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Wheat Responses, Defence Mechanisms and Tolerance to Drought Stress: A Review Article

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ABSTRACT

Wheat (*Triticum aestivum* L.) is one of the major basic stable crops grown worldwide, however, it is sensitive to environmental stresses like drought. With climate change, drought stress is becoming an increasingly severe constraint on wheat production which affects the plant growth and development, physiological functions, grain formation, grain quality and ultimately the yield. Various responses including biochemical, physiological, morphological, and molecular adaptations are shown by plants to survive in the drought stress condition. Drought escape, avoidance and tolerance are important coping mechanisms of wheat plant under drought environment. Several mechanisms such as accumulation of ABA, osmotic adjustment, and induction of dehydrins may confer drought tolerance by maintaining the high tissue water potential. As the root structure and root biomass define the pattern of water extraction from the soil, enhanced root and suppressed shoot growth resulting in higher root: shoot ratio facilitated plants to drought tolerance. The development of drought tolerance varieties becomes an important due to the uneven distribution of rainfall and water shortage. Some growth stage-specific physio-morphological traits are fundamental targets to breed drought-tolerant wheat varieties. Mutation breeding, molecular breeding, genome engineering techniques including gene pyramiding, gene stacking, and transgenics are employed to breed wheat for tolerance to abiotic stresses including drought. Omics decode the entire genome to have better understanding of plant molecular responses that will provide precise strategies for crop improvement. This paper discusses the wheat plant's responses to drought stress, their defense mechanisms and modern techniques for the development of drought tolerant wheat varieties.

Keywords- Drought, Wheat response, defense mechanism, breeding techniques.

I. INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is one of the major stable crops grown in 216.7 million hectares worldwide which is the third-largest crop in terms of area and production with the total production of 765.4 million tons (USDA, 2019). It is a rich source of protein among cereal crops and provides 20% of total calories to nourish 30% of the world population (Shiferaw et al., 2013). It is also the important source of vitamins (e.g. B1, B2, B3 and E), and mineral elements (e.g. Se, Mn, P and Cu). Wheat crop is used as food, animal feed and industrial raw material to prepare alcoholic beverages, starch and straws (Nhemachena and Kirsten, 2017). It has a complex and huge allohexaploid genome (17 GB) composed of three homoeologous sub-genomes with approximately 80% of the repetitive elements and estimated 124,201 annotated genes (Kulkarni et al., 2017). World is currently witnessing enormous changes in climate and temperature owing to global warming which has majorly affected the agriculture sector.

Drought is the meteorological occurrence in the absence of rainfall for a long enough time to cause moisture depletion in the soil and consequently reduction in the water potential of plant tissues (Fatima, 2014). Irregular rainfall due to climate change is likely to further exacerbate water stress leading to a decline in productivity of cereal crops including wheat (Reynolds, M.P. & Ortiz, R. et al., 2010). Wheat is sensitive to environmental stresses like drought and heat mostly at flowering and grain filling stages which negatively impact the yield and quality of grain because of their massive impact on overall plant's growth and development (Lesk et al., 2016). The production of wheat might be waned by 29 % due to the climate change imposed environmental stresses while the demand is predicted to rise by 60 % by 2050 (Manickavelu et al., 2012). Insufficient water because of receding water tables is also detrimental the wheat production (Rodell, M. et al., 2009).

Plant show various responses including physiological, morphological, and biochemical adaptations to maintain normal mechanism for survival, growth and productivity under drought stress. They display different surviving mechanism under drought stress condition. Some agronomic traits included kernel number, grain yield, biomass, harvest index, spike density, thousand grain weight, heading, maturity, and grain filling while the physiological traits included canopy temperature, stem reserve, water status, and photosynthesis are vital for breeding for drought tolerance as these traits contributed to seedling emergence, grain yield, and adaption to drought environments. Canopy temperature, being a good physiological indicator for drought tolerance, may be used as morphological selection tools for developing drought stress-tolerant genotypes. Various modern techniques including molecular breeding, mutation breeding, double haploid, omics, genetic engineering and biotechnological tools are utilized for enhancing the

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tolerance of wheat to drought stress. This review paper explains the wheat crop responses to drought stress, drought tolerance mechanisms and modern breeding approaches to develop drought tolerant wheat varieties.

