Journal of Animal & Plant Sciences, 32(3): 2022, Page: 615-630
ISSN (print): 1018-7081; ISSN (online): 2309-8694
http://doi.org/10.36899/JAPS.2022.3.0462
Review paper

DROUGHT TOLERANCE IN RICE AND ROLE OF WRKY GENES

S. Kanwal*[1], S. Jamil[1], N. Afza[2], I. Ghafoor[3], M. Shehzadi[4], R. Kanwal[2] and M. Z. Iqbal[1]

[1]Agricultural Biotechnology Research Institute, [3]Wheat Research Institute, AARI, Faisalabad
[2]University of Agriculture, Faisalabad; [4]Agronomic Research Station, Farooqabad
*Corresponding author's email: kanwalshamsa32@yahoo.com

ABSTRACT

Anthropogenic alteration in climate has resulted in devastating global issue of drought for rice crop. Drought interferes with all the growth stages of crop by delaying its growth mechanisms, metabolic pathways and reducing the spikelet fertility. Rice plant has developed some morphological and physiological mechanisms to cope with the stress which include reduction in photosynthesis and transpiration, increased stomatal conductivity and density, root to shoot ratio, root length and carbon assimilation. Some biochemical modifications like biosynthesis of various hormones (ABA) and proteins (proline) also help in reducing the yield losses. Marker assisted selection and Quantitative Trait Loci (QTL) mapping are the advanced molecular techniques that played a vital role in developing the improved and stress tolerant rice cultivars. Identification of different stress responsive genes and transcriptional factors especially *WRKY* TFs have provided platform to obtain good crop stand and yield even under stress conditions. Rice possesses more *WRKY* genes (109 *WRKY* TFs in rice) as compared to *Arabidopsis thaliana.* An enormous variation in the expression patterns of *WRKY* genes and their contribution to the amplification of various signaling pathways and regulatory networks has been observed. These transcription factors work by regulating different mechanisms of drought tolerance and by releasing hormones, proteins, reducing-sugars, solutes and by affecting the stomatal conductance and root architecture. The *WRKY* genes work by showing up- and down- regulation to proteins, various protein-protein interactions and cross-regulation of *WRKY* TFs. Advance breeding methods; MAS, GWS, MABC, MARC and biotechnological tools along with different *WRKY* transcription factors have dynamically contributed in developing abiotic and biotic stress resistant rice varieties/cultivars on large scale.

Key words: Drought stress; *WRKY* TFs; QTLs; Biotechnological approaches; Rice breeding

INTRODUCTION

Rice (*Oryza sativa sp.*) is the major staple food of about 3.2 billion population around the world and carries the smallest genome among all the cereal crops (Moin *et al.,* 2017; Dien *et al.,* 2019). Certain yield limiting factors in rice crop cause severe yield loss, for instance more than 50% reduction in yield occurs through abiotic stresses, majorly due to; drought, heat, cold, salinity and oxidative stress (Ijaz *et al.,* 2021; Kanwal *et al*., 2021). About 23 million hectares area of cultivated rice under rain-fed regions suffers from drought (Serraj *et al.,* 2011). Susceptibility to drught stress is mainly due to small root system, waxy cuticle and fast stomata closures (Ji *et al.,* 2012; Pirasteh-Anosheh *et al.,* 2016). Various growth stages of rice respond differently at different levels of drought (Sharifunnessa and Islam 2017; Kumara *et al.,* 2020). Rice plant faces either terminal or intermittent drought stress. Terminal drought leads to water scarcity, causing severe stress to plant and ultimately kills the plant. Whereas, the intermittent drought stress occurs due to inadequate irrigations or rainfalls occurring either once or at intervals during the planting season causing distress in plant growth. Intermittent stress is less lethal as compared to the terminal stress (Polania *et al.,* 2017). Figure 1 elaborates how of rice plans respond to drought stress at morphololological, biochemical and physiological levels.

The provision of information about genome sequences, molecular markers and the inexpensive genotyping has played important role in the practical application of marker-assisted breeding technology on a routine basis (Swamy and Kumar 2013; Chung *et al.,* 2017). In the recent past, extensive study has been done in proteomics, transcriptomics and metabolomics approaches of functional genomics which revealed that the rice plant has evolved a wide range of strategies to cope with drought stress (Shahzad *et al*., 2021b). Moreover, the drought stress responses can be improved by employing different techniques such as marker assisted selection along with conventional breeding methods and by application of different hormones, osmolytes & enzymes and generating transgenic rice varieties (Upadhayaya and Panda 2019).

Transcription factors are classes of genes which play important role in managing the responses to different abiotic and biotic stresses. Among all, the important TFs are NAM, ATAF$_1$/$_2$, dehydration responsive element binding protein (DREB), myeloblastosis (MYB), ethylene responsive element binding factor (AP2/ERF) and WRKY (He *et al.,* 2016). The *WRKY* TFs family has expanded greatly in evolutionary process starting from algae to Arabidopsis and flowering plants through whole genome, segmental and tandem duplications. The WRKY transcription factors domain enhances the plant growth and development and majorly involved in biotic and abiotic stress tolerance processes (Chen *et al.,* 2019). *WRKY* family has widely been identified in various plant species including large number of *WRKY* genes in *Arabidopsis*, wheat, rice, sorghum, soybean, barley, pinus, papaya, poplar (Chen *et al.,* 2012), *Brachypodium distachyon*, *Citrus* sinenses, *Citrus clementine*, *Jatropha curcas*, *Manihot esculenta*, *Malus domestica*, *Oryza sativa. ssp. Japonica*, *in Oryza sativa ssp. Indica*, *Zea mays*, *Solanum lycopersicum* and *Solanum tuberosum* (Liu *et al.,* 2017). The current review focuses on the effects of drought stress on rice crop, and the mechanisms which rice plant has developed for combating stress. Moreover, the major focus is on advance breeding techniques and the working of novel WRKY gene family for drought tolerance in rice.

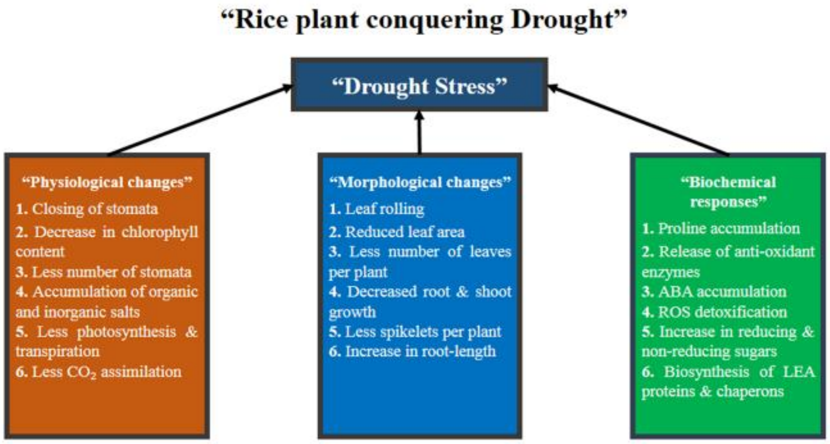

Fig. 1 Response of Rice Plant to drought stress

Drought stress in Rice: During the vegetative phase, the drought stress causes delay in leaf and tiller establishment, reduces the number of panicles per plant and result in low grain production (Singh *et al.,* 2017; Swain *et al.,* 2017). A water tension of -20 kPa in soil at vegetative growth phase results in 50% grain yield reduction in comparison with normal water supply (Swain *et al.,* 2017). Drought suppresses the tillering and expansion of leaf and causes reduction in the leaf area and rate of photosynthesis (Bunnag and Pongthai 2013; Zhao *et al.,* 2020).

The reproductive stage of rice is more affected by drought than the vegetative stage (Shrestha 2019). The most affected stage under drought stress is grain filling (anthesis to maturity) stage which is followed by panicle initiation stage (Sharifunnessa and Islam 2017; Melandri *et al.,* 2020). At flowering stage, drought stress harms the physiological parameters as well as the rice yield (Yang *et al.,* 2019b). It affects spikelet fertility, viable pollen production, panicle exertion, pollen-shedding, germination and embryo development (Shrestha 2019) ultimately reducing final grain yield (Liu *et al.,* 2006; Rang *et al.,* 2011; Zhao *et al.,* 2020).

Effect of drought stress on morphology of rice: Drought stress impairs the germination of the seedling (Padmini *et al.,* 2014), decreases the number of tillers per plant (Ashfaq *et al.,* 2012; Bunnag and Pongthai 2013), plant height (Bunnag and Pongthai 2013; Sokoto 2014), fresh and dry root and shoot weight (Centritto *et al.,* 2009; Ji *et al.,* 2012). Root is the first organ exposed to water stress due to an insufficient or excessive level of water in the soil. The root surface area depends on the root hair development and root diameter and these traits can be improved under water stress in order to increase the improved uptake of soil moisture and to maintain productivity of plant (Koevoets *et al.,* 2016; Kim *et al,* 2020). Coarse deep roots having increased ability of penetration and branching and high root to shoot ratio are found to be significantly contributing to drought avoidance in rice plants (Gowda *et al.,* 2011; Pandey and Shukla, 2015). Rice plant has three adaptive mechanisms for root system under drought stress (i) osmotic adjustment in roots, during relatively small soil water reservoir, (ii) increase in soil root penetration, and (iii) increase in root density, root depth, and the root-to-shoot ratio during large soil water reservoir (Kim *et al.,* 2012; Kim *et al.,* 2020).

Number of leaves (Sokoto 2014), leaf area and index (Kumar *et al.,* 2014; Cal *et al.,* 2019), leaf angle and elasticity in leaf rolling are also affected by the prevalence of drought stress (Pandey and Shukla 2015). Water deficit conditions negatively affects the mineral uptake and metabolism thereby decreasing leaf area and change partitioning of assimilates among different pant organs. Under severe water stress, increased degree of leaf rolling observed in rice leaves (Cal *et al.,* 2019). It is the acclimation response of rice plant, and is used as a principle tool for assessment of drought tolerance (Pandey and Shukla 2015). It results in the reduction of CO_2 which diffuses in leaf and decreases the transpiration rate minimizing leaf dehydration, (Kadioglu and Terzi 2007) and maintains the normal plant water status (Gana 2011). Leaf rolling delays when the cell turgor is maintained, however, increase in leaf rolling under severe drought stress helps in preventing water loss and damage from radiations (Pandey and Shukla 2015). It varies in different rice genotypes showing that it has genetic basis. A large number of QTLs linked to this mechanism are identified in rice (Salunkhe *et al.,* 2011; Grondin *et al.,* 2018).

