REVIEW

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Physiological responses of wheat to drought stress and its mitigation approaches

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Abstract

Drought is a polygenically controlled stress and a major agricultural risk that reduces crop productivity and limits the successful insight of land potential throughout the world. This review article has been divided into two parts, i.e., effect of drought stress on physiology of wheat and potential drought mitigation approaches. In the first part, physiological responses of wheat to stress were discussed. Cell membrane stability, relative water content, early maturity, decreased leaf area, small plant size, increased dry weight and root–shoot ratio, and the whole-plant transpiration rate response to enhanced atmospheric vapor pressure deficit are physiological traits associated with drought tolerance in wheat. Reduction of relative water content closes stomata and thereby reduces stomatal conductance. Osmotic adjustment improves drought tolerance by allowing cell enlargement, plant growth, and stomata to stay partially open and by maintaining CO_2 fixation under severe water deficit. The wheat plant accumulates several organic and inorganic solutes in its cytosol to lessen its osmotic potential for maintenance of cell turgor. Drought affects photosynthesis negatively by changing the inner structure of chloroplasts, mitochondria, and chlorophyll content and minerals. Destruction of the photosystem II (PSII) oxygen releasing complex and reaction center can disturb production and use of electrons, causing lipid peroxidation of cell membrane through the production of reactive oxygen species. In the second part, drought mitigation approaches were discussed. Seed, drought, bacterial, and hormonal priming are common approaches used to lessen the effects of water deficit. Physiological trait-based breeding, molecular breeding, marker-assisted backcrossing, aerial phenotyping, water budgeting, and resource allocation are modern approaches used to develop drought tolerant wheat cultivars. Wheat genotypes produced as a result of a combination of all these methodologies will increase food security regarding the currently changing climate.

Keywords Aerial phenotyping · Priming · Root–leaf relations · Water budgeting · Resource allocation · Osmolyte accumulation · Chlorophyll · Photosynthesis

Introduction

Plants have always been a key to survival for humans, as they are vital to meet the world's food needs by contributing about 82% to total global food production harvested from land resources. Historically, over 3000 species of plants

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have been used to feed humans. Among the plants, wheat is an excellent health building food and an excellent source of minerals, dietary fiber, proteins, and B-group vitamins. It is often grown in rain-fed areas (Geravandi et al. 2011) for its starch and protein that makes it the most important cereal crop globally, and, along with rice and maize, forms an integral part of diets of over 4.5 billion people. The success of wheat in temperate world regions is due to its adaptability and high yields together with its unique flour dough properties which give it a distinct advantage over the other temperate crops (Shewry 2007).

Drought is a polygenic stress (Kilic and Tacettin 2010) that reduces productivity and quality of crops (Waraich et al. 2010, 2011) and also limits the successful realization of land potential throughout the world (Pierre et al. 2012; Liu et al. 2016). The scarcity of water, caused by erratic and poorly distributed rainfall, causes tremendous global losses in agriculture. Russia, for example, has estimated total losses of over US$800 million due to drought and other natural challenges in 2000 alone. Drought affects all plant development stages from germination, vegetative and reproductive growth to grain filling and maturation of the crop (Hossain et al. 2012). Drought reduces nitrogen (N) uptake efficiency and utilization by plants. The deprived nutrient uptake is due to impaired membrane permeability and active transport and reduced transpiration rate resulting in repressed root absorbing power. In semi-arid and arid regions of the world, drought is one of the leading causes of limited agriculture production. Many growth variables and functions of plants are affected by water stress (Nezhadahmadi et al. 2013). Under drought conditions, the intake of CO_2 is reduced due to stomatal closure, and inside the stomata, a high level of oxygen produces reactive oxygen species, caused by the partial reduction of oxygen, and causes rupturing of membranes which become leaky, thereby affecting respiration, photosynthesis, and the overall development of the plant. Reactive oxygen species also seriously damages the production of cellular components such as carbohydrates, nucleic acids, lipids, and proteins (Waraich et al. 2011; Reddy et al. 2014).

Drought is one of the major abiotic stresses that affect at least 60% of wheat production in high-income countries and about 32% of 99 million hectares in low-income least developed countries (Chen et al. 2012). Water deficit might decrease wheat grain yield from 17 to 70% (Nouri-Ganbalani et al. 2009). Daryanto et al. (2016) reported 20.6% yield losses in 40% reduced water. Double ridge to anthesis stage is the most sensitive growth period regarding wheat yield to water deficit because of the negative influence on number of spikelets and ultimately kernels per spike. Water deficit decreases grain yield by affecting anthesis and grain filling period. It is well documented that plant height, biomass, and yield are more sensitive traits to water deficit in comparison with number of spikes and 1000 grain weight.

A number of tillers per plant, kernels per plant, 1000 grain weight, awn length, and peduncle length affect wheat tolerance to drought (Nouri-Ganbalani et al. 2009; Aminzadeh 2010). Drought stress may decrease leaf water potential, consequently lowering turgor, stomatal conductance, and photosynthesis, and, finally, lessening growth and yield of wheat (Chen et al. 2012). Therefore, the study of wheat plant traits in response of drought stress is crucial for its genetic improvement to ensure high yield in water-deficit conditions. This review article describes in detail the wheat physiological responses under drought stress and possible drought mitigation approaches for the future outlook.

