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Morphological, Physiological, Biochemical and Molecular Responses of Wheat vs Drought Stresses: A Review

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Abstract

Drought stress is becoming a serious challenge for international food security. Prevailing climate change, complex nature of genetic response to drought and multifaceted character of drought-associated traits make drought more pronounced. Drought severely impairs plant growth and development, production and performance of crop plants. It causes significant yield reduction and brings shrinkage of farmlands compared to other abiotic factors. Worldwide, wheat is the most important food crop contributing one fifth of total dietary calories and proteins. However, recurrent drought associated with climate change is among the principal constraints to global productivity of wheat (*Triticum aestivum* L.) and *T. durum* L.). Based on genetic variability within and among wheat species, there is morphological, physiological, biochemical and molecular attributes against water stress. This review illustrates, change in these attributes in wheat and functional genomics through transgenic wheat as drought tolerance mechanisms in wheat. Potential challenges and associated opportunities in drought tolerance development in wheat are also highlighted.

Keywords: Climate change, drought tolerance, genetic variability, transgenic wheat.

1. Introduction

Drought is abiotic stress, severely impairs plant growth and development, limits production and the performance of crop plants, causes significant yield reductions on crops and impact on cropping areas, more than any other abiotic factors (Shao *et al*., 2009;Rad *et al*., 2012; Ray *et al*., 2018). Climate extremes are expected to increase with climate change, which may negatively affect crop production mainly due to drought (Troy *et al*., 2015). Due to the existing climatic change, it is assumed that by the year 2025, around 1.8 billion people will face absolute water shortage and 65% of the world's population will live under water-stressed environments (Nezhadahmadi *et al*., 2013). This is due to an imbalance in plant water regime resulting in an excessive evapotranspiration by shoot over water uptake by root (Reynolds *et al.,* 2005). Thus, Drought is most devastating stress, which immediately affects morphological, physiological, biochemical, and molecular characteristics of wheat crop and lead to severe reduction in overall production (Nezhadahmadi *et al*., 2013; Bila *et al*., 2015).

Wheat is the most abundant crop in the world, the first rainfed crop after maize and the second irrigated crop after rice (Portmann *et a.,l* 2010). The two major wheat species, hexaploid bread wheat (*Triticumaestivum L.*; 2n = 6x = 42) and tetraploid durum wheat (*Triticum durum L.;* 2n = 4x = 28), are commercially important. Food and Agriculture Organization (FAO) of the United Nations has estimated 739.9 million tons of wheat production in 2017, which would be down from 760.1 million previous year production (http://www.fao.org/worldfoodsituation/csdb/en/). Wheat contribute about 20% of the total dietary calories and proteins worldwide (Lobell & Gourdji 2012; Shiferaw *et al*., 2013). Despite, the estimated wheat demand to increase by 60% (Manickavelu *et al*., 2012) to 70% (CIMMYT, 2014) by 2050, wheat production might go down by 29% because of climate change imposed environmental stresses such as drought (Manickavelu *et al*., 2012). Zampieri *et a.l* (2017) reported that drought is the main contributor of annual wheat production variability in major wheat production belts throughout the world, which is estimated at around 40%.These predictions indicate that improving drought stress tolerance in wheat has supreme importance for global food security. Continued wheat genetic improvement is thus critically important as it has direct impact on economic development, food security, and international grain trade.

Wheat as a sessile crop plant has different degree of adaptation mechanisms to abiotic stresses such as drought. Therefore, determination of the genetic diversity existing within and between wheat populations remains as basis for elucidation of the genetic structure and for improvement of quantitative traits for drought tolerance. Genetic variability of wheat can be explored with germplasm from its centers of origin, diversity and within wild relative and landraces for drought tolerance (Nevo and Chen 2010; Dvorak *et al*., 2011; Dodig *et al*., 2012). However, drought tolerance is a complex trait that is controlled by numerous genes, each with minor/polygenic effects (Bernardo 2008; Gupta *et al*., 2017). Some of the genes are located as quantitative trait loci (QTL) exhibiting additive and non-additive gene effects. Due to its polygenic inheritance and genotype by environment interaction, drought tolerance typically has low heritability (Blum, 2010; Khakwani *et al*., 2012).Additionally, the inheritance of most QTLs that have been examined sofar have a certain component of epigenetics control (either DNA methylation or histone modification,or both) (Gupta *et al*., 2017). On the face increasing climatic extremes and high demand for wheat for accelerated world population growth, understanding drought tolerance mechanisms in wheat has principal importance. In general, wheat respond to drought stress with a wide range of modifications leading to changes at morphological, cellular, physiological, biochemical, and molecular level **(**Rampino, 2006; Lopes & Reynolds, 2011). Hence, this review focuses on morphological, physiological, biochemical, and molecular responses of wheat to tackle drought stresses.