Effect of drought stress on physiological characters of rice: Physiological characters affected by drought in rice including rate of photosynthesis, conductivity of stomata and water use efficiency (WUE). Moreover, the relativity of water, chlorophyll content, photosystem ll activity, stability of membranes, carbon isotopes distinction and abscisic acid content are also affected by drought (Pandey and Shukla 2015). Drought stress causes the closing of stomata which leads to decreasing chlorophyll content and transpiration rate (Li *et al.,* 2015; Caine *et al,* 2019). Loss of chlorophyll is a negative consequence of abiotic stress and is an important adaptive character in proper growth of plants under drought.

Effect of drought stress on biochemical parameters of rice: Numerous biochemical changes occur in response to drought stress in rice including the accumulation of osmo-protectants like proline, sugar, polyamines and anti-oxidants (Joseph *et al.,* 2015, Pandey and Shukla 2015). Soluble sugars play an important role as an osmo-protectant during water stress (Artadana *et al.,* 2019). The high level of proline in plants enhances the drought tolerance, stimulates the oxidative stress tolerance by antioxidant enzymatic activities (Sharma and Dubey 2005; Dien *et al.,* 2019) and regulates the plant growth during drought (Zandalinas *et al.,* 2018). It also helps plant cell to stabilize the structure of cell membranes and proteins. Accumulated proline plays a significant role to reduce and regulate water loss under water deficit conditions by acting as compatible solute and helps in adjusting osmotic balance. Proline accumulates contribute to stress tolerance in plants by supplying energy for growth and survivor. It is a significant indicator to screen drought tolerant lines in water deficit conditions (Pandey and Shukla, 2015). Rice varieties manifesting enhanced tolerance to abiotic stress were found to have elevated rate of proline biosynthesis. (Dien *et al.,* 2019). Drought stress causes increased accumulation of various reactive oxygen species (ROS), most of which are produced in chloroplast and in mitochondria also, resulting in oxidative stress (Impa *et al.,* 2012). Superoxide anion radicals, singlet oxygen, hydrogen peroxide and hydroxyl radicals are the main reactive oxygen species. Plants exhibit a defense mechanism under drought stress for protection from the detrimental effect of oxidative stress. Plants having increased level of induced antioxidant exhibit improved resistance and tolerance to oxidative damage (Impa *et al.,* 2012, Lum *et al.,* 2014). The significant role of abscisic acid (ABA) in regulating drought stress and mediating plant stress response by activating stomatal movement and stress related genes is described in Fig.2 (Nadarajah and Kumar 2019). The release of ABA significantly increases during drought, salinity, chilling and freezing stress and enhances the plant tolerance to these stresses (Kanwal *et al.*, 2019; Liu *et al.,* 2019). *$ARAG_1$* an ABA-responsive DREB gene, is hypersensitive to ABA signaling and the transcript level of *$ARAG_1$* increases under drought and ABA treatment and increases tolerance to drought.

This gene is overexpressed in roots, inflorescences, immature embryos and germinating seeds (Zhao *et al.,* 2010). Rice *OsbZIP42* is a member of the group E bZIP and is positive regulator of ABA signaling conferring drought tolerance (Joo *et al.,* 2019). PYL10 is one of the ABA receptors (ABARs) and the over-expressed PYL10 transgenic rice shows high RWC, membrane stability index, chlorophyll content, and lower amount of H_2O_2 manifesting both drought and cold tolerance (Verma *et al.,* 2019).

Breeding for Drought Tolerance: In modern breeding, general terms such as marker-assisted selection (MAS), genome-wide selection (GWS), marker-assisted pedigree selection (MAPS), marker-assisted recurrent selection (MARS) and marker-assisted back crossing (MABC) are used. Recurrent selection is a type of varietal improvement method that involves a number of crosses for gathering multiple genes, controlling favorable characters and maintain varietal diversity. This method has been used in rice, maize (Bolaños and Edmeades 1993; Pang *et al.,* 2017) and soybean (Posadas *et al.,* 2014). A male sterile line “Jiabuyu” has been developed which has a dominant male sterility gene (Pang *et al.,* 2017) and is mapped on the chromosome number 8 (Yang *et al.,* 2012).This method is superior to pedigree selection as it gives both improved agronomic traits and enhanced drought tolerance (Pang *et al.,* 2017).

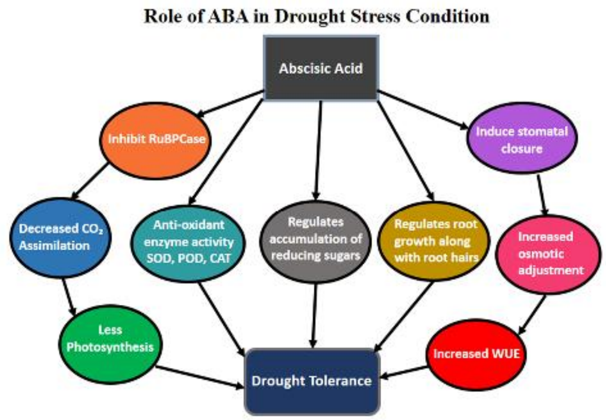

Fig 2 Role of ABA in drought stress condition

Marker-assisted back crossing method is most efficient and widely used for the phenotypic characters that are under control of single gene (Miah *et al.,* 2017; Chukwu *et al.,* 2019). Backcrossing is mostly used in rice breeding for the introgression of targeted genes controlling the particular desirable trait from donor parent to recipient parent along with the high recovery of the recipient parent genome and eliminating the donor parent genome. Drought tolerant rice varieties have been developed by backcrossing the donor lines Basmati, Bg 300, Binam, BR24, Cheng-Hui 448, FR13A, OM1706, OM1723, Tarom molaii and Type3 (having high drought tolerance) with the high yielding (IR64 and Teqing) rice cultivars (Lafitte *et al.,* 2006).

Induced mutation breeding is another approach which plays an important role in creating new genetic sequences of alleles that are not present in nature and these mutants can be introduced as a new variety or may be added in breeding programs (Oladosu *et al.,* 2016). Mutagenic treatments with strong genetic effects and less physiological changes are desirable. Mutation breeding has evolved many mutant rice varieties including Nagina-22 (Poli *et al.,* 2013), NERICA mutant (Sharifunnessa and Islam 2017), DSS1 rice mutant, 2 OsCDPK7 rice mutant (Ansari *et al.,* 2015) and Manawthukha rice mutant that are tolerant to drought stress. In Malaysia, MR219-9 and MR219-4 are drought tolerant high yielding rice varieties derived from MR219 through mutation breeding (Rahim *et al.,* 2012)

QTLs and marker assisted selection: Drought related traits are controlled by several quantitative trait loci (QTLs) (Fleury *et al.,* 2010; Liu *et al.,* 2012) and tolerance against drought cannot be achieved unless the molecular mechanisms involved in grain production are focused while using the techniques of traditional breeding or modern genetics. Thousands of the QTLs have been identified and cloned by using genetic engineering tools (Francia *et al.,* 2005). For the production of new transgenic lines, candidate genes are major targets and molecular approaches use these QTLs for crop improvement (Varshney *et al.,* 2011). Linkage-based QTL mapping involves those mapping populations (which have the traits correlated to drought tolerance) that segregate and identify polymorphic markers, construct the genetic map, and show accurate phenotyping and QTL mapping according to the phenotypic and genotypic data (Fleury *et al.,* 2010).

QTL mapping is not that efficient in providing complete data about the QTLs as many of the inheritance related limitations are associated with mapping-populations. This is because the QTLs are mostly linked with large chromosomal segments having insufficient time for recombination, also the QTLs segregation is linked with the same traits and have inadequate phenotypic variation in diverse mapping-populations (Liu *et al.,* 2012). Many of the QTLs that are related to drought tolerance, show responses to stress at root and shoot level, osmotic adjustment, photosynthesis, stomatal adjustment and hormonal responses. A major QTL *qDTY1.1,* has additive effect on the grain quality at reproductive stage under drought and is present on chromosome 1, flanked by RM431 and RM11943 in the populations of N22/Swarna, N22/MTU1010 and N22/IR64 (Vikram *et al.,* 2011).

Marker assisted selection is not efficient as it functions only with the major QTLs, the minor QTLs are under-represented in the selection process resulting in missed genetic gains. Genomic selection (GS) is highly recommended and is more advantageous as it also deals with the minor genes than the traditional MAS (Hayes *et al.,* 2009). The GS technique shows a combined effect of all the alleles on polygenic traits and is a type of MAS revealing the genetic variation in almost every individual and reduces the time of selection for most traits (Lorenzana and Bernardo 2009). Genotyping-based sequencing (GBS) is a novel approach and tool of NGS having its applications in discovering and genotyping of SNPs in crop plants. This GBS approach works by using restriction enzymes to digest the genomic DNA, ligation of barcode adapter, PCR and then sequence the amplified DNA on a lane of flow cells. (He *et al.,* 2014; Chung *et al.,* 2017).

Role of biotechnological approaches in mitigating drought stress: Genetic engineering has played a key role in developing drought tolerant transgenic rice varieties. Different genes encoding proteins such as kinases, transcription factors, enzymes and some regulatory proteins are involved in developing transgenics with enhanced drought tolerance (Todaka *et al.,* 2015). The transcription factor *OsbZIP23* is the leading regulator of ABA and its over-expression in rice is highly sensitive to ABA at germination and post-germination stages (Xiang *et al.,* 2008; Yang *et al.,* 2019a). Another TF *OsbZIP46* in its active form

OsbZIP46CAI shows drought tolerance in transgenic rice. *AtCYP78A7* protein encodes cytochrome P450 in transgenic brown rice and improves the tolerance to water deficit by keeping the quality and composition of the key nutrients same as present in non-transgenic rice (Nam *et al.,* 2013).

Response of rice plant to drought stress is found to be a multigenic trait at molecular level. Candidate genes showing drought tolerance have been identified in different plants by using genome annotation, functional genomics and molecular physiology (Feuillet *et al.,* 2011). Different proteins related to the drought-responsive candidate genes directly take part in (1) cell protection like osmotic adjustment, repairing, degradation, structural changes, detoxification and (2) the positive correlations with the protein transcription factors DREB, MYB, bZIP and protein kinases to fight with drought (Hadiarto and Tran 2011). Some of the drought tolerant candidate genes, CDPK7 gene accession number LOC-Os03g03660 (Saijo *et al.,* 2000), CIPK03 gene accession number LOC-Os07g48760 and CIPK12 gene accession number LOC-Os01g55450 have been identified in *Oryza sativa* for drought tolerance; showing signal transduction, have protein kinases and other regulatory proteins (Xiang *et al.,* 2007). There are two main groups of the products of stress-inducible genes. The first group involves proteins which protect the plants directly under stress conditions such as protein conferring late embryogenesis, chaperones, antifreeze proteins and enzymes involved in biosynthesis of osmoprotectants. The second group includes those proteins which are involved in signal transduction and regulation of gene expression which are protein kinases and transcription factors.

