shown (Amezcua-Allieri and Rodriguez-Vazquez, 2008) that uptake of metals by plants grown in metal-contaminated soil was insignificant during first 3 weeks. However, then a rapid increase of metal uptake was observed. This may be due to certain stage of development of wheat seedlings. The life cycle of wheat is marked by several critical physiological and morphological stages (Carver, 2009). He and Yang (1999) reported that tillering stage (an important stage of the wheat development) was observed on 28–30 days of the plant growth. Just at this time, the significant increase of Sb concentration in the wheat seedlings was found.

After exposure to Sb during first 12 h, concentration of Sb in leaves of the seedlings grown in water increased two times and increased four times after 24 h. After 5 days of exposure, Sb concentration in leaves of the seedlings grown in the Sb-spiked water increased 20 times compared with control. The accumulation of Sb in roots of the water-grown plants was higher than in leaves. The Sb concentration increased 25 times and 34 times after 12 and 24 h exposure time, respectively. In 5 days, the concentration of Sb in roots was 270 times higher than in roots of control plants.

The uptake of elements by roots and their transfer to leaves proceed differently (Baker and Hall, 1975). During transfer of nutrients and metals from roots to upper plant parts, certain portion of the elements may be selectively removed from the xylem sap. Plants have specific mechanisms that govern the accumulation of nutrients and metals (Liu et al., 1997). The mechanisms control the uptake and distribution of different elements in the plant tissues, thus maintaining their concentrations below the levels that cause toxic symptoms (Clemens, 2001). We may assume that this restriction of the metal transfer from roots to leaves is a specific metal tolerance strategy.

The relationships between Sb concentrations in roots and leaves of the wheat seedlings grown in soil and in water were not the same. There was no correlation between Sb in roots and leaves of the soil-grown plants. The correlation between root and leaf Sb concentrations in the water-grown wheat was statistically significant and positive. It may be speculated that transfer of Sb within the plants grown in water occurs more easily than within the plants grown in soil.

4.5 Uptake of macronutrients and trace elements by wheat seedlings grown in a highly contaminated by Sb medium

The accumulation of Sb influenced the uptake of different elements in wheat seedlings. However, the effects were different for the plants grown in soil and in water. In the soil-grown plants, only statistically significant increase of Co in roots and decrease of Na in leaves were found. Variations in the concentrations of elements in the wheat seedlings grown in the water contaminated with Sb were more marked. The most suffering part of the plants were roots. When the seedlings were grown in the water that contained 50 mg/L Sb, the bioaccumulation of Sb in roots caused a statistically significant decrease of K, Cu, and Pb concentrations (Table 19.1). Under higher Sb concentration in the growth medium, we also observed the decrease of Ca and Na in roots. In seeds of the wheat seedlings that were grown in the water spiked with 150 mg/L Sb, concentration of Ca and Na decreased statistically significantly ($P < .05$) compared with control. The least effect was found in leaves. Growth of the seedlings in the water spiked with 100 or 150 mg/L Sb resulted in a statistically significant decrease of concentration of K. Probably, the bioaccumulation of Sb (its concentration in roots increased more than 100 times compared with control) could lead to partial replacement of some elements by this metalloid and thus result in unbalance in the plant mineral nutrition.

It was reported that decrease of plant K concentration can lead to suppression of photosynthesis. Potassium deficiency may be characterized by reduced plant growth with yellowing of the leaf edges (Pan et al., 2017). It is also known that Cu is a structural element in regulatory proteins. It participates in photosynthetic electron transport, mitochondrial respiration, oxidative stress responses, cell wall metabolism, and hormone signaling (Schulten and Krämer, 2017). In our experiment, the decrease of the plant K and Cu concentrations was the most significant (Table 19.1). The experiment showed that the decrease of the concentrations of essential plant nutrients and increase of concentration of Sb correlate with decrease of the plant biomass.

5. Conclusions

Biogeochemistry of many trace elements in wheat is still poorly studied. The concentrations of the trace elements are relatively low, much lower than in soil. Until the present time, little is known about phytotoxicity of the elements. Available data are very contradictory and hardly comparable.

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CHAPTER

20

Transfer of the wheat heritage of anatolia to future generations

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OUTLINE

1. Introduction

Located in the continents of Asia and Europe and having 78 million ha surface area, Turkey has a total of 11.707 plant taxons, 3.649 (31.82%) of which are endemic (Guner et al., 2012). Almost all of the botanic biological diversity of the European continent is within the borders of our country. The distinction of our country's geographical structure is a factor in this. Its being located at a point, where the Mediterranean and Near East Vavilov Gene Centers, plays an important role in the emergence of particularly grains and garden plants. Turkey is in a very valuable location in terms of the genetic sources of wheat, which is one of the most important agricultural products of the world and in the first place for food safety.

Having an important place in the nutrition of the world, wheat is accepted to have originated from the region, known as the "Fertile Crescent," and it was cultivated in Karacadağ in the Southeast Anatolia region of Turkey and spread to the entire world from this location. There are 27 wild wheat species around the world, and 20 of them are located in our country. These species could maintain their generations until today despite various abiotic and biotic stress conditions (Karagoz and Ozberk, 2010).

Whether it has natural or anthropogenic sources, climate change affects the entire world and threatens food safety. Especially, climate change, caused by the rapid increase of the world population and industrialization, has affected and will affect the world countries at different levels depending on their locations. Turkey is a country which is located in the Mediterranean basin and predicted to be affected with the temperature increase. It is thought that our country that has different climates is going to be affected by climate change in different ways and levels.

It is predicted that particularly agricultural production is going to be affected by climate change. In our country, which is quite rich in terms of grain gene sources, the necessity of taking measures toward the protection of these sources and the development and production of the species resistant to climate change occurred. In this study, the effects of climate change on our country and the world wheat production will be examined, and the strategies that will provide the protection of the wheat gene sources and their transfer to the future generations will be focused on.

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00020-0

2. Our genetic heritage wheat

Wheat and its close relative species Poaceae (Graminea) family are included in the Triticeae tribe. *Triticum* genus, depending on the number of chromosomes, is on the level of three different ploidies such as diploid (2n = 14), tetraploid (2n = 28), and hexaploid (2n = 42) (Feldman et al., 1988). The cultivated kinds of wheat are *Triticum monococcum* ssp. monococcum (diploid), *Triticum turgidum* ssp. dicoccoides (tetraploid) and *Triticum timopheevii* (tetraploid), and *Triticum aestivum* (hexaploid).

Having a single ancestral plant dating back to 13 million years ago, wheat grain has evolved into many species as the result of natural mutations and environmental interactions in time. Interspecies gene exchange has been common in the evolution process of wheat. Tetraploid durum wheat, cultivated at the present, has occurred as the hybridization of the species of *Aegilops speltoides* and *Triticum boeoticum* among its wild relatives and continued its transformation to the species of first *Triticum dicoccum* and then *Triticum durum* with the mutation of the species of *Triticum dicoccoides*. Being a hexaploid, bread wheat (*T. aestivum*) is the natural hybrid of the species of *T. dicoccoides* and *Aegliops tauschii* (Karagoz and Ozberk, 2010).

In global food safety and decreasing poverty, wheat, corn, and rice have vital importance. The prices of these products, being fundamental human calorie sources, are determined with the global balance of supply and demand (Lobell and Gourdji, 2012). Wheat, corn, and rice provide 30% of the food calories of more than 4.5 billion people in 100 developing countries (Hellin et al., 2012). Wheat is in the position of being the fundamental calorie source for many societies around the world having nutritional value; containing rich amino acids; being easily carried, stored; and having wide tolerance limits (Atak, 2017). It provides more than 20% of people's daily calorie need (Peng et al., 2011 a,b). Meanwhile, it is one of the most important protein sources and provides approximately 21% of daily protein intake (Shiferaw et al., 2013).

In Turkey, home to a large number of wild wheat species, there are certified varieties such as 198 bread and 61 durum wheat as of 2016 (Ozberk et al., 2016). Today, hexaploid ones are generally used in the production of bread, baklava, biscuit, pastry, and cake; tetraploids in the production of pasta and bulgur; and diploids, despite being very few, in the production of bulgur and pasta (Demirel, 2013).

As well as the use of wheat grain as human food and animal forage, it is known that its stalks are used in making adobe and mushroom compost, animal breeding, and protecting and treating human and animal health (Atar, 2017).

Wheat, additionally, has an allelopathic interaction with many weeds. The intensive use of chemical herbicides since the Green Revolution has done so much damage to the ecology. It was stated in many studies that wheat's allelopathic effect can be benefited from the production of environmentally friendly bioherbicides (Aydemir and Turkyilmaz, 2019a,b; Disli and Nemli, 2014; Turker et al., 2019; Turkyilmaz and Bayram, 2018).

It is accepted that wheat was cultivated for the first time in a region, particularly around Diyarbakır-Karacadağ, that covers Turkey's Southeast and is named the "Fertile Crescent" (the region that covers Jordan, Syria, and Iraq and extends until Iran's Zagros Mountains and covers their west in the shape of a half-moon) 10000–12000 years ago. Turkey takes the first place in terms of the existence of wheat and its weed relatives. All of the relatives which constitute the modern wheat and are in the first gene pool are in Turkey (Ozberk et al., 2016).

Wheat farming enabled hunter and gatherer communities to become sedentary and the development of many civilizations (Diamond, 1997; Harlan, 1995; Heun et al., 1997). Although it used to grow and be grown only in the geography of the Middle East 10000–12000 years ago, it spread to the entire world and became an important cultivated plant in terms of food safety. Today, it is farmed in more than 140 countries (FAO, 2014), the Scandinavian countries between 67 degrees north parallels in Russia and 45 degrees south parallels in Argentina (Shewry, 2009). Being a temperate species, wheat has no rival by growing in fertile lands of Western Europe as well as the extreme conditions of Asia, Africa, and Australia and with its wide tolerance limits (Atar, 2017; Braun et al., 2010).

It is the grain that has the largest cultivation area (220 million ha) and the highest production amount (729 million tons) after corn and paddy around the world (Peng et al., 2011a; Shiferaw et al., 2013). The International Maize and Wheat Improvement Center (IMWIC) stated that there are almost 80 million wheat farmers around the world today, and by the year of 2050, it will be necessary to produce 60%–70% more than the currently produced wheat (Furbank and Tester, 2011).

The United States, EU, China, India, Russian Federation, Canada, Australia, Argentina, and Turkey make more than 75% of the world's wheat production (FAO, 2004). Mainly planted in the Central Anatolia, Thrace, and Central Anatolia, wheat agriculture can be made all around Turkey (Turkoglu et al., 2016). Planted the most among grains, wheat has 7.8 million ha cultivation area, 22.6 million tones production, and 260 kg/da average yield (TUIK, 2015).

In our country, along with the certified cultivated types, local (village) wheat types are still used. These types are the wheat variations which have been developed with natural and artificial selections for years and suitable for local environmental conditions and traditional cultivation techniques (Jaradat, 2013; Ozberk et al., 2016). Regarding characters, they are not pure and serve as a bridge between cultivated and wild types (Atak, 2017). It is known that local types are cultivated mostly in the areas that are distant from settlements, rocky, sloped, and rugged under extreme conditions with traditional methods. In general, its yield is lower in comparison to the commercial types, and it is stated that it is cultivated because of the reasons of resistance to the conditions like drought and diseases, etc.; not needing much input; and taste (Karagoz and Ozberk, 2010). Among the local types, it was found that the sizes of their cultivation areas were Zerun, White Wheat, Red Wheat, Yellow Wheat, Karakılçık, Kırık, Siyez, Koca Buğday, Topbas, Sahman, and Üveyik Wheat (Kan et al., 2015). However, the cultivation of local types of wheat decreases day by day (Kan et al., 2015; Karagoz, 2014; Morgounov et al., 2016).

3. Climate change around world

Today, all climate scientists accept that there is a deterioration in the world's climate system (Ozturk, 2002). Global warming is the systematical increase of world's surface temperature as the result of natural processes as well as the creation and reinforcement of the greenhouse effect by carbon dioxide (CO_2), carbon monoxide (CO), methane (CH_4), dinitrogen monoxide (N_2O), ozone (O_3), water vapor (H_2O), and chlorofluorocarbon gases (CFCs) which are released into the atmosphere. The increase in the emissions of greenhouse gases has promoted global warming since the industrial revolution of the 1800s (Dellal, 2008). However, the global climate change is the exposition of such climate factors as humidity, precipitation, air movements, drought, etc. depending on global warming (Cepel, 2003).

The issue of climate change was brought into question for the first time with the World Climate Conference of 1979 internationally. The turning point in the field of climate change is that the United Nations General Assembly defined climate change as a shared concern of humanity with its resolution on December 6, 1988, and accepted to establish the Intergovernmental Panel on Climate Change (IPCC) (Ata et al., 2011).

The report that the IPCC prepared in September 2013 remarks that the surface value has averagely increased 0.85°C since the industrial revolution and predicts that if not any measure is taken, the average temperate will increase 1.8−4.0°C more in 2100, and its causes are human activities (Team et al., 2014). English scientist Stern (2007) also predicts that the global temperature will continue to increase between 0.5°C and 1°C in the next decades even if not any greenhouse gas emotion is made starting from today, and the world will get 1.4°C and 5.8°C hotter in the next century providing that no measure will be taken in this matter.

The acceleration in global warming and climate changes exceedingly affect human health and the ecosystems, biodiversity, water resources around world (Akin, 2006; Jiang et al., 2005; Kotir, 2011; Ozturk et al., 2010). It is expected that climate change is going to cause stress on particularly water and other resources, desertification of lands, salinization—and hence their infertility—increase in disease and pests (Akalin, 2014).

One of the most important effects of the climate is the one on agricultural production, and accordingly food safety. Considering that three-fourths of the poor populations around the world live in rural areas (IFPRI, 2009), there is increasing importance of climate change in terms of agricultural production and food safety (Akalin, 2014; Godfray et al., 2011). Together with climate change, it is predicted that the average loss of fertility is going to be 15% by the year 2080 in developing countries (Fischer et al., 2005). According to another scenario, it is thought that after a while the sea level is going to rapidly increase when all ice in the poles melts, and the countries like Germany, Denmark, the Netherlands, etc., whose lands on or under the sea level, are going to be covered with sea waters, become salinized and infertile, so food production is going to decrease and food safety will become under threat (Akin, 2006).

Although the agricultural activities like energy consumption, crop and animal cultivation, fertilization, disinfection, etc. are responsible from 1/5 of the increasing greenhouse gas (Houghton, 2003; Pathak and Wassmann, 2007), they are extremely important for the world population to eat and survive healthily. Agricultural production is also affected by climate conditions at a high rate.

Although temperature and carbon dioxide increase positively affect the yield of agricultural products in some areas for a short term, these constituents cause the extreme climate conditions like drought, salinity, floods, etc. and can negatively affect the product quality and amount (IFPRI, 2009).

The plants that are exposed to abiotic and biotic stress factors can respond by escaping from the stress conditions or showing resistance against them. In order to escape from stress, plants generally change their morphologic structures (number of leaves and area, cuticle thickness, stoma status, root length, etc.) and decrease the effect of stress.

And, the plants that tolerate stress eliminate or recover the effects that stress causes by responding at subcellular (cell wall and membrane), molecular (secondary compounds, polysaccharides, proteins, amino acids), or submolecular (reactive oxygen species) level (Ozen and Onay, 2013; Taiz and Zeiger, 2008). For instance, it was observed in wheat, exposed to the stress of drought, that seedling growth, photosynthetic pigment amount, stoma conductivity, protein amount, and relative water decreased, while malondialdehyde and proline amount increased (Ozdemir, 2012). It was also observed in wheat, exposed to the salinity stress, that germination, seedling growth, and photosynthetic pigment amounts decreased, while the proline amount increased (Turkyilmaz, 2012). In the study, made by Gupta et al. (2013), while wheat's seedling growth and chlorophyll amount were decreasing due to the temperature stress, proline and antioxidant enzyme (catalase, guaiacol peroxidase and superoxide dismutases) activities increased. It can be said that wheat is trying to deal with the stresses of drought, salinity, temperature, etc. with the accumulation of osmolytes.

It is almost not known how plants are affected from the abiotic stress factors caused by climate change and what reactions they can give, but accurate estimations cannot be made about the impact level of the agricultural diseases and pests. It is stated that global warming and climate change are going to allow agricultural diseases and pests to increase and can also be carried to different regions (WMO, 1996). Plant diseases and pests greatly decrease the production and quality of important food products. Mycotoxins and pesticide residuals in food products also threat human and animal health. For this reason, the disease and pest increase that will occur under the changing climate conditions are among the important food safety concerns (Miraglia et al., 2009; Tirado et al., 2010).

The impact of climate change on agriculture can show difference depending on regions and product groups. The grains like wheat, barley, corn, rice, etc. have strategic importance for many regions. Considering that more than one billion people are malnourished around the world (FAO, 2009), climate change is expected to be more effective in agriculture in the future. It is estimated that while the underdeveloped and developing Africa, Asia, and Latin America countries are negatively affected, the European Union countries and the United States are going to be affected positively from the temperature increase until the level of 2°C and negatively from the average temperature increase above 2°C. Although the countries which are in the north parallels like Canada and Russia will be able to perform the agricultural activity in a larger area due to global warming, it is still a matter of debate whether the soil conditions will be suitable for intense agriculture (UNEP, 2006).

4. Climate change in Turkey

Because of its complex climate structure, Turkey is among the countries in the risk group with respect to climate change due to global warming (Bayrac and Dogan, 2016). Because of its being surrounded by seas on its three sides, its topographic structure and orographic characteristics, different regions are going to be affected by climate change in different ways and at different dimensions. The arid and subarid regions like the Southeast and Central Anatolia and subhumid regions without enough water like the Aegean and Mediterranean are going to be affected more in comparison to our other regions (Turkes, 1998).

As the result of the analysis of the General Directorate of Meteorology's climate date starting from the year of 1960, it was found that average temperatures of Turkey increased at a considerable rate in summers, and it also increased in the transition seasons (spring and fall) although it was not as much as summers, but a significant change has not occurred in the temperature of winters. It was also underlined that there was an increasing tendency in fall precipitations, and there was a decreasing tendency in winter almost at the same rate, while there was not any change in other seasons. When the high-definition simulations are analyzed, it is revealed that the characteristics of the typical Mediterranean climate can be seen in larger areas. For example, the Black Sea Region, currently, having a temperate and rainy climate, will carry the characteristics of the typical Mediterranean climate with the increasing temperature (Sen, 2013).

The products that are affected from climate change the most in Turkey are fig, tobacco, watermelon, tomato, potato, apple, seedless grape, wheat, and barley (Engindeniz and Ozturk, 2010). The insufficiency of the spring rains is going to harm the grain production at a large scale. The drought that can occur in the sprouting period of wheat plant can affect the number of plants per square meter; the drought that is seen in the period that takes place from the beginning of the wheat apex's coming to existence until the appearance of the second node on soil can affect the spikelet and flower number; and the drought before the stem extension period can affect the number of fertile flowers in a spike. Grain size is also affected by the stress conditions after pollination. Generally, drought stress decreases wheat's fertility by affecting it with the loss of the number of grains in square meter over the number of fertile spikelet and flower until pollination and with the grain loss after pollination (Soylu and Sade, 2012).

In Turkey, positive temperature anomalies have been observed since 1994, save for the year of 1997. The positive increases in air temperatures have also caused shifting forward in plant phenological periods, particularly. In our country, while the locations where wheat began early heading especially because of climate reasons were the Aegean and Mediterranean coasts and the Southeastern Anatolia regions, the location where it headed the latest was Sivas, Gümüshane, and Van provinces. It was determined that there was shifting to an early time for 40 days/100 years in the heading dates of wheat in general around Turkey, as the result of climate change (Turkoglu et al., 2016).

5. Food safety and climate change

According to a study which was made by the United Nations (DESA, 2015), the world population is predicted to reach 9.7 billion by 2050 and 11.2 billion by 2100. Food is one of the most important resources for the maintenance of life in the history of humanity (Bayram and Gokirmakli, 2018).

Food safety is defined as "access of all human beings to healthy, safe and nutritious food physically and economically in order to sustain an active and healthy life" by the United Nations Food and Agriculture Organization (FAO, 2006). Starting with the Universal Declaration of Human Rights of the United Nations (UN) in 1948, defining "access to food" as "a fundamental human right," 1975 UN (1975), the UN Food and Agriculture Organization (1983), the World Bank (1986), the World Food Program (1989), FAO (1992) and the International Nutrition Conference, organized by the World Health Organization (WHO), and the World Food Summit, organized by the FAO in 1996, importantly dwelled upon food safety (WHO, 2001).

The relationships between food safety and climate change are rather complex (Easterling et al., 2007; Gregory et al., 2005). Climate change affects food safety under four subjects as food provision, accessibility, efficient use, and stabilization of food systems. While these effects can occur with extreme climate events in the short term, they can threaten food safety with the changes in temperature and precipitation regimes in the long term (Glantz et al., 2009).

The impact of climate change on food safety can show differences between important regions. For example, in South Africa, one of the most frequently stated causes of food unsafety is the climate. It can behave both as a continuing problem and a short-term shock (Gregory et al., 2005).

So as to provide food safety, it is important to decrease the negative impacts of climate change on agriculture and take a set of ecologic and economic measures (Kurukulasuriya and Rosenthal, 2003; Ziervogel and Ericksen, 2010).

6. Transfer of wheat to future generations

Together with corn and paddy, wheat is an important grain that provides global food safety. Climate change strongly affects the crop of wheat around the world. In order to provide food safety, wheat's cultivation areas can be enlarged, advanced agriculture and irrigation techniques can be used, the conscious and environmentally friendly use of fertilizer can be increased, ecological agricultural control applications, convenient type selection can be performed (Demirbas and Atis, 2005), and the training of farmers can be encouraged by supporting public and civil society organizations that work on the protection of nature and biological diversity (Ozberk et al., 2016).

The other methods that will increase product number and quality for wheat are the adaptation of wheat to the stress conditions (acclimatization) (Olgun et al., 2005) or the external application of such plant growth regulators as salicylic acid, methyl jasmonate, benzoic acid, gallic acid, etc. that will provide it a systematically gained resistance. There are studies, in which various plant growth regulators are externally applied and succeeded in alleviating the negative effects of the abiotic stress factors like the drought stress (Horváth et al., 2007; Singh and Usha, 2003; Waseem et al., 2006) and the salinity stress (Javid et al., 2011; Kaydan et al., 2007; Khan et al., 2012; Turkyilmaz, 2012) on wheat.

The use of the marker for the selection of the types resistant to stress conditions is another option. Being the genetic material of plants, deoxyribonucleic acid (DNA) is in the form of chromosome pairs each of which come from one parent. The genes that control various features of the plant are found in specific parts of the chromosome (Semagn et al., 2006). Molecular markers are pieces of DNA that refer to a gene area in any genome and display the differences that are sought for. They are effectively used in breeding works due to not being affected by the environmental conditions, being easily observable in any stage of the plant's growth and existing in a large number (Sonmezoglu et al., 2010). The development of the molecular markers encouraged the use of marker-assisted selection (MAS) in the works about increasing the yield, quality, and disease resistance of grains. MAS rapidly replaced

the classical breeding methods that take a very long time. For example, the resistance genes of some bread wheat types were mapped against drought (Di Bianco et al., 2008; Tavakol et al., 2008; Yakisir, 2015), yellow rust, powdery mildew disease, etc. (Porceddu and Blanco, 2008; Ercan, 2008; Sonmezoglu et al., 2010) and molecular markers were developed for marking them. For plant breeders, wild and local types have great importance in the creation of the types that are resistant to abiotic and biotic stresses. It is necessary to rapidly include our country's rich wheat gene resources into the modern wheat breeding programs and the genetic selection should become widespread.

The protection of plant gene resources has vital importance for providing agricultural biodiversity, creating a resource for plant breeding works and food safety (Grausgruber et al., 2016). The protection of plant genetic resources can be achieved either in their natural habitats (in situ) or outside their natural life (ex situ) (Tan, 1998). Ex situ protection can be provided with organizations such as gene banks, seed banks, botanic gardens, cell and tissue culture centers, etc., but it prevents natural evolution.

The in situ protection of wheat, its wild relatives, and their local types is extremely important in terms of food safety. Although there are successful examples of ex situ works, in situ protection works are insufficient. While the protection of seeds in gene banks and botanic gardens, creating their genetic maps, and determination of their molecular markers are very important, their protection in their natural habitats is also important, as much. The wild relatives of agricultural plants constitute a large gene pool and ensure their generations' sustainability despite various stress conditions. As they are in interaction with their environments, their gene pool can be protected only on site. Most of the wild wheat types (20 species) that are found around the world (27 species) are in our country. Together with Karacadağ, which has an important place for not only our country but also the world, the regions, where the wild relatives of wheat intensively exist should also be taken under protection (Ertekin, 2002). Edges of wheat fields and half natural habitats that exist between farms should be protected, as well. It should not be forgotten that there are the living spaces for many plant species which take refuge in the transition areas because of not being able to reside in the cultivated lands (Ozberk et al., 2016).

Today, as the resistance gene of the cultivated types, with high yield but narrow genetic basis, against changing climate conditions is absent, they cannot adapt to the conditions of the environment when they are unconsciously planted outside the region and experience the loss of fertility and quality, and the farmer suffers from economic damage (Atak, 2017). However, the local types are resistant against the stresses unique for this region and changing environmental conditions and have high yield stabilities under stressful conditions. They contain interspecies diversity and provide a genetic resource in the development of new species (Akcura and Topal, 2006; Jaradat, 2013). They do not need very special breeding conditions (Jaradat, 2013). They serve as a bridge in transferring the quantitative characters in long-term breeding programs and the quantitative characters in the short- and midterm programs (Sehirali and Ozgen, 1987; Jaradat, 2013). For this reason, samples should be gathered from the local types which are still cultivated in villages and hamlets in the county of our country, particularly, and they must be populated and protected, and the farmers should be encouraged to use these types.

7. Result

Having been cultivated for the first time in Anatolia and having a very rich genetic diversity in our country, wheat has an important place in terms of food safety. Due to the climate changes with natural or anthropogenic causes, its agricultural production around the world is decreasing, gradually. Anatolia (Turkey) is also the gene center of wheat as for many grains. Taking wild and local types under in situ and ex situ protection, storage, serving to the use of farmers by populating as well as using a gene resource in genetic breeding works have great importance in transferring our wheat heritage to future generations.