Physiological responses

Growth

Drought stress causes considerable variation in germination percentage, seed vigor index, other seedling traits, and membrane stability in bread wheat genotypes (Dhanda et al. 2004). It delays, reduces, or inhibits germination, and seedling vigor of wheat (Ghanifathi et al. 2011; Almaghrabi 2012) and germination stress tolerance index (GSTI) (Moayedi et al. 2009). Seed vigor index is the most sensitive trait influenced under water-deficit conditions, followed by root and shoot length and germination percentage (Moayedi et al. 2009). Reduction of cell membrane stability, relative water content (Geravandi et al. 2011), early maturity, decreased leaf area, small plant size (Nezhadahmadi et al. 2013), increased dry weight and root–shoot ratio (Shi et al. 2014), and the whole-plant transpiration rate response to enhanced atmospheric vapor pressure deficit (Schoppach et al. 2016) are associated with drought tolerance in wheat.

Root–leaf relations

Wheat morphological traits influenced by water deficit include different leaf characters such as shape, area, expansion, size, waxiness, pubescence, senescence, and cuticle tolerance and root traits including length, density, fresh, and dry weight (Nezhadahmadi et al. 2013). Appraisal of leaf water potential is an efficient and reliable way to measure plants' response to water deficit. Water-limiting conditions slowly decreases electron transport of photosystem II, increases the ability for non-photochemical quenching, and finally lowers leaf relative moisture content in wheat (Zivcak et al. 2013). Drought decreases leaf water potential in wheat due to the accumulation of solutes, but genotypic variation may exist in response to water potential under well-watered as well as drought conditions (Nawaz et al. 2014). Leaf water potential also affects different gas exchange characteristics like stomatal conductance, net-photosynthetic rate, and transpiration

rate, etc. Stomatal conductance and transpiration rate decrease with a reduction in leaf water potential in spring wheat (Liang et al. 2002). Leaf waxiness and trichome density may lessen water loss and protect against drought for longer periods (Bowne et al. 2012). In water-deficit conditions, roots continue to increase in size to search for water, but growth in above ground parts such as leaves and shoots are restricted. Deep roots, high water absorbance, and good grain yield of wheat could be achieved during drought by enriching the surface layer with fertilizer. Uneven fertilizer spreading can change root growth and water absorbance (Jin et al. 2015). Quantitative trait loci (QTL) associated with cooler canopy temperatures are linked to root spreading in bread wheat. Roots move deeper under water deficit and closer to the surface during well-watered conditions (Pinto and Reynolds 2015). Root growth and root length density were increased under water deficit with foliar application of 32 ppm of silica (Ratnakumar et al. 2016). Understanding root–shoot communication is crucial to develop drought tolerant wheat varieties. Lessened stomatal conductance may appear in plants grown under water deficit where shoot moisture content remains the same. It is a non-hydraulic maintenance mechanism during drought. Non-hydraulic root-sourced signals assist plants to detect water deficit in roots and are expressed as a change of growth or stomatal conductance in leaves. By selecting cultivars for an earlier start of the non-hydraulic root-sourced signal, advancement in yield and drought tolerance could be achieved in wheat (Liu et al. 2014). The root–shoot ratio increased under osmotic stress to enhance water absorption that is associated with abscisic acid (ABA) concentration in roots and shoots (Mahdid et al. 2011; Nezhadahmadi et al. 2013). Gibberellin A3 (GA3) application to the roots restored leaf elongation in semi-dwarf and tall genotypes growing in restrictive soil; the longest leaves were attained when GA3 was applied to affected roots of tall genotypes (Filho et al. 2013). ABA controls plant growth by refining root development and modifying leaf elongation and expansion during water deficit (Reddy et al. 2014; Farooq et al. 2014). Genetic improvement of root–shoot structure can enhance water and mineral absorbance in wheat under water deficit. The tillering inhibition (tin) gene in wheat strongly affects root–shoot structure. This gene enhances root–shoot ratio and root biomass during early stem elongation and also increases root depth at maturity in near isogenic lines (NILs) of wheat. It also slows down the use of soil water by lowering canopy temperatures, increasing stomatal conductance and stay green during grain filling in these NILs. These changes could increase harvest index and ultimately yield (Hendriks et al. 2016). Low light and low soil moisture enhance responses of roots and shoots significantly in wheat under water deficit. Low light

increases the number of leaves to enhance photosynthesis, while low moisture promotes root development into deeper soil layers for water absorption to maintain high yield during drought (Nagel et al. 2015).