II. WHEAT RESPONSE TO DROUGHT STRESS

Morphological

- Diminishing sprouting and seedling
- Diminishing leaf area and stunted plant height
- Reduction of root and shoot growth
- Decline of spike length & spikelet per spike
- Decrease in grain number, size &weight
- Reduced biomass and grain yield
- Early senescence and maturity

Physiological

- Decrease of stomata size and number
- Stomata closure
- Reduction in stomata conductance
- Decline in photosynthesis & osmoregulation
- Elevated transpiration & respiration
- Decrease in water potential & relative water content
- Decrease in cell membrane stability

Biochemical

- ROS production and detoxification
- Oxidative stress
- Limited carboxylation
- ABA and HSPs accumulation
- Antioxidant enzymes, free radical & solutes accumulation
- Diminishing chlorophyll

Anatomical

- Damage in mesophyll, nuclei, chloroplast and mitochondria
- Xylem and phloem damage
- Reduction in mitosis, cell division, cell enlargement and differentiation
- Changes in cell wall, membrane and thylakoids architecture

Figure 1: Combined changes occurred in wheat under drought stress.

Stomata cover only 5% of leaf surface area but responsible for around 70% water transpiration by plants. It is the aboveground point for entry of carbon dioxide for photosynthesis and exit of water through transpiration (Shahinnia et al., 2016). All plants respond to severe water-deficit condition by closing stomata to avoid water transpiration resulting decrease in leaf's turgor pressure or water potential or the creation of low humidity atmosphere (Khazaei et al., 2010) that consequently decline the inflow of CO_2 into the leaves (Azhand et al., 2015). This makes a more availability of electrons for ROS production and also increases the susceptibility to photodamage (Lawlor, 2009). As the stomatal responses are dependent on soil moisture content rather than leaf water status (Sharifi and Mohammadkhani, 2015), stomata respond to chemical

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signals like ABA that is produced by dehydrating roots although water content in leaves is enough (Blum, 1996).

Besides carbon dioxide uptake, drought causes many changes in plant's regular mechanisms. Some of them are damage in photosynthetic apparatus, change in photosynthetic pigments and components, and alteration in the activity of enzymes of Calvin cycle resulting in crop yield reduction (Sharifi and Mohammadkhani, 2015). Moreover, loss of balance between the formation of ROS and the antioxidant defense is a key factor to limit the growth and photosynthetic ability of plants (Guan et al., 2000). In wheat, as a decline in the activity of Rubisco, an enzyme involved in the first major step of carbon fixation (Flexas et al., 2004), and the disruption of thylakoid membranes which constrain the normal membrane-associated electron carriers and enzyme activities eventually lowers the rate of photosynthesis (Ristic et al., 2008). In wheat, more than 50% of the daily accumulated photosynthese are transported to roots and around 60% of this fraction are respired (Turton et al., 1996). So, respiration rate is also declined as the acute reduction in photosynthesis due to drought. Drought increases the rate of respiratory carbon loss in rhizosphere that reduces the ATP production and enhances the synthesis of ROS (Akter and Islam, 2017). ROS- extremely toxic- may react with proteins, lipids, membranes etc. thereby causes oxidative damage to cells and deactivate their normal functions (Singh et al., 2016). Oxidative stress remarkably increases membrane peroxidation and declines the membrane thermo stability (Savicka and Skute, 2010).