2. Wheat morphological responses to drought tolerance

Morphological traits of wheat has been significantly impacted by drought. Study result showed that vegetative and reproductive stages of crops were affected by drought (Shi *et al*., 2010).Wheat yield losses at vegetative and reproductive stages under drought condition has been reviewed in Nezhadahmadi *et al* (2013). Bilal *et al*. (2015) specified wheat yield under drought stress suffer serious moisture deficit throughout its growth period from seedling to full maturity (Figure 1). Various scholars have reported morphological responses of wheat to moisture stress via above ground; gain yield, plant height, biomass, leaf (area, extension, size, number, and longevity), and below ground; root (extension, dry weight, density, and length, and root to shoot ratio (Nezhadahmadi *et al*, 2013). Under drought condition, decreasing pattern was experienced in above ground morphological traits in wheat (Kilic & Yağbasanlar, 2010). In contrast to the above groundmorphological traits, under drought stress conditions, below ground morphological traits continue to grow to find water. These different growth responses of shoot and root under water limiting conditions could result in high root to shoot ratio, and function as drought avoidance mechanism in drought tolerant wheat genotypes.

Experiments conducted on durum wheat (*Triticum durum L.*) genotypes indicated weak to strong positive correlations of morphological traits. These include plant height, fertile tiller number, with grain number and biomass make the evaluation of high-yielding genotypes in rainfed conditions possible (Liu *et al*, 2015).Morphological traits (such as plant height and tiller number)could therefore be considered as potential indicators for indirect selection of durum wheat with water-deficit stress tolerance. Most agro-morphological traits except root length and associated parameters show decreasing trends under water limiting conditions. In drought susceptible wheat genotypes photosynthetic rate and eventually targeted yielddecrease drastically. Therefore, wheat genotypes with higher performance of agro-morphological traits are considered to have drought tolerance mechanisms. However, since drought is a complex trait and drought tolerance response is carried out by various genes, transcription factors (TF), microRNAs (miRNAs), hormones, proteins, co-factors, ions and metabolites (Budak *et al*., 2015) contribution of morphological traits alone is less significant. This complexity coupled with the large and repetitive genome size of wheat has limited the development of wheat cultivars for drought tolerance by classical breeding.

However, several research finding have been indicated that a strategy of selecting should take into consideration early flowering, long grain filling period, late maturity period, low drought susceptibility index (DSI values<1), a high number of grains per spike, high spike weight and short spike length for increasing yields under drought conditions (Kilic & Yağbasanlar, 2010).

3. Wheat physiological responses to drought tolerance

Physiological changes are consequences of deleterious effects of drought on important metabolic processes as well as responses of various defense mechanisms adapted by plants under drought conditions (Chorfil & Taïbi, 2011). Physiological characters are yield stability parameters and useful for evaluating drought tolerance wheat genotypes (Kadam *et al*., 2017). The principle is to strengthen the synthesis of metabolism, increase intracellular infiltration of substance concentration, reduces osmotic potential, maintain the pressure and normal cell physiological function (Dong *et al*., 2018). Evaluation of wheat genotypes under drought stress illustrated that drought tolerance genotypes accumulate higher concentration of physiological indices such as free proline, glycine, betaine, total sugars and potassium content. These organic and inorganic substances help to maintain osmo-regulation under water stress. Moreover, higher concentration of these solutes gives advantage to wheat plant to tolerate drought stress (Muhammad *et al*., 2016). In tolerant durum wheat genotypes, maintenance of high plant water status and maintenance of photosynthetic rate are major physiological attributes of high yield stability under rainfed conditions (Liu *et al*., 2015). Even though, leaf water status was maintained by unlimited water supply from deeper soil layers, wheat plants regulate its stomata in response to drying signals from the roots in the top drying layer of the soil profile (Blum and Johnson, 1993; Saradadevi *et al*., 2015). Transgenic wheat plants close their stomata rapidly under drought stress conditions and resulted in reduced transpiration and water loss, improving wheat drought resistance (Yu *et al*., 2017). Several studies reported that under drought stress photosynthesis shows direct relationship with wheat grain production due to reduction in stomatal opening, which resulted in low amount of CO_2 fixation that lead to reduction in photosynthetic amount (Mafakheri *et al*. 2010). Lowered photosynthetic amount is an outcome of inhibition of RuBisCO (ribulose-1, 5-bisphosphate carboxylase/oxygenase) enzyme activity and development of ATP under water deficit condition (Dulai *et al*. 2006).