Water relations

Relative water content (RWC) is an important indicator of water status as compared to leaf water potential in wheat under water deficit (Lugojan and Ciulca 2011) and has been utilized for the selection of drought tolerant cultivars in wheat (Bayoumi et al. 2008). Drought applied at later stage of plant growth (after 6 weeks of emergence) has more deleterious effects on water relations, nutrient uptake, growth, and yield than early imposed drought (after 3 weeks of seedling emergence) in wheat (Nawaz et al. 2014). Drought significantly reduces chlorophyll content, membrane stability and RWC of wheat cultivars at flowering stage (Moayedi et al. 2010). Drought stress reduced relative water content by 43% (from 88 to 45%) in four genotypes of bread wheat (Siddique et al. 2000). Reduction of RWC closes stomata that will reduce photosynthesis rate. The scarcity of water impedes osmotic regulation, whereas alternate drying and re-watering induced osmotic regulation that improved plant's water use efficiency under drought conditions. High relative moisture content is a tolerance approach to water deficit and is due to more osmotic regulation (Keyvan 2010). Drought tolerant genotypes maintained high turgor potential and relative water content to signify that limited water had a little effect on their protoplasmic structure as compared to sensitive genotypes which indicate a highly positive correlation between RWC and photosynthetic rate (Moayedi et al. 2010). Maintenance of leaf turgor is an important adaptive mechanism that plays an important role in stomatal regulation and photosynthetic activities under water-deficit conditions (Lipiec et al. 2013).

Chlorophyll content and photosynthesis

Depending upon cultivars, plant growth, and various environmental factors, the ratio between chlorophylls *a* and *b* is 3:1. However, the highest chlorophyll content occurs at the onset of flowering in plants (Simova-Stoilova et al. 2009). Severe drought stress in wheat significantly reduces leaf chlorophyll content (Fotovat et al. 2007) and leaf photosynthesis (Prasad et al. 2011). Reduction of chlorophyll content in wheat is linked with leaf age. Chlorophyll content increased in young leaves due to enzyme activation in light reaction of chlorophyll synthesis but decreased by 13–15% in older leaves due to activation of chlorophyllase and enzyme inactivation under water deficit (Nikolaeva et al. 2010). Physiological performance of nine contrasting wheat genotypes was evaluated under rain-fed conditions

and results showed non-significant variations in chlorophyll content among the susceptible and tolerant wheat genotypes at both vegetative and anthesis stages; however, anthesis stage showed the lowest chlorophyll content (Almeselmani et al. 2011). Variations in chlorophyll content were not only caused by drought stress but also existed among genotypes. High chlorophyll content resulted in better seed yield under water-deficit conditions (Alaei 2011; Arjenaki et al. 2012). Kilic and Tacettin (2010) evaluated yield and physiological attributes of 14 durum wheat cultivars under drought stress and found a positive correlation of grain yield with chlorophyll content, grain filling period, and number of grains per spike. Water deficit is often complemented by high temperatures that increase evapotranspiration and affect photosynthesis and ultimately decrease yield (Mir et al. 2012). Water deficit affects photosynthesis negatively by changing inner structure of the chloroplast, mitochondria and chlorophyll content and minerals (Huseynova et al. 2016). Photosynthesis of C_3 and C_4 plants reduces when RWC and osmotic potential are reduced under drought (Bogale et al. 2011). High functional stability of thylakoid membrane proteins and greater antioxidant capability increased water deficit tolerance in stay green mutant tasg1 of wheat (Tian et al. 2013).

Osmolyte accumulation

Osmotic adjustment as a plant defense mechanism improves drought tolerance of plants (Shao et al. 2005). It permits cell expansion and plant growth with severe water deficit. It also permits stomata to stay partially open and CO_2 fixation to continue during water deficit. Osmolyte accumulation allows cells to manage their dehydration and membrane structural integrity to give tolerance against drought and cellular dehydration (Loutfy et al. 2012). Osmotic adjustment in plants exposed to drought may follow storage of low-molecular-weight organic solutes. The wheat plant accumulates several inorganic and organic solutes in its cytosol to lessen its osmotic potential for maintenance of cell turgor.

Organic solutes

The compatible osmolytes present in higher plants are glycine betaine, proline, and soluble carbohydrates and proteins. Glycine betaine shields cells from water deficit by preserving the osmotic balance between extra and intra cellular environment, alleviating quaternary structure of proteins, e.g., antioxidant enzyme protection and membrane proteins and the oxygen releasing complex of photosystem II (Gou et al. 2015). It also regulates intra cellular osmotic potential, controls pH of cytoplasm, and stabilizes cell membrane structure of wheat in drought stress (Huseynova et al. 2016). The presence of proline is one of the common traits in most of cereals under drought (Marcińska et al. 2013). Drought