Thousands of regulatory elements and proteins have been identified in plants and many of them incorporated in the rice genome in order to study their response to drought stress either by showing suppression or over-expression (Huang *et al.,* 2009; Usman *et al.,* 2017). In rice, WRKY genes encoded transcriptional factors control different biological processes, particularly zinc-finger proteins are widely distributed in rice for regulating stress responses. A zinc-finger "*DST mutant*" shows enhanced drought and salinity tolerance by decreasing the stomatal density (Huang *et al.,* 2009) and another zinc-finger "*OsZFP252*" shows 74-79% high survival rate of rice plant in drought stress (Xu *et al.,* 2008; Yang *et al.,* 2010). Abscisic acid accumulates in guard cells and helps in closing of stomata which reduces water loss during drought (Lim *et al.,* 2015). A major enzyme *LOS5/ABA3* that appears in the end stage of ABA biosynthesis was over-expressed in transgenic rice and the grain yield and grain filling traits were improved during drought stress (Hu and Xiong 2014).

The late embryogenesis abundant (LEA) proteins ranging from 10-30 kDa are found in many plants (Olvera-Carrillo *et al.,* 2011). Over expression of these proteins like *OsLEA3* in rice enhance drought tolerance (Xiao *et al.,* 2007) and *HVA1* (an encoded LEA protein gene) from barley, wheat and rice shows increase in WUE and growth performance under drought (Babu *et al.,* 2004; Chen *et al.,* 2015). The encoding LEA genes *OsLEA3-1* & *OsLEA3-2* also show tolerance to water deficit conditions and minimum yield losses as compared to controlled treatments in severe droughts (Xiao *et al.,* 2007; Duan and Cai 2012).

Overview of WRKY Transcription Factors: WRKY transcriptional factors are responsible for genes regulation that show response at different growth stages of a plant. The gene expression of *WRKY* TFs occurs mainly by binding to the DNA at specific cis-regulatory **W-box** elements, which are short sequences (T)TGAC(C/T) located at the promoter site of gene sequence in DNA (Finatto *et al.,* 2018; Jimmy and Babu 2019). They have an invariant amino acid sequence at the N-terminus which is about 60 residues called the ***WRKY* signatures**, while the C-terminus of WRKY TFs contains a **Zinc-finger** structure of **Cx4-5Cx22-23HxH** or **Cx7Cx23HxC** (Shahzad *et al.,* 2021a; Jimmy and Babu 2019). *WRKY*TFs show expression during various diseases, environmental stresses, seed germination, seed dormancy and other growth related events in higher plants (Rushton *et al.,* 2010; Li *et al.,* 2020). The WRKY proteins also function in immune response mechanisms of a plant such as the mechanical damages and wounding (Hara *et al.,* 2000) and stresses like highly saline soils (Niu *et al.,* 2012; Wang *et al.,* 2012), drought stress (Zhang *et al.,* 2008b), heat shock stress (Li *et al.,* 2010), damages by ultra-violet radiations (Izaguirre *et al.,* 2003), sugar signaling by sugar-responsive elements (Sun *et al.,* 2003), gibberellin signaling in aleurone cells (Zhang *et al.,* 2004) and ABA stimulation (Chen *et al.,* 2010).

- The WRKY domains contain a zinc-finger at the N-terminus and is supported by the evidence that 2-phenanthroline chelates the zinc ions when added to the gel retardation assays, resulting in the non-binding with W-box target sequence in E.coli. An in-variant motif of 60 amino acids sequence has a well-conserved WRKY signature *WRKYGQK* on N-terminus (Rushton *et al.,* 1995; Xu *et al.*, 2020).
- The amino acid sequence on N-terminus binds with the W-box on the targeted DNA sequences. They are highly specific to their promoters in the target DNA. Along with the W-box core, the nearby sequences also play an important role in binding the W-box with the *WRKY* TFs (Eulgem *et al.,* 2000; Yamasaki *et al.,* 2005).
- Yamasaki determined the structure of C-terminal WRKY domain forming a complex with W-box in the DNA of Arabidopsis *(WRKY4)*. He found that a four-stranded β-sheet perpendicular to the helical axis enters the major groove of DNA in the β-wedge

(Yamasaki *et al.,* 2005; Duan *et al.,* 2007; Yamasaki *et al.,* 2012).

The WRKY Gene Family in Rice: Rice (*Oryza sativa.sp)* contains higher number of *WRKY* TFs than in *Arabidopsis thaliana* (Goff *et al.,* 2002; Yuan *et al.,* 2005). Many *WRKY* TFs have identified in *Oryza sativa L.* ssb *indica* and L. ssb *japonica*. The plant transcription factor databases have different number of *WRKY*TFs in indica and japonica by having 111 and 129 *WRKY* TFs respectively whereas Indica has 107 and japonica has 126 coding regions out of these gene models. Only 101 *WRKY* TFs in indica and japonica were classified in groups and the rest are putative gene sequences. These genes mainly responsive to the abiotic and biotic stresses (Jimmy and Babu 2019). Indica rice contains 102 copies of WRKY genes out of which 92 are unique. Two identical copies of *OsWRKY46* are present on chromosome 11 and 12. *OsWRKY55* and *-89* are doubled in indica rice showing the tandem repeats on chromosome 3 and 5 respectively (Ross *et al.,* 2007).

Japonica has two identical copies of *OsWRKY46* at chromosome 11 and 12 but unlike indica, *OsWRKY55* and *OsWRKY89* has only one copy in Japonica. WRKY genes are unevenly distributed in the rice and chromosome 1 has maximum number of *WRKY* TFs (Xie *et al.,* 2005). The densities of *WRKY* TFs on all the 12 chromosomes appear to be same in both japonica and indica. Equal number of *WRKY* TFs are present on the chromosome (1, 2, 5, 6, 10 and 11) while other chromosomes have difference of one or two *WRKY* TFs. Genes on the chromosomes 1, 3, 5, 8, 11, and 12 are present in clustered form (Ross *et al.,* 2007). From the evolutionary analysis of rice *WRKY* TFs, the group 1 WRKY genes are classified into G1a and G1b.

Two differences have found in group 1a and group1b, out of which first difference is, the zinc-finger motif on N-terminus and C-terminus of group 1a is of C_2H_2 type, while the zinc-finger motif on N-terminus and C-terminus of group 1b is of C_2HC, while the second difference is that the group 1a genes has a conserved intron only on the C-terminal of the WRKY domain encoded region. However, the group 1b contains conserved intron on both C-terminal and N-terminal. The group 1 *WRKY* TFs of slime mold and Arabidopsis has highest similarity with the rice group 1a and not the group 1b. So, the only group 1a genes of rice are part of ancestral history of WRKY genes in plants (Jimmy and Babu 2019). The evolutionary study of rice suggests the group1 of *WRKY* TFs as the oldest one because it contains 2 WRKY domains and that the group 2 and 3 have originated from group1 (Ulker and Somssich 2004). A fourth group has also emerged and classified as a set of WRKY genes that has a complete WRKY motif but the Zinc-finger is absent (Ross *et al.,* 2007). Table 1 describes the various groups of WRKY Transcriptional factors traits being controlled.

Table 1 Classification and Role of Different WRKY Transcriptional Factors.

Trait	*WRKY*TFs	Environment	Classification	Reference
Innate immunity	*OsWRKY62*	*Xanthomonas oryzae* pv.*oryzae*	Group lla	Peng *et al.,* 2010.
Semi-dwarf & early flowering	*OsWRKY72*	Salinity,drought ABA & Auxin inducible	Group ll	Song *et al.,* 2010a; Ashwini *et al.,* 2016.
Shoot, sheath, node, collar	Phospho-mimic mutant *OsWRKY53*	*Magnaporthe oryzae* (fungal rice blast)	Group l	Chujo *et al.,* 2014.
High H_2O_2 level	*OsWRKY46*	*Magnaporthe oryzae*	Group lll	Gao *et al.,* 2020.
High H_2O_2 level	*OsWRKY6*	*Magnaporthe oryzae*	Group lle	Gao *et al.,* 2020.
SA & JA pathways	*OsWRKY13*	Drought, Bacterial blight, Fungal Blast	Group lle	Qiu *et al.,* 2007.
Wax deposition on leaf & less internode length	*OsWRKY89*	UV-B , rice blast & white-backed hopper	Group lll	Wang *et al.,* 2007.
Defense system	*OsWRKY11*	Drought, heat & *X. oryzae pv. Oryzae*	Group llc	Lee *et al.,* 2018.
Accumulation of phytoalexins	*OsWRKY76*	Cold stress & Rice blast	Group lla	Yokotani *et al.,* 2013.
Retards root growth	*AtWRKY23*	*Heterodera schachtii*	Group llc	Grunewald *et al.,* 2008.
Numerous and longer lateral & primary roots	*OsWRKY08*	Drought, cold, salinity	Group ll	Song *et al.,* 2010b.
Jasmonic acid	*OsWRKY80*	*Rhizoctonia solani*	Group lle	Peng *et al.,* 2016.
Jasmonic acid accumulation & SA suppression	*OsWRKY45*	*M. oryzae & X.oryzae pv. Oryzicola & M.*	Group llla	Tao *et al.,* 2009.