Monirul *et al* (2015) depicted that Polyethylene Glycrol-induced drought stress caused significant decline in physiological characteristics in susceptible wheat genotype as compared to tolerant genotype, suggesting response variability among genotypes for drought tolerance. Liu *et al.* (2015) explored that durum wheat genotypes tolerant to water-deficit stress has less yield reduction and also had less reduction in chlorophyll content, relative water content and leaf water potential. Hence, durum wheat genotypes tolerant to water-deficit stress maintain a higher photosynthetic rate and leaf water status. Higher leaves chlorophyll contentis significantly correlated with photosynthesis and regarded as encouraging selection trait in crop productivity (Teng *et al*., 2004). Under water stress conditions, decrease in water status and osmotic potential in plants is the ultimate outcome of lower relative water content. Osmoregulation mechanism plays a remarkable role in preserving turgor pressure, which helps in soil water absorption and continue plant metabolic activities for its survival (Bilal *et al*., 2015).

Under drought, Cell-membrane stability (CMS) is another vital important selection criteria of drought tolerant genotypes. Genotype with values less than 50% and with 71-80% are considered as susceptible and tolerant to drought, respectively (Tripathy *et al.* 2000; Bilal *et al*., 2015). In drought tolerant wheat,higher CMS protect the plant from ROS that causes decrease in membrane stabilitydue to production of lipid peroxidation.Physiological responses, includingchlorophyll content, closure of stomata and decrease in the activity of photosynthesis, development of oxidative stress, alteration in the integrity of cell wall, production of metabolites play a crucial role in wheat when water is limiting. Thus, these physiological traits could be consideredas potential indicators for indirect selection of tolerant wheat genotype(s) under drought conditions.

4. Wheat biochemical responses to drought tolerance

In crop plants, significantly accumulated metabolites under drought stress are considered as key metabolites and are correlated with potential biochemical pathways, enzymes or gene locations for a better understanding of the tolerance mechanisms (Ullah *et al.*, 2017).Drought signaling pathways involve crosstalk among various biochemical, which makes breeding for drought tolerance an uphill task (Akpinar*et al*., 2012). Proline is among key biochemicals that accumulate in significant proportions in plants when exposed to various kinds of stress, including dehydration (Hong-Boa *et al*., 2006; Khamssi, 2014). Ithas been associated with several osmo protection roles, including; osmotic adjustment (Marek *et al*., 2009; Zadehbagheri*et al*., 2014), membrane stabilization (Hayat *et al*., 2012), and gene signaling to activate anti-oxidizing enzymes that scavenge reactive oxygen species (ROS) (de Carvalho*et al*., 2013, Kadam*et al*., 2017). Higher accumulation of proline in BG-25, drought tolerant wheat genotype, deliver strong antioxidant defense and play a pivotal role in drought tolerance in wheat (Monirul *et a.l*, 2015).Chorfil & Taïbi (2011) investigated that durum wheat genotypes adapted to arid environment exhibited significantly higher accumulation of proline compared to the less adaptive once.