Plant display diverse responses to cope with drought stress which includes physiological, morphological, and biochemical adaptations (Fahad et al., 2017). Morphological adaptations include extended, deeper and dense root growth and suppressed shoot growth resulting in higher root: shoot ratio, larger green leaf area, and late leaf senescence. Lower osmotic potential, high chlorophyll content, thick and waxy leaf coverings and increased harvest index indicate cellular and biochemical adjustments. Physiological responses include closing of stomata, significant decline of photosynthesis activity, a noticeable oxidative stress, a change in the integrity of cell wall, and production of fatal metabolites (Zvi and Blumwald, 2011). These all are accompanied by signal recognition of roots and loss of turgor pressure with a decrease in leaf water potential, stomatal conductance to CO_2 and growth rates (Nezhadahmadi et al., 2013). Wheat crop adjusted to drought through the improvement of osmoprotective and antioxidant responses (Huseynova, 2012) and significantly a better coordination of positive and negative regulation of gene expression.

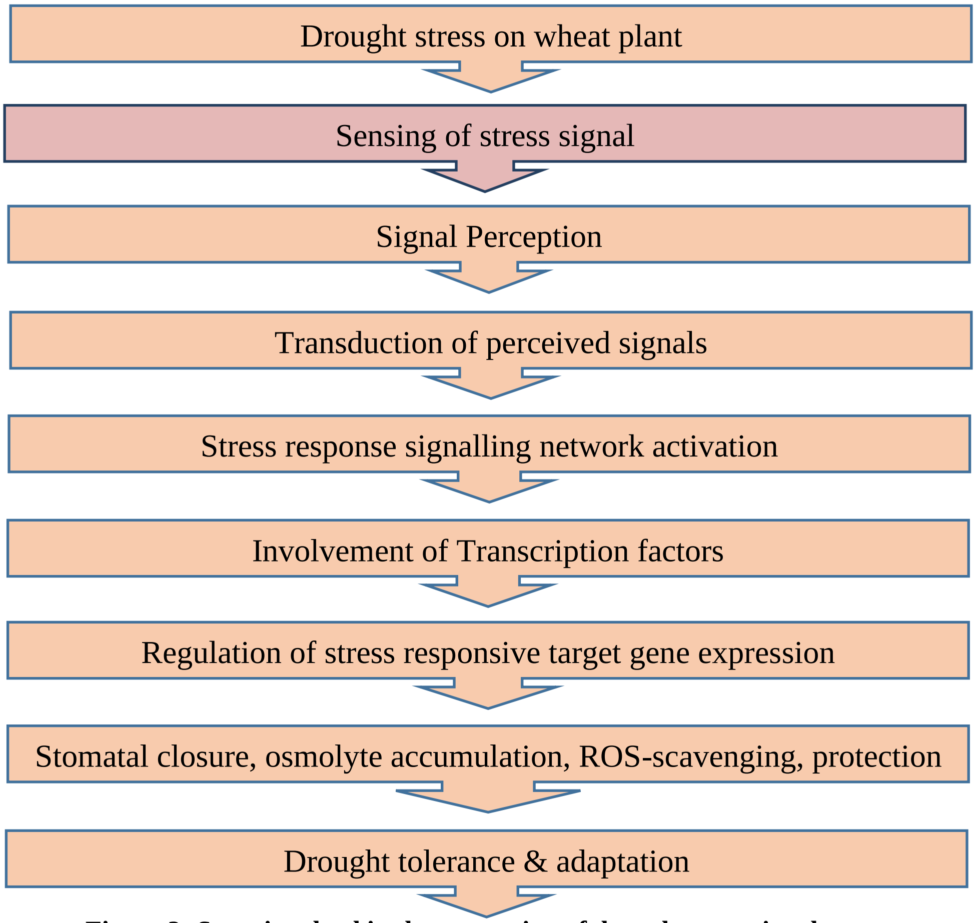

Figure 2: Steps involved in the expression of drought stress in wheat

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III. DROUGHT TOLERANCE MECHANISM

Normally, plant's surviving mechanism to drought is classified into three different groups: drought escape, avoidance and tolerance. In drought escape, plant completes its cycle before the onset of drought when there is sufficient supply of water (Fang and Xiong, 2015). During drought avoidance, plants preserve higher water potential by maintaining the turgor with deeper roots and controlling transpiration through stomata even though there is low water availability in soil. Whereas in drought tolerance, turgor is maintained by osmotic adjustment resulting in increased cell elasticity and reduced its size.