stress resulted in high proline content in wheat with reduced relative moisture and dry matter production (Tatar and Gevrek 2008). Wheat plants accumulate proline to a greater extent than the other osmoregulators, especially in leaves (Farshadfar et al. 2008) as a consequence of increasing collapse of proteins with immediate decline in its synthesis during the grain filling stage under water deficit (Nazarli and Faraji 2011). Proline accumulated under salinity or drought improves tolerance against drastic effects of these stresses (Bajji et al. 2001). It is osmotically active, controls storage of useful N, and plays a major part in membrane stability (Bandurska et al. 2008), scavenging free radicals and buffering cellular redox potential that help wheat plants to combat abiotic stresses. As a signaling controller molecule, it initiates many mechanisms that help in adaptation to drought (Marcińska et al. 2013). Like proline, sugars are also necessary compatible solutes that play a major role in osmoregulation under water deficit. Soluble carbohydrates accumulate in plants as a result of drought (Zhang et al. 2009) in addition to a decline in the net CO_2 integration rate. In extreme dehydrated states, sugars become an essential replacement for water, even more than proline, providing a hydration shell around proteins (Bowne et al. 2012). Wheat genotypes accumulate more soluble sugars during the grain filling period than the pre-anthesis stage under drought stress, and the best stages for the screening of drought tolerant cultivars are grain filling and post-anthesis periods (Farshadfar et al. 2008). High osmotic stress reported to enhance the endogenous level of soluble sugars in wheat from 1.49 mg in control to 2.65 mg per gram of leaves under osmotic stress of − 8 bars (Qayyum et al. 2011). Remobilization of carbon reserves was evaluated in wheat under water deficit and loss in total soluble proteins at 50% field capacity imposed after 14 days of anthesis to maturity was much higher than imposed 14 days later from anthesis (Saeedipour and Moradi 2011). However, a significant relationship was observed among total proteins and grain yield of wheat under rainfed conditions (Farshadfar et al. 2008).

Inorganic solutes

Like organic solutes, inorganic solutes also have a potential significance in water homeostasis and growth during water deficit. Potassium (K) has several functions that include protein biosynthesis, energy status, charge-balance, osmoregulation, and stomatal regulation. It also reduces transpiration and upholds turgor pressure under water-deficit environment. Calcium (Ca) also affects stress reactions of plants and growth by regulating different physiological processes including cell division, cell wall synthesis, stomatal regulation, water and solute movements, respiration, and translocation. These vital elements absorbed by roots are used for water conservation of plants under water deficit as direct

inorganic osmotic solutes or indirect as possible regulators in biosynthesis of the organic solutes (Marcińska et al. 2013).

Silicon enhances photosynthetic gas exchange in wheat by improving water status, inorganic phosphate concentration in leaves and phosphoenolpyruvate (PEP) carboxylase activity under water-deficit environment. It was also reported that the alleviation of drought stress in wheat plants using silicon depends on the upsurge of antioxidant defense capabilities (Pei et al. 2010; Gong and Chen 2012). Ratnakumar et al. (2016) observed that foliar application of 32 ppm of silicon increases RWC, leaf chlorophyll content, and also lower canopy temperatures. Therefore, ortho-silicic acid had a robust influence on lessening drought and reduced the yield losses in wheat under water deficit.

The phenolic compound salicylic acid (SA) (Kang et al. 2013) is a phytohormone and growth regulator that has a vital role in growth and development, ethylene biosynthesis, stomatal behavior, flower induction, and respiration in many plants (Kang et al. 2012). It performs a critical role in plant biotic stress tolerance and is now generally recognized as chief signal transducer during biotic stress (Loutfy et al. 2012). External application of SA also improves plant's abiotic stress tolerance (Kang et al. 2013) including drought (Azooz and Youssef 2010). These studies have mostly been done at physiological levels, proposing that SA induced drought tolerance is linked with an improved antioxidant defense mechanism (Horváth et al. 2007). However, some studies have revealed that alleviation of abiotic stress by SA could be the result of changed expression of the genes encoding heat shock proteins, osmotin, and pathogenesis-related proteins (Kang et al. 2013). It is reported that application of SA at seedling stage to alleviate drought could produce real economic yields of wheat genotypes grown under water deficit. Role of SA on growth improvement of wheat seedlings has also been reported for other stressed environments (Loutfy et al. 2012). Major physiological traits and their significance in term of growth and yield and related QTL with chromosome location under drought were presented in Table 1.

Table 1 Physiological traits and their significance in terms of growth, yield, and related QTLs under drought stress

Traits	Physiological significance	Chromosome	References
Root	Increase root growth	2D, 4D, 3A, 5A, 6A	Bai et al. (2013)
Root hair length	Increase yield by manipulating restrictive mineral and water resources	1A, 2A, 2BL, 6A	Horn et al. (2016)
Root and shoot length	Contribute towards yield	1B	Maccaferri et al. (2016)
Root–shoot ratio	Change growth or stomatal conductance, enhance ABA in roots and shoots	4B	Maccaferri et al. (2016)
Cooler canopy temperature	Linked with normal root spreading	1B, 2B, 3B, 4A, 7A	Pinto and Reynolds (2015)
Water relations	Perform osmoregulation by affecting stomata and photosynthesis rate	7A	Morgan and Tan (1996)
Chlorophyll contents	Increase chlorophyll contents in leaves and influence grain yield	1A, 1B, 2B, 4A, 5A, 5B, 6A, 7A	Peleg et al. (2009)
Chlorophyll contents	Increase chlorophyll contents in leaves and influence grain yield	2B, 4B, 3A, 6A,	Kumar et al. (2012)
Photosynthesis (*Fv/F0)	Increase primary yield of photochemistry of PSII during light reaction (influence grain yield)	1B, 2A, 2D, 4A, 5A, 5B, 6B, 7B, 7D	Czyczyło-Mysza et al. (2011)
Photosynthesis (**Fv/Fm)	Enhance quantum efficiency of PSII and results in increased grain yield	1B, 2A, 2D, 3D, 4A, 4D, 5A, 5B, 6B, 7A, 7B, 7D	Czyczyło-Mysza et al. (2011)
Photosynthesis (**Fv/Fm)	Enhance quantum efficiency of PSII and results in increased grain yield	2B, 3A, 4B, 4D, 6A	Kumar et al. (2012)
Water soluble carbohydrates	Help in osmoregulation, provide hydration shell, affect pre-anthesis and grain filling stages	1A, 1D, 2D, 4A, 6B, 7B, 7D	Yang et al. (2007)
Grain yield	Enhance grain yield	1A, 1B, 5A, 6A	Liu et al. (2013)
Grain yield	Enhance grain yield	2B, 2D, 3A, 3B, 4B, 5A, 5D, 6B	Czyczyło-Mysza et al. (2011)
Grain yield	Enhance grain yield	1B, 3B, 4A	Pinto et al. (2010)