In the course of adaptation to stress environments, plant hormonesregulate diverse processes in plants, which enable adjust to stress. Under water deficits, ABA translocate form roots to leaves and involve in alteration of guard cell ion transport, regulatestomatal closure, reduces water loss and inhibits plant growth (Kim *et al*., 2010; Wilkinson and Davies 2010). Studies indicated that wheat genotypes that accumulate less ABA in their leaves have been associated to drought resistance and those accumulating more ABA havebeen considered sensitive to drought (Quarrie, 1981; Ji *et al*., 2011). On the contrary, high leaf ABA accumulating wheat lines demonstrated better water use efficiency for grain yield than low ABA lines (Innes *et al*., 1984). Auxins is knownas negative regulators of drought tolerance in crop plants.In wheat leaves, drought stress tolerance was accompanied by a decrease in indole-3-acetic acid (IAA) content (Xie *et al,*. 2003). Brassinosteroids (BRs) have also been reported to protect plants against various abiotic stresses (Kagale *et al*., 2007). Application of BR was seen to increase water uptake and membrane stability, as well as to reduce ion leakage arising from membrane damage in wheat plants subjected to drought stress (Sairam, 1994). Hormonal priming increased grain yield, total sugar and protein contents of some bread wheat genotypesunder drought as tolerance mechanism.Seed priming with plant growth regulators like Gibberellic Acid (GA) and Salicylic Acid (SA) can significantly enhance wheat performance in terms of morphological parameters and yield attributes under drought (Ulfat *et al*., 2017). Dong *et al.* (2018) showed that activities of antioxidant enzymes (POD), malondialdehyde (MDA), proline (Pro), glutathione (GSH) and H_2O_2 in wheat seedlings increased under drought stress. Hence, those wheat seedlings with increased antioxidants enzymes activities can be used as indicator of drought resistance during evaluation. In general, co-ordination between different hormone signaling, or hormone signaling and otherpathways such as ROS regulatory mechanisms could be flexible, being altered by timing and types ofstresses, and could be different depending on plant species under stress combinations (Nobuhiro, 2016, Llanes *et al*., 2016).

5. Wheat molecular responses to drought tolerance

Drought stress triggers expression of many genes influencing the metabolism of several bio-chemicals including key enzymes, transcription factors, hormones, amino acids, and carbohydrates (Yang *et al.* 2010). Notable among these include the phytohormone; Abscisic acid (ABA), proline, tryptophan, late embryogenesis abundant

(LEA) proteins, trehalose, raffinose, mannitol, glycine-betaine, and superoxide dismutase (Sivamani *et al*., 2000; Hameed *et al*., 2011; Nio *et al*. 2011). Gene expression experiments have identified several hundred genes which are either induced or repressed during drought stress (Shi *et al*., 2006). In wheat, there are several genes which are responsible for drought stress tolerance and produce different types of enzymes and proteins such as, late embryogenesis abundant (lea), responsive to abscisic acid (ABA), rubisco, helicase, proline, glutathione-S-transferase (GST), and carbohydrates during drought stress (Nezhadahmadi *et al*., 2013). These bio-molecules are involved in dehydration avoidance or dehydration tolerance events such as osmotic adjustment, membrane stabilization, anti-oxidation, scavenging of reactive oxygen species (ROS), and gene regulation (Ashraf, 2010; Yang *et al*., 2010).Gene(s) linked with drought tolerance has enhanced our understanding of this complex phenomenon.

Knowing the genetics of drought tolerance and identifying quantitative trait loci (QTLs) linked with DNA markers help wheat breeders to develop high yielding drought tolerant cultivars (Khan *et al*., 2011). A number of research studies have been carried out to investigate drought tolerance in wheat using DNA markers by interval and GWAS mapping. The DNA markers used includes SSR, SNP, and DArT markers. SNPs are generally more abundant, stable, amenable to automation, efficient and cost-effective than other forms of genetic variants (Rafalski, 2002; Akhunov *et al*., 2009). The research reports elucidated that some QTLs were found to be major QTLs (explaining ~20% phenotypic variation) and stable QTLs (detected in >50% tested environments) (Acuna-Galindo *et al*., 2015; Gupta *et al*., 2017; Gahlaut *et al*., 2017). It has been reported that specific genomic regions of chromosomes 5A and 7A were important for wheat improvement for drought tolerance. Chromosome 7A was considered to be important, since it contains QTL for days to anthesis (DTA), days to maturity (DTM), grain filling duration (GFD), productive tillers per m2 (PTPM) and 1000 grain weight (TGW) together with a QTL affecting drought sensitivity index (DSI) for grain weight per ear (GWPE) linked with wmc0283 (Acuna-Galindo *et al.,* 2015). QTLs were found to be associated with plant height, kernel weight and yield under varying water availability in wheat (Maccaferri *et al*., 2008). However, contribution of QTLs to a trait is often low and QTLs associated with adaptive responses to drought differ across environments, while those that are constitutive are stable across environments (Collins *et al.,* 2008). Dissecting the phenotypic traits into smaller and simpler traits, which show high heritability in genotypes exhibiting drought tolerance, has led to the identification of stable QTLs associated with these traits across diverse environments (Tardieu & Tuberosa, 2010).