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CHAPTER

21

Overview of the prospective strategies for conservation of genomic diversity in wheat landraces

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OUTLINE

1. Introduction

The most domesticated food crop grown in mild temperature is wheat. It is considered to be one of the major crops and included in the list of top three big cereal crops. In the year 2007, the total cultivation of maize crop in the world was approximately 785 million tons, the total cultivation of wheat was approximately 607 million tons,

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00021-2

and the total cultivated rice was approximately 652 million tons (FAO, 2007). Currently, global wheat cultivation was 222 million hectares (USDA, 2016), and its production has boosted from year 1961 to 2015, i.e., 235 to 733 million tons, respectively (FAO, 2014), and forecasted at 771 million tons in 2019. Even in Turkey, estimation of total annual wheat production is 19.6 million metric tons, whose value in 2010 was estimated at approximately US$6.9 billion. Wheat provides various important nutritional components such as carbohydrates, vitamins, phytochemicals, minerals, essential fibers, and amino acids. The cultivation of wheat as a "pioneer crop" happened 10 centuries ago, due to "Neolithic Revolution" (Heun et al., 1997; Nesbitt, 1998; Dubcovsky and Dvorak, 2007). Hexaploid wheat grown in the world is 95% of total cultivation (containing six homologous sets of chromosomes, $2n = 6x = 42$) in nature, and this wheat is known as bread, scientifically called *Triticum aestivum*. The tetraploid (having four times the haploid number of chromosomes, $2n = 4x = 28$) wheat variety is approximately 5% and is known as durum. It is used for various purposes including baking and in making a variety of foods, like pasta (Wrigley, 2009). The wheat having an outer covering of the seed is called hulled wheat (emmer and einkorn) and known as Faro in Italy (Özkan et al., 2011). There is a type of wheat known as spelt which the farmers are still cultivating in the Alpine areas of Europe (Fossati and Ingold, 2001).

The most widely grown cereal crop throughout the world is wheat. The major source of raw materials, food, and feed is also wheat. According to an estimate, there will be an increase in the demand for food to an approximately 40% by the end of 2030 (Harlan, 1992). To overcome this demand, the area of the agricultural land should increase up to 1.5 billion ha along with an annual increase in the yield up to 2%, but unfortunately, the yield is only increasing up to 0.9% since the last decade (Harlan, 1992). The condition is alarming in Europe, especially France, where the yield of the wheat crop has been constant since 1995 (Brisson et al., 2010) and the main reason for this constant yield is the unfavorable climatic change (Newton et al., 2011). Around 50% of the need for calories and proteins daily are overcome by three major crops which are rice, maize, and wheat. Cereals are one of the most important domestic variants of Gramineae family. The dominant food in different parts of the globe is also officially represented by cereals. Their origin and domestication appear to be connected to various ancient civilizations. Thus, wheat among the three major crops, which fulfill the need of the people, has been affiliated with Sumer or Egypt civilization in the Mediterranean region (Harlan, 1992).

While the domestication of natural populations clearly developed emmer and einkorn, the hybridization of cultivated unrelated wild grass *Triticum tauschii* with emmer many years back resulted in the birth of bread wheat (Shewry, 2009). The wheat is a complex polyploidy species that contains more than twice the haploid number of chromosomes. Multiple species of varying ploidy levels formed a genetic combination of *Triticeae* tribe (Dubcovsky and Dvorak, 2007). Thus, three types of species mainly found are the diploid species which has 2x, the tetraploidy species which is 4x, and the hexaploidy which is 6x.

Through archaeological evidence it was proved that in the Iberian Peninsula, wheat was cultivated since the fifth millennium B.C. Following that the Fertile Crescent was responsible for developing wild wheats, traditional wheat varieties, and other crops (Diamond, 2002). However, as a result of migration from the region of Fertile Crescent and also natural and human selection, local wheat landraces developed as shown in Fig. 21.1. During the domestication process and spread, new traits suitable for better adaptation under new environmental conditions were selected by the ancient farmers for domesticated wheat (Charmet, 2011; Peng et al., 2011) (Fig. 21.1). Other traits involved in coselection were the number of spikes and grains along with the height of plants (Peng et al., 2011). The farmers not only preserved the landraces, but they also grew them in the fields to overcome their ethnical, environmental, and even financial needs (Belay et al., 1995). Landraces were developed from the older ones who have the capability to grow in the conditions which are not fruitful for the growth of the regular wheat such as under stress which might be biotic and abiotic, and these landraces not only increase the yield but also facilitate stability (Witcombe et al., 1996). Climate change has affected crop yields across the globe. With exceptional adaptation capacity in the past, landraces are still out-yielding modern cultivars under low-input production systems (Dwivedi et al., 2016). This is also beneficial because these landraces are enriching in the nutrients required by the body. So by keeping in view all these advantages such as its resistance to stresses and its nutritional value, there is a need to increase the yield at the earliest possible time to meet the challenges faced by the world.

Wheat landrace refers to a traditional wheat variety possessing tolerance to stress and producing high-yield stability with moderate level of crop yield under minimum input conditions (Zeven, 1998). It is different from a wheat variety which has been improved for specific traits by the plant breeders. These landraces are the result of the different varieties of the crops which are harvested by the farmers in a normal way, and these varieties are resistant to the factors which cause damage to the normal wheat type (Zeven, 1999). Due to the resisting capability of landraces against the stresses, dry period, chilling weather, these landraces have emerged as a complicated and heterogeneous population (Masood et al., 2005). Studies have depicted that farmers produce wheat landraces in generally remote areas for the purpose of subsistence farming (FAO, 2015). Landraces of barley, maize, rice, and wheat have abiotic stress-tolerant alleles which lead to investigating and conserving landrace germplasm. Investigating landrace

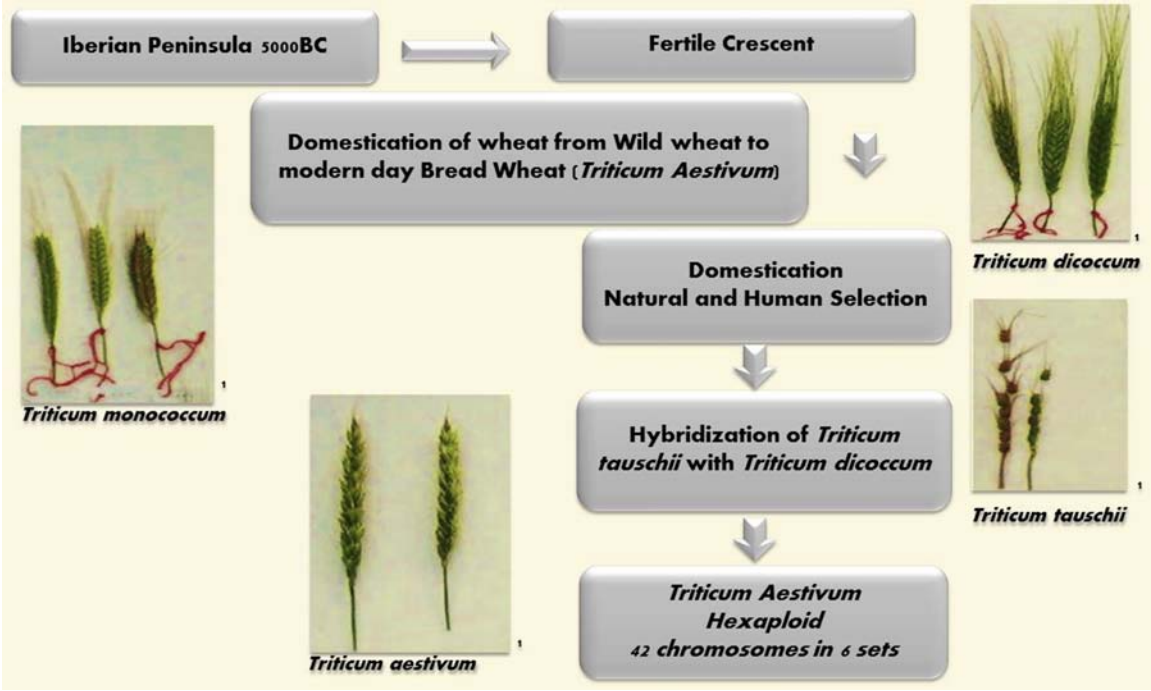

FIGURE 21.1 Domestication of wild wheat toward modern wheat varieties of *Triticum aestivum*. Wheat was cultivated in Iberian Peninsula and later Einkorn or Emmer wheat varieties were cultivated in Fertile Crescent. Wheat over a period of time was domesticated. With natural and human selection, migration and hybridization of modern wheat variety (*Triticum aestivum*) was developed. *Adapted from. Kilian, B., Martin, W., Salamini, F., 2010. Genetic diversity, evolution and domestication of wheat and barley in the fertile crescent. In: Evolution in action. Springer, Berlin, Heidelberg, pp. 137–166.*

germplasm will lead to discovery of more agronomically beneficial alleles to increase productivity and improve adaptation in stress-prone environments (Dwivedi et al., 2016).

It is not practical to use long-lived landraces which have been an important source for further breeding (Collins and Hawtin, 1999). The genetic diversity of unused varieties and species of crops outstandingly assist the enhancement of crop idiosyncratic qualities. The genes discovered can be utilized for breeding new resistant varieties (Reynolds et al., 2007; Gollin and Smale, 1998). Genetic diversity within crop species has reaped notable importance in the current framework of modern intensified agriculture systems. It has been a subject of various studies. Innumerable factors have been identified which caused depletion in genetic diversity and shattering of natural gene reserve. These factors include population outburst, urbanization, fast industrial growth, plant breeding, modern agriculture, and fleeting industrialization (Rauf et al., 2010).

Triticum monococcum L., also called as einkorn (diploid species, 2n = 14), *Triticum dicoccum* also called as emmer (tetraploid species), and the third species *Triticum spelta* L., also called as spelt (hexaploid species) are considered to be among those species which are harvested by farmers (Suchowilska et al., 2010). Einkorn is grown in Southeast European countries, Turkey, Italy, Spain, Germany, and Swiss countries (Wieser et al., 2009). Emmer is considered to be a crop grown in countries like Italy, Turkey, India, and Ethiopia (Marino et al., 2009). Spelt is grown in the area including the Germany, Swiss, European countries, and the Czech Republic (Troccoli and Codianni, 2005). The two species of wheat emmer and spelt are grown in the field by farmers not only because they are enriched in the nutritional components but also they both are highly resistant to the unfavorable factors present in the environment (Suchowilska et al., 2010). High resistance is depicted by spelt to environmental factors such as abiotic stress and disease regarding agronomic characteristics. Spelt can be produced under unfavorable conditions such as high altitudes, cold and wet soils (Campbell, 1997). In recent years, 50% yield losses have been observed as a result of stem rust epidemics, and both spelt and emmer are found resistant to this dangerous disease (Beard et al., 2006).

Several benefits of high genetic diversity may be unfolded. Genetic diversity within crop variety acts as a cushion against the eruption of epidemics. It was noted that a mixture of defenseless and resistant plants had increase in the performance of susceptible type along with delayed evolution of new pathotypes (Zhu et al., 2000). Genetic diversity overcame the pitfall of phenotypic diversity such as reduced polymorphism and laborious nature of fieldwork (Rauf et al., 2010). Landraces consists of a wide allelic variation with stress-adaptive traits. It is necessary to exploit this genetic diversity which requires more attention and work.

2. Wheat cultivation

Wheat was cultivated 10,000 years ago, which resulted in the progress of human enlightenment (Willcox, 1998), wheat is a constant crop to transfer food through migration from one place to another. People started cultivating important crops including wheat because of the important traits which include:

a. Increased size of grain along with thriving seed germination and seedling growth in cultivated farms and
b. Development of an undemolished seed, which prevented natural diffusion of seeds and ultimately allowed mankind to reap and gather seeds at an ideal time.

It has been believed that different traits appear at different stages as proposed by the history of habituating progression of wheat (Feldman and Sears, 1981). Such as, earlier grain size has become greater by a change in the grain thickness and linear measure, and later it was followed by lessening in the shape of grain. Archaeological data and molecular genetics have permitted the reconstruction of domestication events that lead to the production of landraces, old cultivars, and later, modern cultivars (Dvorak et al., 1998; Willcox, 1998). In Turkey, an event in wheat domestication resulted in the emergence of hexaploid (6x) bread wheat through hybridization between a tetraploid (4x) and a diploid (2x) species (Hammer et al., 1996). Afterward, this hexaploid species spread around the Caucasian region and subsequently throughout the world.

According to an estimate, the loss in the crop genetic diversity is approximately 75% in the last 100 years (Hammer et al., 1996; Witcombe et al., 1996). This genetic loss is very much alarming for the world because it is an ultimatum for the food security as a long term. It needs an immediate attention of the world not only to preserve but also to grow these landraces as they provide protection against the shortage of food and also provide good quality wheat in the face of food uncertainty. Farmers are lagging behind in the preservation of the diversity of the wheat genetics (Zeven, 2000). It has been depicted by several research reports from Turkey that out of the total wheat cultivating areas in the country, the share of local landraces was under 1%, whereas, a very high rate of sharing of modern wheat varieties was reported in Turkish agriculture (Mazid et al., 2009). Thus, in the Turkish wheat crop, a decline has been observed in genetic diversity. Environmental changes are also causing the elimination of the landraces (Mercer and Perales, 2010). Consequently, the wheat with different genetic diversity is lost. Moreover, as a result of the rise in population, the farmers have replaced the landraces with the crops that have a high yield to overcome their needs. This resulted in production of crop low in nutritional benefits (Distelfeld et al., 2007).

3. Origin of wheat landraces

Wheat has evolved a large diversity of genotypes due to human skill, natural interference, and years of wheat cultivation. Evidence from the past proves that many farmers have used wheat crops to create new bread (Zeven, 2000). This is mainly because of the changes in the environment, socioeconomic conditions, and cultural applications. Furthermore, different factors like agriculture practices and agroecological conditions have posed stress on the available cultivars (Motzo and Giunta, 2007). Owing to these factors, we see many varieties of the crop, e.g., *T. monococcum*, *T. dicoccum*, *T. spelta* which can be called as landraces.

Landraces and local varieties have survived since ancient times and are expected to contribute to new agricultural practices (organic or sustainable farming), adversities in environment (Atkinson et al., 2008), quality (Gitay et al., 2001) and security (Parry et al., 2004) of food. The huge genetic diversity of these landraces is necessary for food stability (Dhillon et al., 2004). These landraces possess many useful genetic traits that are utilized by many farmers to cultivate bread with high yield. On the contrary, many of the varieties are not genetically stable and do not possess uniform traits (Morris and Heisey, 1998). This might have originated by the combination of homozygous and heterozygous traits. So, it is of vital importance to characterize these varieties (Brown, 2000). Characterization of the genes providing stability to the wheat crops is also necessary. Two software tools (geNorm and NormFinder) have been formulated to select the genes showing more stable expression under given experimental conditions. Thus, expression stability of some candidate genes has been analyzed via these tools (Vandesompele et al., 2002). This information may help in strengthening the already unstable and susceptible wheat varieties.

Obsolete cultivars and landraces are a significant part of the gene pool because the broad intraspecific genetic diversity of crops is represented by them from which arise new cultivars (Vojdani and Meybodi, 1993; Zou and Yang, 1995). In contrast to modern wheat cultivars, the original varieties have high biomass, and they can also extract high levels of water from the soil, so in order to compensate this problem, many are of the view to put these characters

either by breeding or by molecular biology (Sourour et al., 2010). Moreover, the mineral content is also low in comparison to those of landraces. These include copper, zinc, iron, and magnesium (Genc et al., 2005; Distelfeld et al., 2007). It can be suggested that this phenomenon may have occurred due to the presence of low minerals in the soil of old cultivars (Distelfeld et al., 2007; Khoshgoftarmanesh et al., 2010). Valuable characteristics have been shown by the landraces, which are formed through the selection performed by farmers and a combination of natural selection (Keller et al., 1991; Tesemma et al., 1998).

4. Genetic diversity of wheat landraces and adaptation to climate change

The pivot of variation of durum and bread wheat landraces has been switched by monocultures of natural and healthy genotypes. This degradation of genomes damaged novelty and diversity of both phenotypic and genotypic traits and biotic stress resistance or abiotic stress tolerance; in contrast to pure wheat which was deficient with wide modifications in genetic frameworks that were present in landraces. Genetic variation facilitates production.

Climate affects yield and growth of the crops. Over the 20th century, an increment of $0.6 \pm 0.2^{\circ}C$ has been observed in the global averaged surface temperatures, accompanied by severe changes in intensity and precipitation of some extreme climate phenomena (Gitay et al., 2001). Change in climate alters quality and yield of the wheat. Another major stress to global wheat production is fungal diseases. Fungal diseases result in the occurrence of the rust disease particularly on the leaves and stems (Newton et al., 2011). All three rusts, i.e., stripe rust caused by *Puccinia striiformis* West. f. sp. tritici Eriks., leaf rust by *Puccinia triticina* Eriks., and stem rust by *Puccinia graminis* Pers. f. sp. *tritici* Eriks., and E. Henn. (Pgt), greatly affect bread or common wheat (Bariana et al., 2007). To make the situation worse, the low output of landraces as a result of climatic change pose a great threat to the families of the poor farmers. To overcome this problem, the farmers started using the seeds of modern wheat that resulted in the increase of the yield (Zeven, 1999). But on the other side, this could cause loss of few or whole landrace populations or even entire minor species of wheat.

To improve crop yield and stability under continuous changes in climate and stress conditions, the most practical approach was to develop new wheat varieties. A few steps need to be taken to encourage the public to use the landrace and to cultivate them in their fields:

1. Creating awareness among the farmers and the public to inform them about the landraces importance.
2. Update the farmers about the landraces detail and then compare the knowledge of your landrace with the procedures they adapt for their practices.
3. Share your experience as well as your seed of landrace with the farmers that reside in whereabouts.
4. Payback the farmers with some goods who has kept the multifariousness and also to the farmers who preserve them.
5. Create the market which only focuses on the products of the landraces and brief the farmers about their cultivation (Newton et al., 2011).

The improvement in the available genetic diversity using landraces in breeding programs to counter harsh environmental conditions and quality of end product is a practical strategy. Yet the existing polymorphism in various wheat landraces need to be protected (Nazco et al., 2014a, 2014b; Lopes et al., 2015a). Infinium iselect 9K wheat SNP array investigated wheat landrace resistance to five *P. triticina* and one *P. striiformis* f. sp. *tritici* race. Eleven QTL along with various other markers were identified resistant to leaf rust (Kertho et al., 2015).

4.1 Drought tolerance

Inadequate water supply combined with high temperature is the sole factor for the limitation of crop productivity (Araus et al., 2002). Currently, drought is a significant threat for food supply and crop yield worldwide. Tolerance to drought is crucial for steady and increased food production. The domestication of wild wheat genetic diversity as that of wild wheat has affected its genome and decreased diversity. One trait majorly affected is drought tolerance. Many cultivated wheat species are adapted to artificial environmental conditions and not drought tolerant. Yield under drought is related to collective dry matter at maturity in durum, bread wheat, and barley (Fischer and Wood, 1979). While, it was reported that out of 39 wild emmers, 33% showed higher resistance when subjected to osmotic stress as compared with control (Blum, 2005). Moreover, it is observed that several *Aegilops* species, wild

Triticum species, and durum lines accumulated a higher biomass under limited water supply (Rafi et al., 1992). Studies have also proved high spike allocation has helped boost yield (Araus et al., 2002).

A wide analysis of emmer by allozyme and DNA marker variation has shown greater genetic diversity in association with environmental factors. For high drought tolerance, wild emmer is found very popular, and some of *T. dicoccoides* have almost thrived fully in arid conditions as well as in arid desert environments. As compared to durum wheat, emmer has good productivity and stability under limited water conditions. This predicts that wild emmer has allelic traits that can be utilized for a higher yield purpose. Therefore, *T. dicoccoides* can be used for producing drought-tolerant crops. The leaf and root transcript profiling of *T. dicoccoides* TR39477 (tolerant variety) and TTD-22 (sensitive variety) has shown these genes to be responsive in the drought stress mechanism (Budak et al., 2013b). Moreover, metabolite and transcript profiling of TR39477 (tolerant variety) and A24-39 (sensitive variety) proved various regulation in different cultivars under drought stress. Cloning of TdicTMPIT1 taken from wild emmer root tissue which is expected to be associated with drought stress showed an increased expression when this cultivar was subjected to osmotic stress (Lucas et al., 2011).

5. Improvement of wheat landraces in modern time and future

It is estimated that world population is increasing at the rate of 90 persons per minute. This high rate of population is confined to the developing countries. This is creating the population pressure on the world's food reservoir. To feed such a huge population, it is essential to increase production of wheat at minimum by rate 1.6%. To achieve this it is crucial to develop high-yielding wheat varieties that are tolerant to both biotic and abiotic stresses (Khan et al., 2013). Since the two leading cereal crops are wheat and maize, both cereal crops make up around 80% of total cereal requirement of developing countries (Hoisington et al., 1999). Wheat has a greater world trade than for all other crops combined (Curtis, Rajaram & Gómez, 2002).

To enhance the production and the yield of these valuable crops, we need to have breeding techniques in our account. For the successful breeding, we critically need genetic diversity among the gene pool of our target crop. The larger gene pool provides a critical resource for agriculture (Brozynska et al., 2015). Various landraces such as Ethiopian landraces are rich in variation (Mengistu et al., 2016). Another study on Iran revealed high existing genetic diversity within populations of landraces especially in durum wheat (Fayaz et al., 2019). Genetic improvement of crops depends on variant gene expression leading to more optimal development and growth in a given environment. Allelic diversity can be increased by exotic parents (Reynolds et al., 2007). An enormous amount of genetic information about these crops has been collected. Access to these data resources is vital to fight against world hunger (Hoisington et al., 1999). It is worthy to be noted that some modern wheat and other food crop cultivars have genetic similarity and a narrow genetic base. So the use of new genetic resources is critical for producing genetically diversified crops. The artificial selection particularly by the farmers has resulted in the rise of wheat landraces (Belay et al., 1995). This hybrid of natural, as well as the artificial selection, has broadened the genetic basis of the wheat gene pool in the domesticated wheat areas that have ultimately led to the conservation and evolution of valuable genetic characteristics (Keller et al., 1991; Tesemma et al., 1998).

The most focused area in the today's world is the stability of crops regarding yield and stress. These landraces have the efficient resistance to various domestic stresses (Li et al., 1997) that eventually result in the good yield stability (Tesemma et al., 1998). Due to the following rationales, the landraces and old-time cultivars are thought to have a broad genetic pool with valuable characteristics. These landraces also have the broad intraspecific genetic diversity of crops that aids in the new cultivars arisen (Vojdani and Meybodi, 1993; Zou and Yang, 1995). A new genetic diversity is being exploited by the bread wheat breeding program of the International Maize and Wheat Improvement Center (CIMMYT), Mexico, starting from interspecific hybridization of the ancestral genomes of bread wheat (Mujeeb-Kazi et al., 1996). This led to development of "MasAgro Biodiversidad," one of the first platforms to understand wheat germplasm in association with software tools and data (Halewood et al., 2018).

These landraces are also gifted with the broad content of proteins and valuable characteristics of grain quality, e.g., some landraces of common wheat (*T. aestivum*) have high protein content (Rodriguez-Quijano et al., 1990; Keller et al., 1991; Beihai, 1992; Yang and Liang, 1995). Improved drought adaptation has been resulted from the crosses between synthetic wheat and elite wheat cultivars (Trethowan et al., 2005). These varieties led to the development of five different varieties named Safed Lerma, PV 18, Sonalika, Kalyan Sona, and Chhoti Lerma. Following their development, these varieties were commercialized later. Therefore, it is said that the introduction of these varieties laid the foundation of Green Revolution in India. The dwarf wheat introduced in this period had extensive valuable characteristics like highly responsive to inputs, high level of disease resistance, and nonlodging nature. By the grace

of these qualities, a high yield and improved seed quality were observed for these varieties of dwarf wheat. Later in 1970–75, new varieties were developed by crossing these dwarf lines with the native wheat varieties (William et al., 2011).

5.1 Systematic development of wheat

A systematic procedure is something which requires a series of steps starting from the scratch to reach the desired goal. The systematic development and improvement of wheat started in 1905. Since then it is achieving many developmental successes. Howard, an imperial botanist at Pusa Bihar, pioneered this systematic development of wheat. Real breakthroughs have been resulted due to these systematic wheat developments particularly in the productivity of wheat. Spectacular advances in wheat research have made the wheat system more sustainable with high-yield efficiency and productivity. India has achieved magnificent wheat development from the Green Revolution era. It is clearly revealing the fact that 630%, 123%, and 226% improvement has been achieved in production, area, and quality, respectively, from 1965 to 2007 (Shiva, 2016). Varieties released in India during 1975–2003 had a higher yield. A significant gain in wheat productivity was observed in these varieties for 5–6 years. Wheat varieties, developed from the landraces like HD 2329, HUW 234, WH 147, Sanalika, Lok 1 and Kalyan Sona prevailed in the wheat-cultivated regions because of their flexibility to the native environment, maturity duration, wider disease resistance, plant height, grain quality, remarkably high yield potential, and other desirable agronomic traits (William et al., 2011).

Many hilly areas face low productivity of wheat due to several reasons, major of which is slower seed replacement rate. For this purpose, a technique of wheat cultivation is used known as System of Wheat Intensification (SWI), in which plant density is properly sowed allowing for sufficient aeration, sunlight, moisture, and nutrient availability. Thus, the proper root system is developed from the early stage of crop growth. SWI ensures high potentiality to provide a high yield per kilogram of agricultural inputs like seed, fertilizer, etc. per drop of water.

5.2 Yield enhancement by genetic manipulation

The genetic manipulations are the key to obtain better qualities with wider genetic variations. Genes encoding the high disease resistance, reduced plant height, and efficient viral resistance were introduced during Green Revolution in crops. The impact of this manipulation demonstrated tremendous genetic resources that can be used for the production optimization. Genetic manipulation can lead to the hybrids of wheat with better and enhanced characteristics which are expected to be required in future. For these genetic manipulations, what we need is the identification of our target genetic resource and of course, access to it (Hoisington et al., 1999).