*Maximum primary yield of photochemistry of PSII

**Maximum quantum yield of PSII

Reactive oxygen species

A decline in the net-photosynthetic process under water-deficit conditions is also associated with conflicts in biochemical routes of a non-stomatal nature, triggered by oxidation of chloroplast lipids and variations in the assembly of pigments and proteins. Production of reactive oxygen species (ROS) enhanced in response to drought stress (Kashif 2013); however, the major source of ROS production is electron transport chain which operates in chloroplasts. Destruction of the photosystem II (PSII) oxygen releasing complex and reaction center can disturb production and use of electrons, resulting in the production of ROS that subjected cell membrane to lipid peroxidation (Wang et al. 2014). High concentrations of singlet oxygen ($^1O_2$), superoxide radicals (O_2), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH) resulted in oxidative damages to plants depending upon their endogenous levels. ROS may react with deoxyribonucleic acid, lipids, and proteins, leading to oxidative damage, inactivation of enzymes, and destroyed cellular structures associated with photosynthesis by impairing the normal functions of cells (Miller et al. 2010; Huseynova et al. 2016). ROS production is linear with the severity of water stress that triggered the peroxidation of membrane lipids and break down of nucleic acids. Cell organelles, i.e., chloroplasts, mitochondria, and peroxisomes are cytological locations and first target of active oxygen species, as well. Nitric oxide-mediated alternative pathways boosted photosynthesis under water deficit by circumventing severe decrease in electron transport chain of photosynthesis and finally inhibiting ROS production and oxidative damage in wheat leaves (Wang et al. 2016).

Antioxidant enzymes

Production of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and glutathione peroxidase (GPx) in response to water stress is an adaptive mechanism well-known in plants. Plants enhance the activity of peroxidases and glutathione against water stress induced oxidative damage. APX is the most important antioxidant enzyme of water–water and ascorbate–glutathione (ASH-GSH) cycles which scavenge superoxide radicals and H_2O_2 in the chloroplast under water-deficit conditions (Gill and Tuteja 2010). Drought stress influenced plant–water relations which modulated the antioxidant defense system and resulted in APX synthesis (Selote et al. 2004). Similarly, in wheat cultivars, APX activity varied depending on leaf developmental stage and duration of drought. Wheat plants subjected to mild drought enhance leaves' APX activity, whereas prolonged water deficit decreased its activity because of the increased production of malonic dialdehyde (MDA) (Nikolaeva et al. 2010).

The simultaneous and sequential action of various antioxidant enzymes like CAT and POD plays key role in the survival of plants under changing environments. These enzymes also play a vital role in the regulation of ROS in cell through triggering and deactivation of H_2O_2 (Sairam et al. 2005). SOD, glutathione reductase, and APX significantly contribute to the reduction of ROS produced due to water deficit (Hernández et al. 2012). Being scavengers of hydrogen peroxide, CAT and POD converts toxic levels of endogenous H_2O_2 into water and oxygen. Likewise, CAT activities were examined in wheat leaves subjected to severe drought and increased activity of CAT was noted, especially in susceptible cultivars (Simova-Stoilova et al. 2010).

Foliar applied antioxidants have been described to noticeably reduce the drastic effects of drought on plant growth and metabolism (Malik et al. 2015). Ascorbic acid as an antioxidant has a key influence on cell division, differentiation, and growth of plants (Athar et al. 2009; Malik and Ashraf 2012). Foliar applied ascorbic acid alleviates drought by influencing stomatal closure, nutrient uptake, total chlorophyll content, protein synthesis, transpiration, flowering, and photosynthesis (Xu et al. 2015). Foliar applied ascorbic acid increased wheat yield and chlorophyll content linked with leaf water potential regulation by moving minerals from leaves to flowers and by enhancing the CAT and APX activity (Hafez and Gharib 2016).