		grisea		
Effects root & shoot growth	*OsWRKY56*	Submergence	Group lVb	Viana *et al.,* 2018.
Basal defense & Xa_1- mediated resistance	*OsWRKY10*	*X. oryzae pv. oryzae*	Group llc	Choi *et al.,* 2020.
GA signaling pathway & leaf aleurone cells	*OsWRKY71*	Bacterial blight, SA, MeJA and ACC	Group lla	Liu *et al.,* 2007.
Rice protoplast & SA signaling pathway	*OsWRKY30*	Drought & Xoo	Group la	Shen *et al.,* 2012.
SA dependent	*OsWRKY33*	Pathogen infections	Group l	Koo *et al.,* 2009.
Rice epidermal cells	*OsWRKY24*	*Pyricularia oryzae* & NO signaling	Group l	Yokotani *et al.,* 2018.
Aleurone cells release ABA	*OsWRKY77*	ABA signaling	Group llc	Xie *et al.,* 2005.
Defense system & lateral roots formation	*OsWRKY31*	*Magnaporthe grisea* & Auxin	Group lle	Zhang *et al.,* 2008a.
Defense system	*OsWRKY52*	*Magnaporthe grisea*		Wang *et al.,* 2005.
H_2O_2 formation & callose deposition	*OsWRKY22*	*Magnaporthe oryzae*	Group lllb	Abbruscato *et al.,* 2012.
Plant defense	*OsWRKY6*	*Xoo & SA* pathway	Group lld	Hwang *et al.,* 2011.
Defense response	*OsiWRKY*	*Xoo* & mechanical wounding	Homologous Group is llc	Guo *et al.,* 2004.
Normal rice leaf growth	*WRKY68* protein	Bacterial leaf blight *(Xoo)*	Group lld	Yang *et al.,* 2016.
Plant defense response & flag leaf	*OsWRKY47*	Drought, Cold & Rice blast	Group ll	Raineri *et al.,* 2015.
Express in Roots, SA pathway & senescing leaves	*OsWRKY23*	*Pyricularia oryzae* Cav	Group ll	Jing *et al.,* 2009.
Expressed in lateral root & root tips, reproductive organs	*OsWRKY28*	Arsenate	Group lla	Wang *et al.,* 2018.
Defense system	*OsWRKY19*	Blast disease (M. oryzae)	Group lll	Kim *et al.,* 2012.
Changes in RSA, tillers number & grain weight	*OsWRKY74*	Phosphate (Pi) starvation, Fe, N & cold stress	Group lll	Dai *et al.,* 2015.
Expressed in roots, young & mature leaves, inflorescence	*OsWRKY45*	Drought, salinity, ABA, *P. oryzae* & *Xoo*.	Group lll	Qiu and Yu 2009.

Role of WRKY TFs for Drought Tolerance in Rice: 103 *WRKY* TFs of WRKY family have identified in rice. Four genes out of these 103, are up-regulated by drought while 13 by both salt and drought stress. Two *WRKY* TFs are up-regulated by drought but down-regulated by cold stress. One gene is regulated by drought but suppressed by cold and salinity (Ramamoorthy *et al.,* 2008).

OsWRKY72 shows tolerance against drought in rice and is induced by NaCl, PEG, ABA and high temperature. It shows high sensitivity to mannitol, NaCl and ABA (Song *et al.,* 2010a). This TF is an up-regulatory gene and is stimulated by abscisic acid released in aleuron cells (Li *et al.,* 2015). *OsWRKY72* imparts tolerance to salinity in rice as it shows higher expression during salts stress in different rice varieties like Rasi & Tellahamsa (Ashwini *et al.,* 2016). Another gene *OsWRKY11* is induced by drought in rice seedlings. The over-expression of *OsWRKY11* along with HSP101 promoter which shows the drought and heat tolerance and results in slower leaf-wilting (Wu *et al.,* 2009). Research shows that *OsWRKY11* binds to *RAB21* promoter, enhances the heat and drought tolerance in transgenic rice (Shi *et al.,* 2018). A *WRKY*TF *OsWRKY30* has identified in rice which is activated by MAP Kinases (Shen *et al.,* 2012). *OsWRKY30* has two WRKY domains and belongs to group la. It is induced by *M. grisea* infection and phytohormones SA (salicylic acid) and JA (jasmonic acid) is discussed in Table. 1. The SA antagonizes JA by showing response against disease resistance (Ryu *et al.,* 2006). The over-expression of *OsWRKY30* shows a dramatical increase in drought tolerance in rice. (Shen *et al.,* 2012).

A rice zinc-finger protein “DST mutant” shows drought tolerance by decreasing the distribution of stomata and enhancing the closing of stomata in rice. Similarly, over-expression of the zinc-finger protein *OsZFP252* increases the drought tolerance by accumulation of soluble sugars and proline and increase the plant survival upto 74-79% (Oladosu *et al.,* 2019). The *SbWRKY30* works as a transcriptional factor (localizes in the nucleus) and is positively regulated by drought stress. The heterologous expression of

SbWRKY30 shows enhanced drought tolerance in rice by affecting the root architecture. Moreover, *SbWRKY30* transgenic rice has higher proline content, SOD (superoxide dismutase), POD (peroxidase) and CAT (catalase) activities. In rice *SbWRKY30* shows tolerance to environmental stresses by up-regulating some stress-related genes (Yang *et al.,* 2020).

The heterologous expression of *AtWRKY57* induces drought tolerance in transgenic rice. This over-expressing of *AtWRKY57* also contains salt tolerance. Firstly it showed drought tolerance in *Arabidopsis thaliana* and then introduced in rice to check whether it shows the same expression or not (Jiang *et al.,* 2016). Similarly, the WRKY gene *ZmWRKY58* when over-expressed, enhances the drought tolerance in rice by increasing the RWC (relative water content) and hence plant survival. The *ZmWRKY58* has isolated from maize and its expression pattern indicates that it is induced by drought, salt and abscisic acid. Moreover, the *ZmWRKY58* is also present in onion and yeast (*ZmWRKY58* can interact with the *Z2mCaM*, suggesting its function as calmodulin binding proteins and promotes abiotic stress tolerance). In rice, *ZmWRKY58* causes delay in germination and inhibits the post-germination (Cai *et al.*, 2014). Ectopic expression of *ZmWRKY33* and *ZmWRKY58* in *Arabidopsis thaliana* and *Oryza sativa* improve the salinity and drought tolerance respectively (Shi *et al.,* 2018).

OsWRKY13 is a transcriptional repressor of *OsWRKY45-2* but suppresses the *OsWRKY45-1* under drought stress and binds to the W-box sequence. It shows cross-talk between abiotic and biotic stresses in rice. This transcriptional factor is induced in the leaf vascular tissue, guard cells and bacterial infection, where another TF *SNAC1* increases the tolerance to the drought stress (by inducing stomatal closure) and some bacterial infection. The *OsWRKY13* makes antagonistic cross-talk between drought and disease resistance pathway It suppress the *SNAC1* and *WRKY45-1* (Xiao *et al.,* 2013). *OsWRKY47* belongs to the gourp-ll of WRKY gene family and is the positive regulator of drought stress. Overexpression of *OsWRKY47* in transgenic PSARK::IPT plants shows enhanced tolerance to drought. *OsWRKY47* has sequences similar to the regions of *CRSSP* and *CaMBP* promoters, its gene expression profile in the flag leaves of PSARK::IPT plants shows the differential expression of *OsWRKY47* and reduction in chlorophyll content hence2, enhancing drought tolerance (Raineri *et al.,* 2015). Another *WRKY* TF *0sWRKY80* is induced by different factors including *Rhizoctonia solani* infection in rice, exogenous jasmonic acid (JA) and ethylene (ET) (Peng *et al.,* 2016). Its overexpression increases disease resistance and in rice it is up-regulated in roots, leaves and stems showing drought tolerance (Ricachenevsky *et al.,* 2010). Figure 3 gives an overview of how *WRKY* TFs enhance the tolerance to drought stress.

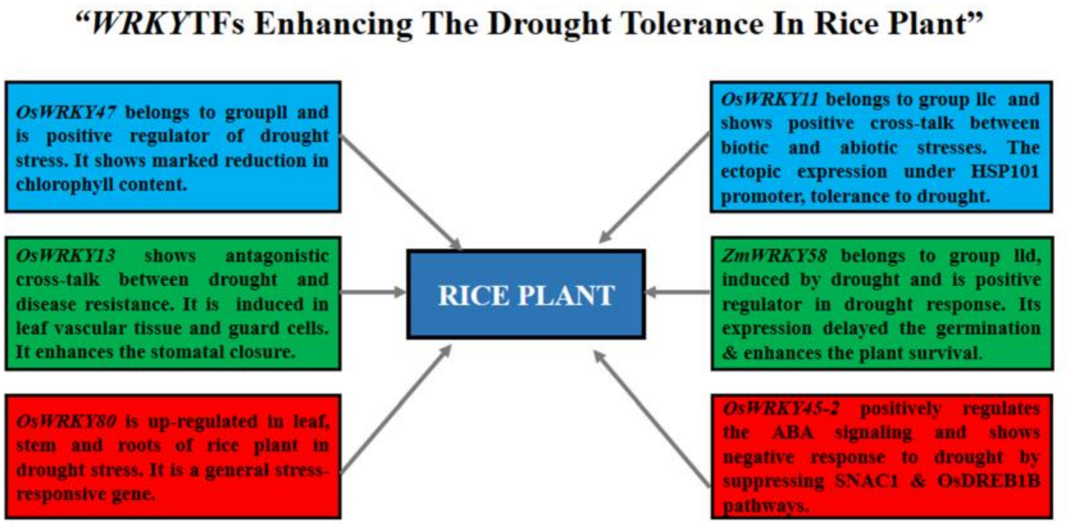

Fig. 3 WRKYTFs Enhancing the Drought Tolerance in Rice Plants

Conclusion: To conclude, it is evident from aforementioned illustrations that rice plant is highly susceptible to drought. Drought negatively influences the rice plants at different growth stages. In order to overcome the damages from water deficiency, and cope with the stress this crop has adapted morphological, biochemical and physiology parameters accordingly. The advanced techniques have improved the understanding of rice genome QTLs and *WRKY*TFs resulting in development of more precise drought tolerant rice types focusing only on attributes and mechanisms which directly interfere with their development and production under drought stress conditions.

REFERENCES

Abbruscato, P., T. Nepusz, L. Mizzi, M. Del Corvo, P. Morandini, I. Fumasoni, C. Michel, A. Paccanaro, E. Guiderdoni, U. Schaffrath, J.-B. Morel, P. Piffanelli and O. Faivre-Rampant (2012). OsWRKY22, a monocot WRKY gene, plays a role in the resistance response to blast. Mol. Pl. Pathol. 13: 828-841.

Ansari, M.U.R., T. Shaheen, S. Bukhari and T. Husnain (2015). Genetic improvement of rice for biotic and abiotic stress tolerance. Turk J. Bot. 39: 911-919.

Artadana, I., I. Dewi and J. Sukweenadhi (2019). The performance of three local rice (Oryza sativa L.) cultivar from East Kalimantan - Indonesia under drought stress at early seedling stage. *IOP* Conference Series: Earth Environ. Sci. 293: 012021.