A possible genetic resource can be exemplified by the *Tripsacum*, which is considered to be related to the wild maize. It represents an unaltered genetic resource in the face of biotic and abiotic stress. We can use this rich resource of desired genes through apomixis. This would be the best way of apomixis and other hybrid technologies leading to quality trait improvements. The second thing which we need to address for the genetic manipulations is the ownership of genetic resources. We have to break the monopoly of the giant groups/companies over the genetic resources and ensure the availability of these resources to the public. The key to open the new horizons in the field of wheat breeding is the use of genetic engineering and other molecular biology applications. These techniques, particularly molecular biology and genetic engineering, ensure the efficient use of available genetic resources. The effective and frequent use of our technological tools is very important to meet the world's challenges related to food security (Hoisington et al., 1999).

Next, the effective screening of landraces is required to understand the agronomic, physiological, and breeder's concept underlying target traits. The collection of nonadapted germplasm of wheat landraces is also very important for the genetic manipulations. By this method, we will be able to screen the extent of variation available. It will help us in the selection of parents with the desired traits that will enable us to develop the segregating populations. These segregating populations will be helpful in isolating the genes controlling traits of interest and could be characterized as the quantitative trait loci (QTL). These potentially useful alleles will then be introduced into target genome, and their value for breeding can be evaluated against the best existing varieties. The outcome of this work will be sustainable genomics leading to predictive wheat breeding (Collins et al., 2008). Various tools and resources have been developed in recent years. These tools have been instrumental in identifying and characterizing various complex traits in different studies including identification and characterization of QTL (Snape et al., 2007); these are stretches of a genome that are linked to genes that affect the trait. Commercial genetically modified (GM) traits have been

developed for insect resistance, herbicide tolerance, shelf-life, virus resistance and oil composition in a variety of crop species which are quite successful (Halford, 2012).

5.3 Allelic variations among landraces

Maintenance of diversity in breeding programs is essential; however, it is also important for the diversity to address allelic variation for major concerned traits. Allele mining identifies allelic variation of related traits within genetic resources. Genetic resources are subjected to allelic variation screening for the identification of known functional genes and DNA sequence (Bhullar et al., 2010), and this is achieved through various molecular techniques (Kumar et al., 2010). A significant source of functional allelic diversity and differential allelic frequency is by segregation of valuable alleles from landraces or genetic resources. New functional allelic diversity for powdery mildew resistance has been identified through deliberate selection of bread wheat landraces (Bhullar et al., 2009). Likewise, new allelic variation for quality and texture of grain has been found in old Mexican and Mediterranean landraces (Ayala et al., 2013). Keeping in view the colossal capacity of finding new alleles for genes of known function, work is in progress for screening wheat germplasm collections in international research institutes (Kumar et al., 2010). Identity of new markers linked to the trait of interest through genome-wide association studies (GWAS) will immensely provide advantage to the breeders, chiefly after confirmation of key markers linked with complex traits. Such as, the wheat association mapping initiative (WAMI), genotyped with the 9K and 90K single-nucleotide polymorphism (SNP) chip, is now providing a markers set linked with complex traits (Lopes et al., 2015b; Sukumaran et al., 2015).

5.3.1 Abiotic stress resistance through allelic variations

One of the important stresses that most of the crops face is the abiotic stress. The reasons behind increasing abiotic stresses are climate change which includes drought, and high temperature, and carbon dioxide concentration (Curtis and Halford, 2014). Plant breeders improve crop yield and resilience against abiotic stresses such as excessive or inadequate supply of water, extreme temperatures, frost, high wind, salt, and other osmotic stresses (Halford et al., 2015).

To cope with abiotic stresses, scientists are more headed toward the allelic variation that would lead to the resistance in the desired crop. The importance of allelic variation can be observed by the fact that the genome of the elite and modern bread wheat varieties is a mixture of chromosomal segments that arose 10,000 years back from landraces. This marks the separation between the domestication of hexaploid wheat and the birth of modern plant breeding. Use of alleles that facilitate the adaptation to new environmental challenges like new pests and disease stress, drought and thermal stress, and reduced nitrogen inputs, is an efficient piece of strategy for wheat breeders to ensure valuable genetic gains (Gupta et al., 2008).

5.4 Improvement through human selection

Over the millions of years, the human is selecting the wheat plants having desired yield and quality. Farmers used to select the best seed from the annual harvest to sow the next year due to which wheat has changed to a good extent over the subsequent millennia. This human selection has led to the significant improvement in wheat breeding. About 90% of total wheat production consists of bread wheat. Durum wheat is also important in some regions. In the ancient times, wheat with the large-sized grains was developed by the human selection (Shewry, 2009). Selection process in durum wheat has produced varieties producing higher yields with low micronutrient content. These varieties can be helpful in biofortifying modern varieties (Sciacca et al., 2018). Moreover, development of semidwarf wheat by Norman Borlaug, photoperiod insensitivity, accelerated crop development, and enhanced disease resistance were among the significant improvements that were made in the 20th century (Araus et al., 2008).

5.4.1 Evolution of dwarf wheat

The spring wheat (*T. aestivum*), *T. durum* (bread wheat), and *T. dicoccum* (emmer) have been grown in the subcontinent, particularly India, on a commercial basis from the prehistoric times. *Triticum sphaerococcum* is considered as an extinct variety in India. Wheat production rose steeply in 1964 with the onset of the Green Revolution, when the cultivation of local wheat landraces was gradually abandoned and landraces were replaced by the newly introduced, more improved, highly productive and genetically uniform semidwarf wheat cultivars. The achievement of these cultivars is likely the most imperative event in the past of modern agricultural research and allowed the

wheat importers viz. Pakistan and India to become wheat exporters. The cultivars Mayo 64, Sonora 63, Lerma Rojo 64, and Sonora 64 led the foundation of dwarf wheat in India. Not only this, around 613 segregating lines based on CIMMYT, Mexico, were also grown in this era (William et al., 2011). Yield breakthrough has been seen not only in India, but also in Turkey, Afghanistan, Pakistan, and many other countries due to the development of semidwarf and dwarf varieties (Pitic 62, Penjamo 62, Sanora 64, Lerma Rojo 64, Siete Cerros, etc.) at CIMMYT (Khan et al., 2013).

Due to the extensive adoption of improved semidwarf varieties during the second half of the 20th century, genetic variation in wheat was extensively narrowed down. The low HI plant height and general lateness of the wheat landraces have led to their restricted cultivation to some marginal areas or organic farming systems, thus discouraging breeding programs from exploiting and evaluating them as parents in hybridization. The HI was found lower in Mediterranean landraces as compared to modern semidwarf cultivars. Among the subpopulations of landraces, greater HI was identified within the eastern Mediterranean landraces. A study using 52 durum landraces collection that were classified based on dispersal (northern and southern) of durum wheat across the Mediterranean basin showed that HI was high within the southern landraces that came from dry and warm areas (Moragues et al., 2006). Their results suggested high capacity of southern landraces to assign biomass into grains and an improved capability to set grains under stress. Similarly, higher HI was found in eastern Mediterranean landraces in this study that might indicated their high water use efficiency during later plant stages as compared to cooler area landraces which is depicting adaptation to drought conditions.

Yet, breeders are now convinced that local wheat landraces are a source of putatively lost diversity and may possibly confer new genes or alleles for improving commercially important traits (Lopes et al., 2015a). Introgression of such genes or alleles into modern wheat cultivars would be extensively useful, particularly in breeding programs for suboptimal environmental conditions. Although Mediterranean wheat landraces have been particularly identified as valuable sources because of their enormous genetic variation and the occurrence of accessions possessing high abiotic stress tolerance, biotic stress resistance, and enhanced grain quality (Nazco et al., 2012; Lopes et al., 2015a), the huge genetic distance between modern wheat cultivars and all landrace subpopulations depicts the reduced utilization of durum landraces in durum breeding programs.

5.5 Improvement through natural hybridization

Modern wheat varieties emerged by natural hybridization of three grassy weed species approximately 1000 years ago. The hybridization of wheat thousands of years ago and the natural mutation caused by the wheat domestication around the world is the reason behind the variation of wheat breed in these past 70 years. As a matter of fact, all the modern crops from grasses and garden flowers to wheat and rice are distinct from the varieties that existed at the time when the earth was formed. Two basic breeding methods have been used by the plant breeders:

5.5.1 Conventional crossing

During the conventional crossing, genes from the complementary wheat parents are combined to generate new genetic combinations (not new genes) in the offspring. This has led to the development of valuable characteristics like higher yield and disease and insect resistance.

5.5.2 Incorporation of genes

This method involves the incorporation of the genes residing in the ancestral or related species of modern wheat into the target wheat variety. It is important to note that this procedure is not genetic engineering, but the crossing is carried out to introduce the genes. Furthermore, the method utilizes the variation already found in wheat's lineage.

5.6 Use of tilling for quality improvement

TILLING (targeting induced local lesions in genomes) is the method to mutate the genes by using chemical mutagens. This is a nontransgenic and reverse genetic method, which is used to enhance the quality trait potential in a polyploid crop plant (Colbert et al., 2001).

The importance and use of TILLING can be exemplified by the physiochemical analysis of waxy starches. These waxy starches have important and novel physiochemical properties. It is observed that this waxy starch trait is encoded by three genes. Wheat, in which only two genes are functional, produces starch with intermediate levels of amylopectin. These three genes are made up of 246 alleles. These alleles have been identified by TILLING. Wild type to the null activity of the three genes is encoded by these alleles. A wheat variety with the

two homozygous mutated genes was created through TILLING. The phenotype lack of these waxy starches was achieved by deleting the third gene, so TILLING can be used as a tool for creating as well as identifying genetic variations (Slade et al., 2005). The existing methods for TILLING are quite expensive and complex, yet it is very efficient.

6. Wheat modification and its importance

In the 1960s, developmental efforts, experimental lines, and the novel or modified varieties were shared with the researchers around the world. Moreover, wheat production in Mexico, India, and Pakistan was significantly enhanced. This resulted into the improved food reservoirs for the millions of people who otherwise would have starved to death (Jones, 2014). All farmers, including wheat farmers, are subjected to rely on plant breeders for the development of different varieties of seeds with the required characteristics like pest and disease resistance and ability to face constantly varying climatic conditions (Poehlman and Sleper, 1995).

Scientists all over the world are attempting to understand the full wheat genome, just like we have mapped the human genome. The sequence of the wheat genome is very much needed to manipulate the wheat varieties for the better future (Kingsbury, 2009). Such kinds of research should not be restricted to wheat but should be extended to the rest of the food crops to achieve 66% agriculture production in 2040 to match the population growth because the nutritional needs can only be fulfilled by the development of healthy plants (Bickel et al., 2000).

6.1 Wheat modification in Pakistan

It is estimated that Pakistan, India, China, Canada, Australia, European Union, Turkey, Ukraine, and Russia produce about 80% of total wheat. Pakistan being the eighth major producer of wheat, participates in the wheat production by 3.17% with a cultivated area of 3.72%. Wheat occupies the central position in agriculture and economic progress of Pakistan because of its central position in the list of food crops (Shuaib et al., 2010). Ancient breeding practices focused mainly on the per hectare yield enhancement rather than on quality. So, wheat varieties developed at that time were lacking in the quality. Now the wheat breeders in Pakistan are mostly concerned about the wheat yield with the superior quality. That is why they are attempting to develop new varieties with mentioned characteristics. However, unfortunately Pakistan has been facing the food deficit for some years. During recent years, harsh weather conditions in Pakistan have adversely affected agriculture and particularly food supply. This has been a hint toward growing threats of food shortage in coming times (Economist Intelligence Unit, 2012).

It is worth noting that wheat in Pakistan had the wide agro-climate range and expected to have efficiently high yield because of its growing practices in different areas of varying climate conditions. Now the main focus should be on the investigations for their biochemical composition because these crops fulfill the nutritious demands and also ensure food security in Pakistan (Chowdhry et al., 2000). Adoption of technology and farm management practices is another important factor that has increased wheat supply in Pakistan (Tariq et al., 2014).

7. Molecular biology in genetic diversity evaluation and modern wheat improvement

The aim of genetic improvisation of crop plants is to select most suitable germplasm carrying desirable traits such as high yield, better nutritional quality, suitable color or aroma, etc. Such traits of interest are not evaluated from the plants directly; however, these are assessed from various sources linked closely with the trait. Such tags employed to choose the most superior germplasm are termed as markers. Due to increase in the availability of genetic sequences and high technological advancement in sequencing strategies, we can develop genetic markers for breeding. Genotyping by sequencing (GBS) or SNP markers is the whole genome approach which have been instrumental in identifying marker-trait associations and novel alleles for desirable traits for GWAS (Lopes et al., 2015a; Sukumaran et al., 2015). SNP also identified small population bottlenecks and selection occurring on distinct or various functionally equivalent alleles in different areas of geographic range of wheat (Cavanagh et al., 2013).

Genetic markers in plant breeding and genetics can be classified into two categories, viz. DNA markers and classical markers (Xu, 2010). Polymerase chain reaction with other systems was developed by DNA markers, based on varying techniques and polymorphism detecting methods. Other techniques developed with PCR

were southern blotting, nuclear acid hybridization, and DNA sequencing, such as amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), simple sequence repeats (SSR), SNP, etc. (Collard et al., 2005). Several studies have the most efficient tool to evaluate genetic diversity of wheat germplasm is SSR markers. The assessment of subpopulation structure due to their wide genomic distribution, codominancy, high polymorphism, maximum reproducibility, and simplicity of analysis (Royo et al., 2010; Hao et al., 2011; Oliveira et al., 2012; Ruiz et al., 2012; Laidò et al., 2013; Sahri et al., 2014; Khan et al., 2015). Classical markers include cytological markers, morphological markers, and biochemical markers (Jiang, 2013).

Genetic diversity can be easily identified by using any of the above data types either pedigree, morphological, biochemical, or DNA molecular marker (Singh et al., 2013). Sequencing is also now becoming inexpensive and soon it will be possible to utilize it regularly in breeding programs (Poland and Rife, 2012) such as for genetic diversity evaluation (El-Basyoni et al., 2013). Furthermore, it is expected that a combination of de novo sequencing and resequencing would help to efficiently explore important genetic variation (Brozynska et al., 2015). The utilization of landraces in the developmental process of populations may significantly foster the genetic diversity and will alter the frequency of genes or alleles, thus creating the possibility to detect novel genes or alleles.

7.1 Marker-assisted breeding

Molecular breeding approaches target on specific regions on the DNA and therefore are called as marker-assisted breeding (MAB). This is often taken from QTL mapping of the quantitative trait (Witcombe et al., 2008). MAB involves numerous modern plant breeding strategies, comprising marker-assisted selection (MAS), marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS), and genome-wide selection (GWS) or genomic selection (GS) (Ribaut et al., 2010). Marker-assisted selection (MAS) is a breeding approach that involves integration of detection and selection of DNA marker with a conventional breeding program. It is widely used under the banner of physio-morphological characters regarding yield under drought condition. DNA markers used in this area are SSRs (Xgwm136 and NW3106) linked to genes that control coleoptile length, respectively (Gulnaz et al., 2011). Other markers linked to dwarfism (Rht) genes are often associated with HI (Pearce et al., 2011). Besides these, transcriptional factors like dehydration-responsive element binding protein (DREB) possess a huge potential for PCR-based selection and are very much utilized in MAS (Wei et al., 2009). The DArT molecular marker was helpful in evaluating genetic diversity. In durum landraces of Iran, it has proved diversity among populations (Fayaz et al., 2019). Though, the isolation of this factor is very tedious and hard mainly because it belongs to such a gene family that contains sequences showing high similarity.

7.2 Transgenic method

Another method is the transgenic method, which allows the transfer of genetic loci to the wheat and only desired gene will be introduced. This can be incorporated into the elite wheat varieties to get high yield. In one case, the over expression of DREB from cotton and *Arabidopsis thaliana* was done in wheat that produced transgenic lines which showed a high level of drought tolerance (Guo et al., 2009). In another study, a barley protein HVA1 was also over expressed in wheat, and same results were observed. Moreover, transgenic wheat obtained from *Arabidopsis* DREB and HVA1 also showed good drought tolerance (Yang et al., 2010). This was performed using novel techniques and also by agrobacterium-mediated genetic transformation (Checker et al., 2012).

7.3 Proteomics

The recent studies on wheat tolerance are focused towards proteome analysis. This intends to target special proteins and understand their function under stress. In an experiment, two wild varieties of wheat (TR39477 and TTD22) were tested along with the modern wheat (T. turgidum). The analysis was done on the 2-DE gel and nano-scale liquid chromatographic ionization tandem mass spectrometry and 75 differently expressed proteins were detected. The comparison of these can provide a more vivid output that will allow us to examine the roles of various proteins in drought resistance (Budak et al., 2013a).

TABLE 21.1 Genetic diversity of global wheat landraces studied in recent years.

Sl. no.	Recent research developments	Country/region	Reference
1	Salinity-tolerant varieties	Afghanistan	Shamaya et al. (2017)
2	Durum wheat variety tolerant to local environment	Iran	Fayaz et al. (2019)
3	Distinct genotypic and phenotypic variation was documented	Israel/Palestine	Frankin et al. (2019)
4	Durum wheat variety adapting to semiarid environment	Middle East	Abu-Zaitoun et al. (2018)
5	High-density molecular characterization and association mapping in Ethiopian durum wheat landraces	Ethiopia	Mengistu et al. (2016)

8. Conservation and utilization of wheat landraces

Wheat landraces are an important genetic resource to maintain food security in current and changing climates. Knowledge of the need for the conservation of biodiversity is now globally recognized; however, present conservation activities are centered on wild plant species. Immense genetic variation in domesticated species is present in traditional wheat varieties, i.e., landraces, which are maintained by traditional farming communities. To broaden domestic wheat genetic background wheat landraces are required. However, these landraces are strictly in danger by genetic extinction mainly because these are exchanged by modern genetically uniform varieties (Villa et al., 2005). Wheat landrace conservation is linked to understanding relation among diverse landraces and environment (Zhang et al., 2006). In recent years, various studies were conducted to understand wheat landraces of different localities (Table 21.1).

During the period 1970–90, much of the landrace genetic resource has been gathered and preserved in national as well as international gene library (Frison et al., 2011). Moreover, some of the wheat landrace diversity has been preserved and used by the farmers resulting in continuous cultivation and evolution (Brush and Meng, 1998). Both the preservation methods have their own merits and demerits. The total comfort of wheat landrace entirely depends on preserving and cultivating them in the field. Farmers cultivate the landraces and preserve them only if landraces overcome their communal, commercial, and ethnical needs. Moreover, farmers consider all the good traits as being precious for dissipation and preserve the landrace which has the capability to overcome utilization needs (Brush and Meng, 1998). Evolution of traits by selecting and crossing traits is nature's way of preserving genes. These can help in preservation of landraces (Burbank, 1921; Hawkes, 1958; Harlan, 1975, 1976; Peloquin, 1983). Accelerated spike growth causes reduction in number of florets and low grains per unit area under high preanthesis temperatures (Fischer, 2011; González et al., 2011).

Wheat landraces are not only important economically, but also their preservation and cultivation are associated to the people's racial, societal, and official values. However, in the case of the poor and single farmers, the reasons for growing and preserving landraces are his economic stability and survival (Le Boulc'h et al., 1994). Mirza Gökgöl, a scientist in Turkey has collected wheat landraces from all over the country in the early 20th century and characterized them for diversity. He identified around 18,000 types, out of which 256 novel varieties were recognized. In his opinion, Turkey contains all wheat varieties growing in the world, along with the fact that Turkish wheat landraces have infinite value among global wheat breeders (Karagöz, 2014). He is trying to breed yields under harsh conditions with agricultural systems responsible for migrating varieties. In two countries, namely Turkey and Iran, wheat landraces are still grown, though on a smaller area, and it is estimated that this diversity source may be lost speedily if not properly preserved and protected. The conservation of wild wheat varieties along with landraces which were replaced by new valued, profitable varieties lacked adaptive capabilities. These old varieties and other wheat species need conservation as an important source of genetic diversity.

9. Conclusion

Wheat landraces are a valued, profitable, and crucial source of genetic diversity in the field of agriculture which has been partially used in breeding programs around the world. Most of their genetic diversity is still conserved and not completely exploited. Genetic erosion occurred due to replacement of wheat landraces with high-yielding varieties. Many developing countries were affected by this, while even in developed countries, landraces were scarcely cultivated due to their low yields and vulnerability to diseases. Their low yield trait could be the result of their genetic heterogeneity as well as the intercropping competition that can possibly be minimized by converting a landrace into desired homozygous genotypes. However, wheat landraces along with old cultivars have better quality attribute than high-yielding cultivars under natural and low-input farming systems. Also, compared to modern cultivars, landraces are well adapted under stress and varying stresses and climates as a result of diverse genetic structure, buffering capacity, and a collective variation of morphophysiological characters conferring adaptability to stress environments. New approaches are rising to develop modern wheat landraces based on manifold crosses and selection from durum, einkorn, emmer, and bread wheat populations in combination with site-specific selection on location and to attain highly resilient wheat genotypes for domestic production. To ultimately improve wheat production, it is essential to exploit genetic variation in wheat landraces in especially changing future climate change.

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CHAPTER

22

Next-generation sequencing in bread wheat

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OUTLINE

1. Introduction

Wheat (*Triticum aestivum* L.; family Poaceae) is one of the most significant cereal crops in the world. With a food of 20% of the world population, wheat production and yield has increased twice over the past 40 years that may be attributed to selection breeding (Berkman et al., 2012). However, the future demand for wheat is increasing with the exponential growth in population. According to an estimate, the world population will be 9.6 billion by 2050, so wheat yield needs to increase by 1.6% each year. It is, therefore, necessary to explore full potential of the wheat genome. However, the application of conventional sequencing methodologies to study wheat genomics is limited due to its complex allohexaploid genome (approximately 17 gigabasepairs (Gb) size). The complex genome may be a hybridized product of the three diploid (AA, BB, and DD) genomes with each diploid subgenome of approximately 5 Gb size. The diploid A subgenome derived from *Triticum urartu* and the B diploid subgenome as unknown relative of *Aegilops speltoides* hybridized making a tetraploid, i.e., *Triticum turgidum*. It is further hybridized with the diploid D subgenome derived from *Aegilops tauschii* resulting a hexaploid (*T. aestivum*) genome (Chantret et al., 2005; Marcussen et al., 2014). These diploid genomes share 90% identity with each other (Kawaura et al., 2009).

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00022-4

TABLE 22.1 Different kinds of next-generation sequencing methods ad their characteristics.

NGS platforms	Library preparation	Template preparation	Sequencing technology and detection	Advantages	Concerns
Illumina	The library contains DNA or RNA templates	Through bridge amplification	Sequencing by synthesis and detection by fluorescence	Enormous data	Short reads, long run time
Roche	The library contains DNA or RNA templates	By emulsion PCR	Sequencing by synthesis and detection by fluorescence	Longer read, lengths small data files	Less data and homopolymer formation
Ion torrent	The library contains DNA or RNA templates	By emulsion PCR	Sequencing by synthesis and Δ pH detection	Low cost and very fast	Less data and small reads
SOLiD	The library contains DNA or RNA templates	By emulsion PCR	Sequencing by synthesis and detection by fluorescence	High-quality data	Short reads and long run time

The information was derived from Del Chiericoet al. (2015) and Nguyen et al. (2018).

Wheat genome analysis is more challenging—firstly due to its large size that is five times larger than the human genome, and secondly due to the ploidy level, the hexaploid nature. The presence of gigantic zones of highly repetitive DNA sequences and retroelements (Winfield et al., 2012; Brenchley et al., 2012) further convoluted wheat genome analysis. The limitations in sequencing of long repetitive regions also complicated wheat genome sequencing (Berkman et al., 2012). During the past decade, several reference genomes for diploid and hexaploid wheat (based on the *T. aestivum* cultivar Chinese Spring) were generated to understand the complex genome (Brenchley et al., 2012; Clavijo et al., 2017; Zimin et al., 2017). The International Wheat Genome Sequencing Consortium (IWGSC) generated a gold standard quality reference genome of hexaploid wheat, i.e., Refseq V1. The reference sequence represents 94% of the wheat genome. With 21 sequenced chromosomes, it provided information regarding locus and order of total 107,891 genes. It further offered identification of more than 4.7 million molecular markers (IWGSC, 2018).

Next-generation sequencing (NGS) is preferred for its potential to sequence extensive genomes in a less time with low cost compared with traditional Sanger sequencing technology. Recently, 454 and Roche platforms were used to sequence approximately 20,000,000 bp in just 4 h. This chapter explores the importance of NGS in wheat functional genomics and research. Various NGS platforms have been compared in Table 22.1.

2. Next-generation sequencing

Hundreds of millions of parallel sequencing reads have made NGS a method of choice (Hert et al., 2008). Solexa (Illumina), Roche 454 (Pyrosequencing), Ion Torrent, and sequencing by ligation (SOLiD) are the few well-known NGS technologies. Furthermore, cyclic-array sequencing and emulsion PCR have played a vital role in whole-genome sequencing (Mardis, 2008).

2.1 Pyrosequencing (sequencing by synthesis)

Introduced in 2005, pyrosequencing is considered to be one of the first second-generation sequencing technologies. It was commercially used with Roche's 454 sequencing instrument (Ansorge, 2009). The procedure involves production of light produced with the release of pyrophosphates (PPi or β- and γ-phosphates) while adding a single dNTP in the chain elongation step. The light is then harvested/detected by a sensor (Ronaghi et al., 1998). As for all NGS platforms, pyrosequencing cleaves DNA into small fragments and then ligated to generic adaptors. Each adaptor is attached with a microbead. Each bead is assigned to a single well. Primers specific to the adaptors are used to amplify each DNA fragment for several cycles using emulsion PCR. After getting several copies of a single fragment, sequencing is preceded, while PPi is detected each with addition of a single dNTP. Four dNTPs are used one by one followed by washing steps. The light signal is proportional to the quantity of ATP produced. In the presence of ATP, luciferase changes luciferin to oxyluciferin to emit light. The road map of pyrosequencing reaction has been elaborated in Fig. 22.1.