Drought mitigation approaches

Priming

Seed priming is highly effective in improving germination, emergence, and vigor of seedling in many crops. As already discussed above, drought stress early in the season is more destructive than late-stage water shortage. The simplest way to improve germination is by hydro-priming (use of water); however, under stress conditions, scientists reported that osmopriming (halo-priming, chemo-priming, hormonal priming) is highly effective for improved seedling vigor. Under abiotic stresses like water stress, much of the injury occurs at cellular level and antioxidant defense response due to oxidative damage (Hameed et al. 2011). Seed priming with osmoprotectant repairs and protects nucleic acids, increases the synthesis of proteins, as well as repairs cellular membranes. In wheat use of growth promoters (Yasmeen et al. 2013), osmoprotectants (Hameed and Iqbal 2014) and antioxidants (Farooq et al. 2013; Malik et al. 2015) were successfully used to mitigate effects of drought.

Bacterial priming (plants inoculation with growth promoting bacteria) is an effective approach to ameliorate adverse effects of water deficit in wheat. Inoculation of wheat with *Azospirillum brasilense* NO40 and *Bacillus amyloliquefaciens* 5113 strains decreased the transcript

levels of enzymes activated during drought stress. This was due to combined morphological, physiological, and metabolic effects on host plants by these bacteria (Kasim et al. 2013). Inoculation of wheat with endophytic actinobacteria increased wheat yield by producing plant hormones, enhancing soil mineralization and N availability under drought (Yandigeri et al. 2012). Likewise, *Burkholderia phytofirmans* strain PsJN inoculation of wheat significantly reduced severe effects of drought on RWC and CO_2 assimilation rate and consequently improved photosynthesis, water use efficiency (WUE), and chlorophyll content in comparison with control (Naveed et al. 2014).

Drought priming (plants pre-exposure to mild water deficit) is also used to lessen effects of severe drought during the grain filling period of wheat. It changes protein expression and enhances photosynthesis and ascorbate peroxidase activity to enhance wheat yield under drought during grain filling period (Wang et al. 2014).

Hormonal priming (application of plant hormones) is currently being used to alleviate adverse effects of drought in wheat. For example, Liu et al. (2016) investigated the effect of polyamines (PA) in wheat during grain filling under water deficit. Spermidine (SPD) and spermine (SPM) negate the effects of severe drought. The influence of PA on wheat grain filling under water deficit is linked with endogenous ethylene (ETH), abscisic acid (ABA), and Zeatin (Z) + Zeatin riboside (ZR). Polyamines, SPM and SPD, enhanced the concentration of ABA and Z + ZR and lessened ETH release, which resulted in enhanced grain filling of wheat under water deficit.

Foliar application

Foliar application is very efficient, because chemicals provided by foliar sprays are readily available to plants (Arif et al. 2006). Application of minerals like magnesium, potassium, calcium, and vitamin-A helps in scavenging the ROS produced in wheat under severe drought. Several scientists successfully used foliar application of potassium in wheat against drought tolerance (Aown et al. 2012). Yasmeen et al. (2012) reported that *Moringa oleifera* leaf extract (MLE) has several plant growth hormones which not only increased plant yield but also enhanced drought tolerance. Later on, Yasmeen et al. (2013) successfully used a foliar spray in wheat to mitigate harmful effects of drought. Malik et al. (2015) observed the effectiveness of methods of application of ascorbic acid in wheat and reported that application of ascorbic acid in the rooting medium was most effective, followed by foliar application and seed priming. Wheat seed treatment with an organic osmolyte "Glycinebetaine" (Mahmood et al. 2009) as well as its foliar application (Qian Quan et al. 2006) was also reported to be effective for drought mitigation.

Breeding strategies

Plant breeding for enhanced water productivity is crucial to fulfilling increasing food demand due to water-deficit conditions in agriculture that will reduce food security in coming years (Davies and Bennett 2015; Hall and Richards 2013). Drought tolerance is the ability of a plant to sustain itself under water deficit. Induction of drought tolerance via breeding is difficult because of its polygenic nature. Usually, screening tests like chlorophyll fluorescence are used to evaluate wheat genotypes for drought tolerance (Sayar et al. 2008). Scientists have worked on seedling (Kashif 2013) as well as physiological (Sayar et al. 2008) responses of wheat to drought. In the conventional breeding programs, it is challenging to control the polygenic nature of drought stress tolerance mechanisms (Khan and Iqbal 2010). However, biotechnology has given solutions for this problem. Two major biotechnological approaches, i.e., molecular marker-assisted selection (MAS) and plant genetic engineering are being used to identify and induce drought tolerance in crop plants (Gosal et al. 2009). However, despite of the technological advancements, the success of MAS in developing drought tolerance is still due (Zhao et al. 2008). Mutation and double haploid techniques have been found effective in breeding for drought tolerance (Njau et al. 2006). A dwarf mutant (s-dwarf) of wheat has been produced in China (Zhang et al. 2005). Similarly, by the use of haploid breeding and mutagenesis, two mutant wheat lines DHML-9 & DHML-50 have been developed which appeared drought tolerant (Khan et al. 2001). Drought tolerance in wheat can be enhanced by the use of water stress-related genes and QTLs (Budak et al. 2013).