Drought signaling gene expression is categorized into ABA-dependent and ABA-independent pathways as ABA is the first line of defense against drought (Budak, *et al*., 2013), figure 2. ABA-dependent signaling consists of two main gene clusters (regulons) regulated by ABA-responsive element-binding protein/ABA-binding factor (the AREB/ABF regulon) and the MYC/MYB regulon (Budak*et al*., 2015). NAC and WRKY TFs provide crosstalk between these pathways. ABA accumulation during the expression of drought tolerance isknown to bring about a reduction in ethylene production and an inhibition of ethylene-induced senescence and abscission (Thameur *et al*., 2011). Significant genotypic variation in the accumulation of ABA in wheat leaves under water stress has been demonstrated in most of the studies conducted in wheat (Quarrie and Jones, 1977; Henson and Quarrie, 1981; Quarrie, 1981; Ji *et al*., 2011; Du *et al*., 2013).

It has been reported that expression of two genes, TaCRT1 (calreticulin $Ca2^+$-binding protein) and DREB1A (dehydration responsive transcription factor) greatly induced in roots of drought stress tolerant, BG-25 than drought stress susceptible, Bijoy(Monirul *et al*., 2015). These, imply that the expression of the two genesinvolvement in generegulation associated with drought tolerancemay be linked with the survival of wheat plants under drought conditions. In addition, it was indicated that higher antioxidant capacities in roots of water deficit wheat genotype further implicate that this genotype is efficient in scavenging ROS generated by drought stress.Reverse transcription-PCR by Khateeb*et al* (2017) on the assessment gene expression level for a drought stress response gene (DHN15.1) showed increased DHN15.1 transcript level in drought tolerant Karaka, *T. durum* landrace. Karakshowed long shoots (48% relative to its control), the longest roots (45% relative to its control) and the highest proline content (483% relative to its control). According to the investigation, this landrace appeared to be a good donor for drought tolerant genes due to its drought tolerance mechanisms. Under stress conditions,alternative splicing of some mRNAs coding for transcription factorshas been reported in wheat (Egawa *et al*., 2006).Molecular genetic understanding of genes and networks for stomatal patterning, size, and density regulation in wheat enable modulation of stomatal index in wheat and improve Transpiration Efficiency (TE) under drought stress (Kulkarni *et al*., 2017).

In wheat, a number of functional genomics studies were undertakenfor identification of drought responsible gene expression. For instance, transgenic wheat using HVA1 gene for ABA-responsive late embryogenesis abundant protein has improved transgenic wheat biomass under drought stress situation (Sivamani *et al*., 2000). Transgenic wheat expressing DREB1 gene from Arabidopsis showed better tolerance to drought under glasshouse conditions (Pellegrineschi *et al*., 2004). Significantdifferences in stress indices revealed that the SeCspA transgenic wheat lines possessed significantand stable improvement in drought tolerance over the control plants (Yu *et al*., 2017). Thus, suggesting that over expressing a synthetic bacterial cold shock protein, SeCspAgene confers drought tolerance.

6. Challenges and opportunities in crop plants drought tolerance development

Key challenges in breeding drought tolerant crop plants have been discussed by several scholars (Ashraf, 2010; Blum, 2010; Khakwani *et al.,* 2012; Kosová *et al.,* 2014*)*. Congruently, the following factors are known to be challenges in developing drought tolerant wheat cultivars. These are: Timing (growth stages), genetic diversity, intensity of drought, complex and the large size wheat genome, low heritability and quantitative/polygenic nature of drought responsive traits, epistatic QTL interactions, genotype and environment interaction and concomitant occurrences of biotic and abiotic factors.

Genetics of drought tolerance/sensitivity is complex, and the associated traits are complex and polygenic, thus making the task of developing drought-tolerant cultivars difficult. However, the current high throughput technologies to carryout precise phenotyping, dissection of wheat genome through (transcriptomics, proteomics, metabolomics, genotyping and SNP chip assay) and bioinformatics softwares employed put optimism to identify drought tolerant wheat. Therefore, recent technologies such as high-throughput phenotyping, next generation sequencing (NGS), and genetic engineering should be utilized for drought tolerance improvement in wheat (Mwadzingeni *et al.,2015*).

7. Conclusion

Drought intensity and occurrence increases due to climate change. It adversely affect wheat yield and yield related components globally. Genetic dissection of wheat using high throughput phenotyping and genotyping help to explore wheat genetic diversity for drought tolerance. It should also, be noted that drought does not occur independent from other abiotic stresses and is normally associated with heat stress (Jha *et al*., 2014). Application of omic sciences to identify gene (s) or gene region (s) and gene transfer technology give confidence to develop drought tolerant wheat cultivars, hence to enhance future wheat breeding program.