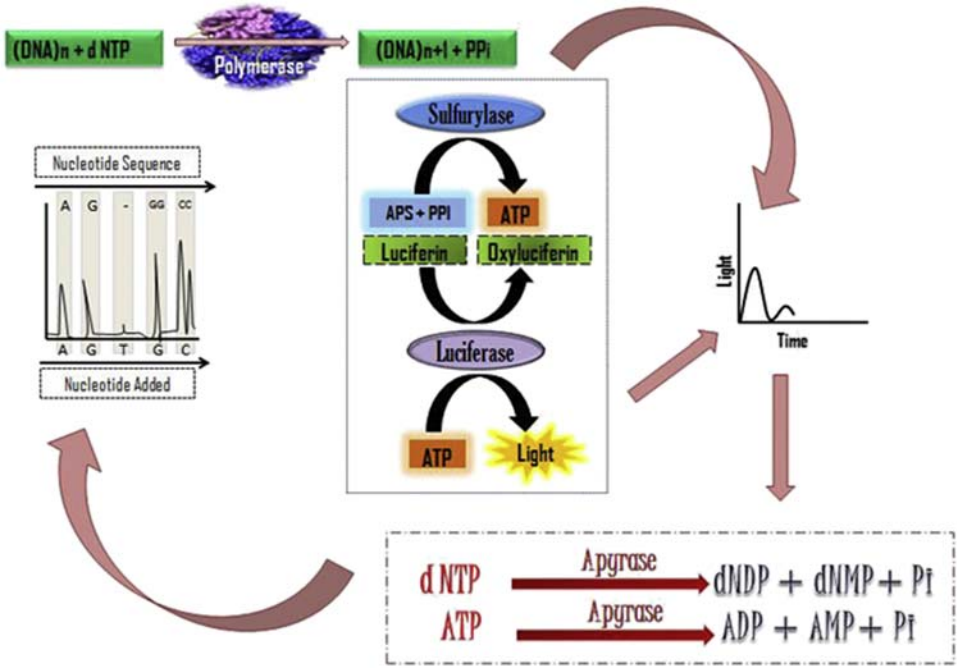

FIGURE 22.1 **An overview of pyrosequencing reaction.** In the pyrosequencing reaction, a DNA polymerase integrates dNTP complementary to the template strand. Pyrophosphate (PPi) is released in the reaction. Sulfurylase converts adenosine 5′ phosphosulfate (APS) and PPi to ATP. Luciferase converts ATP to light, which is detected by a charge-coupled device, camera. The results can be visualized in a pyrogram, and the fluorescence is proportional to the amount of dNTP integrated.

2.2 Illumina (cyclic reversible termination)

David Klenerman and Shankar Balasubramanian, two British biochemists, developed Solexa for DNA sequence analysis. The procedure was commercialized in 2006. Illumina is sensitive, time efficient, and cost-effective as compared with other NGS techniques and the Sanger method. Illumina has two steps:

Step 1 starts with genomic DNA fragmentation. DNA adapters are then attached and loaded onto a glass slide (the flow cell). In each flow cell, one end of the adapter-ligated DNA binds with a complementary oligo (termed as oligo 1) covalently linked to the surface. The other end of the adapter-ligated DNA binds with oligo 2, which is covalently attached adjacent to oligo 1 on the surface. Attachment of both ends of the fragment will form a bridge-like structure. Next, the amplification of the DNA starts with addition of dNTPs and the polymerase. The following PCR cycle initiates with the denaturation of the newly formed complementary strand and template. In each channel of the flow cell, heavy clusters of amplified DNA duplexes are formed as a result of repetitive cycles of bridge amplification.

Step 2 starts with denaturation, annealing with sequencing primers and addition of dNTPs tagged with specific reversible fluorophores. The fluorophores are detected by the addition of the next base and tris(2-carboxyethyl) phosphine that removes the fluorophore from the previously inserted nucleotide base (Pettersson et al., 2009; Bentley et al., 2008).

2.3 Ion torrent

In 2010, Life Technologies introduced high-throughput intermediate technique for DNA sequencing. The technique was based on the formation of a covalent bond in synthesizing DNA strand triggered by a polymerase. As a result, a proton and pyrophosphate are released. Lowering of pH occurs in the surrounding environment due to the release of proton. The change in pH is then used to determine the growing strand (Pareek et al., 2011; Rothberg et al., 2011). Single-stranded template-amplified DNA is sequenced with a sequencer having microwells on a semiconductor chip. Deoxynucleotide triphosphates (dNTPs) and DNA polymerase are added into wells. Biochemical reaction takes place by the release of hydrogen ions due to the incorporation of a single dNTP in the growing chain.

Change in pH is detected by ion-sensitive field effect transistor present underneath the wells. Free dNTPs are washed out before every next cycle.

3. Next-generation sequencing–based genotyping of wheat

NGS was used to generate a draft DNA sequence of the wheat complex genome (IWGSC, 2018). NGS helps in exploring epigenetic changes, transposons copy number variations, population genetics (genome-wide association studies and exome capture), and NGS-dependent gene cloning and functional genomics.

To deal with the complications in enormous wheat genome, the 21 chromosomes of common wheat cultivar Chinese Spring were divided by flow cytometric sorting. Bacterial artificial chromosome (BAC) libraries were constructed from each chromosome arm into physical maps. Firstly, chromosome 3B was sorted effectively owing to its large size. In 2008, the BAC clones of chromosome 3B enabled the construction of physical map (Choulet et al., 2010). Presently, all chromosomes or chromosome arms of common wheat (Chinese Spring) have been sorted, and their physical maps have been generated (http://www.wheatgenome.org/Projects/IWGSC-Bread-Wheat-Projects). Furthermore, the sequences of several chromosomes (1AS, 1BS, 3DS, 5DS, 7DS, 1AL, 1BL, 4A, 5A, 6A, 6B, and 7B) were made available (Hernandez et al., 2012; Barabaschi et al., 2015; Holušová et al., 2017).

In 2012, whole-genome shotgun sequencing along with pyrosequencing technology successfully sequenced Chinese Spring and generated a fivefold coverage genome sequence of the hexaploid wheat. As a result, 94,000–96,000 genes were predicted (Brenchley et al., 2012). The approach of draft genome sequence distinguished the highly conserved regions of gene copies in each chromosome. Another technique of NGS, Illumina technology, was used to sequence 21 chromosomes of common wheat and generated 10.2 Gb genome (IWGSC, 2018). In 2017, mate-pair libraries were constructed to generate a new assemblage that covered 78% of the whole genome (Clavijo et al., 2017). In addition to this, another genome-wide assembly was reported in 2017 that was generated by two different technologies—the short Illumina reads (NGS, the second-generation sequencing) and the long Pacific Bioscience reads (third-generation sequencing) (Zimin et al., 2017).

More than 90% of hexaploid genome was generated by combining two sets of sequences assembled using the MaSuRCA and FALCON assemblers. Recently, IWGSC generated a gold standard quality reference genome of hexaploid wheat, i.e., Refseq V1.0. This reference sequence represents 94% of the wheat genome comprising 21 chromosomes and also provides the information regarding locus and order of total 107,891 genes (IWGSC, 2018).

3.1 Map-based cloning

Map-based cloning is a typical approach in forward genetics, where the gene locus or gene-of-interest demands map-based gene cloning (Clavijo et al., 2017). Map-based cloning in plants includes outbreeding the mutant organism to generate a mapping population (Mooney and McGraw, 2007). Markers linked to targeted genes can be detected and used to monitor yeast artificial chromosome (YAC) or BAC libraries. The targeted gene clone can then easily be isolated. As a result, genetic and physical maps of different plant species can be made available. In addition to these maps, reference genome sequences are also necessary that aid the map-based cloning in identification of shorter regions of the genomes. Although genetic mapping technique helps to link a gene mutation to its phenotype, it is time-consuming. So the advent of NGS resolves these hurdles and opens the new horizon in forward genetics (Gardiner et al., 2018). A mutation causing a phenotype can efficiently be identified by sequencing of the mutant line. To exemplify, a novel 120 Mb *Arabidopsis* clock mutant *early bird 1* (ebi-1) and the wild-type *Wassilewskija 2* (Ws-2) genomes were sequenced (Ashelford et al., 2011).

3.2 Genome-wide association studies

Exploring genetic variations in wheat is a difficult task. Genome-wide association study (GWAS) is the most effective way to look for the genetic variations and their influence on the phenotype. Previously, single nucleotide polymorphism (SNP) microarrays were used to acquire genome-wide insights in different wheat genomes. SNP microarray is cost-effective, compared with NGS, enabling fast screening of the associated genes. It helps understand the marker traits linked in maps construction and the ancestral relationships among populations. However, NGS has replaced SNP microarrays due to its sensitivity in detection and the ability to identify the genetic diversity

(Wang et al., 2014). Furthermore, NGS-based genotyping can unravel the novel genetic diversity and can help analyze the in-depth population genetics.

GWAS is an effective approach to discover natural variations within the genomes. GWAS enables detection of multiple historical recombination events and genetic markers associated with phenotypic measurement in bread wheat. It connects a phenotype with a genotype and detects quantitative trait loci (QTL) for important traits associated with yield, disease resistance, grain quality, and heat tolerance (Mondal et al., 2016; Tadesse et al., 2015; Arruda et al., 2016; Liu et al., 2017). Genetically diverse panel of lines are utilized by GWAS in wheat that display adequate variation in the traits being measured, generally over multiple growing seasons and different environments. The members of these panels were sequenced, and the detected SNPs were linked to phenotypes with the help of mixed linear model or generalized linear model approach (Bradbury et al., 2007). Different studies have explored GWAS to identify QTLs for different traits in wheat. Studies with GWAS explored that *TaGW8* gene is responsible for kernel size in hexaploid wheat (Yan et al., 2019). GWAS also revealed QTLs for heat tolerance (Maulana et al., 2018) and spikes-related traits (Liu et al., 2018). QTLs for disease resistance have also been discovered like QTLs against different *Puccinia* (a pathogenic fungus) species including *Puccinia striiformis, Puccinia triticina, and Puccinia graminis* (Maccaferri et al., 2015; Gao et al., 2016; Prins et al., 2016). In addition to these, it also has identified QTLs for resistance to powdery mildew (Liu et al., 2017). In 2017, it was successfully used to examine preharvest sprouting traits in hexaploids (Zhou et al., 2017). It was also carried out to reveal the QTLs for yield-associated traits of common wheat within different populations in different regions such as Mexico (Sukumaran et al., 2015) Kazakhstan (Turuspekov et al., 2017), Pakistan (Ain et al., 2015), and Scandinavia (Bellucci et al., 2015). QTLs for high yield under normal and drought stress conditions were also linked (Mwadzingeni et al., 2017). Furthermore, GWAS was used to identify QTLs for the wheat stalk to serve as biofuel feedstock by enzymatic degradation (Bellucci et al., 2015).

Genotyping-by-sequencing (GBS) recently has appeared an effective approach for GWAS in hexaploid wheat. GBS multiplexed samples of the complex genome and explored the millions of SNP markers used to discover genetic diversity.

3.3 Next-generation sequencing–based exome capture assay

Exome capture along with the NGS technologies is an effective approach for the detailed analysis of the wheat genome. With the help of this technique, a complement of exons in a genome can be sequenced (Hodges et al., 2007). Exome capture can detect the variants related to significant traits (Mascher et al., 2013), specifically appraised from 2735 hexaploid Cadenza and tetraploid Kronos ethyl methane sulfonate–induced mutants (Krasileva et al., 2017). In Pakistan, exome capture assay was used to detect the induced mutations in the genome of hexaploid wheat variety "NN-Gandum-1" (spring wheat resistant to leaf and yellow rust). A total of 104,779 SNPs were detected in hexaploid wheat subgenomes (A, B, and D) (Hussain et al., 2018). In 2012, variation among eight UK wheat landraces by using NimbleGen captured 56.5 Mb wheat exome. More than 5 million SNPs were successfully identified (Winfield et al., 2012). Along with this, 107 Mb NimbleGen gene-based probe set was used to explore 62 accessions, which discovered 1.57 million SNPs and 161,719 small indels in wheat genome (Jordan et al., 2015).

4. Targeted-induced local lesions in genomes

Targeted-induced local lesions in genomes (TILLING) is a well-known technique in molecular biology using chemical mutagens to bring changes at single nucleotide level. After the treatment of seeds with chemical mutagens, plants are raised to several generations where stable inherited mutations are achieved. The process starts with DNA extraction from seeds of mutated plants and storing rest of the seeds from all samples to create a genetic library (Slade and Knauf, 2005).

This technique was first developed for fully sequenced diploid genomes. The complex genome of wheat was a challenge for TILLING as the mutations maybe obscured by the multiple copies of the same gene (Slade et al., 2005). A TILLING library for genetic modification of bread wheat and durum wheat was created to check its potential for modifying complex genome. The refined A-genome diploid species of wheat was designated first podium for TILLING and was established in the diploid wheat (*Triticum monococcum*). In bread wheat, *T. monococcum is occupied as a prototypical for the study of genes, characters, and alleles*.

Commercially important four genes were targeted, i.e., *WAXY* gene and three lignin biosynthesis pathway genes—COMT1, HCT2, and 4CL1, and chief gene is complicated in starch amalgamation (Dubcovsky and Dvorak, 2007; Wang et al., 2012). There are opinions in theory that information for gene task in the diploid wheat necessity has to be transportable into the hexaploid wheat. But multiple homologous replicas obscure the function mode in the polyploidization. However, TILLING population is obligatory to make in polyploidy wheat. Many TILLING populations for the tetraploid and hexaploid wheat have been testified (Dong et al., 2009; Lindqvist Appell, 2005). Waxy gene could not be mutated through traditional breeding due to lack of genetic variability at one of the waxy loci. Locus-specific PCR primers for waxy gene were developed, resulting in the identification of 250 alleles in the commercial wheat. Genetic modifications were analyzed through bioinformatics tools. No phenotypic results were observed during the screening of triple homozygous mutant with mutation in two waxy loci through conventional breeding (Slade and Knauf, 2005). Identification and generation of mutant level leads to the confirmation that TILLING has the ability to modify polyploidy genome. Possessions for durum and bread wheat by Uauy et al. (2009) were measured as a second exertion. It included 1368 tetraploid and 1536 hexaploid M2 plants (Hazard et al., 2012). The mutation thicknesses with a 1/38-kb mutation rate were extraordinary for hexaploid and for tetraploid, i.e., 1/51 kb. These TILLING plants were considered useful and informative in recognizing gene function (Uauy et al., 2009). Mutations in SBEIIa enzymes produced nontransgenic wheat plants, which are consulted as high-amylose innards and with novel starch functionality (Botticella et al., 2011). Mutations were established as another case in SBEIIa and were aimed at both bread wheat and durum varieties. They have comparable variations in resistant starch and amylose content (Hazard et al., 2012). Expectantly, every wheat gene, with speedy buildup of evidence from genomics, would have mutant identified rapidly for functional studies.

Yet, the conventional TILLING platforms are deliberated as much time overwhelming and tiresome (Till et al., 2006). It was added with online entree (http://www.wheat-tilling.com/) used to accessibly identify triumph alleles and for >90% of wheat genes. Moreover, to authenticate mutations, predesigned SNP-based primers were made accessible (Ramirez-Gonzalez et al., 2015). Such a supply was used to make enduring stocks of mutant lines that could ease characterization of wheat gene function. More recently, there were supplementary tools in genome-editing technologies to create DNA variation for the polyploid wheat (Shan et al., 2014). In this regard, all three homeologs' widespread editing of marker genes has been reported (Gil-Humanes et al., 2017).

Allelic diversities within species can be analyzed through TILLING efficiently (Till et al., 2006). With introduction of NGS, TILLING technologies have been improved on the principle of Illumina sequencing in which multiple pool templates are designed to detect single nucleotide mutations (Tsai et al., 2011). A well-organized genome excision system must have more optimization for wheat and must be equipped with more adaptable applications that comprise targeted gene supplement or allele replacement (Zhao et al., 2016; Gil-Humanes et al., 2017).

5. Dynamic wheat transcriptomes

During plant development and adaptation, genome substructure has been delivered for mapping actively transcribed regions to abiotic and biotic stresses. For empathy of expression patterns of all genes and their harvests, transcriptome profiling was performed for the wheat genome. Root transcriptomes in Chinese Spring are assembled by de novo assembly from RNA-seq reads with the help of 454-GS-FLX and HiSeq platforms (Challa and Li, 2018). For the in-depth analysis of gene function and regulation, the evidence would ease as well in their complex biological processes and communication system. The cDNA microarrays have been the prime component for a precise wheat transcriptomic analysis (Wan et al., 2008; Gao et al., 2012; Zhang et al., 2014). In 2004, high-density microarrays of the publicly available wheat EST (expressed sequence tag) resource containing 26,382 sequences were obtained based on 35 individual cDNA libraries, which represented highly specific developmental stages of various tissues of grains and seedlings. However, there was inadequate expression evidence from microarrays attributed to the immobile nature of probes that was mostly reliant on the genome annotation quality. Expression levels were found illustrative for cDNA arrays, and by hybridization indications, indirect dimension of gene expression levels was petite on precision for the fortitude of real transcript figures in specific cell lines or tissues (Wang et al., 2009). For complete transcriptional landscape, a systematic survey has been performed through NGS for RNA sequencing. Although it showed genome-wide gene activity in quantitative terms, it revealed alternative splicing (Feng et al., 2017; Filichkin et al., 2010; Li et al., 2014).

Study by Pfeifer et al. (2014) has fixed a good specimen for an operative RNA-seq analysis. It might offer more useful and consistent information regarding the transcript reads. In wheat grain, the cell type-specific summarizing of transcriptome for homologous genes has acknowledged distant coexpressing bands. Wheat endosperm

enlargement comprises expression outlines that might imitate the spatiotemporal arrangements of gene functions. No global genome supremacy was predictable, although there was cell type- and stage-dependent genome ascendancy. The subgenome interfaced, and its evidence and discrete cell types in wheat grains revealed to have its possessions on gene transcriptions.

6. Invisible variations in wheat genome

For crop enhancement, currently breeding databases focus on SNP-based markers. It is accompanied to the traits of curiosity, as they represent a stable source between wheat concurrences of phenotypic diversity. SNP analysis–based tactics, however, do not consider other stimulating forms of genomic alteration. Latest studies in crops have projected their influence on phenotypic difference. Three main sources have been acknowledged that were the variations that might occur across an assortment of wheat landraces: high compatible transposable element (TE) variability, alongside epigenetic and hereditary diversity. It was recommended that epigenetic variants could potentially be used in breeding programs. Their contributions alongside to trait dissimilarity assessed classical genetic disparity (Gardiner et al., 2018).

6.1 Epigenetic variations

Heritable changes in the genome, with no change in the nucleotide sequence, are brought about by DNA methylation or modification in the histone proteins. Epigenetics show phenotypic variations. Epigenetic variations successfully affect transcriptional activities and phenotypic characters, without changing the DNA sequence. Small RNAs are involved in histone modification and DNA methylation. These findings were observed while studying the variable changes during the process of DNA methylation and histone modification. These variations particularly affect the phenotypic characteristics of the crop plant. For plant communal, an epigenetic trait was recognized and was considered distinct as a sturdily heritable phenotype. This alteration was considered to be deprived of DNA sequence modification (Wolffe and Matzke, 1999). Agronomically, important characters with epigenetic states exist such as difference in flowering plants (Feng et al., 2017). In maize, there was disease confrontation (Jordan et al., 2015), and in oil palm, altered fruit development has occurred (Ong-Abdullah et al., 2015). Epigenetic controls included histone alteration, DNA methylation, and noncoding RNA gene silencing. In *Arabidopsis thaliana*, it was revealed that constitutive gene expression patterns were related to increase gene body of methylation and that if promoters were methylated, then there was expression of genes at diminished/lower levels (Gardiner et al., 2018).

Genome-wide DNA methylation in wheat representative differential methylation was considered in subgenomes A, B, and D (Gardiner et al., 2015). More recently, Gardiner categorized genome-wide epigenetic discrepancy and designated the assemblage of Watkins landrace diversity. Landraces reformed wheat diversities locally. It was not a topic to discriminate breeding, and consequently, a pool of multiplicity represented imitating their wide variation for different growing surroundings. They found a topographical module that may specify a response to methylation patterns by indigenous environmental situation to selection that is linking methylation with local variation for salt acceptance. A gold standard methodology is assumed that is uniting gene imprisonment and bisulfite management (bisulfite sequencing) for the application of a genome-wide survey (Olohan et al., 2018).

6.2 Transposon copy number

Plant genomes have both protein coding and noncoding regions. These noncoding regions include introns, noncoding RNA, repeat sequences, and transposable elements. The noncoding regions regulate gene expression and play a vital role in genome organization (Wang et al., 2014).

Plant TEs are particularly divided into two main classes: class I TEs, known as RNA elements or retrotransposons that move by a *copy-and-paste* mechanism involving an RNA intermediate, and class II TEs are also known as DNA transposons that translocate through a *cut-and-paste* mechanism that does not involve any intermediate molecules. TEs specifically play an important role in crop genome advancement. In crop plant genomes such as maize and wheat, an enormous expansion has been suffered by TEs and covered 85% of the genome. Characteristically highly repeated DNAs were methylated to repress expression and its inversion for the sustained genome stability (Kim and Zilberman, 2014).

The most active transposable elements in eukaryotes are the inverted-repeat transposable elements (Jiang et al., 2003; Kikuchi et al., 2003; Yang et al., 2007). They are members of the tandem inverted repeat family of DNA transposons. The sizes of nonautonomous miniature inverted-repeat transposable elements (MITEs) are 10−100 bp, prevalent in eukaryotic genomes only. MITEs are found in organisms with more copy number genes such as maize and rice and have strong linkage with these genes (Choulet et al., 2010; Zhao et al., 2016). They mainly influence the expression, when inserted in the introns, promotors, or regions with regulatory sequences of the genes.

Epigenomic diversity at huge scale happened across a wheat landrace assemblage. It was alongside of TE copy number difference. It was shown that high copy number of Gypsy retrotransposons and CACTA DNA TEs accounted for much of the discrepancy, which tends to be linked with intergenic regions. In the practice of TE expansion, it could be compared with the Chinese Spring reference variety. They also established variation for the inferior copy number Mariner and Harbinger MITEs athwart the assortment, respectively. They both are linked with genic sections. TEs could hypothetically have, therefore, a vivid effect on the gathering and directive of genes. As a key player in phenotypic variation, TEs have given an additional source of variation to breeders' disparity (Gardiner et al., 2018).

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CHAPTER

23

Genomic selection in wheat breeding

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OUTLINE

1. Introduction

Genomic selection (GS) is a model-based approach in plant breeding that utilizes genomic estimated breeding values (GEBVs) of breeding lines to predict breeding outcomes in an effective and efficient manner. It basically establishes links between phenotypes and genetic markers to accelerate the genetic gain in plant breeding (Wang et al., 2018). Initially, it was established in the animal breeding because of inability of animals to replicate and the high cost of phenotyping (Rutkoski et al., 2017). GS gained limelight in plant breeding because it achieves more and comprehensive selection as compared with other conventional breeding tools that mostly rely on phenotype selection. It uses genomic prediction models based on genome-wide prediction markers and phenotypic traits of the training population (TRN) to predict the GEBVs of the testing population (TSN) that only have genotypic data. Then the GEBVs of those lines in TSN will be utilized to process the selection for the next breeding cycle as described in Fig. 23.1 (Lorenz et al., 2011). However, the advancement of GS in plant breeding field is relatively far away behind as compared with animal breeding, in which the initial implantation was performed in 2007 based on the simulated data in maize (Bernardo and Yu, 2007).

GS is a sensitive selection process that even accounts small-effect markers with potential to interfere with significance of test. It has showed significant advantages in plant breeding as compared with traditional marker-assisted selection (MAS) especially for complex quantitative traits with low heritability and regulated by various loci with small effects. It is able to capture more variations and to improve selections that involve genome-wide spread genetic markers. Moreover, GS reduces breeding cycles by improving the genetic gain per unit time, which is demonstrated by the breeder's equation ($G = \frac{ir\sigma_A}{Y}$, where G denotes gain per year, i denotes selection intensity, r denotes selection accuracy, σ_A denotes square root of narrow sense heritability, and Y denotes time in years for a cycle of selection). According to the equation, larger genetic gain can be achieved, compared with traditional phenotypic selection (PS),

Climate Change and Food Security with Emphasis on Wheat
https://doi.org/10.1016/B978-0-12-819527-7.00023-6

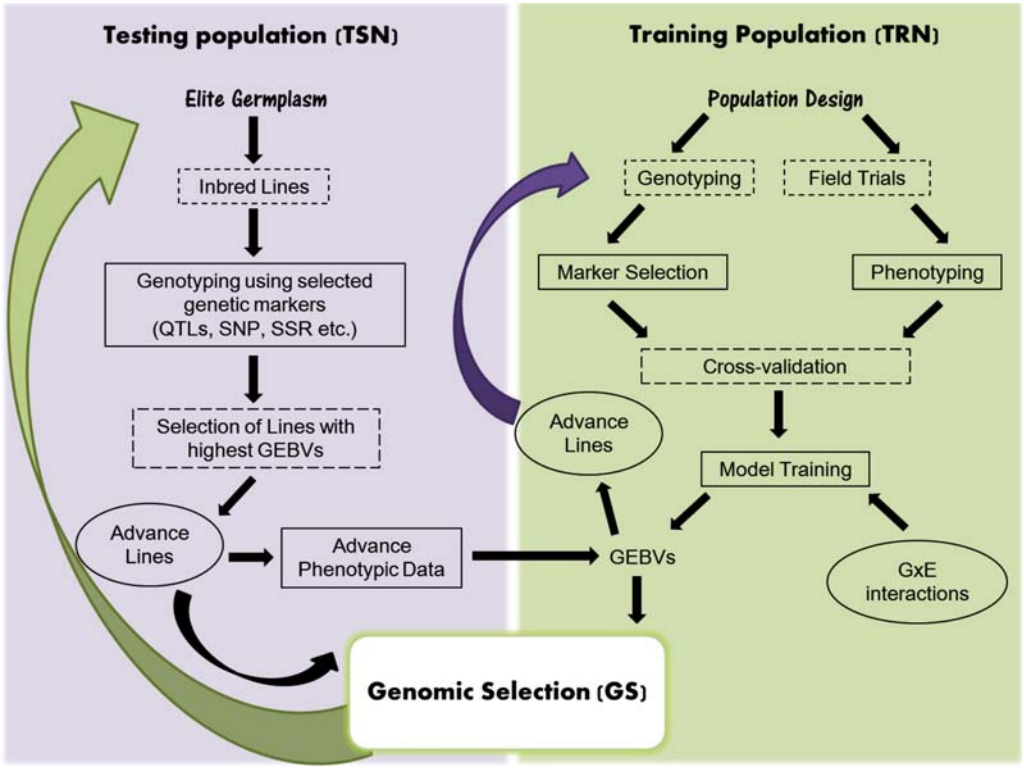

FIGURE 23.1 **An overview of genomic selection in plant breeding.** The genomic selection involves two populations including training population (TRN) and testing population (TSN). TSN is the main population for a breeding program whose outcomes are predicted using genotypic and phenotypic data of TRN. The accuracy of prediction depends upon genomic estimated breeding values (GEBVs) calculated through specially designed genomic model for trait under study. Various other factors affecting GEBVs include genomic × environment interactions, phenotype of both TSN and TRN, selection of genetic markers, and variation in the advance lines. *Information retrieved from Rutkoski, J.E., Heffner, E.L., Sorrells, M.E., 2011. Genomic selection for durable stem rust resistance in wheat. Euphytica 179, 161–173 and Wang, X., Xu, Y., Hu, Z., Xu, C., 2018. Genomic selection methods for crop improvement: current status and prospects. The Crop Journal 6, 330–340.*

by reducing the duration of breeding cycles, which allows lowering the cost of phenotyping in a long term. The development of next-generation sequencing (NGS) technology resulted in the reduction in the cost of the genotyping, consequently inspiring the extensive application of GS in different breeding programs of the plant community to enhance genetic gains and speed up crop selection.