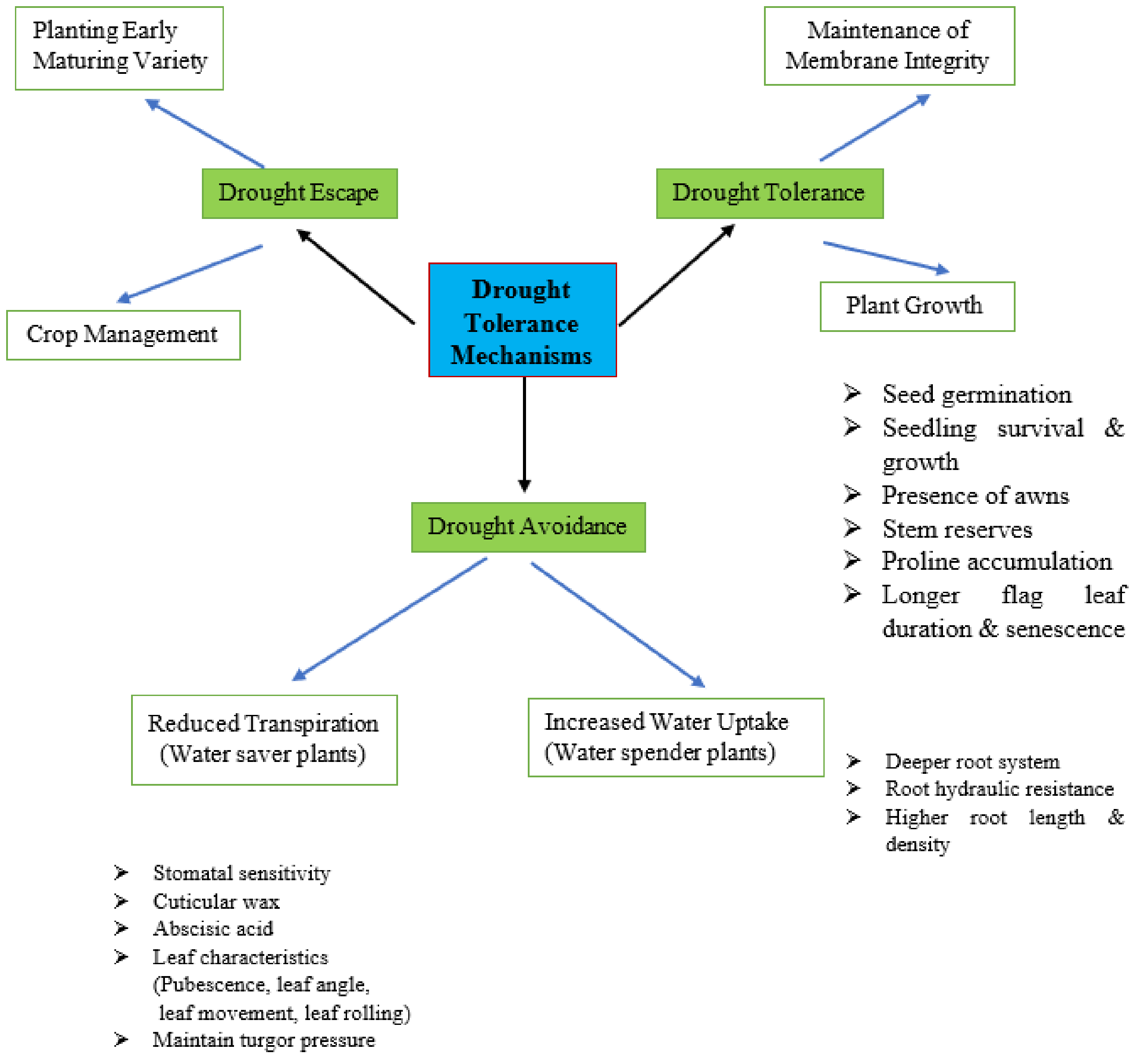

Figure 3: Schematic overview of drought tolerance mechanisms in wheat

As flag leaf contribute 30-50% of assimilates during grain filling (Sylvester-Bradley et al., 1990), flag leaf stomatal features are vital to cope drought stress. Smaller size and increased density of stomata in flag leaves of wheat promote transcription efficiency (Kulkarni et al., 2017) which were found to be connected with water stress tolerance in wheat varieties (Shahinnia et al., 2016). Drought tolerant spring wheat cultivars such as Anmol, Moomal, Bhittai, Sarsabz have smaller sized stomata, lower stomata conductance and ability to maintain higher relative water content under drought stress (Baloch et al., 2013). Relative water content is the meaningful determinant of drought tolerance as it indicates the membrane stability and balance between

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water supply and evapotranspiration. In drought-sensitive genotypes, senescence was first appeared in flag leaves and then in older leaves. Stay green (SG), an important physiological character, helps wheat plant during drought stress condition (Budak et al., 2013). The green leaf area in the post-anthesis period sustains carbon assimilation (Thomas, H. & Smart, C.M., 1993) and contributes to grain-filling and grain yield through the remobilization of stem reserve to grains (Rebetzke, G.J. et al., 2016). As temperature tolerant traits are linked with drought tolerant traits, rubisco is an important enzyme that shows an excellent affinity for CO_2 in drought-tolerant wheat. Therefore, this property can be applied for the development of drought-tolerant varieties (Cossani and Reynolds, 2012).

Various mechanisms such as osmotic adjustment, accumulation of ABA and induction of dehydrins may confer drought tolerance by maintaining high tissue water potential (Lambin et al., 2001). Osmotic adjustment is a process of overproduction of different types of organic compatible solutes (Serraj and Sinclair, 2002). Compatible solutes, low-molecular-weight highly soluble compounds, are generally nontoxic even at high cytosolic concentrations (Pinhero et al., 2001). They defend plants from stress through helping in osmotic adjustment, detoxifying ROS, stabilizing membranes, and structures of enzymes and proteins (Blum, 2016). Osmotic adjustment, an important trait in delaying dehydrative damage in water-limited environments, continually maintained cell turgor and physiological processes (Taiz and Zeiger, 2006). It helps to maintain the cell water balance with the active accumulation of solutes in