Water use (WU), water use efficiency (WUE), and harvest index (HI) are key parameters to get high wheat yield under water deficit. These parameters require strategic trait-based breeding and genetic partitioning of water-deficit adaptive mechanisms (Cobb et al. 2013; Lopes et al. 2014). Root breeding (example of strategic trait-based breeding) is an imperative strategy for drought tolerance in wheat. This includes four root traits for breeding, i.e., deeper root system, enhanced density at depth, lessened density at surface, and increased root hairs for declined opposition to the movement of water from soil to roots. First of all, for controlled and for field conditions, a screening procedure must be repeatable, heritable, cost efficient with a low genotype by environment interaction. Then, germplasm may be screened for root traits, and the best donor parents selected for backcrossing. The first parent (donor) may have low yield, poor quality, and disease resistance but possess desired root traits. The second parent (recurrent) should be with good quality, average yield, and disease resistance but lacking desired root traits. Cross the selected parents to produce the F_1 generation. Backcross F_1 plants with the recurrent parent (BC$_1$) to

produce the BC_1F_1 generation followed by the BC_1F_2 generation. Select plants from BC_1F_2 with desired root traits to form the BC_1F_3 generation. Again backcross BC_1F_3 plants with the recurrent parent (BC_2) to produce the BC_2F_1 generation, and this process must be repeated up to the BC_2F_3 generation. From BC_2F_3, plants with desired root traits can be selected and evaluated for yield at multiple locations under drought, leading to the development of new wheat cultivars having the ability to withstand drought stress as well as having a high yield. This strategy needs a careful choice of field locations and years that permit expression of deep roots. It also requires crossing of germplasm and careful selection to allow assessment of root expression among cultivars that are alike for some phenological traits especially flowering time (Wasson et al. 2012).

Aerial phenotyping

Low-cost unmanned aerial systems (UAS) have real potential for swift proximal dimension determination of plants in agriculture. Recently used methods in plant breeding for phenotypic characterization of breeding material in field conditions need significant resources regarding time, cost, and labor. High-resolution observations can be executed for small plot research using UAS for field-based high-throughput phenotyping (HTP). UAS also enable quick evaluation of several field plots at a time (Haghighattalab and Pérez 2016). Imaging technology is a new strategy for phenotyping characters related to yield and resource efficiency (Nakhforoosh et al. 2016). In a study, three transgenic wheat lines were used for checking the expression of alfalfa aldose reductase gene during permanent drought. These lines were grown at 20% water capacity to achieve permanent drought under controlled conditions. The semi-automatic phenotyping system was used to examine stressed and control plants giving computerized watering, thermal, and digital imaging. Results showed that transgenic wheat plants have a higher yield (green biomass) than non-transgenic plants under drought. Thermal imaging revealed that leaf temperature of stressed non-transgenic wheat plants was increased, while leaf temperature of transformed wheat plants remained the same under normal as well as drought conditions. Phenotyping offered a comprehensive data that depicts an improvement in physiological traits of transgenic stressed wheat plants during the early growth phase under water deficit (Fehér-Juhász et al. 2014). However, aerial phenotyping has some limitations for greenhouse experiments. For example, soil volume in the pot is smaller as compared to field for root development leading to reduced accessibility of nutrients and adequate water to the plant. Soil environment plays major part in the growth of plants, and therefore, it is difficult to make predictions from greenhouse experiments. Phenotyping during water deficit is especially interesting, because

the decrease in soil moisture is linked with an increase in mechanical impedance (an effect difficult to repeat in pots) in the field. In fact, the choice of phenotyping in greenhouse and field experiments depends upon the objectives of phenotyping and heritability of the character along with logistical concerns for data collection. For instance, there is no possible three-dimensional or time-based choice to assess high atmospheric CO_2 in the field (Araus and Cairns 2014). Sankaran et al. (2015) reported that the unmanned aerial vehicle (UVA) method revealed the enormous potential for high-throughput phenotyping in wheat breeding under field conditions. Parent et al. (2015) used an imaging platform to phenotype huge segregating populations of wheat by connecting physiological traits with the genetics of the characters. They found 20 QTL for physiological traits; some of these QTL expressed strong influence explaining 26–43% genetic variation on chromosome 1A and 1B. This means that genotype × environment interaction may be reduced in the greenhouse. Co-location of QTL found in the field and also in imaging platform revealed that they have a common genetic basis at the same loci. Co-locating QTL were identified for different physiological parameters like average growth rate, transpiration rate, leaf expansion rate, and WUE in imaging platform with spike number, grain number, grain weight, harvest index, and yield in the field. It is concluded that phenotyping is adequate for the screening of wheat genotypes in the field (Lopes et al. 2014).

Water budgeting

Irrigation has a major role in enhancing crop yield and accounts for 20% of cropland and 40% of food production in the world (Shen et al. 2013). Several physiological and morphological methods have been developed to lessen the effect of water-deficit stress, extending from drought avoidance to tolerance. Plants avoid water deficit through deep rooting, leaf area reduction, early flowering, and WUE mechanisms. WUE is the ratio between above ground biomass and water consumed during plant growth. Under water deficit, grain yield can be presented regarding WU, WUE, and HI, i.e., Grain yield = WU × WUE × HI (Salekdeh et al. 2009).