2. Approaches to improve genomic selection accuracy in wheat

The prediction accuracy of GS in early generation can be achieved by improving the rate of genetic gain per unit time (Bassi et al., 2016). Generally, the accuracy is evaluated by the Pearson correlation between the empirically estimated breeding values (BVs) and the GEBV (Lorenz et al., 2011). Many studies have investigated those factors in different plant breeding programs. The accuracy of GS could be affected by TRN size, the heritability of the trait, and the effective number of loci in marker density if the genetic markers and quantitative trait loci (QTL) are in perfect linkage disequilibrium (Bassi et al., 2016). For example, studies identified that the accuracy of GS enhances with the increase of the size of TRN and the density of genetic markers (Heffner et al., 2011b; Lorenz et al., 2011). He et al. (2016) demonstrated that the predictive ability of GS could be improved by using the historical data as TRN and effective filtering genotypes. However, when the QTL and markers are not closely linked, the accuracy is affected by the genetic relationship between TRN and TSN (Bassi et al., 2016). In these cases, higher accuracy could be achieved by increased levels of relationship between TRN and TSN and the optimization of TRN (Isidro et al., 2015). In the next few sections, some of other factors that determine the GS accuracy reported in recent studies will be covered.

2.1 Genomic selection models

Various genomic prediction models have been deployed to improve the accuracy of GS. However, many of which present a negligible variation, and linear combination of different models in GS did not seem to improve the accuracy of prediction accuracy as well (Heslot et al., 2012; Juliana et al., 2017b). Heslot et al. (2012) has compared multiple models including random regression best linear unbiased prediction (ridge regression, RR-BLUP), the weighted Bayesian shrinkage regression (wBSR), Bayesian Lasso (BL), reproducing kernel Hilbert space (RKHS), random forest (RF), and so on. They observed quite similar level of accuracy between most of those test models, however, under such conditions, the selection of models in GS would be determined based on the difficulty of the model to be implemented, the reliability across different traits and datasets, and the efficiency of computation (Heslot et al., 2012). According to those considerations, RR-BLUP, BL, and wBSR are recommended models in their study. It needs to mention that despite the fact that RKHS regression model was overfitting and relatively complex, it provided higher accuracy than all of other models, suggesting more genetic signals and noises were captured by the model (Heslot et al., 2012). Overall, under the similar accuracy, models that are easy to be implemented and require less computational time are commonly preferred in GS studies. Genomic models and their features have been mentioned in Table 23.1 for further understanding. Moreover, some other studies also evaluated the differences between the additive and nonadditive GS models. Generally, nonadditive models, such as models including epistasis effect, resulted in higher prediction accuracy than additive models (He et al., 2016; Mirdita et al., 2015).

2.2 Genotype × environment interactions

In plant breeding, genotype × environment interactions (G × E) are a great challenge for GS researches, as these interactions are often evaluated within the same environment or considered as noise. However, these interactions amplify variation in phenotypes of cultivars across environments for the reason that plants respond differentially to environments and the integration of G × E interactions into GS models enables the selection of stable and high-performance cultivars (Bassi et al., 2016; Rutkoski et al., 2017). Since G × E interactions in the GS model improve the genomic prediction power by taking advantages of genetic correlations between environments (Heslot et al., 2014), developing efficient models to integrate G × E interaction terms is essential, which will be discussed in the following section.

Back to a few years ago, Burgueño et al. (2012) being the first researcher improved the genomic prediction power by developing the multienvironment model for GS. In this reported work, they applied the factor analytic (FA) structure for G × E interactions in GS using an International Maize and Wheat Improvement Center (CIMMYT) wheat population evaluated in four environments. Based on their results, multienvironment models outperformed single-environment models in across-environment predictions. However, when used to predict the performance of newly developed lines, this approach failed to improve the predictive ability (Burgueño et al., 2012).

After that, a new approach for G × E was proposed by Heslot et al. (2013) to characterize the estimates of allele effect, instead of line effect, at each environment to identify the outlier environments. In unbalanced data, despite the fact that all genotypes are not presented in all environment, the allele effects are presented in all environment (Rutkoski et al., 2017). The authors utilized a highly unbalanced elite barley phenotypic data to demonstrate their approach in analyzing multienvironment trials. In addition to the estimates of allele effect, they characterized the environments based on the accuracy of prediction between environments (Heslot et al., 2013). However, the large variance components in this data set bring tremendous difficulty in estimating the correlation matrix among environments. To solve this issue, they employed a reduced data set with only 61 commercial checks and cultivars to be released to develop the correlation matrix. Although those genotypes reduced G × E interactions compared with all lines in the data set, G × E patterns from those genotypes are able to represent the whole G × E patterns, as evidenced by the high correlation between the among-environment correlation matrix and accuracy matrix between environments (Heslot et al., 2013). It is worth to note that the FA structure mixed model proposed by Burgueño et al. (2012) suffers from the convergence issues in such large and unbalanced data sets due to singularity issues; as a comparison, their genomic selection model BL was able to be converged successfully. In addition, the approach to optimize the ratio of TRN was proposed to predict the target population of environments. The GS model was trained by removing the environment with less predictive ability; as a consequence, the prediction accuracy of GS was increased from 0.54 to 0.61.

Similarly, in the context of whole-genome genotyping, Lopez-Cruz et al. (2015) demonstrated the benefits of using GS model comprising marker × environment (M × E) interaction in modeling G × E. Compared with standard multienvironment mixed models, this approach can be easily implemented and interpreted. Most importantly, this

TABLE 23.1 Models used for genomic selection and their respective features.

GS models	Abbreviations	Algorithms	Average accuracy (cross-validated)	Feature	References
Random regression best linear unbiased prediction (ridge regression)	RR-BLUP	Regression algorithm	0.56	Predictor assumes that all of the markers have a common variance, therefore, this model shrinks equally for each marker effect.	Lorenzana and Bernardo (2009), Kang et al. (2008)
Bayesian ridge regression	BRR	Linear regression (including normal distribution)	0.55	Model makes the same assumptions as that of RR-BLUP, but the shrinkage level is predicted with a Bayesian hierarchical model.	Pérez et al. (2010), Heslot et al. (2012)
Weighted Bayesian shrinkage regression	wBSR	Bayesian multinomial logistic regression	0.56	It is an expectation maximization algorithm for the BayesB model with higher computational efficiency.	Hayes and Goddard (2001), Heslot et al. (2012)
BayesCπ	—	Markov chain Monte Carlo	0.55	It assumes a common marker effect variance for all of the markers with nonzero effects, but rather than using a fixed π, it estimates π. (π is defined as prior distribution for the additive SNP effect).	Heslot et al. (2012), Plummer et al. (2006)
BayesB	—	Monte Carlo Markov chain	0.58	It relaxes the assumption of common variance across marker effects made by RR-BLUP.	Gao et al. (2015)
Bayesian Lasso	BL	Modified least angle regression algorithm	0.56	It provides interval estimates that can guide variable selection.	De Los Campos et al. (2009), Heslot et al. (2012)
Reproducing kernel Hilbert space	RKHS	Reproducing kernel Hilbert space algorithm	0.59	It uses a kernel function to convert the marker data set into a set of distances between pairs of observations that results in a square matrix to be used in a linear model.	Heslot et al. (2012)
Random forest regression	RF	R package "RandomForest"	0.54	It is machine-learning method that they can capture different relationships between markers and phenotypes. Its regression trees grown on bootstrap samples of observations using a random subset of predictors to define the best split at each node.	Heslot et al. (2012), Ali et al. (2012)
Support vector regression	SVR	R package "e1071"	0.41	It is machine-learning method that they can capture different relationships between markers and phenotypes. SVR uses linear models to implement nonlinear regression and simultaneously minimizes an objective function that accounts for both model complexity and the error in the training data.	Drucker et al. (1997), Meyer et al. (2019)

TABLE 23.1 Models used for genomic selection and their respective features.—cont'd

GS models	Abbreviations	Algorithms	Average accuracy (cross-validated)	Feature	References
Artificial neural networks	NNET	It includes algorithms for reinforcement learning, classification, and regression	0.55	It is machine-learning method that they can capture different relationships between markers and phenotypes. It is modeled loosely after the human brain, and it is designed to recognize patterns. It is system of simple interconnected neurons or nodes.	Gardner and Dorling (1998), Heslot et al. (2012)
Genomic best linear unbiased prediction mixed model	GBLUP	Linear regressions	0.54	The method adapts a standard mixed effects linear model for obtaining pedigree-based best linear unbiased predictions.	Gianola et al. (2018)
Empirical Bayes	E-Baye	Maximization algorithm	0.54	It is a differential parameter shrinkage method for an oversaturated.	Heslot et al. (2012), Lorenzana and Bernardo (2009)
Elastic net regression	Elastic net	Multiple regressions	0.54	It combines the penalties of ridge regression and lasso to get the best of both.	Heslot et al. (2012)

model decomposes effects into common within environments and deviations that are specific to environment, thus enabling to distinguish the genomic regions affected by main effects those are persistent across environments and specific effects those are accounted for G × E interactions. In the situation that the sets of environments had positively and similarly correlated environments, the most optimized outcome can be generated as predicted by the model. The authors compared the accuracy of GS in three different models including within-environment analysis, across-environment model without G × E, and across-environment model using M × E. Based on the observations, the prediction accuracy of M × E model was significantly higher than the one from the model without G × E; thus, it displays similar or higher accuracy than the one from the within-environment model.

Another way to evaluate G × E interactions is to group the environments into megaenvironments (MEs) to minimize the G × E pattern within MEs (Heslot et al., 2014). Lado et al. (2016) utilized a genomic BLUP (GBLUP) mixed model to predict either overall or by-environment selection for different sets of environment from a large advanced wheat population in 35 location−year combinations. They characterized G × E interactions including variance component estimation and correlation between environments by applying additive main effect and multiplicative interaction, genotypic main effect and genotype × environment interaction matrix (GGE), and graphical representation through augmented biplots. To reduce G × E interactions, all environments in their data set were divided into three MEs based on a GGE2 augmented biplot. By using this approach, they were able to get the information from relatives that have been evaluated in different environments and to predict new genotypes before phenotyping by modeling the correlation matrix across environments. In addition, higher predictive ability was achieved by using this approach.

One of the strategies to integrate G × E into GS models is to omit the correlations between environments for G × E (Heslot et al., 2014). This has been exemplified by some studies, such as FA structures, which utilized multiplicative mixed model to evaluate the covariance between environments by considering that G × E has no correlations between environments (Burgueño et al., 2012). However, the usage of such models is limited by some other issues such as convergence issues and incapability of predicting lines for a new environment in highly unbalanced multienvironments trials (Burgueño et al., 2012; Heslot et al., 2014). Another approach, namely, factorial regression, evaluates G × E by finding the environmental factors associated with G × E (Heslot et al., 2014). When environmental covariates are integrated into the model, they produce a large number of covariates, each of which is responsible for a small amount of variance of total variance, impeding its implantation into GS models (Heslot et al., 2014). To resolve this issue, Heslot et al. (2014) proposed an approach of integrating crop modeling for environment data into GS to predict G × E. The environmental data, which are daily weather data in their study, are physiologically integrated into the crop model to find covariates of stress, reducing the dimensions of environment data to some covariates at each growth stage of crop. After that, the covariates are utilized as independent variables in statistical models for estimating

and predicting effects. With this approach, they are able to model genome-wide markers and to differentiate their responses to the environments. Although the gain of GS in this study was small, the approach provides a great deal of understanding the genetic architecture of G × E interaction and predicting genotypes-based wheat data.

In summary, more applications to evaluate G × E interaction are mushrooming, aiming to characterize the interactions between genotype and environments efficiently in highly unbalanced trails (Crossa et al., 2016; Cuevas et al., 2017; Jarquín et al., 2014; Lado et al., 2016; Sukumaran et al., 2017; Ward et al., 2019). All these methods may hold great promise because they can be referenced, improved, or extended in different breeding programs.

2.3 Platforms for high-throughput phenotyping

With rapid advancement in NGS technology, phenotyping has become a limiting factor for genetic gains in plant breeding as it is time consuming. However, reliable phenotypes, in addition to genotyping, are essential for obtaining the desirable accuracy of genomic prediction model training. Currently, a great deal of efforts has been put forth to develop programs for high-throughput phenotyping (HTP) in various crops to generate in-depth and large-scale phenotyping with high accuracy and low cost (Araus and Cairns, 2014). Based on imaging technologies and remote or proximal sensing, platforms have been established for field-based HTP including three categories: infrared thermometry and thermal imaging, visible/near-infrared spectroradiometry, and red, green, and blue light color digital photography (Araus and Cairns, 2014). The relevant information can be found in the review written by Araus and Cairns (2014). Recently, measuring various traits in wheat, for example, vegetation indices (Haghighattalab et al., 2016), plant height (Holman et al., 2016), and disease resistance (Devadas et al., 2015), has become feasible based on development of HTP platforms. Therefore, the application of phenotypes from HTP platforms into GS becomes promising.

Since HTP platforms are designed to realize relatively accurate phenotypic data collection in large scale, it is reasonable to expect that those data can serve as the primary input for model training. Watanabe et al. (2017) used unmanned aerial vehicle (UAV) remote sensing to collect the data of sorghum plant height and applied the data into genomic prediction. Their results were slightly lower compared with traditional manual measurement; however, the capability in reducing the labor and cost is significant. The applications of HTP platforms are still at early stage; however, HTP platforms are well recognized to be the flagship method in the long run. More importantly, HTP platforms enable the collection of time series data over plant growth, providing the opportunity to directly compare the traits at the same growth stage and allow plant breeders to make selections at early growth stages of plant (Sun et al., 2019; Watanabe et al., 2017).

The traits from HTP platforms are used for the prediction of complex primary traits by applying correlations between the primary and secondary traits. Rutkoski et al. (2012) integrated normalized difference vegetation index and canopy temperature into the multitrait genomic prediction model to predict grain yield in a CIMMTY wheat population; average of 70% improvement was observed in the predictive ability of GS within a population. Similar improvements have been achieved in different researches; some of the researches include Crain et al. (2018), Juliana et al. (2019), Krause et al. (2019), Montesinos-López et al. (2017), and Sun et al. (2017, 2019). Such studies demonstrated the potential of integrating HTP platforms into GS either within a population or across populations. Although available platforms for HTP are still lagging behind the technologies for genotyping, it is anticipated that more traits will become accessible, and the accuracy of the data and the performance of HTP platforms will be improved as well.

3. Application of genomic selection in wheat

Wheat (*Triticum aestivum* L.) is an important economic crop that fed the world and has a very large genome with roughly about 16 Gbp in hexaploid (Poland et al., 2012). The advancement of NGS has provided the opportunity to apply GS in breeding programs of wheat. The first GS study in wheat was published by De los Campos et al. (2009) using the data from Global Wheat Program of CIMMYT, with a conclusion that GS based on genomic markers improved the predictive ability of GS models. Genotyping by sequencing (GBS) and diversity array technology (DArT) are mostly used marker platforms for GS studies (Juliana et al., 2017b; Poland et al., 2012). Based on the study of Heslot et al. (2013), despite higher accuracy of GS observed from GBS than DArT marker platforms, it was primarily attributed to the increase in the number of genetic markers from GBS. Similar conclusion was drawn by Juliana et al. (2017a), who reported that GBS markers in GS were slightly better than DArT makers, and the combination of markers from GBS and DArT (whole-genome profiling approaches) did not improve the accuracy of predication of GS. GS has been utilized by various quantitative traits in wheat, including disease resistance (Juliana et al., 2017a;

Rutkoski et al., 2012), grain yield (Heffner et al., 2011b; Poland et al., 2012), and other traits (Heffner et al., 2011a; Manickavelu et al., 2017; Velu et al., 2016). In the following part, some of those applications and the breeding strategies in wheat will be highlighted.

3.1 Wheat grain yield and genomic selection

As a complex quantitative trait, grain yield is regulated by various genes and influenced by the interactions between environments and genes (Heffner et al., 2011b). Grain yield is an important economic trait, which has been investigated in most of GS studies of wheat. The first GS study in wheat utilized the grain yield data from CIMMYT (De Los Campos et al., 2009). The authors concluded that GS for grain yield based on genomic markers was better than using pedigree alone for the reason that genomic markers are able to capture the variations within family as a result of Mendelian sampling. Later on, Crossa et al. (2016) also studied the ability of prediction for wheat grain yield from CIMMYT by testing several models for GS but utilized less genomic markers than de los Campos et al. (2009). They concluded that GS can be utilized effectively for the selection of lines without phenotypes and the improvement in the genetic gain is expected when the number of genetic markers increases (Crossa et al., 2016). The accuracy of genomic prediction for grain yield can be varied from moderate to high in different breeding backgrounds and schemes. Breeders also have worked on different approaches to further improve the genomic prediction accuracy. Burgueño et al. (2012) demonstrated that multienvironment GS models greatly improved the prediction accuracy for grain yield than simple linear models; Helsot et al. (2014) observed that the prediction accuracy of GS models was improved by 11.1% on average for grain yield when GS was incorporated with crop modeling and environmental covariates. He et al. (2016) confirmed that historical data and filtering genotypes enhanced the prediction ability of grain yield.

3.2 Wheat disease resistance and genomic selection

GS approach has great potential to improve the complex quantitative disease resistance for the breeders of wheat. Since quantitative disease resistance is controlled by many genes with small effects, it is difficult to be overcome by pathogens. Wheat is constantly threatened by multiple biotic stresses, in which the rust and Fusarium head blight (FHB) are two of most popularly studied diseases using GS approach.

Ornella et al. (2012) utilized GS to identify the predictive ability for yellow rust and stem rust using CIMMYT wheat populations. GS within population and environment yielded a correlation greater than 0.50 between predicted and observed values, and including information from other environments or population improved the genomic prediction between populations and environments (Ornella et al., 2012). Rutkoski et al. (2015a) designed a case study for wheat stem rust using historical data; their results showed that the optimization of historical training population, such as population size and relativity, was more predictive than randomly selected subsets. Rutkoski et al. (2015b) compared realized gain from GS and PS based on equal selection intensities over 2 years. It was observed that genetic gains per year from GS were similar to PS, but genetic variance was significantly reduced in GS. Juliana et al. (2017b) compared three different genomic prediction models to evaluate the BVs of adult plant and seedling resistance to stripe rust, stem rust, and leaf rust. Most of the evaluated models showed similar prediction accuracy; however, an average of 42% improvement in accuracy was observed by using models based on genomic marker compared with the accuracy from the least square approach that utilizes selected loci (as fixed effects).

Rutkoski et al. (2012) analyzed several models for genomic prediction to predict FHB resistance traits including deoxynivalenol (DON) levels based on three marker sets: FHB QTL-targeted markers, genome-wide markers, and both marker sets. In general, ridge regression (RR) and RKHS regression models are the most accurate approaches, while genome-wide marker provided higher accuracies than QTL-targeted makers for most traits except DON (Jiang et al., 2015). Jiang et al. (2015) investigated the factors influencing the genomic prediction accuracy of the genotypic variation of FHB resistance for European wheat varieties based on both single nucleotide polymorphism (SNP) and simple sequence repeat. In their study, the prediction accuracy was only marginally impacted by the marker density; thus, SNP arrays ranging from low to medium density are applicable for GS of FHB resistance. Arruda et al. (2015) developed GS models for predicting traits correlated with FHB resistance in wheat, and they compared the prediction accuracies of GEBVs based on different variables including imputation methods, statistical models, marker density, training population size, relationship matrices, and relatedness between training and testing populations. They found that each factor affects the prediction accuracy to distinct extent. The imputation methods exert no visible differences on prediction accuracy; RR-BLUP was found to be superior to other models; the reduction in marker density, population size, and the relatedness yet lowers the prediction accuracy. In addition, pedigree relationship

matrix of behaviors is worse in terms of prediction accuracy when compared with marker-based relationship matrix. Based on desirable prediction accuracy in these studies, typical from moderate to high, the authors believe that GS is a promising approach for FHB resistance in wheat.

In addition to rust and FHB, some other diseases' effects on wheat have also been investigated using GS. For example, Juliana et al. (2017b) performed a comparative study between the influences of GS models and whole-genome marker platforms on multiple plant disease resistances including Stagonospora nodorum blotch, Septoria tritici blotch, and tan spot resistances in wheat. Moderate to high prediction accuracy was observed for those disease resistances by using genomic prediction models, which were 48% higher than using least square approach. These results lead to the same conclusion that implementing GS would be beneficial to achieve high prediction accuracies in wheat breeding for disease resistance (Juliana et al., 2017a).

3.3 Genomic selection and other traits

The quality of wheat is largely determined by the features of traits such as baking quality, softness of flour, milling quality, and protein content, which constitute the essential properties of wheat. Heffner et al. (2011a) compared the accuracy of prediction between MAS, PS, and GS in multiple traits by including those quality traits in a winter wheat population. The average prediction accuracy of GS was 28% better than MAS, but slightly less accurate than PS. However, this study still reveals the potential value of GS as it is superior to MAS and PS in terms of cost and gain per unit time (Heffner et al., 2011b). Ward et al. (2015) applied GS to study a series of wheat quality traits including protein, gluten, starch, moisture content, and so on, based on a new model, namely, differentially penalized regression, resulting similar accuracy compared with prediction from RR using covariates. Furthermore, many series of GS studies have been carried out for different traits of interest in wheat, for example, nutritional traits (Manickavelu et al., 2017; Velu et al., 2016), plant height (Ward et al., 2015), days to heading (Isidro et al., 2015), and lodging tolerance (Heffner et al., 2011b). More in-depth information of the applications of GS in different traits is available in Poland and Rutkoski (2016), Rutkoski et al. (2017), and Sweeney et al. (2019).

4. Summary

In theoretical and practical studies, the primary goal of breeding is to enhance the genetic gain. According to the breeder's equation, the major way for GS, compared with traditional PS, to increase the genetic gain is to reduce the breeding cycle. However, in practical wheat breeding, other parameters in the equation determine the rate of genetic gain from GS. For example, in addition to the selection accuracy as we discussed, breeders apply the selection intensity differently at each breeding cycle depending on the generation, inbreeding value, and the prediction accuracy increased by updating the TRN, and the heritability for the trait of interest determines the effective population size required in the breeding program (Bassi et al., 2016; Lorenz et al., 2011). As a consequence, those factors that govern the genetic gain from GS also affect the cost of GS in a breeding program at each cycle. Therefore, when enhancing the rate of genetic gain from GS, the cost required for GS breeding schemes should be considered to optimize the resource allocation. A great number of studies have illustrated many questions for the application of GS in wheat breeding, and we have discussed some of the potential solutions in this chapter. However, the advance of GS in the practical wheat breeding programs is still limited, which is restricted by the complex breeding goal and resource related to each breeding program and the requirement of large computational resource from the complexity and the efficiency of GS models. Therefore, to explore the high potential of GS into wheat breeding, more researches are expected to perform; especially the development of new technologies, such as HTP, would be valuable to GS because they are capable of improving the phenotyping accuracy and reducing the cost.

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CHAPTER

24

Wheat genomics and genome editing

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OUTLINE

1. Introduction

Wheat is an invaluable, staple food crop. It constitutes 17% of crop acreage worldwide and provides essential sustenance for around 40% of the global population. In an average diet, wheat makes up 20% of the total consumable calories and protein. Although wheat production has shown a steady, significant increase during the last four decades, recent years have represented fatigue, causing the lowest global wheat stocks since 1949. Subsequently, wheat prices have soared, peaking in 2018 at US $10 a bushel, compared to US $4.50 in 2017. Adding to this, to meet increasing food demands wheat growth rate must be increased at a rate of 2% per annum, without any addition to sowing acreage (Gill et al., 2004). To meet this challenge head on, new levels of approaches need to be employed in relation to the structural and functional genomics study of the wheat.

Wheat is largely adapted to temperate climatic zones. To utilize wheat reference genome for development of new wheat varieties, knowledge of previous research and current molecular marker tools is essential. Wheat understated flexibility when it comes to surviving within a wide range of climate conditions is largely responsible for its success as a food crop globally. This adaptability can mostly be attributed to the allohexaploid structure of common wheat

(*Triticum aestivum* L.) genome. Its haploid contains three subgenomes/monoploids (each subgenome, i.e., A, B, and D has seven chromosomes). The diploid ancestors of the three subgenomes have been identified, though there has always been a debate concerning the ancestor of B genome for a common wheat (Gill et al., 2004). During meiosis division, common wheat behaves as a diploid plant. Additionally, its genome can be aneuploidy-tolerating due to the presence of triplicate genes. All these genomic features facilitate wheat genome research greatly (Gupta et al., 2008), particularly when considering the set of 42 nullisomic-tetrasomics, the whole set of monosomics, and the entire set of 42 ditelocentrics, which have been produced (Hossain et al., 2004) alongside of more than 400 segmental deletion lines (Endo and Gill, 1996).

1.1 Contributions of wheat genetic resources

The genus *Triticum* originated almost 10,000 years ago in the important area of the Middle East, the Fertile Crescent. *Aegilops* (goatgrass) plays a significant role in the evolution of wheat, which originated following two successive hybridizations (polyploidization) events. During the first hybridization event, a wild Emmer (domesticated species is *Triticum turgidum* tetraploid, $2n = 4x = 28$) was evolved from two diploid species, *Triticum urartu* (AA; $2n = 2x = 14$) (Petersen et al., 2006) and an unidentified *Aegilops* species. Followed by a second hybridization event between this tetraploid wheat (*T. turgidum*) and a diploid *Aegilops tauschii* species, giving rise to allohexaploid wheat (*T. aestivum* L., $2n = 6x = 42$, AABBDD) (Nesbitt and Samuel, 1996; Petersen et al., 2006). This is the cultivated variety of wheat, commonly known as bread wheat and makes up around 95% of the global wheat production.