Ashfaq, M., M. S. Haider, A.S. Khan and S.U. Allah (2012). Breeding potential of the basmati rice germplasm under water stress condition. Afr. J. Biotecnol. 11: 6647-6657.

Ashwini, N., R.S. Sajeevan, M. Udayakumar and K.N. Nataraja (2016). Identification and Characterization of OsWRKY72 Variant in Indica Genotypes. Rice Sci. 23: 297-305.

Babu, R.C., J. Zhang, A. Blum, T.-H.D. Ho, R. Wu and H. Nguyen (2004). HVA1, a LEA gene from barley confers dehydration tolerance in transgenic rice (Oryza sativa L.) via cell membrane protection. Pl. Sci. 166: 855-862.

Bolaños, J. and G. Edmeades (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. Field Cr. Res. 31: 253-268.

Bunnag, S. and P. Pongthai (2013). Selection of Rice (<i>Oryza sativa</i> L.) Cultivars Tolerant to Drought Stress at the Vegetative Stage under Field Conditions. Amer. J. Pl. Sci. 04: 09-08.

Cai, R., Y. Zhao, Y. Wang, Y. Lin, X. Peng, Q. Li, Y. Chang, H. Jiang, Y. Xiang and B. Cheng (2014). Overexpression of a maize WRKY58 gene enhances drought and salt tolerance in transgenic rice. Pl. Cell, Tissue and Organ Cul. (PCTOC) 119: 565-577.

Caine, R. S., X. Yin, J. Sloan, E. L. Harrison, U. Mohammed, T. Fulton, A. K. Biswal, J. Dionora, C. C. Chater, R. A. Coe, A. Bandyopadhyay, E. H. Murchie, R. Swarup, W. P. Quick and J. E. Gray (2019). Rice with reduced stomatal density conserves water and has improved drought tolerance under future climate conditions. New Phytologist, 221(1): 371-384.

Cal, A. J., M. Sanciangco, M. C. Rebolledo, D. Luquet, R. O. Torres, K. L. McNally and A. Henry (2019). Leaf morphology, rather than plant water status, underlies genetic variation of rice leaf rolling under drought. Pl. cell & environ. 42(5): 1532-1544.

Centritto, M., M. Lauteri, M.C. Monteverdi and R. Serraj (2009). Leaf gas exchange, carbon isotope discrimination, and grain yield in contrasting rice genotypes subjected to water deficits during the reproductive stage. J. Exp. Bot. 60: 2325-2339.

Chen, H., Z. Lai, J. Shi, Y. Xiao, Z. Chen and X. Xu (2010). Roles of arabidopsis WRKY18, WRKY40 and WRKY60 transcription factors in plant responses to abscisic acid and abiotic stress. BMC Pl. Biol. 10: 281.

Chen, L., Y. Song, S. Li, L. Zhang, C. Zou and D. Yu (2012). The role of WRKY transcription factors in plant abiotic stresses. Biochem. Biophy. Acta. 1819: 120-128.

Chen, Y.S., S.F. Lo, P.-K. Sun, C.-A. Lu, T.H.D. Ho and S.M. Yu (2015). A late embryogenesis abundant protein HVA1 regulated by an inducible promoter enhances root growth and abiotic stress tolerance in rice without yield penalty. Pl. Biotech. J. 13: 105-116.

Chen, X., C. Li, H. Wang and Z. Guo (2019). WRKY transcription factors: evolution, binding, and action. Phytopathol. Res. 1: 13.

Choi, N., J.H. Im, E. Lee, J. Lee, C. Choi, S.R. Park and D.-J. Hwang (2020). WRKY10 transcriptional regulatory cascades in rice are involved in basal defense and Xa1-mediated resistance. J. Exp. Bot. 71: 3735-3748.

Chujo, T., K. Miyamoto, S. Ogawa, Y. Masuda, T. Shimizu, M. Kishi-Kaboshi, A. Takahashi, Y. Nishizawa, E. Minami, H. Nojiri, H. Yamane and K. Okada (2014). Overexpression of phosphomimic mutated OsWRKY53 leads to enhanced blast resistance in rice. PloS one 9: e98737-e98737.

Chukwu, S.C., M.Y. Rafii, S.I. Ramlee, S.I. Ismail, M.M. Hasan, Y.A. Oladosu, U.G. Magaji, I. Akos and K.K. Olalekan (2019). Bacterial leaf blight resistance in rice: a review of conventional breeding to molecular approach. Mol. Biol. reports 46: 1519-1532.

Chung, Y.S., S.C. Choi, T.-H. Jun and C. Kim (2017). Genotyping-by-sequencing: a promising tool for plant genetics research and breeding. Horticulture, Environment and Biotechnol. 58: 425-431.

Dai, X., Y. Wang and W.-H. Zhang (2015). OsWRKY74, a WRKY transcription factor, modulates tolerance to phosphate starvation in rice. J. Exp. Bot. 67: 947-960.

Dien, D. C., T. Mochizuki and T. Yamakawa (2019). Effect of various drought stresses and subsequent recovery on proline, total soluble sugar and starch metabolisms in Rice (*Oryza sativa* L.) varieties. Pl. Produc. Sci. 22(4): 530-545.

Duan, M.-R., J. Nan, Y.-H. Liang, P. Mao, L. Lu, L. Li, C. Wei, L. Lai, Y. Li and X.-D. S (2007). DNA binding mechanism revealed by high resolution crystal structure of Arabidopsis thaliana WRKY1 protein. Nucleic Acids Res. 35: 1145-1154.

Duan, J. and W. Cai (2012). OsLEA3-2, an Abiotic Stress Induced Gene of Rice Plays a Key Role in Salt and Drought Tolerance. PLOS ONE 7: e45117.

Eulgem, T., P.J. Rushton, S. Robatzek and I.E. Somssich (2000). The WRKY superfamily of plant transcription factors. Trends in Pl. Sci. 5: 199-206.

Feuillet, C., J.E. Leach, J. Rogers, P.S. Schnable and K. Eversole (2011). Crop genome sequencing: lessons and rationales. Trends in Pl. Sci. 16: 77-88.

Finatto, T., V.E. Viana, L.G. Woyann, C. Busanello, L.C.d. Maia and A.C.d. Oliveira (2018). Can WRKY transcription factors help plants to overcome environmental challenges? Gene. Mol. Biol. 41: 533-544.

Fleury, D., S. Jefferies, H. Kuchel and P. Langridge (2010). Genetic and genomic tools to improve drought tolerance in wheat. J. Exp. Bot. 61: 3211-3222.

Francia, E., G. Tacconi, C. Crosatti, D. Barabaschi, D. Bulgarelli, E. Dall'Aglio and G. Valè (2005). Marker assisted selection in crop plants. Pl. Cell, Tissue and Organ Cult. 82: 317-342.

Gana, A (2011). Screening and resistance of traditional and improved cultivars of rice to drought stress at Badeggi, Niger State, Nigeria. Agric. Biol. J. North Amer 2: 1027-1031.

Gao, X.-q., X.-y. Sun, Y.-y. Peng, Y.-y. Huang, M.-Q. Liu and X.-y. Weng (2020). WRKY Transcription Factor Functions as a Transcriptional Regulator of Xylanase Inhibitor RIXI, Involved in Rice Disease Resistance to Magnaporthe oryzae. J. Pl. Biol. 63: 177-188.

Gowda, V.R.P, A. Henry, A. Yamauchi, H. E. Shashidhar, and R. Serraj 2011. Root biology and genetic improvement for drought avoidance in rice. Field Crops Res. 122(1): 1-13.

Goff, S.A., D. Ricke, T.H. Lan, G. Presting, R. Wang, M. Dunn, J. Glazebrook, A. Sessions, P. Oeller, H. Varma, D. Hadley, D. Hutchison, C. Martin, F. Katagiri, B.M. Lange, T. Moughamer, Y. Xia, P. Budworth, J. Zhong, T. Miguel, U. Paszkowski, S. Zhang, M. Colbert, W.L. Sun, L. Chen, B. Cooper, S. Park, T.C. Wood, L. Mao, P. Quail, R. Wing, R. Dean, Y. Yu, A. Zharkikh, R. Shen, S. Sahasrabudhe, A. Thomas, R. Cannings, A. Gutin, D. Pruss, J. Reid, S. Tavtigian, J. Mitchell, G. Eldredge, T. Scholl, R.M. Miller, S. Bhatnagar, N. Adey, T. Rubano, N. Tusneem, R. Robinson, J. Feldhaus, T. Macalma, A. Oliphant and S. Briggs (2002). A draft sequence of the rice genome (Oryza sativa L. ssp. japonica). Sci. (New York, N.Y.) 296: 92-100.

Grondin, A., S. Dixit, R. Torres, C. Venkateshwarlu, E. Rogers, T. Mitchell-Olds, P.N. Benfey, A. Kumar and A. Henry (2018). Physiological mechanisms contributing to the QTL qDTY3.2 effects on improved performance of rice Moroberekan x Swarna BC2F3:4 lines under drought. Rice 11: 43.

Grunewald, W., M. Karimi, K. Wieczorek, E. Van de Cappelle, E. Wischnitzki, F. Grundler, D. Inzé, T. Beeckman and G. Gheysen (2008). A role for AtWRKY23 in feeding site establishment of plant-parasitic nematodes. Pl. Physiol. 148: 358-368.

Guo, Z.-J., Y.-C. Kan, X.-J. Chen, D.-B. Li and D.-W. Wang (2004). Characterization of a rice WRKY gene whose expression is induced upon pathogen attack and mechanical wounding. ACTA BOTANICA SINICA-ENGLISH EDITION- 46: 955-964.

Hadiarto, T. and L.-S. Tran (2011). Progress studies of drought-responsive genes in rice. Pl. cell reports 30: 297-310.

Hara, K., M. Yagi, T. Kusano and H. Sano (2000). Rapid systemic accumulation of transcripts encoding a tobacco WRKY transcription factor upon wounding. Mol. & Gener. Gene. MGG 263: 30-37.

Hayes, B.J., P.J. Bowman, A.J. Chamberlain and M.E. Goddard (2009). Invited review: Genomic selection in dairy cattle: Progress and challenges. J. Dairy Sci. 92: 433-443.

He, J., X. Zhao, A. Laroche, Z.-X. Lu, H. Liu and Z. Li (2014). Genotyping-by-sequencing (GBS), An ultimate marker-assisted selection (MAS) tool to accelerate plant breeding. Front. Pl. Sci. 5: 484.

He, G.H., J.Y. Xu, Y.X. Wang, J.M. Liu, P.S. Li, M. Chen, Y.Z. Ma and Z.S. Xu (2016). Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in Arabidopsis. BMC Pl. Biol. 16: 116.