the cytoplasm thereby decreases osmotic potential and increases gradient for water influx; as a consequence, it minimizes the damaging effects of drought (Morgan et al., 2002). It also facilitates a better translocation of pre-anthesis carbohydrate partitioning during grain filling whereas high turgor maintenance leads to higher photosynthetic rate and growth (Serraj and Sinclair, 2002). Plants underwater stress shift focus to ABA production for downstream activation of signaling and tolerance mechanisms which lowers the grain filling and ultimately the yield; therefore, the balance between yield and drought tolerance needs to be scrutinized (Alvarez et al., 2014). ABA, usually known as the "stress hormone" - acts as a first line of defense against drought- usually increases in response to multiple environmental stresses including drought (Finkelstein et al., 2002). Thus, ABA content has been used as selection index for screening wheat underwater deficit and contrasting parents for its production have been crossed.

Although it was identified that increased yield depend upon pattern of water stress in that specific environment (Palta et al. 2011), wheat genotypes with a deeper, dense, extended, and high radial hydraulic conductivity display an improved yield and drought tolerance. As the root structure and root biomass define the pattern of water extraction from the soil (Prasad et al., 2018), enhanced root and suppressed shoot growth resulting in greater root: shoot ratio facilitated plants to drought tolerance (Xu et al., 2013). More efficient root with 20% faster root descent extracted water effectively from sub-soil (roots below 60 cm) resulting yield aids of 0.32–0.44 t/ha in wheat (Lilley and Kirkegaard, 2011). 50% increase in root: shoot ratio was found in wheat in response to drought (Rauf et al., 2007) which enhanced root growth while subsequent suppressed shoot growth was occurred due to the increase level of abscisic acid (Xu et al., 2013). Crop varieties extracting moisture from deeper zones (60– 120 cm) maintain higher stomatal conductance and cooler canopy temperature (Pask and Reynolds, 2013). Deeper roots enhance moisture uptake (Uga et al., 2013), whereas transcription factors from LBD gene family improve root architecture (Li et al., 2016). In addition to improved root traits, better crop transpiration efficiency (TE) - measured as biomass produced per unit of water transpired by a plant- is critical to protect yield under limited availability of soil moisture (Condon et al., 2004). As TE is linked to deeper root system, these two traits need to be simultaneously improved.