Wheat is one of the few crops that can be considered truly global, with a cultivation range covering most of the world. *Triticum* constitutes plenty of domesticated cultivars and wild (landraces) species. The main center of origin is Southwestern Asia, ranging from the Mediterranean coast in the west to the Tigris Euphrates plains in the east. In this area, a mixed population of diploid and polyploidy *Triticum* species is coexisted and exhibited a remarkable morphological and ecological diversity. In order to conserve diversity, numerous species of *Triticum* have been sampled from this area and are currently preserved in various genetic resource centers, for instance, the CIMMYT headquarters in Mexico.

Much has been reported about the lack of utilization in genetic resources available within the *Triticum* collections. In relation to this, Chapman (1989) observed the scope of genetic resources (wild materials and landraces) in wheat breeding, however, and found it challenging to estimate. Therefore, he examined that the collections stored in these resources may have been employed 10% of all historic hybrids based on the lineages of cultivars released recently. Current efforts of CIMMYT to develop a full lineage database of the wheat genetic resources worldwide (Wheat IS, the International Wheat Information System) has allowed the estimate of contributions from landrace and wild material to modern varieties/cultivars by providing lineage information that dated back to the true ancestors of landrace. More recently, in-depth analysis on the flow and use of wheat genetic resources has been performed which revealed that the lineage of modern wheat varieties/cultivars has gradually increased the number of different landraces during the past 30 years, and therefore the biogeographical origins of the landraces has been expanded (Smale et al., 1996). Furthermore, the contribution of numerous specific genes, particularly on the wheat phenotype, can be traced back directly from the genetic resources.

1.1.1 Dwarfing genes

Norin 10, a Japanese cultivar, was found to have two major dwarfed genes, *Rht1* and *Rht2*. These genes reduce (or dwarf) the wheat plant height, and it is believed that this is inherited from a Japanese landraces. Norin 10 along with 16 other varieties were crossed with Mexican local varieties by Norman Borlaug and Borlaug Rockefeller; the resulting productivity was significantly higher than that of other nondwarfed (tall) cultivars. Therefore, it was assumed that this was caused by a reduction of lodging in dwarf varieties, from which tall genotypes were particularly susceptible. Additionally, tall varieties were not very responsive to fertilizer inputs. The obtained varieties from this cross were further tested in India and Pakistan. Most significantly, this development led to what is now known as *the Green Revolution* (Ortiz and Mowbray, 2007). Originally, it was thought that these genes, *Rht1* and *Rht2*, caused increased production directly by reducing lodging through height minimization. Now, it is known that they may have some other direct consequences on yield along with the better uptake of nutrients and tailoring capacity (Gale et al., 1985).

1.1.2 Rust resistance genes

Fungal pathogens are the most destructive, diversified group of crop pathogens. Currently, yellow, stem, and leaf rust are three of the most widespread diseases in wheat. Historically, fungicides have bestowed a level of control, but choice of chemicals is sometimes limited, especially in developing states where there is a lack of funds and

knowledge. However, particularly for races of rust pathogens, many genes have been discovered that contribute to resistance. Introgression of these genes into wheat varieties has partially eliminated the need for fungicides (Smale et al., 1996). As an example, a single gene has been successfully introgressed/transformed into multiple varieties, imparting resistance to particular pathogenic races of the rust.

For leaf resistance, >40 genes are known, of which 12 are originated in the wheat species other than *T. aestivum* and *T. turgidum*. Along with this, in a total of 41 known genes for stem (black) rust resistant, 20 genes are also originated in the wheat species other than *T. aestivum* and *T. turgidum*. Surprisingly, several genes which are originating from *T. aestivum*, come from landraces. However, some of the above resistance sources have now been reverted to susceptible, since the pathogen strains have been mutated and now become virulent against certain resistant genes. Due to this, more efforts are underway to recognize and transform genes which give durable resistance. Numerous such genes have already been identified and integrated into modern wheat varieties, including the *Lr34* (leaf rust resistance gene) gene originally found in the Fontana spring wheat cultivar (McIntosh, 1992). According to a report, approximately 50% of wheat varieties had the *Lr34* gene simultaneously inserted with several modifier genes in the late 20th century (1980s and 1990s), which imparted stable leaf rust resistance, and are now grown worldwide.

In terms of stem rust resistance, the *Sr2* (stem rust resistance gene) gene appears to be critical, which when mixed with other unknown genes, created durable resistance. This *Sr2* gene was identified from awned wheat, Emmer, a tetraploid wheat variety, and has since been wildly integrated into numerous wheat varieties, contributing outstanding resistance levels. Additionally, a linked DNA marker has been developed that permits fast, efficient recognition and manipulation of the resistant gene. Furthermore, incorporation of these resistance genes, including both *Lr34* and *Sr2*, showed genetic advancement in the grain. It is likely that without these gains the Green Revolution would not have occurred.

1.1.3 *Veery wheat lines*

In addition to the examples previously mentioned, genetic resources have contributed not only genes but also transfer of the full chromosomal fragments, helping toward crop development efforts. Perhaps the most notable of these is the *1By1R*, which included a simple translocation of genes between a rye and wheat cultivar "Kaukaz" from the former Soviet Union. The *1By1R* translocation exhibits several genes from rye, which confer resistance to many diseases (including fungal and viral pathogens) alongside an adaptation to marginal land (Villareal et al., 1991). Since its discovery, this fragment has been integrated into more than 60 wheat varieties, including the dynamic *Veery* lines (a spring bread wheat lines for several environments), which occupy more than 50% of all arable land for wheat in the developing countries, covering almost 40 million hectares (Skovmand, 1997).

2. Wheat genomics

Wheat contains large amount of carbohydrates, minerals, and protein. It is consumed by 30% of the human residents and serves as an essential food source. Due to the climatic shift, wheat cultivation is reduced by 5.5% in 2000 and 2008 (Lobell et al., 2011). Unfortunately, for the past 10 years, global wheat yield was not satisfactory in accordance to our needs. In 2050, worldwide population would be expected to cross 9 billion. Researchers and cultivators are facing this challenge of growing wheat manufacturing around by 70% to overcome upcoming loads (Tilman et al., 2002). Fertilizer and other valuable input expenses are increasing. Variation in the climate causes stress conditions on wheat plants and the rising competition among edible and nonedible uses, and the decreasing annual crop growth aggravates the situation (Judge, 2010). A model on science-based developments in wheat breeding and genetics, following the food prints of 1960s Green Revolution, will be necessary to tackle these challenges.

Common bread wheat is an allopolyploid with 21 pairs of chromosomes. However, genetically, bread wheat acts like a diploid because the homologous pairing between the chromosomes is halted due to the involvement of *Ph* (pairing homoeologous) genes (Martinez-Perez et al., 2001). Because of high proportion of the repetitive transposable elements (TEs) (Wicker et al., 2011) besides relevant genes, the size of each of the subgenomes (A, B, D) is greater, estimated approximately up to 5.5 GB. Along with this, a reference genome for bread wheat sequencing could not be generated owing to large and repetitive nature of the genome. Coding sequences that comprised <2% of the wheat genome were focused in early studies. However, more than 1 million ESTs (expressed sequence tags), 40,000 unigenes (a genes cluster performing a specific function), and 17,000 full-length cDNA (complementary DNA) sequences were generated as a consequence of coordinated efforts for the exploration of the wheat genome (Mochida et al., 2009).

The studies on individual gene, establishment of different techniques like microarrays, marker sets for targeted genome wide association and expression are now being enabled and facilitated by these genetic resources. Approximately 7000 ESTs (Qi et al., 2004) have been allocated to specific bin of chromosome providing initial view of the localization of subgenome and organization of chromosome. To assemble the gene spaces of *A. tauschii* and *T. urartu* (Jia et al., 2013) (diploid species in bread wheat), many high-throughput and low-cost sequencing technologies have been employed.

Around 60,000 gene sequences were specified to the subgenomes of bread wheat variety "Chinese Spring" through the use of assembled sequence data (Illumina, Incorporated, San Diego, CA) for *Triticum monococcum* and *A. tauschii,* in which cDNAs from *Aegilops speltoides* helped in gene assemblies of the bread wheat (Brenchley et al., 2012). Next-generation sequencing (NGS) has made this easy to extract information about the genes of hexaploid bread wheat and also its diploid wild relatives and therefore, a large number of single nucleotide–based polymorphic markers were developed (Krasileva et al., 2013). However, limited information was available on the position and distribution of genes present on each chromosomes of the bread wheat.

2.1 Repetitive DNA

Repetitive DNA content, TEs, and sequence repeat spacers in subgenomes (A, B, and D) were assessed throughout the whole genome of wheat. It was estimated that high copy number of repeats represented by 20 mers (Kurtz et al., 2008) contain more than 1000 copies which correspond to 24%–26% of the sequence reads from the frequently defined repeats (1.7–8.9 kb). After analyzing the transposons distribution, it was found that subgenome A chromosome as compared to B or D (A > B > D) was abundant in retrotransposons. The scheme for elements of class II (DNA transposons) was reversed (D > B > A). Retrotransposons with long terminal repeats (LTR) showed noticeable differences exhibiting ample gradient across the three subgenomes, different from Class I or II elements. The LTR retrotransposons may, therefore, represent older elements reconstructed through polyploidization and the current TE amplification or deterioration.

It is suggested that the progenitor B genome had lower number of LTR retrotransposons and polyploidization, thereby modifying transposon activity with a high coherence of recent amplifications into the B genome. It was assumed that the dynamics for amplification/degeneration of each genome was similar. A considerable reduction to 19.6% in the TE content was observed linked with 0.8% (615 Mb) of the chromosomal survey sequences (CSSs) representing contigs that contained high-confidence genes (Choulet et al., 2014). There was a twofold increase in non-LTR retrotransposons except few while reduction in the neighboring genes of class I elements were observed. Class II elements showed a decrease of 67% while Harbinger and miniature inverted repeats were the minor TEs to be enriched (Hollister and Gaut, 2009).

2.2 Protein-coding genes

In the CSS assemblies, the interpretation of protein-coding gene order has its base in contrast to interpret genes into associated grasses (*Hordeum vulgare, Oryza sativa, Sorghum bicolor,* and *Brachypodium distachyon*) also accessible in RNA-seq data and full-length cDNAs (fl-cDNAs) (Mochida et al., 2009) in Chinese Spring wheat. A total of 976,962 loci having 1,265,548 well-defined splicing variants were identified, 133,090 loci fall into high-confidence gene calls as their sequence was homologous to related grass genes. The genes were subdivided into four groups (HC1 to HC4) based on the coherence of length of reference gene occupied by predicted locus. For wheat transcript assignment, approximately 124,201 genes were notated on individual sequences on the chromosome arm, and the remaining 6.7% were not detected in the CSS assemblies. HC1 covers 55,249 (44%) of the designated loci of chromosomes that represents the functional genes covered at least 70% of the length of the supported evidence.

HC genes, fragmented in the assembly, could therefore be termed as gene fragments and pseudogenes. Further sequencing can improve the scope and quality of generic sequences to which these genes be assigned (Lang et al., 2018). Based on the level assembly completion and the rate of detection of HC1 genes, it is estimated that wheat genome comprises 106,000 genes coding functional proteins. 32,000–38,000 genes in hexaploid wheat support the claim of estimated functional protein genes for each diploid subgenome and are continuous with findings in relevant diploid species (Jia et al., 2013; Krasileva et al., 2013). Over 96% of community wheat CSS gene sets mapped by ESTs (HarvEST), comprising 89% which link to HC gene-coding loci, representing that the assemblies of CSS comprise a high characterization of the present gene listing of the wheat bread genome. This may be underestimated because 69% of the most complete gene loci (HC1) spliced alternatively with 3.5 transcripts per locus on average.

More than 300,000 individual protein-coding transcripts are encoded by hexaploid bread wheat. In all the three subgenomes, the proportion of genes showing AS appear similar and is in accordance with the complexity of transcription reported for plant species such as *Arabidopsis thaliana* and *H. vulgare* (Marquez et al., 2012).

2.3 Gene distribution and order

One of the gene classification over the three subgenomes exposed excessive amount of gene loci on the B subgenome (35%) associated with the D and A subgenomes that hold (32%) and (33%), respectively. The gene distribution was not in accordance at the chromosome level. Furthermore, these subgenomes differed from one another prior to polyploidization or showed that drivers that determine the layout of the genome behave at the regional level and not at the subgenome level.

Compatible to the observation in rye (Martis et al., 2013) and with wheat chromosome 3B complete sequence (Choulet et al., 2014), syntenic chromosome contained 53.4% of HC genes compared to *B. distachyon*, *O. sativa*, and *S. bicolor*. Synteny level for D genome chromosome was higher as compared to that for chromosome A (51%) and B (50%). Syntenic conservation was lower in LC (low confidence) gene in comparison to HC genes. LC genes were generated due to frequent generation of gene fragments by double-stranded repair mechanisms or are pseudogenes that were fragmented after they diverged from the other sequenced grass genomes, some LC genes might be functional as suggested from the retained synteny to other grass genomes (Wicker et al., 2011). To regulate the amount of gene preservation over homologous chromosomes, assemble the protein families from HC genes through sequence resemblance (Lang et al., 2018).

With the 4AL chromosome exception, the genes upon entire chromosome arms assembled through their consistent homologs. The arrangement of clustering detected in 4A is compatible along two translocations of fragments from 7BS and 5AL chromosome arms and a well-known pericentromeric inversion (Hernandez et al., 2012). All potential cluster topologies have established among genes regarding the A, B, and D genomes. The conservation patterns propose that the gene content of the D genome chromosomes is mainly close to the A and B homologous chromosomes than to each one. This inspection challenges a model of branching evolutionary interactions among the A, B, and D genomes but is consistent with models of interlinked hybridization within the Triticeae (Civan et al., 2013) and verify phylogenomic investigates which propose that the D genome is a result of homoploid hybrid phylogenetics among A and B genome lineages more than 5 mya (Marcussen et al., 2014).

The preservation of gene copies in A, B, and D genomes provides evidence that they were structurally autonomous and independently paired during meiosis (Griffiths et al., 2006). An excessive amount of subgenome independence has also being studied in the arrays of expression of gene. The GenomeZipper method (Mayer et al., 2009) integrates the syntenic preservation of gene sequence in grasses (Moore et al., 1995) to generate a virtual gene sequence within wheat, with high-density SNP-build genetic maps (Luo et al., 2013) with the known gene sequence of completely ordered grass genomes (Paterson et al., 2009). The amount of genes attached to each chromosome extended from 2125 chromosome 6B to 4404 chromosome 2D.

In general, the locations of GenomeZipper-figured locations are 21,221, 22,051, and 22,813 genes in the A, B, and D genomes, respectively. The population sequencing (POPSEQ) genetic map indicated consistency with the gene function to the GenomeZipper (99.8%) and flow-sorted chromosomes (99.4%). A number of redundant collections of 75,183 HC genes into the 21 bread wheat chromosomes via syntenic conservation or genetic mapping have been located. Gene duplication was frequently detected in wheat occurring through polyploidization or from tandem or integrated duplication related along replication (Zhang, 2003; Li et al., 2003a). The inference from HC1 genes projected that genes are duplicated onto every chromosome among 29.7% (chr. 2B) and 19.1% (chr. 7B) (Lang et al., 2018). This may be due to the chromosome-shotgun sequences or whole genome that collapse greatly preserved duplicates.

Among the three subgenomes, no substantial changes have been observed in the percentage of duplication. In each chromosome, equally 73% duplicates are placed onto one of the chromosome arms, proposing that there might be tandem duplicates which occur by uneven replication-dependent chromosome breakage and crossing-over (Koszul et al., 2004) or by the TEs activity. The comparison of wheat subgenomes and intrachromosomal duplicates in foxtail millet rice, barley, sorghum, and maize was found as 17%–20% (Paterson et al., 2009; Schnable et al., 2009).

2.4 Related species

Data from sequence of seven bread wheat species related to ancestors in A, B, and D subgenomes were organized and arranged (Lang et al., 2018). Along with this, illumina whole genome sequence data were collected from pair of tetraploid wheat cultivars (AABB) *T. turgidum* "Strongfield" (initiating in Canada) and *T. turgidum* "Cappelli" (initiating in Italy), and also from *A. speltoides* (SS) the diploid genome. These data being incorporated along complete genome data sequence from (Ling et al., 2013) *Aegilops sharonensis* (SshSsh), *A. tauschii*, *T. monococcum* (AAmm), and *T. urartu* (AAuu) (Jia et al., 2013). In the nonexplained genomes of *A. sharonensis, T. monococcum, A. speltoides,* and *T. turgidum*, interpreted grass genomes of proteins and *T. aestivum* gene type have proposed on the sequence construction (Mayer et al., 2012; Tanaka et al., 2008).

To define the core wheat genes and loss after polyploidization or gene retention, gene families and genes in the diploid, tetraploid, hexaploid, and genomes have been linked. Gene loss largely affected genes families of diploid genomes in *A. tauschii* (Jia et al., 2013) and *T. urartu* (Ling et al., 2013) when comparing with the subgenomes of hexaploid wheat (Brenchley et al., 2012). On the other hand, singletons were not generally subject to loss of gene later polyploidization. Loss patterns have been detected dependent on the considered gene family.

Extremely related gene retention proportions have been seen for whole bread wheat subgenomes in relationship to *A. tauschii* [0.91 (A), 0.96 (B) and 0.91 (D) against *T. urartu*] and against *A. tauschii* and *T. urartu* 0.91 (A), 0.94 (B), and 0.89 (D). Gene loss in the hexaploid D subgenome seemed slightly lesser than the most olden A and B subgenomes (Buggs et al., 2012). It was inferred that bread wheat subgenomes from the A genome ancestor (*T. monococcum and T. urartu*), B ancestor (*A. speltoides* and *A. sharonensis*), the D ancestor (*A. tauschii*), also the *T. turgidum* tetraploid genome have an ortholog in the genomes. They have identical percentage of genes (60.1%−61.3%) with entirely connected diploid genomes.

2.5 Molecular genetic maps

During the late 1980s, some efforts were primarily made toward molecular markers mapping on wheat genome (Chao et al., 1989). Only then in 1990, an organized production of molecular maps in wheat started, coordinated wheat genome molecular maps, with the association of International Triticeae Mapping Initiative (ITMI). Separate committee groups arranged the chromosome maps for each of the seven diverse homologous individuals.

Integrated maps including many more variety of molecular markers (mainly the microarray-derived diversity array technology or simply the DArT, SSR, SN, and AFLP) have also been produced in wheat. Consensus maps, which provide data from various genomes, or several maps were fused with a particular inclusive map (Somers et al., 2004). Recently, more than 2500 genomic SSR (gSSR) markers are mapped and accessible in wheat, to classify basic recombination measures in population breeding and gene map. Besides gSSRs, some 300 EST-SSR would be present on wheat genome (Yu et al., 2004). Furthermore, gene functional markers (FMs), gene-targeted markers (GTMs), and random DNA markers (RDM) were utilized to identify genes liable for single traits and to develop MAS using possibilities in wheat breeding.

2.6 In situ hybridization in wheat

The rRNA, foreign DNA fragment, and repeated DNA structures were isolated in bread wheat using in situ hybridization utilizing radioactively labeled probes (Mukai et al., 1993; Pedersen and Langridge, 1997). Afterward, the genome in situ hybridization (GISH whole genomic DNA just as probe), multicolor FISH (McFISH, simultaneous recognition of multiple probes), and fluorescence in situ hybridization (FISH) were utilized. FISH was also used to physically map rRNA multiple gene stock (Ma et al., 2001; Zhang et al., 2004b), individual structures and RFLP markers (Li et al., 2003b; Turnbull et al., 2003) and also for identifying and localizing foreign chromatin introgressed within wheat (Schwarzacher et al., 1992; Mukai and Gill, 1991).

FISH is a novel high-resolution procedure, which utilizes superstretched flow-sorted chromosomes (extended DNA fiber-FISH) (Yamamoto and Mukai, 2005; Lavania et al., 2003) to finely map DNA sequences (Fukui et al., 2001) and to confirm successful integration of transgenes into wheat genome (Jackson et al., 2001). Bacterial artificial chromosomes (BACs) were also used as probes for BAC-FISH procedure that facilitated the differentiation among the three subgenomes. BAC-FISH further used in the recognition of specific chromosomes molecular cytogenetic markers and intergenomic translocations (Zhang et al., 2004a). BAC-FISH additionally facilitated in restricting of genes (BACs bearing genes) and also in analyzing evolution and association of genome (Li et al., 2013) between wheat and its families (Zhang et al., 2004b; Gupta et al., 2008).

2.7 Present status and future prospects

Wheat has a wide genome (16,000 Mb) with 80% of the repetitive structures. Wheat crop, thus, remained a challenging crop for genomics studies. A huge EST sets and compact molecular maps (both physical and genetic) and the quantitative trait loci (QTL) enabled genome determination of poor and rich gene areas. The accessibility of markers related to important economic feature also permitted improvement of main strategy of marker-assisted selection in several states and promoted map-dependent cloning of several genes. The functional genomics resources containing RNA interference (RNAi), tilling map alongside with certain novel methodologies like mapping corporation and epigenetics were effectively utilized for wheat genomics (Gupta et al., 2008).

3. Genome editing

Entire plant traits outcome from a composite array of physiological, developmental, and biochemical procedures summarizes into phenotypes. The genetic traits include both the regulatory and compositional directions in the individual cells and the developing plant (Petolino, 2015). Current biological techniques have employed devices permitting the organized modification of the plant DNA sequence. The combined effect of DNA-binding domain and nucleases is utilized in tools for editing genome. They efficiently can identify and edit a particular DNA sequence (Urnov et al., 2010). Specifically strategies like zinc-finger nucleases (ZFNs), transcription activator-like effectors nucleases (TALENs) (Bogdanove and Voytas, 2011), meganucleases (Stoddard, 2011), and clustered regularly interspaced short palindromic repeats/CRISPR-associated (CRISPR/Cas) were successfully utilized to induce on-target DNA nicks on both strands (Shan et al., 2013). The nick can then induce natural repair pathways that can be programmed accordingly. The genome editors allow numerous types of genetic variations extending from rearrangements, mutation in single nucleotide to deletion of large sequences, integrations of nucleotides, etc. (Curtin et al., 2012). A brief comparison of CRISPR, ZFNs, and TALENs has been done in Table 24.1.

3.1 Zinc-finger nucleases

ZFNs are enzymes which produce double-stranded breaks (DSBs) in DNA at specific sites (Carroll, 2011). ZFNs have a site for binding DNA, a chain of two-finger modules that identify an exclusive 6-bp hexamer, and a DNA-cleaving domain most certainly a FokI nuclease (Carlson et al., 2012). The DNA is then modified with the ligation of DSBs (Gupta et al., 2012). The zinc-finger protein (ZFP) Cys_2His_2 delivers the greatest possible structure in creating appropriate ZFNs through the required specificities of sequence (Pabo et al., 2001). The ZFP contains around 30 amino acids and possess a $\beta\beta\alpha$ structure that becomes stable through the zinc ions chelation to preserve Cys_2His_2 amino acids (Thakore and Gersbach, 2015). The ZF motif attaches to the sequence of DNA within the genome through the integration of its α-helix within the DNA double helix major groove (Pavletich and Pabo, 1991). The amino acids at locations -1, $+1$, $+2$, $+3$, $+4$, $+5$, and $+6$ of the zinc finger on the α-helix are accountable for specific sequence association of ZFNs through the sequence of DNA (Elrod-Erickson and Pabo, 1999; Shi and Berg, 1995). Each finger attaches a triplet DNA sequence. Several zinc-finger motifs are required to recognize and

TABLE 24.1 Comparison of approaches used in genome editing.

Approach	Mechanism of action	Important components	Efficiency	Target site requirements	References
ZFNs	Protein nucleases recognize target DNA.	FokI endonuclease with finger domain connected through zinc ions.	Variable	Binding sites for Cis_2His_2 residues of FokI endonuclease.	Carlson et al. (2012)
TALENs	Protein nucleases recognize target DNA.	FokI endonuclease along with TALEN.	High as compared to ZFNs	12−15 bp distance between two enzymes binding to the DNA fragments.	Bitinaite et al. (1998)
CRISPR/Cas9	gRNA recognizes target DNA.	gRNA and Cas9 protein as vector.	High efficiency	gRNA and PAM sequence before target gene site.	Bitinaite et al. (1998)

bind DNA strands (Beerli et al., 1998; Jia et al., 2013; Liu et al., 1997). Furthermore, the transcription repressor domain, FokI cleavage domain, methylase domain, and/or transcription activator domain may be connected with ZFP (Alwin et al., 2005; Mani et al., 2005). An overview of mechanism of action of gene editing by ZFNs FokI endonucleases has been illustrated in Fig. 24.1.

3.2 Transcription activator-like effector nucleases

TALENs are the effector proteins, first observed in *Xanthomonas* bacterial infection that alters transcription of certain genes in the host plants (Boch and Bonas, 2010). TALENs are considered an effective genome editing tool, alternative to ZFNs (Joung and Sander, 2013). TALENs contain nonspecific FokI endonucleases linked with DNA-binding domains. Similarly, TALENs induce DSBs in a way similar to ZFNs. Highly conserved amino acids of 33−34 amino acids are observed in the DNA-binding domain of TALENs having two hypersensitive residues at position 12 and 13. Each module recognizes specifically a single nucleotide base.

Repeat variable di-residues (RVDs) are the 12th and 13th positions that display substantial association with particular nucleotide identification. RVD is considered crucial in nucleotide base recognition. The dimeric FokI endonuclease domain cleaves DNA nonspecifically (Bitinaite et al., 1998; Mani et al., 2005). The number of amino acid residues among the FokI cleavage domain, and the DNA-binding domain and the number of bases among two separate TALEN-binding sites are essential considerations influencing the TALENs activities. On the other hand, the TALENs can be transiently expressed as mRNA that may reduce the probability of their integration into the genomes.

TALENs technology is effectively utilized in *O. sativa* (Li et al., 2012). The disease-resistant rice has been generated where the promoter region *Os11N3* gene in bacterial blight was targeted. TALENs editing is considered more efficient than ZFNs partly due to easy design and the infinite series of target sequences (Joung and Sander, 2013). To this end, knockout mutants of *A. thaliana* have been efficiently generated by using TALEN technology (Cermak et al., 2011).