Hu, H. and L. Xiong (2014). Genetic engineering and breeding of drought-resistant crops. Ann. review Pl. Biol. 65: 715-741.

Huang, X.-Y., D.-Y. Chao, J.-P. Gao, M.-Z. Zhu, M. Shi and H.-X. Lin (2009). A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. Genes Dev 23: 1805-1817.

Hwang, S.-H., S.W. Yie and D.-J. Hwang (2011). Heterologous expression of OsWRKY6 gene in Arabidopsis activates the expression of defense related genes and enhances resistance to pathogens. Pl. Sci. 181: 316-323.

Ijaz, W., S. Kanwal, M.H.N. Tahir and H. Razzaq (2021). Gene action of yield related characters under normal and drought stress conditions in Brassica napus L. Pakistan J. Bot. 53(6): 1979-1985.

Izaguirre, M.M., A.L. Scopel, I.T. Baldwin and C.L. Ballaré (2003). Convergent responses to stress. Solar ultraviolet-B radiation and Manduca sexta herbivory elicit overlapping transcriptional responses in field-grown plants of Nicotiana longiflora. Pl. Physiol. 132: 1755-1767.

Impa, S.M., S. Nadaradjan, and S.V.K. Jagadish (2012). Drought stress induced reactive oxygen species and anti-oxidants in plants. In Abiotic stress responses in plants. Springer, N. Y. 131-147.

Ji, K., Y. Wang, W. Sun, Q. Lou, H. Mei, S. Shen and H. Chen (2012). Drought-responsive mechanisms in rice genotypes with contrasting drought tolerance during reproductive stage. J. Pl. Physiol. 169: 336-344.

Jiang, Y., Y. Qiu, Y. Hu and D. Yu (2016). Heterologous Expression of AtWRKY57 Confers Drought Tolerance in Oryza sativa. Front. Pl. Sci. 7.

Jimmy, J.L. and S. Babu (2019). Variations in the Structure and Evolution of Rice WRKY Genes in Indica and Japonica Genotypes and their Co-expression Network in Mediating Disease Resistance. 15: 1176934319857720.

Jing, S., X. Zhou, Y. Song and D. Yu (2009). Heterologous expression of OsWRKY23 gene enhances pathogen defense and dark-induced leaf senescence in Arabidopsis. Pl. Growth Regula. 58: 181-190.

Joo, J., Y.H. Lee and S.I. Song (2019). OsbZIP42 is a positive regulator of ABA signaling and confers drought tolerance to rice. Planta 249: 1521-1533.

Joseph, A., M. K.V and R. V (2015). A Study on the Accumulation of Proline- An Osmoprotectant Amino Acid under Salt Stress in Some Native Rice Cultivars of North Kerala, India.

Kadioglu, A. and R. Terzi (2007). A dehydration avoidance mechanism: Leaf rolling. The Botani. Review 73: 290-302.

Kanwal, S. M.H.N. Tahir, H.A. Sadaqat, and B. Sadia. (2019). Development of high yielding types of Brassica napus L. under salinity stress. Pakistan J. Bot. 51(4): 1185-1190.

Kanwal, S., M.H.N. Tahir and H. Razzaq (2021). Principal component analysis and assessment of Brassica napus l. accessions for salt tolerance using stress tolerance indices. Pakistan J. Bot. 53(1): 113-118.

Kim, S.-H., T. Oikawa, J. Kyozuka, H.L. Wong, K. Umemura, M. Kishi-Kaboshi, A. Takahashi, Y. Kawano, T. Kawasaki and K. Shimamoto (2012). The bHLH Rac immunity1 (RAI1) is activated by OsRac1 via OsMAPK3 and OsMAPK6 in rice immunity. Pl. Cell Physiol. 53: 740-754.

Kim, Y., Y. Chung, E. Lee, P. Tripathi, S. Heo and K. Kim (2020). Root response to drought stress in rice (*Oryza sativa* L.). Inter. J. Mol. Sci. 21(4): 1513.

Koevoets, I.T., J.H. Venema, J.T.M. Elzenga and C. Testerink (2016). Roots Withstanding their Environment: Exploiting Root System Architecture Responses to Abiotic Stress to Improve Crop Tolerance. Front. Pl. Sci. 7.

Koo, S.C., B.C. Moon, J.K. Kim, C.Y. Kim, S.J. Sung, M.C. Kim, M.J. Cho and Y.H. Cheong (2009). OsBWMK1 mediates SA-dependent defense responses by activating the transcription factor OsWRKY33. Biochem. Biophysi. Res. Communications 387: 365-370.

Kumar, S., S. Dwivedi, S. Singh, B. Bhatt, P. Mehta, E. Rajamanickam, V. Singh and O. Singh (2014). Morpho-physiological traits associated with reproductive stage drought tolerance of rice (Oryza sativa L.) genotypes under rain-fed condition of eastern Indo-Gangetic Plain. Ind. J. Pl. Physiol. 19: 87-93.

Kumara, S., S. K. Dwivedia, S. Basub, G. Kumarc, J. S. Mishraa, T. K. Koleya, K. K. Raoa, A. K. Choudharya, S. Mondala, S. Kumara, N. Bhaktaa, B.P. Bhatta, R. K. Pauld and A. Kumar (2020). Anatomical, agro-morphological and physiological changes in rice under cumulative and stage specific drought conditions prevailed in eastern region of India. Field Cr. Res. 245:107658.

Lafitte, H.R., Z.K. Li, C.H.M. Vijayakumar, Y.M. Gao, Y. Shi, J.L. Xu, B.Y. Fu, S.B. Yu, A.J. Ali, J. Domingo, R. Maghirang, R. Torres and D. Mackill (2006). Improvement of rice drought tolerance through backcross breeding: Evaluation of donors and selection in drought nurseries. Field Cr. Res. 97: 77-86.

Lee, H., J. Cha, C. Choi, N. Choi, H.-S. Ji, S.R. Park, S. Lee and D.-J. Hwang (2018). Rice WRKY11 Plays a Role in Pathogen Defense and Drought Tolerance. Rice (New York, N.Y.) 11: 5-5.

Li, S., X. Zhou, L. Chen, W. Huang and D. Yu (2010). Functional characterization of Arabidopsis thaliana WRKY39 in heat stress. Mol. and cells 29: 475-483.

Li, J., R.-Y. Qin, H. Li, R.-F. Xu, C.-H. Qiu, Y.-C. Sun, H. Ma, Y.-C. Yang, D.-H. Ni and L. Li (2015). Identification and analysis of the mechanism underlying heat-inducible expression of rice aconitase 1. Pl. Sci. 233: 22-31.

Li, W., S. Pang, Z., Lu and B. Jin (2020). Function and mechanism of WRKY transcription factors in abiotic stress responses of plants. Pl. 9(11): 1515

Lim, C.W., W. Baek, J. Jung, J.H. Kim and S.C. Lee (2015). Function of ABA in Stomatal Defense against Biotic and Drought Stresses. Inter. J. Mol. Sci. 16: 15251-15270.

Liu, J.X., D.Q. Liao, R. Oane, L. Estenor, X.E. Yang, Z.C. Li and J. Bennett (2006). Genetic variation in the sensitivity of anther dehiscence to drought stress in rice. Field Cr. Res. 97: 87-100.

Liu, X., X. Bai, X. Wang and C. Chu (2007). OsWRKY71, a rice transcription factor, is involved in rice defense response. J. Pl. Physiol. 164: 969-979.

Liu, W., J.C. Reif, N. Ranc, G.D. Porta and T. Wurschum (2012). Comparison of biometrical approaches for QTL detection in multiple segregating families. TAG. Theor. Appl. Gene. Theoretische und angewandte Genetik 125: 987-998.

Liu, Q.-N., Y. Liu, Z.-Z. Xin, D.-Z. Zhang, B.-M. Ge, R.-P. Yang, Z.-F. Wang, L. Yang, B.-P. Tang and C.-L. Zhou (2017). Genome-wide identification and characterization of the WRKY gene family in potato (Solanum tuberosum). Biochemi. Syste. Ecol. 71: 212-218.

Liu, J., M. Hasanuzzaman, H. Wen, J. Zhang, T. Peng, H. Sun and Q. Zhao (2019). High temperature and drought stress cause abscisic acid and reactive oxygen species accumulation and suppress seed germination growth in rice. Protoplasma, 256(5): 1217-1227.

Lorenzana, R.E. and R. Bernardo (2009). Accuracy of genotypic value predictions for marker-based selection in biparental plant populations. *TAG.* Theor. Appl. Gene. Theoretische und angewandte Genetik, 120: 151-161.

Lum, M. S., M. M. Hanafi, Y. M. Rafii, and A. S. N. Akmar. 2014. Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice.J. Anim. Plant Sci. 24(5): 1487-1493.

Melandri, G., H. Abd-Elgawad, D. Riewe, J. A. Hageman, H. Asard, G. T.S. Beemster, N. Kadam, K. Jagadish, T. Altmann, C. Ruyter-Spiraand and H. Bouwmeester (2020). Biomarkers for grain yield stability in rice under drought stress. J. exper.Bot. 71(2): 669-683.

Miah, G., M. Rafii, M.R. Ismail, M. Sahebi, F.S.G. Hashemi, O. Yusuff and M.G. Usman (2017). Blast disease intimidation towards rice cultivation: A review of pathogen and strategies to control. J. Ani & Pl. Sci. 27: 1058-1066.

Moin, M., A. Bakshi, A. Saha, M. Dutta and P.B. Kirti (2017). Gain-of-function mutagenesis approaches in rice for functional genomics and improvement of crop productivity. Brief Funct. Genomics 16: 238-247.

Nadarajah, K. and I. S. Kumar (2019). Drought response in rice: The miRNA story. Int. J. Mol. Sciences 20(15): 3766.

Nam, K.-H., K.J. Nam, J.H. An, S.-C. Jeong, K.W. Park, H.-B. Kim and C.-G. Kim (2013). Comparative analysis of key nutrient composition between drought-tolerant transgenic rice and its non-transgenic counterpart. Food Sci. Biotechnol. 22: 1-7.

Niu, C.F., W. Wei, Q.Y. Zhou, A.G. Tian, Y.J. Hao, W.K. Zhang, B. Ma, Q. Lin, Z.B. Zhang, J.S. Zhang and S.Y. Chen (2012). Wheat WRKY genes TaWRKY2 and TaWRKY19 regulate abiotic stress tolerance in transgenic Arabidopsis plants. Pl. cell environ. 35: 1156-1170.