Increase in transpiration efficiency could enhance WUE of wheat under drought, leading to higher HI and consequently higher yield (Siahpoosh et al. 2011). Improved WUE through crossing and selection for enhanced transpiration efficiency can lead to the selection of wheat genotypes with high yield under terminal drought stress (Pierre et al. 2012). Xue et al. (2014) investigated wheat yield and WUE in water-deficit conditions. The results showed that new wheat genotypes have high WUE, biomass, and yield under water deficit. These high yielding genotypes have more number of spikes/m^2 and 1000-grain weight. Water consumption and WUE of wheat cultivars have been

evaluated in many experiments. The findings revealed that wheat genotypes having short vegetation periods (low WUE and less yield) were more severely affected by water deficit compared to the cultivars that had longer vegetation periods (high WUE and more yield) (Varga et al. 2015). Aquaporin's (AQPs) are considered the chief source of water, CO_2 and small uncharged solutes transport via cell membrane of plants, thus connecting leaf CO_2 acceptance from the intercellular air spaces to the chloroplast with water loss corridors. AQPs seem to contribute in regulating dynamic changes in leaf, stem, and root hydraulic conductivity in response to environmental changes such as drought (Moshelion et al. 2015).

Resource allocation

Plants store and reallocate micro and macronutrients during their life cycle. Resource allocation depends on the life cycle stage of plants and the reproductive system under investigation (Bennett et al. 2012). A research experiment was performed to see the silicon effect on physiology and yield of wheat in water deficit from flowering to maturity. The results depicted that water deficit increased electrolyte leakage (36%) and silicon concentration in the shoot. Severe water deficit decreased yield by 38%. Application of silicon at 30 kg ha^{-1} helped in mitigating the effects of drought by reducing electrolyte leakage (16.5%) and increasing superoxide dismutase activity, grain K, flag leaf, and grain silicon concentration (Karmollachaab et al. 2013). Zhou et al.'s (2015) variation in C and N allocation, growth, and yield of wheat induced through arbuscular mycorrhizal fungi (AMF) during water deficit. Drought applied at flowering stage decreased photosynthetic C gain, transpiration and stomatal conductance of wheat, while AMF improved all these traits. It also increased N concentration in roots, but decreased it in grains. AMF enhanced growth and ultimately yield by improving photosynthesis during water deficit. In a recent study, three levels of drought stress (severe, moderate, and well-watered) and two levels of N (low and high N) were applied to wheat genotypes. Plants under severe water deficit along with low N showed a substantial reduction in photosynthesis rate, chlorophyll content, and grain yield and reduced grain filling duration (GFD). On the other hand, plants under severe drought along with high N showed drought tolerance through maintenance of less negative leaf water potential, high chlorophyll, and Rubisco content; lower lipid peroxidation linked with high ascorbate peroxide and superoxide dismutase activity. These plants also exhibited delayed senescence, enhanced GFD, and reduced yield decrease. High N nutrition alleviated water deficit in wheat by improving photosynthesis and oxidative defense during vegetative growth (Abid et al. 2016).

Future outlook and main conclusions

The implications of water shortages around the globe will continue to worsen with significant challenges to food production. The challenges brought on by climate change and variability in the world due to global warming will likely have negative impacts on the global grain production, in particular on the crops that feed the world—wheat, rice, and maize. Continued research needs to focus on the use of climate smart agriculture technologies that will reduce the deleterious effects of the stresses. Almost in every part of the globe, crops are grown under suboptimal conditions, thereby limiting their potential, and reducing food availability. The most affected people are the smallholder farmers who live on less than US\$2 day^{-1}, who fail to meet their food demand, causing poverty, hunger, and decreased health. Wheat supports billions of people directly and indirectly and is a staple food for millions of individuals globally. Among several other constraints including heat and low soil fertility, drought poses significant yield losses in wheat and also reduces wheat quality. These stresses impose biochemical, structural, and morphological changes in wheat causing yield losses. The implications of drought will have a highly negative impact on millions of people who depend on wheat directly for their calories.

Low-cost field phenotyping through easy to handle tools of drought tolerance-related characters should be used as an essential strategy in the breeding pipeline. Advancement in technology in terms of phenotyping equipment should also be considered along with strategies used to describe and control variation in the field for wheat under water deficit. It can be achieved using suitable experimental designs, choice of the true characters, and, finally, an appropriate combination of diverse datasets, analysis, and applications, including forecast models. A well-organized combination of all components is required for further application of high-throughput phenotyping to develop drought tolerant wheat varieties in future. As water requirements of wheat vary from region to region, proper water budgeting of wheat is required. For this purpose, WUE regarding yield should be considered. Aquaporin proteins should be inserted via genetic engineering in wheat as these are the principal transporter of water in plants to enhance water use efficiency of modern wheat cultivars during drought stress. Besides physiological investigations, molecular studies are required for better understanding of allocation of resources (such as C and N) during drought water deficit to increase wheat yield. To counter future challenges of drought stress in wheat, new wheat cultivars having the ability to withstand water deficit should be developed together with the application of advances in cultural practices that increase wheat potential on a sustainable basis.

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