3.3 Clustered regularly interspaced short palindromic repeats/CRISPR-associated proteins

Several strategies have been adapted by bacteria to control genetic variations and defend against invading pathogens. Some of these strategies are mutating cell surface receptors, abortive infection, modification through restriction enzymes and CRISPR systems (Shen et al., 2013). CRISPR is a predominant adaptive immunity in bacteria which enables them to develop a genetic memory of previous genetic infection through sequence specificity (Chang et al., 2013). The mechanism of CRISPR includes two elements: (1) a guide RNA (gRNA) specific to the sequence of target DNA and (2) a CRISPR-associated nonspecific endonuclease protein (Fig. 24.2).

Cas protein functions as a pair of molecular scissors, while the gRNA guides the Cas protein to its target sequence. gRNA is modified to target multiple variable nucleotide sequences. Protospacer adjacent motif (PAM) region, situated downstream of target DNA, is also responsible for target recognition. PAM region differentiates between the cell and foreign nucleic acid sequences.

The gRNA consists of two different segments of RNA in its natural form: CRISPR RNA (crRNA) and transactivating CRISPR RNA (tracrRNA). The crRNA is complementary to the target sequence of DNA, and, therefore, may recognize the sequence to be cleaved (Anders et al., 2014). Designed crRNA to the target can target virtually any nucleic acid sequence. The function of tracrRNA is to hold crRNA within the Cas complex. The crRNA, tracrRNA, can be engineered as a solitary sequence known as single-guide RNA (sgRNA) (Shen et al., 2013; Mali et al., 2013).

CRISPR/Cas induces DSBs. Cells may repair DSBs or eventually, the cell may disintegrate. There are two lineages of the repair pathways—the nonhomologous end joining (NHEJ) and the homology-directed repair (HDR). NHEJ can be utilized for genome editing if downregulation/silencing of a sequence is required. NHEJ may ligate the DSBs, however, and is susceptible to error and might insert or delete nucleotides (the indels) (Hahn et al., 2018; Dueva and Iliakis, 2013). Knock-in procedures and intended repairs utilize HDR where a homologous template is provided for a directed and programmed repair.

Several different known Cas proteins are accessible to use Cas9 nuclease from *Streptococcus pyogenes*. SpCas9 is the most frequently utilized nuclease in CRISPR-based editing. SpCas9 can recognize NGG (N indicates all nucleotide) as PAM motif and may generate a DSB along blunt ends at the target location (Zhang et al., 2014). Cas9 nickase is a mutated Cas9 protein that produces nick at single-strand rather than the DSB. Cas9 nickases can be utilized to induce

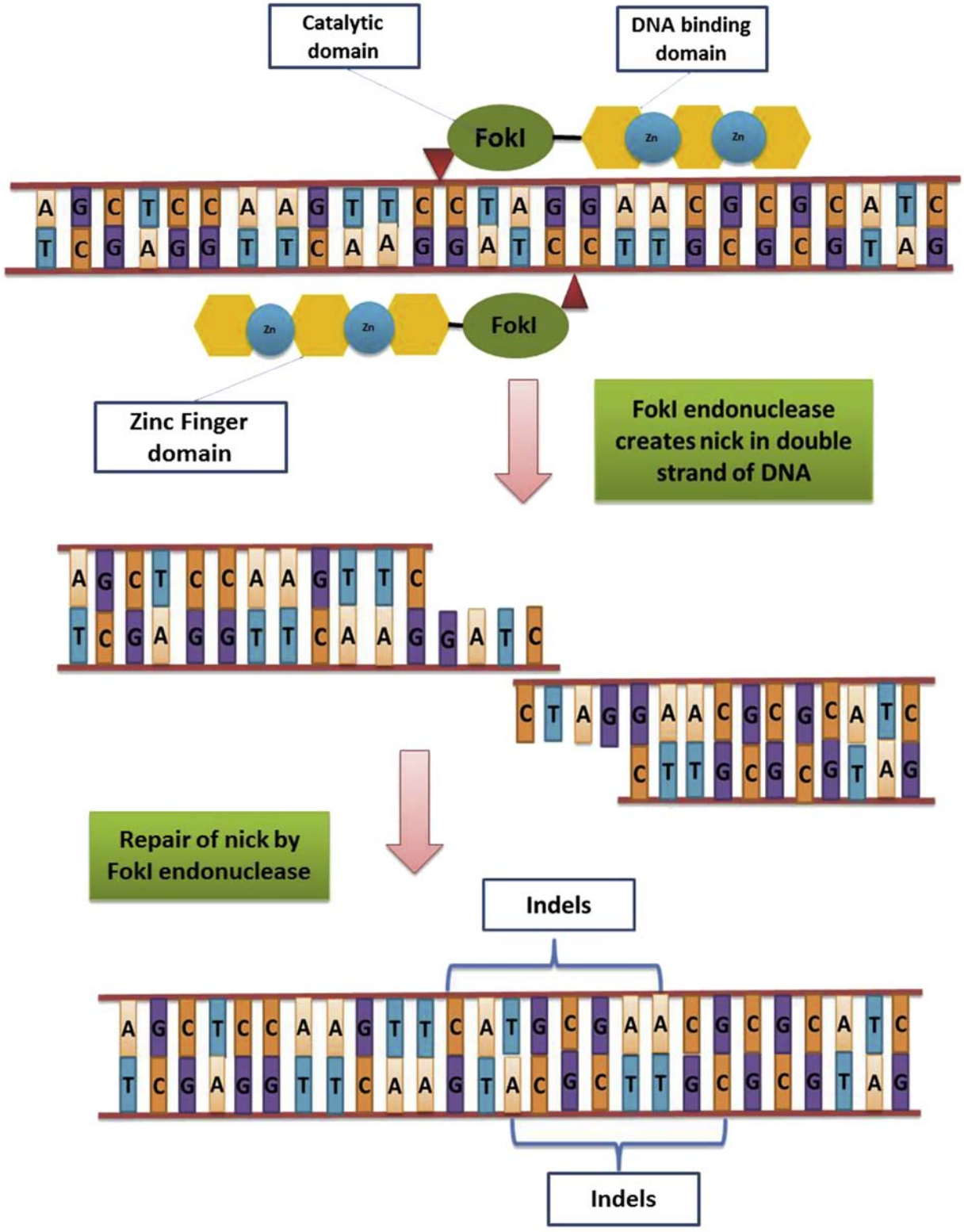

FIGURE 24.1 Mechanism of action of gene editing by zinc-finger nucleases (ZFNs) FokI endonuclease. The production of ZFNs that identify and cleave particular target sequences can be efficiently designed. Zinc fingers precisely attach to triplets of DNA. The existence of 64 triplet alternates in the genome creates it stimulating to project ZFNs which attach every single triplet variant. *Information retrieved from Dreier, B., Beerli, R.R., Segal, D.J., Flippin, J.D., Barbas, C.F., 2001. Development of zinc finger domains for recognition of the 5′-ANN-3′ family of DNA sequences and their use in the construction of artificial transcription factors. Journal of Biological Chemistry 276, 29466–29478; Dreier, B., Fuller, R.P., Segal, D.J., Lund, C.V., Blancafort, P., Huber, A., et al., 2005. Development of zinc finger domains for recognition of the 5′-CNN-3′ family DNA sequences and their use in the construction of artificial transcription factors. Journal of Biological Chemistry 280, 35588–35597; Jamieson, A.C., Miller, J.C., Pabo, C.O., 2003. Drug discovery with engineered zinc-finger proteins. Nature Reviews Drug Discovery 2, 361–368.*

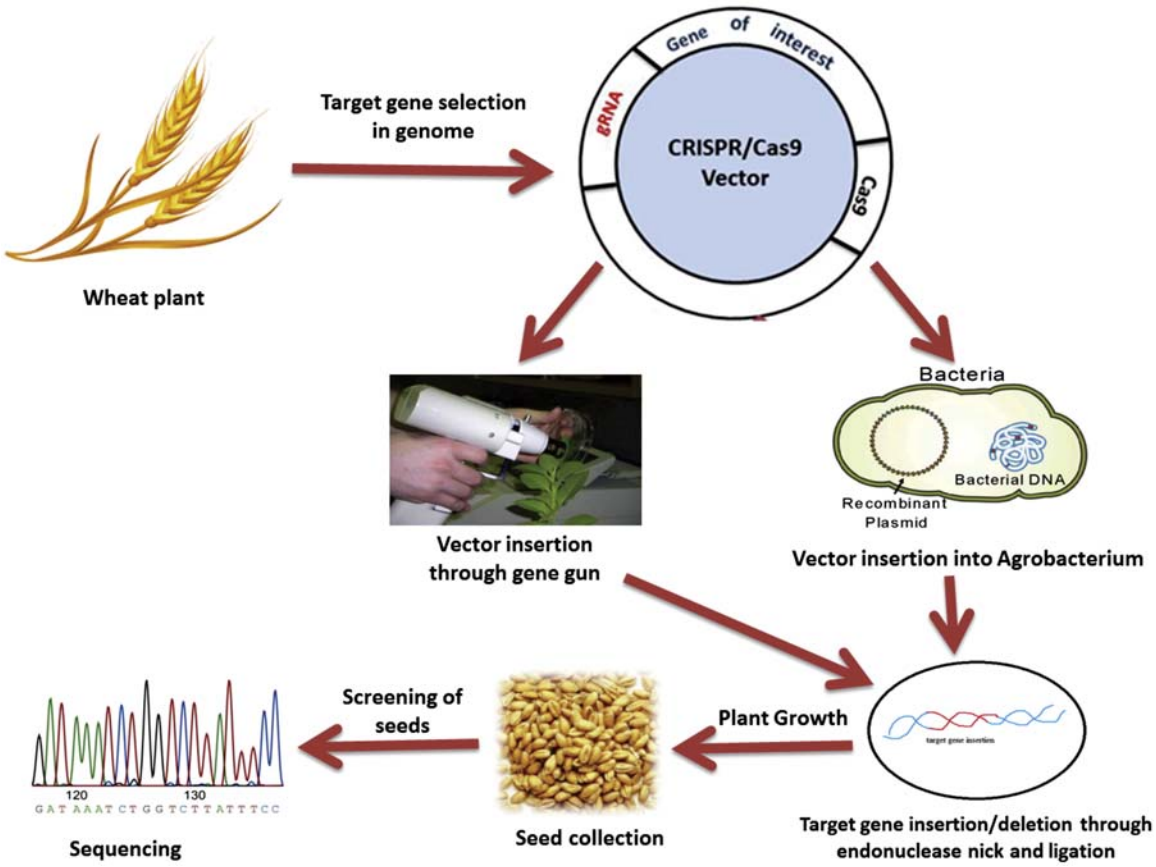

FIGURE 24.2 Flow scheme diagram of genome editing in bread wheat plant using CRISPR/Cas9.

single-strand breaks at two locations followed by the repair. Staggered nicks producing long overhangs allow additional control upon introducing a DNA fragment designed for HDR repair (Hahn et al., 2018). This may impart more specificity and may reduce the off-targets (Jinek et al., 2012).

Another Cas protein is Cpf1 obtained from *Prevotella* and *Francisella* bacterial species. Cpf1 functionally varies from SpCas9 in three ways: (1) Cpf1 identifies TTN as a PAM motif. It hence could be an improved choice for DNA regions targeting through high AT content rather than the Cas9, (2) Cpf1 generates a staggered double-stranded (overhangs), instead of the blunt end, nick generated by SpCas9, and (3) Cpf1 protein is smaller than SpCas9 and does not need the presence of a tracrRNA. The gRNA essential for Cpf1 therefore be smaller and cost-effective (Kim et al., 2016).

*Sa*Cas9 isolated from *Staphylococcus aureus* is an ortholog of Cas9 and belongs to Cas9 family. It, however, recognizes NNGRRT as a PAM sequence. The size of *Sa*Cas9 protein is much smaller than *Sp*Cas9. Due to its smaller size, its insertion in plasmid vectors is easier to deliver it to the cells when compared with SpCas9 (Richter et al., 2012).

CRISPR/Cas system is an adaptive immune system present in Archaea and approximately 60% of the bacterial community. The system employs short noncoding RNA sequences, CRISPR array, and Cas proteins. Three phases are known—acquisition, expression, and interference/immunity. First, foreign genetic elements known as spacers acquired from invading/foreign sequences are integrated into specific repeat sequences. The spacers, each flanked with repeats, constitute a CRISPR array. The Cas proteins are produced and the CRISPR array is transcribed and matured into crRNAs. The plasmid or the invading phages are targeted thus facilitated by a Cas protein and crRNAs complex.

Great diversity among CRISPR/Cas systems exists even though they share similarities (Gasiunas et al., 2012). There are three major CRISPR/Cas system types (I–III), which are categorized by the signature protein. Cas proteins and repeat sequences of the linked array of CRISPR are further divided into subtypes (e.g., I–A to I–F) based on the occurrence of subsets (Barrangou and Marraffini, 2014; Richter et al., 2012).

3.3.1 *Transgenerational CRISPR-Cas9 activity facilitates multiplex gene editing in allopolyploid wheat*

In crops, the multiplexed gene editing based on CRISPR-Cas9 provides a great technique to modify various genomic regions simultaneously managing several agronomic traits. The construct was manufactured by mixing the tandemly arrayed units of tRNA−gRNA to produce heritable mutations in TaLpx-1, TaMLO, and TaGW2 genes of hexaploid wheat. Considering all three homologous copies, gene knockout was successfully produced. The massive increase in seed mass and grain weight was brought by TaGW2. In the early generation of plants, nonmodified gRNA targets can be edited by CRISPR-Cas9 in the next generations. Plant genetically modified with CRISPR-Cas9 can be crossed with a normal line of interests to get improvement in crop plant (Wei et al., 2018).

The genetic variation in conventional breeding or mutant wheat lines and its wild progenitor are the key sources of valuable allelic diversity for further improvement in characters. CRISPR-Cas9 with a potential of multiplex genome editing holds enormous promise in overcoming the restrictions of availability of genetic diversity in conventional breeding. It is also a helpful tool in modifying the agronomic traits of plants (Nissim et al., 2014; Xie et al., 2015). Wheat protoplasts following the first description of genome editing based on CRISPR-Cas9 were regenerated. CRISPR-Cas9 was successfully utilized in transforming the immature embryos of wheat plant including linear RNA plasmids, ribonucleoprotein complexes, and the linear DNA fragments (Zhang et al., 2016; Upadhyay et al., 2013).

In humans, first multiplexed gene editing reported cells employed CRISPR-Cas9 locus and multitarget protospacers were combined in a single pre-crRNA array. It was further modified into gRNAs, Cas9, and the endogenous RNase III. The resulting complexes of ribonucleo-proteins were capable of promoting mutations on various target sites (Cong et al., 2013). Moreover, certain gRNAs having self-promoters within a single construct was found promising in rice, maize, wheat, tomato, *Arabidopsis*, and maize (Ma et al., 2015; Li et al., 2013).

Successful attempts were made utilizing Csy4 nuclease and a 28-bp recognition site with gRNAs from tandemly arrayed units in human cells and in various plant species (Cermak et al., 2017). In rice, functional multiplex gene editing was accomplished by using tRNA spacers in adjacent gRNAs under the control of a single promoter. The use of tRNA spacers in the polycistronic gene transcript might promote endogenous RNA processing system (Xie et al., 2015). In immature wheat embryos functionality of gRNAs generated by either endogenous tRNA or Csy4 ribonuclease processing systems were effectively utilized (Cermak et al., 2017). One of the construct of multiplex gene editing comprised gRNAs targeting the TaLpx-1, TaMLO, and TaGW2 genes. The grain width, thousand grain weight, grain length, and grain area were negatively linked with the A genome homolog of TaGW2 gene (Qin et al., 2017). Silencing of TaLpx-1 gene encoding 9-lipoxygenase rendered resistance of wheat to *Fusarium graminearum*. Resistance was observed in wheat against powdery mildew with knockout alternations in all three homologs of TaMLO (Zhang et al., 2004b; Wang et al., 2014). The gRNAs were to target the TaGW2 gene in conserved regions of all three genomes to check the achievability of all two, three, or only one of the gene homologs in allopolyploid genome of wheat, the TaLpx-1 gene in the area conserved in just two genomes, and the TaMLO gene in the A genome particular region. Genome editing in wheat protoplasts using gRNAs was validated with multiple gene construct. The potential of the multiplex gene editing construct to influence agronomic traits was explored by studying the effects of alternations in the TaGW2 gene on simple scored seed morphology traits controlled by this gene. In wheat lines, mutations in the multiplex gene editing construct progenies showed that the transgenerational CRISPR-Cas9 activity is a significant source of novel mutations that can be utilized to acquire alternations across several sites targeted by the gRNAs. This activity of transgenerational gene editing can also be exploited for reconstructing the breeding lines of wheat genomes by crossing them with the plants expressing CRISPR-Cas9 constructs (Wang et al., 2014).

A single promoter with an array of gRNA-tRNA can be used to bring heritable changes in the wheat genome at multiple targets (Xie et al., 2015). The results of the experiments were assessed by comparing the morphology of normal and *gw*2 knockout seeds confirming the success of the experiment. The mutations were observed in all three copies of TaGW2 gene. The grain weight and grain width were negatively linked with TaGW2 functionally active A homolog before these results, while two other studies suggest that A genome negatively influences the grain length (Jaiswal et al., 2015). Mutation in TaGW2 homologs with CRISPR eliminated the function of these genes and substantially increased the grain weight, grain length, area, and width. TaGW2 homologs in genomes B and D were also suggested to have the same functions as a genome homologs and may have additional effects on physical appearance, i.e., phenotype of seed. This multiple gene-editing strategy is quite useful in editing complex wheat genome, which has at least three homologous copies for maximum genes. The gRNAs should be designed to specifically target the gene in one homolog or target several of the duplicated genes, or it should target several genes from a defined selective genome. The use of single polycistronic RNA-gRNA/Cas9 construct can be used to bring multiple allelic changes in wheat plant genome (Simmonds et al., 2016).

However, it was recommended that this strategy was more successful in polyploid plants as compared to diploid plants. NGS results of CRISPR-Cas9-edited plants identified precise somatic gene editing in a portion of the cells in leaf tissues, indicating ongoing CRISPR-Cas9 action. The successful recovery of edited genes in the new generation of transgenic plants provided a path for successful heritable variation through CRISPR-Cas9. Compatible with the results, plants were recovered successfully with several targets edited in the scions taken from a plant having the active CRISPR-Cas9 multiplex gene-editing construct. Moreover, another advantage of the transgenerational CRISPR-Cas9 movement in multiplex gene-editing construct expressing plants is that it offers the possibility for gaining lines having different mixtures of mutations across different targets. For traits with a complex genetic basis, these lines can be used to study additive and/or epistatic interactions between numerous edited gene variants and to select the most ideal combinations of novel alleles (Simmonds et al., 2016). Recently, the transgenerational CRISPR-Cas9 was used to induce efficient variants at multiple target sites in tomato F1 plants. The useful mutations in the wheat breeding lines not willing to transformation could be tempted by crossing these lines with the wheat lines resonant with the CRISPR-Cas9 constructs. The strategy delivers an effective method for the systematic transfer of beneficial edited genes into the breeding programs (Rodriguez-Leal et al., 2017).

3.3.2 *TaDREB2 and TaERF3*

Numerous techniques such as T-DNA insertions and EMS mutagenesis have been used to generate random mutations. Developments in technology stimulate the finding of genome editing methods such as TALENs- and ZFNs-enabled targeted gene editing (Bortesi and Fischer, 2015). More recently, a more precise genome editing tool, the CRISPR/Cas, was found to be simple, effective, and a more customized approach for crop improvement (Doudna and Charpentier, 2014).

More recently, Cas9D10A (Cas9 nickase alternate) has been used for further specific editing of genomes. Numerous genome editing experiments for crop improvement were accomplished in both dicots and monocots, e.g., *S. bicolor* (Jiang et al., 2013), *A. thaliana* (Li et al., 2014), *Nicotiana tabaccum* (Gao et al., 2015), *O. sativa*, and *Nicotiana benthamiana* (Li et al., 2015). Certain shortcomings are there in CRISPR-Cas9 application in certain plant species (Peng et al., 2016). The hexaploid nature of the wheat genome marks this plant a significant version for studying and optimizing the genome editing method.

Drought, salt concentration, and micronutrient deficiency are the abiotic stress factors mainly responsible for losses in wheat production every year (Araus et al., 2008; Budak et al., 2015). Plants may defend these conditions by expressing several different genes in a comprehensive signal mechanism (Golldack et al., 2014). The main factors controlling the expression of these genes are transcription factors, which activate/deactivate the molecular pathways (Singh et al., 2002). A CRISPR-Cas method is a flexible tool for genome editing. CRISPR-Cas9 application within the wheat protoplast directed selective editing of transcription factors of stress accessible ethylene-responsive factor 3 (*TaERF3*) and stress accessible dehydration responsive element-binding protein 2 (*TaDREB2*) genes. Editing of *TaERF3* and *TaDREB2* was performed with short-lived expression of Cas9 protein and small guide RNA within the protoplast of wheat. The efficiency of wheat protoplast mutagenesis was verified with using T7 endonuclease assay, sequencing, and restriction enzyme digestion assay. Numerous off-target areas were considered for designed sgRNAs. The genome-editing specificity was then verified through amplicon sequencing. Results, considering the currently available tools, suggested that CRISPR-Cas9-based genome editing in wheat can be an optimal tool for crop improvement (Kim et al., 2018).

Several studies record the effect of DREB genes on enhanced drought tolerance (Lata and Prasad, 2011). Overexpression of DREB members in *Arabidopsis* and soybean increased the drought resistance without affecting the growth parameters (Nakashima et al., 2014). Similarly, DREB2 and DREB3 genes were overexpressed in wheat and barley enabling them to resist drought conditions (Morran et al., 2011). These proteins were found to occur more abundantly in root tissue when compared with leaf tissues (Lucas et al., 2011). In maize, genetic variation in the promoter region of DREB2 showed differential response toward drought conditions. In root development, ERF3 has an important role and that the cytokine response is activated by its interaction with Wox11 protein (Zhao et al., 2015). This interaction is important in the development of root hairs and root elongation in drought tolerance (Cheng et al., 2016).

In Chinese Spring (wheat variety), TaDREB2 and TaERF3 were upregulated with drought stress. To conclude, DREB2 and TaERF3 were crucial genes responsible for abiotic stress tolerance, drought in specific. The plasmid pJIT163-2NLSCas9 under TaU6 promoter site and selected sgRNAs were expressed. It was concluded that codon-optimized Cas9 for rice can be utilized in an efficient manner in wheat. Although the transformation efficiency was lower from the previous studies (Shan et al., 2014), the acquired rate of the transformation was enough for the targeted genes to be edited and validated by three different mutation techniques. As compared with TaERF3,

the rate of efficiency of mutation was low in TaDREB2. The reason for the low mutation rate may be due to the location of the chosen sgRNA sites.

There are several concerns regarding the specificity of genome editing using the CRISPR/Cas system (Schaefer et al., 2017; Sharpe and Cooper, 2017). To find out the specificity of genome editing, NGS of the off-target regions was performed based on the homology of sgRNA in comparison to several regions in wheat. For TaDREB2, three amplified regions of off-targets were sequenced through amplicon sequencing and two different online tools including CRISPR-GA (Guell et al., 2014) and Cas analyzer (Park et al., 2017) were used for analyzing the results. Both programs generated results that were in accordance with one another.

Random mutations that occur or arise due to the nature of the PCR amplification process is controlled by the minimum frequency parameter present within Cas analyzer. Due to high GC content in the amplicon of choice during the reaction, it caused random insertions/deletions in both wild-type and mutant samples (Park et al., 2017).

Off-target genome editing efficiency with PAM sequence was low for TaDREB2 as compared to the target sequence. CRISPR/Cas is an efficient genome editing tool and has the potential to manipulate the wheat genome resulting in the production of improved performing crop (Kim et al., 2018).

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CHAPTER

25

The economic aspects of climate risks and food insecurity

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OUTLINE

1. Climate risks

Global warming is real. Our planet is warming, from one pole to the other. According to National Geographic, the global average surface temperature has increased by approximately 1°C (1.6°F), even more in the sensitive regions since the early 1900s (Global Warming Effects, n.d.). The more concerning part is the fact that the adverse effects of such a rise in the global temperature are not waiting for some far-flung future. They are appearing on the face of earth right now. The sea ice and mountain glaciers are melting, the precipitation (rain and snow fall) patterns are shifting, ecosystem is changing, and the animals are migrating, to name a few.

Ice is melting around the globe, particularly at the north and south poles. The big thaw includes Arctic sea ice, ice sheets covering Greenland and West Antarctica, and mountain glaciers. The number of mountain glaciers in Montana's Glacier National Park has decreased to less than 30 from 150 in 1910 (Glick, n.d.). Most of the remaining glaciers have shrunk to approximately two-thirds of their size. As per National Geographic, most of the park's namesake glaciers will disappear within the next three decades (Glick, n.d.). Similarly, glaciers in Himalaya (India) are melting at such an accelerated speed that the scientists believe that most of these glaciers on the eastern and central areas will virtually disappear from the world's map by 2035 (Glick, n.d.). Also, Kilimanjaro's famed snows have also melted almost 80% since 1912 (Glick, n.d.).

Additionally, the precipitation (rain and snow fall) rates, on average, have increased across the globe. Yet, some of the planet's regions are experiencing more severe drought, which has increased the drinking water shortages and risks of

https://doi.org/10.1016/B978-0-12-819527-7.00025-X

wildfires and lost crops. The rising temperature intensifies the water cycle, causing increased evaporation. It causes more storms at one end and contributes to drying over some particular land areas on the other end. As a result, the areas located far from the storm-affected areas experience less precipitation, causing increased risk of drought, whereas the storm-affected areas experience increased precipitation, increasing the risk of flooding. The 2017 flooding in California provides a great example in this regard, which followed a prolonged and intense drought (Nuccitelli, 2017).

As winters have become milder and shorter, the earth's ecosystem is changing. For many species, the climate influences key stages of their life cycle such as reproduction, blooming, and migration. The climate change has changed the timing of these events in some parts of the planet. For instance, 16 out of 23 species of butterflies arrived earlier in California due to changing of their migration timing (CCSP, 2008). Also, earlier springs are resulting in earlier nesting for more than 25 species of migrating birds on the US North Coast (IPCC, 2014a,b). Globally, butterflies and birds are breeding 4 days earlier with every passing 10 years, whereas frogs and other amphibians are breeding 8 days earlier (Poloczanska et al., 2013).