Oladosu, Y., M.Y. Rafii, N. Abdullah, G. Hussin, A. Ramli, H.A. Rahim, G. Miah and M. Usman (2016). Principle and application of plant mutagenesis in crop improvement: a review. Biotech. Biotechnological Equip. 30: 1-16.

Oladosu, Y., M.Y. Rafii, C. Samuel, A. Fatai, U. Magaji, I. Kareem, Z.S. Kamarudin, I.i. Muhammad and K. Kolapo (2019). Drought Resistance in Rice from Conventional to Molecular Breeding: A Review. Int. J. Mol. Sci. 20: 3519.

Olvera-Carrillo, Y., J. Luis Reyes and A.A. Covarrubias (2011). Late embryogenesis abundant proteins: versatile players in the plant adaptation to water limiting environments. Pl. Sig. & Behavior 6: 586-589.

Padmini, S., A. Mahender, P. Smita, B.C. Marndi and G.J.N. Rao (2014). Characterization of some Indian native land race rice accessions for drought tolerance at seedling stage. Aust. J. Cr. Sci. 8: 324-331.

Pandey, V. and A. Shukla (2015). Acclimation and Tolerance Strategies of Rice under Drought Stress. Rice Sci. 22: 147-161.

Pang, Y., K. Chen, X. Wang, J. Xu, J. Ali and Z. Li (2017). Recurrent selection breeding by dominant male sterility for multiple abiotic stresses tolerant rice cultivars. Euphytica 213: 268.

Peng, Y., L.E. Bartley, P. Canlas and P.C. Ronald (2010). OsWRKY IIa Transcription Factors Modulate Rice Innate Immunity. Rice (New York, N.Y.) 3: 36-42.

Peng, X., H. Wang, J.C. Jang, T. Xiao, H. He, D. Jiang and X. Tang (2016). OsWRKY80-OsWRKY4 Module as a Positive Regulatory Circuit in Rice Resistance Against Rhizoctonia solani. Rice (New York, N.Y.) 9: 63-63.

Pirasteh-Anosheh, H., A. Saed-Moucheshi, H. Pakniyat and M. Pessarakli (2016). Stomatal responses to drought stress. 24-40.

Polania, J., I.M. Rao, C. Cajiao, M. Grajales, M. Rivera, F. Velasquez, B. Raatz and S.E. Beebe (2017). Shoot and Root Traits Contribute to Drought Resistance in Recombinant Inbred Lines of MD 23-24 × SEA 5 of Common Bean. Front. Pl. Sci. 8: 296-296.

Poli, Y., R.K. Basava, M. Panigrahy, V.P. Vinukonda, N.R. Dokula, S.R. Voleti, S. Desiraju and S. Neelamraju (2013). Characterization of a Nagina22 rice mutant for heat tolerance and mapping of yield traits. Rice 6: 36.

Posadas, L.G., K.M. Eskridge, J.E. Specht and G.L. Graef (2014). Elite Performance for Grain Yield from Unadapted Exotic Soybean Germplasm in Three Cycles of a Recurrent Selection Experiment. Cr. Sci. 54: 2536-2546.

Qiu, D., J. Xiao, X. Ding, M. Xiong, M. Cai, Y. Cao, X. Li, C. Xu and S. Wang (2007). OsWRKY13 mediates rice disease resistance by regulating defense-related genes in salicylate- and jasmonate-dependent signaling. Mol. Pl.-microbe interactions: MPMI 20: 492-499.

Qiu, Y. and D. Yu (2009). Over-expression of the stress-induced OsWRKY45 enhances disease resistance and drought tolerance in Arabidopsis. Environ. Exp. Bot. 65: 35-47.

Rahim, A.H., K.Z. Shafika, M.A.R. Bhuiyan, M.K. Narimah, R. Wickneswari, M.Z. Abdullah, L.P.K. Anna, H. Sobri, I. Rusli and R. Khairuddin abdul (2012). Evaluation and characterization of advanced rice mutant line of rice (Oryza sativa), MR219-4 and MR219-9 under drought condition. Int: R. and D. Seminar 2012: Res. Dev Seminar 2012. Malaysia.

Raineri, J., S. Wang, Z. Peleg, E. Blumwald and R. Chan (2015). The rice transcription factor OsWRKY47 is a positive regulator of the response to water deficit stress. Pl. Mol. Biol. 88: 401-413.

Ramamoorthy, R., S.Y. Jiang, N. Kumar, P.N. Venkatesh and S. Ramachandran (2008). A comprehensive transcriptional profiling of the WRKY gene family in rice under various abiotic and phytohormone treatments. Pl. Cell Physiol. 49: 865-879.

Rang, Z.W., S.V.K. Jagadish, Q.M. Zhou, P.Q. Craufurd and S. Heuer (2011). Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. Environ. Exp. Bot. 70: 58-65.

Ricachenevsky, F., R. Sperotto, P. Menguer and J. Fett (2010). Identification of Fe-excess-induced genes in rice shoots reveals a WRKY transcription factor responsive to Fe, drought and senescence. Mol. Biol. reports 37: 3735-3745.

Ross, C., Y. Liu and Q. Shen (2007). The WRKY gene family in rice (Oryza sativa). J. Integ. Pl. Biol. 49: 827-842.

Rushton, P.J., H. Macdonald, A.K. Huttly, C.M. Lazarus and R. Hooley (1995). Members of a new family of DNA-binding proteins bind to a conserved cis-element in the promoters of α-Amy2 genes. Pl. Mol. Biol. 29: 691-702.

Rushton, P.J., I.E. Somssich, P. Ringler and Q.J. Shen (2010). WRKY transcription factors. Trends Pl. Sci. 15: 247-258.

Ryu, H.-S., M. Han, S.-K. Lee, J.-I. Cho, N. Ryoo, S. Heu, Y.-H. Lee, S.H. Bhoo, G.-L. Wang, T.-R. Hahn and J.-S. Jeon (2006). A comprehensive expression analysis of the WRKY gene superfamily in rice plants during defense response. Pl. cell reports 25: 836-847.

Saijo, Y., S. Hata, J. Kyozuka, K. Shimamoto and K. Izui (2000). Over-expression of a single Ca2+-dependent protein kinase confers both cold and salt/drought tolerance on rice plants. The Pl. J. for cell and Mol. Biol. 23: 319-327

Salunkhe, A.S., R. Poornima, K.S.J. Prince, P. Kanagaraj, J.A. Sheeba, K. Amudha, K. Suji, A. Senthil and R.C. Babu (2011). Fine mapping QTL for drought resistance traits in rice (Oryza sativa L.) using bulk segregant analysis. Mol. Biotechnol. 49: 90-95.

Serraj, R., K. McNally, I. Slamet-Loedin, A. Kohli, S. Haefele, G. Atlin and A. Kumar (2011). Drought Resistance Improvement in Rice: An Integrated Genetic and Resource Management Strategy. Pl. Produc. Sci. 14: 1-14.

Sharifunnessa, M. and M.T. Islam (2017). Effect of drought stress at different growth stages on yield and yield components of six rice (Oryza sativa L.) genotypes. Fundamental and Applied Agric. 2: 285-289.

Shahzad, R., S. Ahmad, S. Jamil, A. Nisar, Z. Amina, S. Saleem, M.Z. Iqbal, R.M. Atif and X. Wang. (2021a). Harnessing the potential of plant transcription factors in developing climate resilient crops to improve global food security:

Current and future perspectives. Saudi J. Bio. Sci. 28(4): 2323-2341.

Shahzad, R., S. Jamil, S. Ahmad, A. Nisar, S. Kanwal, R.M. Atif, M.Z. Iqbal, Z. Ali, A.I. Ghazy and A.A. Khan (2021b). Omics approaches for improving abiotic stress tolerance in rice: recent advances and future prospects *In Frontiers in Plant-Soil Interaction*, Elsevier Amsterdam, Netherlands. pp: 199-220.

Sharma, P. and R.S. Dubey (2005). Drought Induces Oxidative Stress and Enhances the Activities of Antioxidant Enzymes in Growing Rice Seedlings. Pl. Growth Regu. 46: 209-221.

Shen, H., C. Liu, Y. Zhang, X. Meng, X. Zhou, C. Chu and X. Wang (2012). OsWRKY30 is activated by MAP kinases to confer drought tolerance in rice. Pl. Mol. Biol. 80: 241-253.

Shi, W.-Y., Y.-T. Du, J. Ma, D.-H. Min, L.-G. Jin, J. Chen, M. Chen, Y.-B. Zhou, Y.-Z. Ma, Z.-S. Xu and X.-H. Zhang (2018). The WRKY Transcription Factor GmWRKY12 Confers Drought and Salt Tolerance in Soybean. Int. J. Mol. Sci. 19: 4087.

Shrestha, J (2019). Drought Stress in Rice (*Oryza Sativa* L.). Available at: https://www.linkedin.com/pulse/drought-stress-rice-oryza-sativa-l-jiban-shrestha/ (Accessed: 26 July 2019).

Singh, B., K.R. Reddy, E.D. Redoña and T. Walker (2017). Screening of Rice Cultivars for Morpho-Physiological Responses to Early-Season Soil Moisture Stress. Rice Sci. 24: 322-335.

Sokoto, M. (2014). Response of rice varieties to water stress in Sokoto, Sudan Savannah, Nigeria. J. Biosci. and Medi. 2: 68.

Song, Y., L. Chen, L. Zhang and D. Yu (2010a). Overexpression of OsWRKY72 gene interferes in the abscisic acid signal and auxin transport pathway of Arabidopsis. J. Biosci. 35: 459-471.

Song, Y., S. Jing and D. Yu (2010b). Overexpression of the stress-induced OsWRKY08 improves osmotic stress tolerance in Arabidopsis. Chi. Sci. Bull. 54: 4671-4678.

Sun, C., S. Palmqvist, H. Olsson, M. Boren, S. Ahlandsberg and C. Jansson (2003). A novel WRKY transcription factor, SUSIBA2, participates in sugar signaling in barley by binding to the sugar-responsive elements of the iso1 promoter. Pl. Cell 15: 2076-2092.

Swain, P., A. Raman, S.P. Singh and A. Kumar (2017). Breeding drought tolerant rice for shallow rainfed ecosystem of eastern India. Field Cr. Res. 209: 168-178.

Swamy, B.P.M. and A. Kumar (2013). Genomics-based precision breeding approaches to improve drought tolerance in rice. Biotech. Advances 31: 1308-1318.