Utilization of genetic variation in wheat varieties

The development of drought tolerant varieties becomes important due to the uneven distribution of rainfall and water shortage (Danish and Zafar-ulHye, 2019). The natural progenitors of cultivated crops have drought tolerance characteristics that lost during cultivation of modern lines can be used in the improvement of the latest crop varieties (Ashraf et al., 2009). As an ancestor of modern wheat- *Aegilops tauschii*- which offers the most promising source of drought related genes and their gene regions is more drought tolerant than *Triticum* and wild emmer wheat (*T. dicoccoides*) species, it can be used to develop stress resistant wheat varieties. A group of Creole wheat landraces which introduced to Mexico from Europe have rare but beneficial alleles thereby showed better adaptation to different abiotic stresses including drought (Vikram et al., 2016). Likewise, the Japanese landrace "Aka Komugi" has dwarfing allele Rht8c that contributes to breeding of drought tolerant wheat (Grover et al., 2018). In addition to *T. aestivum* landraces - one of the major groups of genetic resources (Mwadzingeni et al., 2017) - other domesticated wheat species such as *T. durum*, *T. turgidum*, *T. compactum*, *T. sphaerococcum*, *T. polonicum* and *T. turanicum* ("Kumut") are also the sources of valuable alleles for breeding drought tolerant wheat (Nemtsev et al., 2019).

Some growth stage-specific physio-morphological traits such as early vigor (Rebetzke et al., 1999), coleoptile length (Rebetzke et al., 2007), leaf rolling (Kadioglu and Terzi, 2007), carbon isotope discrimination (Kumar and Singh, 2009), flag leaf senescence (Hafsi et al., 2013), leaf chlorophyll content

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(Ramya et al., 2016), glaucousness for photoprotection (Bi et al., 2017), plant height (Su et al., 2019) and root system architecture (RSA) (Lopes and Reynolds, 2010) traits are important targets to breed drought-tolerant wheat varieties. Large-scale identification of drought-related QTLs or genes is required due to the complex nature of stress-related dehydration genes. Plant respond to drought stress through altering their gene expression and protein production and some protein expressed under drought stress are dehydrin, glutathione S-transferase, vacuolar acid invertase, and late embryogenesis abundant (LEA) proteins (Anderson and Davis, 2004).

IV. BREEDING APPROACHES

Modern breeding techniques has addressed the limitations of classical breeding approach by incorporating biotechnological tools to overcome cross-sexual barriers or create novel variability in the crop species, or to improve the reliability of the selection programs (Langridge, P. et al., 2019). The marker-assisted breeding uses the molecular marker profiling in segregant populations to select the superior individuals for the trait of interest. Molecular markers resolve many limitations of morphological and biochemical methods as they are not influenced by the environmental or developmental stage and can detect DNA-level variations (Ashraf et al., 2014). SSRs are the most preferred markers for the assessment of genetic diversity, molecular genetic mapping of wheat (Abbasov, 2018) because of their multi-allelic nature, co-dominant inheritance and high reproducibility (Sajjad et al., 2018). Genes controlling root architecture and stomatal development have significant role in soil moisture extraction and its retention which have been targets for molecular breeding of drought tolerant wheat. The foremost target in the development of drought-tolerant crops are the genes governing the protection and maintenance of cellular structure and functions (Rivero, R.M. et al., 2009).