The climate change has led the animals on the move as well. Approximately half of all life is moving. Sandflies, which host leishmaniasis-causing parasite, have moved into northern Texas while they were once primarily tropical affliction (Kaffenberger et al., 2017). Mosquitoes are moving to higher elevations due to rising thermostats, thus causing malaria to now appear in the higher up mountain slopes in Ethiopia and Columbia (Siraj et al., 2014). Marine life is moving four times faster as compared with the ones on the land, which are moving more than 10 miles per decade (Chen et al., 2011).

2. Food insecurity

Food security has continuously been defined over time. According to the definitions provided by the UNICEF and FAO, food security is a multilayered concept that serves four purposes: (1) food availability, (2) economical and physical food access, (3) cultural and dietary food utilization, and (4) food stability in terms of its provision. Unfortunately, climate change affects all four pillars of food security. Through these pillars, it channels its way to impact food production and distribution channels, livelihood assets, human health, as well as changing market flows and purchasing power. More devastatingly, the impact of global warming is both short- (resulting from more intense and more frequent extreme weather conditions) and long term (caused by precipitation patterns and global temperatures).

The FAO has been using its traditional tool named Prevalence of Undernourishment to monitor hunger at local and global levels. The tool worked based on the occasional data on food consumption available for a few countries and an aggregated country-wise data available for most countries, to produce an estimate for the number of people who do not have enough access to food in one way or another. Later, the FAO adopted the methodology of Food Insecurity Experience Scale, which comprises eight questions. It has two prime features: firstly, the data can be disaggregated because it is a survey-based measure; therefore, countries most affected by food insecurity can be identified, and secondly, it makes estimating prevalence of food insecurity measureable at different levels of severity.

3. Economics of climate change

The increasing global temperatures negatively impact the overall economic activities in the long run. However, there are a number of ways in which global warming will influence economic growth, i.e., through security threats, mass immigration, lost productivity, and damage to property and infrastructure. The impact of climate change is widespread due to economic, political, and financial integration of the world's economies. In the race of combating global warming, there will be winners and losers, but the balance between them turns increasingly negative as the temperatures rise.

Climate change is expected to alter the severity and frequency of extreme weather events. It brings with it infrastructure and property damages. The Hurricane Sandy is a prime example in this regard. It flooded most of the New York City in 2012. Additionally, the rising sea levels are also likely to harm economic output as a consequence of people suffering damage to their homes and businesses becoming impaired. Although the initial economic response to recover such damages would appear in the form of a positive gross domestic product, the world economy will face severe challenges once it realizes that such extreme weather discrepancies are a permanent feature of the environment.

For instance, many economists and researchers would feel that there is no point in replacing capital stock until and unless there is a permanent or semipermanent solution to prevent any further future damages or if there is an opportunity to shift the business to a safer ground. At the worst, moving the business to a safe haven would result in permanent loss of output and capital stock, and at the best, it would only include a small period of disruption when the business relocates. But the damage will become increasingly permanent as the global temperatures continue to climb.

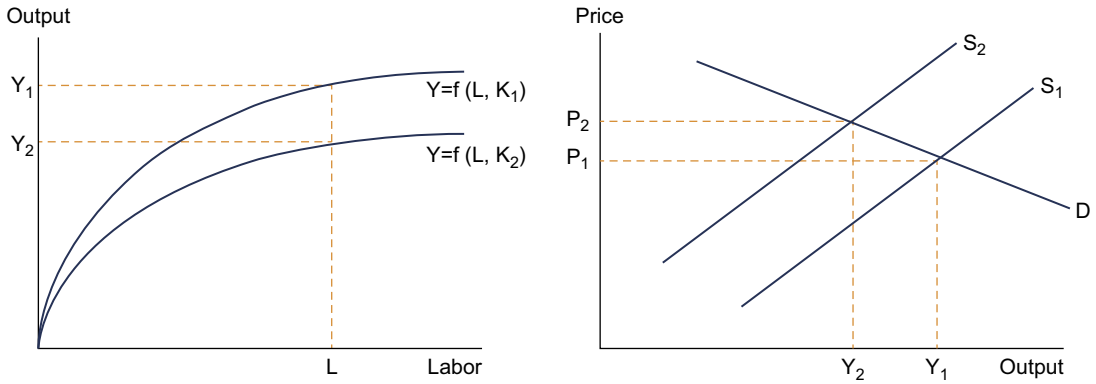

FIGURE 25.1 Global production function and demand and supply effects.

In an attempt to demonstrate the likely effect of climate change on output, the production function presented in Fig. 25.1 can be utilized. The figure shows a fall in the production capacity of the world economy if less capital stock is available due to the climate risks. It translates into a downward shift in the production capacity as each labor produces less output. However, lesser capital stock would not be the only reason behind lower labor productivity. Higher global temperature will also impair those working outside, promote the spread of infectious diseases, and may affect overall food security of the planet. Such variables are expected to cause greater social unrest and incapacity, which reduce both the amount and productivity (effectiveness) of the labor available to produce output.

Such effect of damage from climate change on global output productivity can also be seen in the form of a supply and demand framework. Overall, global warming is likely to bring a supply shock in the world economy. It tends to construct supply at any given price, which eventually will cause the supply curve to move in the backward direction, i.e., from S_1 to S_2. As can be seen from the figure, it will result in a decrease in the level of output Y_2 and an increase in the level of prices P_2. It leads us onto the possible inflationary effects of climate change on world economy. It indicates the fact that higher global food prices will squeeze consumers' income.

Moreover, another way through which the rising inflation seems to materialize is in the form of land unavailability. The increasing global temperatures will eventually make some of the areas of the planet inhabitable and, with this, would come mass migration. Therefore, alongside, such socioeconomic and political implications of the climate change will increase the demands for the ever-decreasing land. Putting it in other words, the population of the planet would have to squeeze down to a small proportion of the land and live in an increasingly concentrated space. However, in a similar fashion to food inflation, the effects of mass migration will be mitigated with some other areas becoming more habitant.

The above analysis is based on a ceteris paribus, which means that the world population is assumed not to respond to climate change. In this scenario, an opportunity cost must also be considered. Although it is probable that preventive measures over the time will be taken to avoid the economic costs of global warming, it will introduce a short-term economic cost as the resources will be directed toward more productive uses. For this reason, Mendelsohn et al. (2016) elaborated that the most severe impact of global warming comes through the use of immediate, inefficient, and aggressive mitigation policies. It requires a temporary economic shift from consumption to investment. As the cost of mitigation increases, budget constraints become increasingly important.

In addition to output prices, the energy costs are also likely to add to inflation as a consequence of global warming. As the weather conditions tend to become harsher, we are likely to demand greater amounts of energy for both warming our living and working environments during the winters and cooling them when we experience warmer summers. It will affect the world economy in two ways: the energy demand will shift, and the supply will shrink because of the increased inefficiency of the existing energy stations due to higher and harsher temperatures. Moreover, governments' step toward green energy will further add to energy inflation in the short- to medium term because taxes will be imposed on coal-derived electricity.

4. Quantifying the global economic value of climate change

The economic value of the global crisis is huge. The world population is continuously growing. As per an estimate, it is expected to grow to almost 10 billion by 2050 (Cho, 2018). It will result in not less than 3.4 billion more mouths to

feed. Also, the middle class' growing desire to consume dairy and meat in the developing countries will add to this scenario, and the global demand for food can increase from 60% to 98% in the coming years (Cho, 2018).

Researchers, with the use of highly sophisticated modeling and estimation techniques, are trying to calculate how each 10th of a degree of global warming is to cost in economic terms. However, the research work carries with it large bands of uncertainty for one reason or another—vagaries of human behavior and almost unpredictable response of the planet to build up greenhouse gases, in this case.

As per a major report issued by 13 federal agencies of the United States in 2018, if the outcomes of global warming are not tackled timely, the country's economy would cut down by not less than 10% by the end of this century (Davenport and Pierre-Louis, 2018). Such a decrease in the American gross domestic product equals to more than double the losses of the Great Recession 10 years ago. The most recent report has precisely estimated the economic cost to be $32 billion from infrastructure damage, $118 billion from sea level rise, and $141 billion from heat-related deaths, among others, by the end of the century (Davenport and Pierre-Louis, 2018).

As a matter of fact, a previous report issued in 2014 had suggested, through robust research that the country had already started to suffer the tangible impacts of climate change, i.e., more severe wildfires and heat waves, torrential downpours in wet regions, forest dying under the assault of heat-loving insects, and increasing water scarcity in dry regions (Gillis, 2014). Such sweeping changes have been observed in the presence of an average of 2-degree increase in the global temperatures. However, if the greenhouse gases continue to emit at the rapid pace, the warming is expected to increase by 10 degrees by the end of this century (Gillis, 2014).

A month before the issuance of the 2018 report, the Intergovernmental Panel on Climate Change issued its most specific and alarming report to date. This report talked about the severe humanitarian and economic crisis expected to hit the world over the next two decades (Davenport, 2018). If the current state continues to exist, the planet will soon be facing severe droughts and poverty. The expected economic cost of the crisis is to be $54 trillion (Davenport, 2018). For saving the world's economy from the severe impact of the climate change, the economy must be transformed within a few years. In this regard, the greenhouse gas emissions must be slowed down to avoid 2.7-degree increase in global temperatures (Davenport, 2018).

According to the solutions provided in the report, heavy prices or taxes must be imposed on carbon dioxide emissions (Davenport, 2018). Perhaps, the rate must be as high as $27,000 per ton by the end of the next century (Davenport, 2018). However, such a bold move is not practically possible particularly in the United States, which is the second largest greenhouse gas emitter behind China and the world's largest economy at present. Despite such impossibility in vision, the lawmakers in the world including California, the European Union, and China have enacted carbon-pricing programs.

The economic impact of climate change will fall differently on countries depending upon their market conditions. According to Mendelsohn et al. (2000a), if the global temperatures increase by 2.5 degrees by the end of this century, then the cumulative market impact cost will not exceed 0.1% gross domestic product. However, the cost will vary from country to country (Mendelsohn et al., 2000a). For instance, low-latitude countries are expected to harm, whereas high-latitude countries are forecast to gain from the warming. But if the global temperature crosses the extreme limit of 2 degrees, then it will increase damages and reduce benefits (Mehdelsohn et al., 2000a).

In a similar fashion, Mehdelsohn et al. (2000b) elaborated on the economic impact of climate risks if the global temperatures cross the limit of 2 degrees over the next four decades. According to their research, a cumulative effect of 0.3% loss in gross domestic product will be observed under such conditions (Mehdelsohn et al., 2000b). However, the agricultural sector will suffer the most. Only the economies of the member states of the Organization of Economic Cooperation and Development will gain, whereas rest of the economies will suffer (Mehdelsohn et al., 2000b). They also elaborated on the fact that individual countries do not always follow continental averages; for this reason, the Ricardian model utilized by the researchers predicts a 0.04% gain to 2060 gross domestic product (Mehdelsohn et al., 2000b).

In the same vein, Stern (2006) estimated an average loss of more or less 5% of global gross domestic product over the next two centuries considering the baseline scenario of global temperatures remaining between 2.4 and 5.8 degrees by the end of 2100. Additionally, as pointed out earlier, the Intergovernmental Panel on Climate Change (2014) estimated a loss of 0.2%–2% of gross domestic product per annum if the warming reaches to 2 degrees. However, the report further estimated accelerated damages if the warming crosses the limit of 3 degrees (IPCC, 2014a,b).

5. Economic value of climate change with regard to food insecurity

The above demand and supply diagram demonstrates not only a decrease in labor productivity but also an increase in prices. It provides basis to the inflationary impact of climate change on world economy. Agricultural yields

are sensitive to weather conditions. For this reason, severe climate shifts resulting in frequent droughts are most likely to reduce crop yields in areas with inevitable food production. Although we must admit the fact that other regions will become more suitable for food production and new drought-resistant crops will be developed soon, food price inflation will continue to climb as the level of warming becomes even greater.

5.1 Economic impact of crop risks

As per the findings of a recent study conducted by the PNAS concluded that the yields could fall by 35% by 2100 due to increased salinity and ozone, and water scarcity if the greenhouse gas emissions continue on their current trajectory (Scheelbeek et al., 2018). Another study conducted by the PNAS on the crop of maize in the United States found that the overall yield of the crop could be cut down in half by just an increase of 4 degrees in the global temperatures. Such an increase in the earth's temperatures could happen by 2100 if the greenhouse gas emissions continue at the same pace (Tigchelaar et al., 2018). The study also indicated the fact that the production of maize would still be dropped by at least 18% if the global warming is limited to under 2 degrees, which is the current goal of the Paris climate accord (Tigchelaar et al., 2018).

The researchers also remain concerned to the finding that the top four maize exporters of the world, which includes the Ukraine, Argentina, Brazil, and the United States, would suffer simultaneous crop failure of 10% or more with a 2-degree increase in the temperature. With the 4-degree increase, the odds would swell up to a staggering 86% (Tigchelaar et al., 2018). Pointing to the crisis of sharply reduced crops, Peter De Menocal, director of the Center for Climate and Life and Dean of Science at Columbia University, explained that the additional impact on crop yields will amplify the divide between rich and poor while impacting the poorest because the world already faces the trouble of feeding its current population (Cho, 2018).

80% of the world's crops are rainfed. The farmers remain dependent on predictable weather to produce their crops. However, the climate change has been altering the rain patterns throughout the globe. Therefore, the farmers are facing extreme weather conditions. Precipitation becomes intense with an increase in the temperatures because the warmer air holds more water. The precipitation events are becoming more common with every passing year. They directly damage crops and decrease the yields.

Continuing in the same vain, more extreme weathers will lead to faster evaporation of water. It would result in more water shortages and droughts. Thus, the farmers will soon be facing the problem of having less water for irrigation just when it is needed the most. As a matter of fact, more than 10% of the world's crops are irrigated with groundwater that is not renewable. Putting it in simple words, the planet's aquifers are being drained faster than they are filling. It is a problem of large scale, which will continue to increase, as the planet will heat up (Cho, 2015).

Moreover, the extreme weather tends to alter the rain and flood behaviors of the planet. The growing intensity of sea level rise and tropical storms is inevitable under the umbrella of global warming. They can drown crops. Moreover, as the increased flooding can transport pollutants such as manure or sewage from roads, lawns, and farms to the agricultural lands, there is an increased chance for the toxins and pathogens to find their way to the food on our tables.

All of these findings unambiguously indicate the fact that the world needs to increase yields by setting up productive production. But the sky is not that clear. The scientists believe that the impacts of climate change in the form of sea level rise, increasing levels of carbon dioxide, drought, extreme weather, and higher temperatures tend to jeopardize the quantity and quality of our food supplies.

Additionally, the economic impact of crop failures due to inadequate rainfall is huge. The extreme weather conditions often translate into severe droughts (Zaveri et al., 2018), which increase poverty and decrease key development outcomes in the developing countries (Dercon, 2004). For instance, it has been found in the previous studies that rainfall variability has accelerated the spread of HIV (Burke et al., 2015), violence toward women (Sekhri and Storeygard, 2014), local tax revenues (Sanoh, 2015), land invasions (Hidalgo et al., 2010), gender wage gap (Mahajan, 2017), food prices (Hill and Porter, 2017), and agricultural wages (Mueller and Quisumbing, 2011).

5.2 Economic impact of meat and fisheries crisis

Climate change is likely to negatively impact the coastal fisheries and fishing communities. Fishing community, who primarily relies on inland fishery resources, remains vulnerable to climate risks. Major physical impacts of global warming for this community realize in the shape of sharpening of gradient structures, a rise in average temperature, changes in ocean currents, and rapid and large increases of freshwater discharges, which often triggers an

increase in chemical nutrients typically phosphorous, resulting in severe reduction in water quality and lack of oxygen. For this reason, access to water resources and other arrangements become a key to future sustainability.

The global fisheries landing is estimated to be approximately between 80 and 85 million per annum. It brings about $100 billions annually (Swartz et al., 2013). As per a recent study, the annual catch of fisheries is about 130 million (Pauly and Zeller, 2016). This industry directly or indirectly supports the livelihood of at least 700 billion people around the globe, which makes up to 10%–20% of the total population (Bianchi et al., 2014). Also, fish provides approximately 3 billion annually with 20% of their animal protein need (Bianchi et al., 2014) along with other micronutrients (Golden et al., 2016). Several studies have suggested that the rapid climate changes, directly or indirectly, pose a major threat to world fisheries particularly in the long run (Pörtner et al., 2014).

Changes in ocean conditions such as oxygen levels and circulation, pH, salinity, sea ice extent, and temperature cause shifts in timing of biological events (Pörtner et al., 2014), changes in primary and secondary productivity, and shifts in distribution range of marine species (Clark et al., 2003; Rose, 2005). Also, the maximum body size of fish is decreased due to the warmer weathers (Cheung et al., 2013). Overall, the combined effect of changes in ocean productivity and predicted distributional shift under climate risks changes species composition (Beaugrand et al., 2015). It eventually leads to redistribution of maximum catch potential in both high-latitude regions and tropics (Cheung et al., 2010). Such variability has large implication for people depending upon fish for income and food, and thus fisheries contribution to global economy (Sumaila et al., 2011; Barange et al., 2014). The changes discussed above make climate change to alter the fisheries subsidies (Sumaila et al., 2016), costs (both fixed and variable) (Lam et al., 2011), and revenues (price × landings).

5.3 Economic impact of freshwater crisis

In normal times, groundwater provides 40% of the fresh drinking water. In the recent times, the percentage swelled up to 65% (Cho, 2015). The farmers around the world have been growing high value water-hungry crops including oranges, tomatoes, walnuts, and almonds. During the droughts, which are also a result of the increasing global temperatures, the farmers tend to drill wells deeper than usual for the purpose of tapping groundwater as it drops by two feet with every passing year (Alley and Alley, 2017)—another effect of the world's rising temperatures.

It means that the planet's aquifers are being drained faster than they are filling (Cho, 2015). An aquifer is a geological formation that contains or channels water (Salama et al., 1999). The global use of groundwater increases by 3% each year particularly in the areas of Asia, Central America, and North America (Brown, 2001). Most of this water is used for irrigating the crops to feed the world's growing population. Therefore, if the water is overdrawn, there can be serious consequences about it. Primarily, it causes water tables to fall, which would mean that some wells would no longer reach water. It will also cause land subsidence because removal of water from soil makes it to collapse and drop (Bouwer, 1977).

Moreover, if freshwater is below the ocean, or is very deep, overpumping can cause the saltwater to move upward or inland. It often results in saltwater intrusion, which contaminates the fresh drinking water. Additionally, overpumping of the aquifers can cause them to collapse (Glennon, 2004). It eventually destroys their ability to store water forever. As per the report of Center for Investigative Reporting, California has lost more than 6 trillion gallon capacity of aquifers in this manner (Cho, 2015). Also, a study in Japan has found that the pumped groundwater that ends up in the ocean causes the sea levels to rise as well (Pokhrel et al., 2012).

According to the United Nations, water scarcity in a particular area occurs when the available water levels drop 1700 m^3 per year, i.e., 4600 L per person per day (UN Water, n.d.). Water scarcity is declared in an area when the freshwater passes the threshold of 1000 m^3 per year or 2700 L per person per day. Any country facing less than 500 m^3 per year or approximately 1400 per person per day experiences water scarcity (UN Water, n.d.). By this comprehensive definition of the United Nations, almost 49 countries on this planet are water stressed. Twenty-one of these countries face absolute water scarcity, whereas nine of them are at the verge of falling scarce to freshwater soon (UN Water, n.d.).

The global water scarcity will have serious economic implications (Gleick, 1993). Primarily, it will impact the businesses worldwide as it leads to difficulties in staying competitive and higher operating costs. Therefore, for international firms, the cost of water scarcity is high particularly where the margins shrink precariously (Hoekstra and Hung, 2005). It eventually causes the firms to take water access as a competitive advantage and relocate when and where necessary (Autry et al., 2013). For instance, any business will prefer to areas with lowest water risks, i.e., areas with easy access to healthy water resources such as relocating by a river basin, river, or lake.

Overall, the lack of water will have a domino effect for the business industry: it causes lack of job opportunities, i.e., population decline, decrease in tax revenues, incomes go down, local commerce declines, and cities and the surroundings shrink to a dangerous level (Cho, 2015). According to the UNESCO, industry accounts for approximately 60% of total water use in high-income nations. The bottom line of this discussion is that businesses need water (World Water Assessment Program (United Nations), 2006).

The water scarcity is also likely to economically impact the agricultural industry, which despite being highly dependent on it continues to contribute to it. In places such as Morocco, land use loss for agricultural purposes and environmental deterioration has been costing approximately 350 million American dollars. Primarily, water scarcity impacts the Middle East, China, and India, which are experiencing serious freshwater scarcity and drought conditions. It causes the countries to reduce their crop production. Thus, the food prices spike dangerously. As per a report, the drought conditions in China threatened or affected 8.7 million livestock, 182 million hectors of agricultural land, and 95 million people (Guarino, 2017).

According to a recent report of the World Bank Group (2016), many expanding countries are likely to witness a decline in their gross domestic product for as much as 6% in the next three decades due to erratic and uncertain water supplies and water shortages along with elevated incomes and rising populations. Such a decline is more significant for the areas where the water supply is currently meeting the demands but prospects for this to continue remain bleak. The most prominent areas in this regard include the Middle East, East Asia, and Central Africa.

Moreover, the current water crisis is attributed to not only inadequate rainfall, poor storage and delivery system of water, and other similar factors but the growing competition among people and industry as well. As agriculture and industry expand in some of the areas of the world such as India, the needs of the people, when it comes to freshwater, are minimized primarily due to the fact that precedence in this area is often given to construction, energy development, agriculture, and industry.

More dangerously, freshwater crisis in the form of lack of drinking water and increase in food prices cause population migration to the areas with easy access to water. It also gives rise to regional conflicts (Sorri, 2016). More importantly, water scarcity causes food shortages while raising food prices (Hanjra and Qureshi, 2010). It often results in hindered trade with developing economies. It eventually gives rise to civil unrest in the long run. Overall, it can be concluded that freshwater crisis has indirect impact on food processing industries and direct impact on irrigated and rainfed agriculture.

6. Policy recommendations

In an attempt to achieve a world without the challenge of food insecurity by 2030 or sooner, scaling up the actions to improve the adaptive capacity and resilience of food systems in response to climate extremes and variability is imperative. Disaster risk reduction and management, and climate change adaptation, in this regard, must be integrated in short- to long-term national and international practices, programs, and policies. Here are a few policy recommendations in this vein.

- Freshwater scarcity can be addressed in several practical manners such as increasing the numbers of desalination plants, upgrading sewage systems, improving farming practices, and increasing storage infrastructure through water recycling. Primarily, governments must invest into the infrastructure to address the water scarcity problem in the long run. As economist Richard Damania puts it in words, high economic dividends can be earned with improved water stewardship because if governments respond to just 25% of the water shortage problems, water losses decline dramatically and even vanish in some of the areas.
- Another silver lining with regard to global water crisis has been witnessed in California. Over the past four decades, the state has implemented strict water restriction in an attempt to address its drought issue. The enhanced water management helped the state get out of the droughts unharmed.
- A more effective way to deal with the problem of freshwater scarcity is to make use of more efficient water-using fixtures. As a matter of fact, approximately 40% of all freshwater resources are being consumed in restrooms. Such consumption can be reduced through the use of no-water urinals and high-performance toilets.
- The greenhouse gases pollution must be reduced in an attempt to avoid the 2.7-degree increase in the global temperatures. If the target is achieved, 45% of the emission levels will be reduced by 2030 and 100% by 2050. In this regard, the use of coal as an electricity source must be reduced. Currently, coals produce 40% of electricity around the globe, which must be cut down to 7% (Davenport, 2018). In a similar fashion, the use of renewable energy resources such as solar and wind, which currently stands at 20% of electricity production, must be increased to as much as 67% (Davenport, 2018).

- Reduction of disaster risks must be made a part of broader strategies instead of just embracing it at the times of responding to extreme events. In this regard, particular attention must be made on development of drought- and heat-resistant vegetal varieties. Such vegetation must have the ability to grow not only in tropical countries but also in temperate countries with high temperatures.
- Another prospect in this context comprises the social protection instruments that must be well designed to ensure regularity and predictability. They must be aligned with climate risk management to enable households to better engage in more profitable agricultural and livelihood activities. It will guarantee continuous access to food and minimum incomes.
- Increasing resource-use efficiency, reducing food wastes and losses, and rebalancing diets toward less animal-sourced food would make a fruitful contribution in this direction.
- Far greater access to information for smallholder farm families, to intelligent investment and credit, and to technologies in developing countries will help them making their livelihood more resilient to climate risks by adjusting their food production system and practices.
- Combined adaptation can also be achieved through agricultural diversification and sustainable intensification with the creation of both locally and rural–urban-linked off-farm opportunities. It would enhance the resilience of the population to absorb the climate shock to their gross domestic product.

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Climate Change and Food Security with Emphasis on Wheat

Edited by Munir Ozturk and Alvina Gul

Understand the potential of wheat to address global food security issues and the challenges faced due to climate change

- Explores the biotic and abiotic effects of climate change on wheat production and biotechnological utilization
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Climate Change and Food Security with Emphasis on Wheat is the first book to present the full scope of research on wheat improvement, revealing the correlations to global issues including climate change and global warming which contribute to food security issues. Wheat plays a key role in the health of the global economy. As the world population continuously increases, economies modernize, and incomes rise, wheat production will have to increase dramatically to secure it as a reliable and sustainable food source. Since covering more land area with wheat crops is not a sustainable option, future wheat crops must have consistently higher yields and be able to resist and/or tolerate biotic and abiotic stresses that result from climate change.

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Munir Ozturk, PhD, DSc, Plant Ecophysiology, is a Professor Emeritus in the Department of Biology and Centre for Environmental Studies at Ege University in Bornova, Izmir, Turkey, and Vice President of the Islamic World Academy of Sciences in Amman, Jordan. He also serves as Consultant Fellow in the faculty of Forestry at Universiti Putra Malaysia, Malaysia, and is a Distinguished Visiting Scientist, ICCBS at Karachi University in Pakistan. His research focuses include Eco-Physiology, Conservation and Management of Plant Diversity, Biosaline Agriculture, Biomass and Bioenergy, Medicinal and Aromatic Plants, Biomonitoring, and Wastewater Recovery.

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An imprint of Elsevier
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ISBN 978-0-12-819527-7
9 780128 195277