Tao, Z., H. Liu, D. Qiu, Y. Zhou, X. Li, C. Xu and S. Wang (2009). A Pair of Allelic WRKY Genes Play Opposite Roles in Rice-Bacteria Interactions. Pl. Physiol. 151: 936-948.

Todaka, D., K. Shinozaki and K. Yamaguchi-Shinozaki (2015). Recent advances in the dissection of drought-stress regulatory networks and strategies for development of drought-tolerant transgenic rice plants. Front. Pl. Sci. 6: 84.

Ulker, B. and I. Somssich (2004). Ülker B, Somssich IE. WRKY transcription factors: from DNA binding towards biological function. Curr Opin Plant Biol 7: 491-498. Current opinion in Pl. Boil. 7: 491-498.

Upadhyaya, H. and S.K. Panda (2019). Chapter 9 - Drought Stress Responses and Its Management in Rice. In: Advances in Rice Research for Abiotic Stress Tolerance, M. HasanuzzamanM. FujitaK. Nahar and J. K. Biswas (Eds.). Woodhead Publishing: 177-200.

Usman, M.G., M. Rafii, M. Mohammad Yusoff, O. Yusuff, M. Ismail and G. Miah (2017). Molecular analysis of Hsp70 mechanisms in plants and their function in response to stress. Biotech. Gene English Reviews 33: 1-14.

Varshney, R.K., K.C. Bansal, P.K. Aggarwal, S.K. Datta and P.Q. Craufurd (2011). Agricultural biotechnology for crop improvement in a variable climate: hope or hype? Trends Plant Sci, 16: 363-371.

Verma, R.K., V.V. Santosh Kumar, S.K. Yadav, S. Pushkar, M.V. Rao and V. Chinnusamy (2019). Overexpression of ABA Receptor PYL10 Gene Confers Drought and Cold Tolerance to Indica Rice. Front. Pl. Sci. 10.

Viana, V.E., N. Marini, C. Busanello, C. Pegoraro, J.A. Fernando, L.C. Da Maia and A. Costa de Oliveira (2018). Regulation of rice responses to submergence by WRKY transcription factors. Biologia Plantarum 62: 551-560.

Vikram, P., B.P.M. Swamy, S. Dixit, H.U. Ahmed, M. Teresa Sta Cruz, A.K. Singh and A. Kumar (2011). qDTY1.1, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. BMC Genetics 12: 89.

Wang, H.H., K. Xie, K.L. Wu and Z.J. Guo (2005). Isolation of a rice WRKY gene OsWRKY52, whose expression is induced by Magnaporthe grisea. Progress in Biochem. Biophy. 32: 937-946.

Wang, H., J. Hao, X. Chen, Z. Hao, X. Wang, Y. Lou, Y. Peng and Z. Guo (2007). Overexpression of rice WRKY89 enhances ultraviolet B tolerance and disease resistance in rice plants. Pl. Mol. Biol 65: 799-815.

Wang, F., X. Hou, J. Tang, Z. Wang, S. Wang, F. Jiang and Y. Li (2012). A novel cold-inducible gene from Pak-choi (Brassica campestris ssp. chinensis), BcWRKY46, enhances the cold, salt and dehydration stress tolerance in transgenic tobacco. Mol. Biol. Reports 39: 4553-4564.

Wang, P., X. Xu, Z. Tang, W. Zhang, X.-Y. Huang and F.-J. Zhao (2018). OsWRKY28 Regulates Phosphate and Arsenate Accumulation, Root System Architecture and Fertility in Rice. Front. Pl. Sci. 9: 1330-1330.

Wu, X., Y. Shiroto, S. Kishitani, Y. Ito and K. Toriyama (2009). Enhanced heat and drought tolerance in transgenic rice seedlings overexpressing OsWRKY11 under the control of HSP101 promoter. Pl. Cell Reports 28: 21-30.

Xiang, Y., Y. Huang and L. Xiong (2007). Characterization of Stress-Responsive CIPK Genes in Rice for Stress Tolerance Improvement. Pl. Physiol. 144: 1416-1428.

Xiang, Y., N. Tang, H. Du, H. Ye and L. Xiong (2008). Characterization of OsbZIP23 as a Key Player of the Basic Leucine Zipper Transcription Factor Family for Conferring Abscisic Acid Sensitivity and Salinity and Drought Tolerance in Rice. Pl. Physiol. 148: 1938-1952.

Xiao, B., Y. Huang, N. Tang and L. Xiong (2007). Over-expression of a LEA gene in rice improves drought resistance under the field conditions. Theor. & App. Gen., Theoretical and Applied Genetics. 115: 35-46.

Xiao, J., H. Cheng, X. Li, J. Xiao, C. Xu and S. Wang (2013). Rice WRKY13 regulates cross talk between abiotic and biotic stress signaling pathways by selective binding to different cis-elements. Pl. Physiol. 163: 1868-1882.

Xie, Z., Z.-L. Zhang, X. Zou, J. Huang, P. Ruas, D. Thompson and Q.J. Shen (2005). Annotations and functional analyses of the rice WRKY gene superfamily reveal positive and negative regulators of abscisic acid signaling in aleurone cells. Pl. Physiol. 137: 176-189.

Xu, D.-Q., J. Huang, S.-Q. Guo, X. Yang, Y.-M. Bao, H.-J. Tang and H.-S. Zhang (2008). Overexpression of a TFIIIA-type zinc finger protein gene ZFP252 enhances drought and salt tolerance in rice (Oryza sativa L.). FEBS Letters 582: 1037-1043.

Xu, Y., H. Xu, B. Wang and X. Su (2020). Crystal structures of N-terminal WRKY transcription factors and DNA complexes. Protein & cell, 11(3): 208-213.

Yamasaki, K., T. Kigawa, M. Inoue, M. Tateno, T. Yamasaki, T. Yabuki, M. Aoki, E. Seki, T. Matsuda, Y. Tomo, N. Hayami, T. Terada, M. Shirouzu, A. Tanaka, M. Seki, K. Shinozaki and S. Yokoyama (2005). Solution structure of an Arabidopsis WRKY DNA binding domain. Pl. Cell 17: 944-956.

Yamasaki, K., T. Kigawa, S. Watanabe, M. Inoue, T. Yamasaki, M. Seki, K. Shinozaki and S. Yokoyama (2012). Structural basis for sequence-specific DNA recognition by an Arabidopsis WRKY transcription factor. The J. Biochem. 287: 7683-7691.

Yang, S., B. Vanderbeld, J. Wan and Y. Huang (2010). Narrowing down the targets: towards successful genetic engineering of drought-tolerant crops. Mol. Pl. Sci. 3: 469-490.

Yang, Z., X. Xie, X. Huang, F. Wang, Z. Tong, Y. Duan, T. Lan and W. Wu (2012). Mapping of Sanming dominant genic male sterility gene in rice. *Yi* Chuan Hereditas 34: 615-620.

Yang, S., L. Zhou, L.-y. Miao, J.-n. Shi, C.-q. Sun, W. Fan, J.-p. Lan, H. Chen, L.-j. Liu, S.-j. Dou, G.-z. Liu and L.-y. Li (2016). The expression and binding properties of the rice WRKY68 protein in the Xa21-mediated resistance response to Xanthomonas oryzae pv. Oryzae. J. Integ. Agric. 15: 2451-2460.

Yang, S., K. Xu, S. Chen, T. Li, H. Xia, L. Chen, H. Liu and L. Luo (2019a). A stress-responsive bZIP transcription factor OsbZIP62 improves drought and oxidative tolerance in rice. BMC Pl. Biol. 19: 260.

Yang, X., B. Wang, L. Chen, P. Li and C. Cao (2019b). The different influences of drought stress at the flowering stage on rice physiological traits, grain yield, and quality. Scientific Reports 9: 3742.

Yang, Z., X. Chi, F. Guo, X. Jin, H. Luo, A. Hawar, Y. Chen, K. Feng, B. Wang, J. Qi, Y. Yang and B. Sun (2020). SbWRKY30 enhances the drought tolerance of plants and regulates a drought stress-responsive gene, SbRD19, in sorghum. J. Pl. Physiol. 153142.

Yokotani, N., Y. Sato, S. Tanabe, T. Chujo, T. Shimizu, K. Okada, H. Yamane, M. Shimono, S. Sugano, H. Takatsuji, H. Kaku, E. Minami and Y. Nishizawa (2013). WRKY76 is a rice transcriptional repressor playing opposite roles in blast disease resistance and cold stress tolerance. J. Exp. Bot. 64: 5085-5097.

Yokotani, N., M. Shikata, H. Ichikawa, N. Mitsuda, M. Ohme-Takagi, E. Minami and Y. Nishizawa (2018). OsWRKY24, a blast-disease responsive transcription factor, positively regulates rice disease resistance. J. Gen. Pl. Pathol. 84: 85-91.

Yuan, Q., S. Ouyang, A. Wang, W. Zhu, R. Maiti, H. Lin, J. Hamilton, B. Haas, R. Sultana, F. Cheung, J. Wortman and C.R. Buell (2005). The institute for genomic research Osa1 rice genome annotation database. Pl. Physiol. 138: 18-26.

Zandalinas, S.I., R. Mittler, D. Balfagón, V. Arbona and A. Gómez-Cadenas (2018). Plant adaptations to the combination of drought and high temperatures. Physiologia Plantarum 162: 2-12.

Zhang, Z.-L., Z. Xie, X. Zou, J. Casaretto, T.-H.D. Ho and Q.J. Shen (2004). A rice WRKY gene encodes a transcriptional repressor of the gibberellin signaling pathway in aleurone cells. Pl. physiol. 134: 1500-1513.

Zhang, J., Y. Peng and Z. Guo (2008a). Constitutive expression of pathogen-inducible OsWRKY31 enhances disease resistance and affects root growth and auxin response in transgenic rice plants. Cell Res. 18: 508-521.

Zhang, L., X. Wang, Y. Bi, C. Zhang, Y. Fan and L. Wang (2008b). Isolation and functional analysis of transcription factor GmWRKY57B from soybean. Chinese Sci. Bull. Chine. Sci. Bull. 53: 3538-3545.

Zhao, L., Y. Hu, K. Chong and T. Wang (2010). ARAG1, an ABA-responsive DREB gene, plays a role in seed germination and drought tolerance of rice. Annals of Bot. 105: 401-409.

Zhao, W., L. Liu, Q. Shen, J. Yang, X. Han, F. Tian and J. Wu (2020). Effects of water stress on photosynthesis, yield, and water use efficiency in winter wheat. Water 12: 2127.