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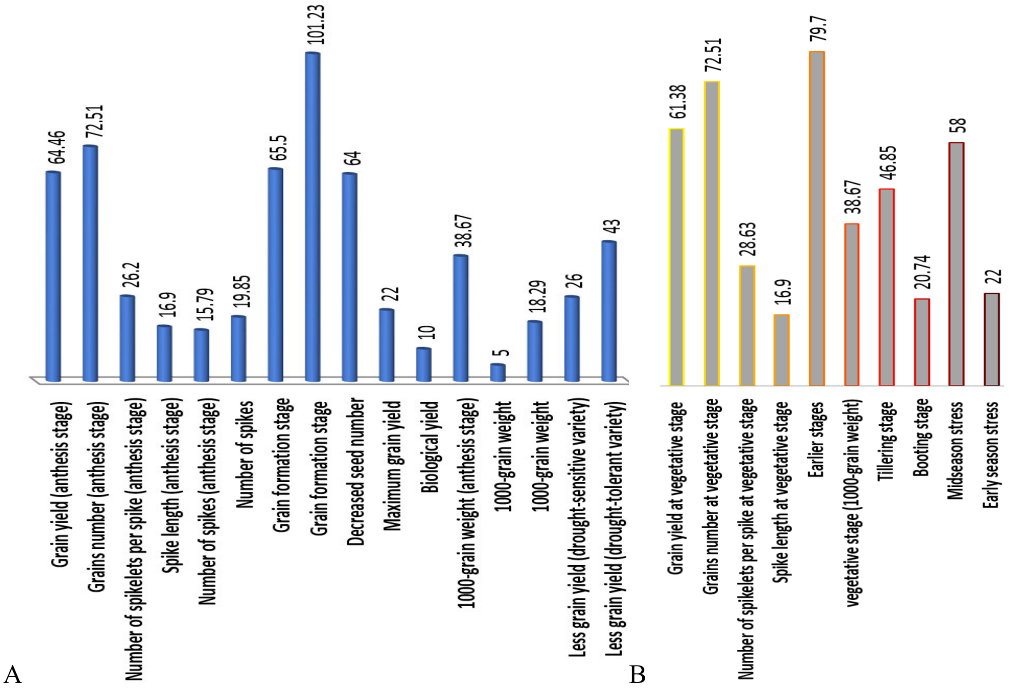

Figure 1. Percent yield losses at reproductive growth stages under drought in wheat (A) and percent yield losses at vegetative growth stages under drought in wheat (B) (modified from Nezhadahmadi *et al*., 2013).

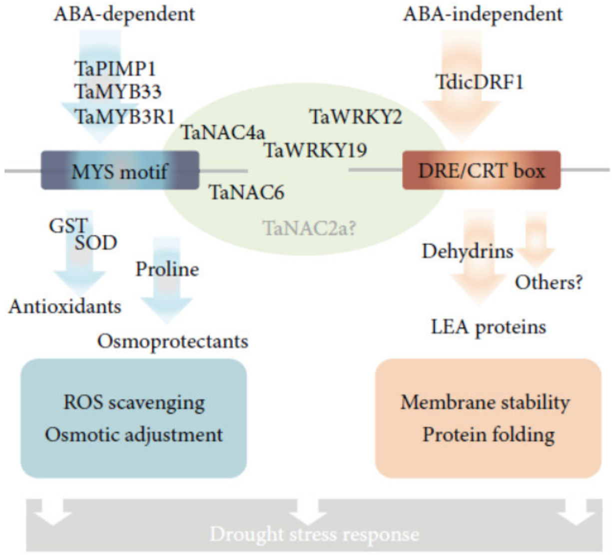

Figure 2. ABA-dependent and ABA-independent pathways of stress response. MYB and DREB TFs are given as examples to ABA dependent and-independent routes. While ABA-dependent pathways appear to recruit antioxidant and osmo protectant mechanisms, ABA-independent pathways generally involve protective proteins. NAC and WRKY TFs provide crosstalk between these pathways; where some members, such as TaNAC4 and TaNAC6, may predominantly act in an ABA-dependent fashion, some members maybe closer to ABA-independent pathways. In several cases, such asTaWRKY19, both pathways are employed. It should be noted that both pathways are highly intermingled, and functions of several regulators, such as TaNAC2a, as well as entire pathways are yet to be elucidated (Budak *et al.,* 2013).