Double haploid complement the conventional breeding to speed the release of new drought tolerant varieties as it provides higher polymorphism in limited quantity of experimented lines. Two drought-resistant wheat varieties Jinghua 1 and Jinghua 764 in China; Malika in Morocco; Florin in France; Gk Delibab in Hungary were developed by using the doubled haploid technique (Pauk J et al., 1995). Furthermore, double haploid genotypes DH1 and DH2 under drought condition found superior than checks in Egypt (Bakhshi N et al., 2017). The high production cost, limitation on number of crosses and low haploid generation facilities restricted the use of double haploid technique.

Mutation breeding, another way to create variants for drought adaptation, has been applied using elite germplasm for cultivar development in wheat. Let us take the example of “Sharbati Sonora”, which is an early maturing cultivar of wheat and developed by gamma radiation of a Mexican cultivar; this made a major contribution to the wheat production in India (Raina et al., 2016). 11 drought-tolerant wheat mutant lines were recognized by using gamma ray radiation (Sen et al., 2017). Al-Naggar and Shehab-El-Deen (2012) used gamma rays and EMS mutagens in six Egyptian bread wheat varieties to produce drought-tolerant mutants which exceeded 20% grain yield over parents under drought condition. Mutation breeding has potential to create novel stress tolerance alleles even if it is less common as compared to other breeding methods.

Integrated genetic engineering and biotechnology approaches open up new opportunities for enhancing the existence of narrow genetic base of wheat crop. Gene pyramiding, gene stacking, and transgenics are some genome engineering techniques which are employed to develop improved drought tolerant wheat varieties (Budak et al., 2015). Karolina et al. (2019) found an important function of wheat genes P5CS and P5CR in controlling tolerance to water deficits by analyzing their expression under drought stress. Hua et al. (2019) identified target genes in wheat which could be exploited through genetic engineering to improve drought tolerance. The overexpression of TaNAC69, HVA1, CAT TaDREB2, and TaDREB3 genes in transgenic wheat improved water use efficiency and produced more shoot biomass and yield under drought conditions (Pellegrineschi A et al., 2004).

Table 1: Development of drought-resistant wheat varieties by foremost wheat-producing countries.

Countries	Drought resistant wheat varieties	References
China	Keyi26, Nongda 36, Nongda 183, Shijiazhuang 407, Huabei 187, Taigu 49, Yulin3, Mazhamai, Xuzhou 14, Jinmai 33, Jinmai 2148, Hezuo 2, Datouchunmai, Xindong 2, Jinmai 33, Kehan 9, Xinkehan 9, Inmai 47, Shijiazhuang 8, Cang 6001, Cangmai 02, Cangmai 6005, JM-262, Xihan No. 2, Longchun 23, Luhan7, Luhan 2, and Yannong 19.	Ling H et al., 2018 Yu L et al., 2017 Li Q et al., 2018 Yu L et al., 2018
India	Shekhar, WH 1142, HD1467, Harshita, N59, and BRW 3723	Gupta A et al., 2018 Shyamal KT et al., 2014 Degu WT, 2015

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Russia	Sarrubra, Sarrosa, Saratovskaya 29, Svetlana, Milturum, and Cesium	Morgounov A et al., 2003 Morgunov AI, 1992
USA	Greer, Joe, Plains Gold Avery, SY Monument, Tatanka, WB-Grain field, TAM112, White Sonora LCS Chrome, LCS Mint, and T158	Jourdan MB et al., 2016-17 Reddy SK, 2014
Canada	Stettler, Lillian, AC Barrie, and Strongfield	Fleury D., 2018 Ashe P. et al., 2017
Pakistan	Chakwal50, NARC 2009, Tijaban-10, Dharabi-11, NRL 2017, Pakistan-13, Pakistan-13, Shahkar-13 and NIFA-Lalma, , Tatara, AZRC-1, Siran-2007, Raj, Chakwal-87, Rawal-97, Pothwar-93, Kohsar-95, Chakwal-97, GA-2002, Ehsan-16, Barani-17, Fateh Jang-16	Akhtar A. et al., 2017 Farooq A. et al., 2017 Ghulam MS et al., 2014 Krishna DJ et al., 2017 Muhammad I et al., 2018 Waheed A. et al., 2018
Australia	1:ZIZ12, 12:ZIZ12, 56:ZIZ12, 134:ZWB12, Allora Spring, Farmer's Friend, King's Jubilee, Steinwedel, Kord CL Plus, drysdale, Wyalkatchem, and Estoc	Donald GM & Leary RO, 2016 Peter M & Don M., 2019 Trethowan R et al, 2016
Turkey	Karahan-99, Gerek-79 and Alka quality, Saricanak-98, Altay-2000, Dagdas-94, Katea-1, and Kirac-66	Ahmed M et al., 2009 Yoruk E et al., 2018 Cheng L et al., 2016

Omics techniques

Recent progress in technology has led to the development of high-throughput like "omics" for crop improvement. Omics - a study of an organism's genes, transcripts, proteins, and metabolites - decode the entire genome to have better understanding of plant molecular responses that will provide precise strategies for crop improvement (Jain et al., 2019). Genomics, proteomics, and metabolomics are three main omics approaches which unravel the whole genetic expression, proteins and metabolites respectively (Krugman et al., 2011). The metabolomics profiling showed that drought-resistant genotype is characterized by the higher accumulation of tricarboxylic acid cycle intermediates and drought-related metabolites including proline, glucose, glycine and trehalose.

A common response to drought includes differential expression of heat shock proteins, cytochrome P450, dehydrins, glutathione transferase, proteinase inhibitors, and regulatory proteins such as transcription factors which is similar in both monocot and dicot plants. In a water stress tolerant wheat genotypes, multiple TFs such as WRKY, basic leucine zipper (bZIP), and NAC were expressed differentially as compared with susceptible genotype (Ergen et al., 2009). Some molecular approaches for drought tolerance in wheat have been broadly described; it includes the protection of proteins by LEA proteins (e.g. dehydrins) and chaperone proteins (e.g. heat shock proteins), signal transduction cascade and transcription activation/regulation, stimulate the production of chemical antioxidants (ascorbic acid and glutathione), and enzymes reducing the toxicity of ROS (SOD, glutathione S transferase), collection of osmolytes (proline, glycine betaine, trehalose, mannitol, myo-inositol) (Yamaguchi-Shinozaki and Shinozaki, 2006). TFs in response to certain drought-tolerant markers regulate transcription of genes related with drought-tolerant mechanisms. Regulation is classified into two sets: first includes protein-coding genes that protect the plant from the effects of dehydration while second group contains genes for the regulatory proteins mainly TFs (Shi et al., 2010). Recently, many transcription factors (TFs) involved in various abiotic stresses have been found and engineered to improve stress tolerance in crops (Wang et al. 2016).

Agronomic approaches

Among the agronomic approaches, water conservation techniques increase water use efficiency; nutrients management moderates soil temperature, reduces evaporation losses, minimize pollution; chemical and biological control protect the wheat from damage due to drought stress; adaptation mechanisms are effective as operational management by translating weather information.

Table 2: Agronomy management practices for drought mitigation

Water conservation techniques	Nutrient management	Planting time	Biological control	Chemical control
Improved water harvesting techniques	Balanced use of nutrients at proper	Early sowing or as soon as adequate	Inoculation of arbuscular	Exogenous application of hormones, antioxidant

Minimum tillage Weed management Seed priming	time and stage Straw mulching	rainfall/moisture available or plant early maturing cultivars	mycorhizal fungi Ameliorating plant growth and development	enzymes, biochemical solutes and osmoprotectants to seed or growing wheat

(Source: Zulkiffal, M. et al., 2021)

V. CONCLUSION

Currently, Agriculture is majorly affected due to the enormous changes in climate and global warming. As the increasing demand on existing resources is not achievable in today's time, there is an immediate necessity of high-yielding stress-tolerant crops to maintain the balance between crop produce and increasing human demand. Environmental stresses including drought negatively affect the yield and grain quality of wheat crop thereby the production of drought tolerant wheat varieties becomes vital. Various breeding approaches are employed to breed the wheat varieties for the tolerance to drought and meet the demand of increasing world's population.

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