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Review Article

A critical review on the improvement of drought stress tolerance in rice (*Oryza sativa* L.)

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Abstract

Abiotic stresses are the primary threat to crop production across the globe. Drought stress is primary abiotic stress which is considerably limiting the global rice production and putting the food security at higher risks. Drought tolerance (DT) is a multigene trait which is influenced by various stages of development in rice plant. Tolerance as well as susceptibility of rice to drought stress is carried out by different drought-response genes and other components of stress. Plant researchers have used various methods such as, genetic manipulation and marker-assisted techniques for development of new rice cultivars with improved tolerance to drought stress. The aims of this review are to present recent advancements and illustrate current approaches to breed a robust drought-resistant rice genotypes by using classical breeding and advanced molecular techniques. We also shed light on all available information regarding the role of significant hormones in DT, QTL for drought-related traits, QTL for rice yield, global strategies for the improvement of DT in rice, DT genes, and selection supported by markers.

Keywords: cultivar; drought tolerance; genes; MAS; QTL; rice

Introduction

Rice (*Oryza sativa* L) is the most staple food of more than 50% of the world's population (Hadiarto *et al.*, 2010; Rasheed *et al.*, 2020c), which meets the 80% caloric needs of the majority of the population predominantly in the Asian countries (Rasheed *et al.*, 2020a, 2020b). Due to its good taste, rice can be cooked with other food products to get an improved taste and nutritional values (Rohman *et al.*, 2014; Rathna Priya *et al.*, 2019). Many rice genotypes contain certain pigments which limit the development of atherosclerotic plaque, because it has anti-oxidative properties (Rohman *et al.*, 2014). Rice growth and yield are significantly affected by abiotic factors. Drought stress is one of the most severe threats to global rice production, causing a

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significant decline in rice yield (Swamy and Kumar, 2013; Sahebi *et al.*, 2018). Drought stress causes many problems in Asian counties like China, Bangladesh, Bhutan, and Nepal due to the changing pattern of annual rainfall (Miyan, 2015). Salinity, low precipitation, low and high temperature, and higher intensity of light etc., are major casual factors for drought stress in rice. These factors restrict the availability of water to the plant. This is a kind of water stress called drought stress (Salehi-Lisar and Bakhshayeshan-Agdam, 2016). Water-related issues are not consistent throughout the years lead to the imbalance in quantity and distribution of rainfall (Hijmans and Serraj, 2009; Khan *et al.*, 2018), however, they occur with expected frequency in a particular area (Serraj *et al.*, 2015). About 42 million ha of rice-producing area faces the problem of drought stress (Yang *et al.*, 2019) and there is a huge gap between the actual (4 t/ha) and potential (10 t/ha) due to the presence of various abiotic stresses (Oladosu *et al.*, 2019).

The shortage of freshwater for rice plants is main issue in the low production of rice (Gosal *et al.*, 2009), as for producing 1 kg of rice, about 3000 litres of water is required. Hence, drought stress can potentially cause yield losses up to 100%, depending on plants growth stage. This reduction in yield can be reduced by using different plans to assist the farmers in safeguarding maximum rice production to maintain global yield level (Oladosu *et al.*, 2019). Continuous loss of underground and aboveground water resources is the main reason for water shortage. Continued drought stress could damage plant growth and cell elongation. Effects of drought stress at reproductive stages cause genetic sterility and embryo abortion (Ozga *et al.*, 2017). Drought stress decreases photosynthesis rate by injuring photosynthetic pigments, reducing leaf expansion, gas exchange rate, enzyme activities and thus lead to the decrease in yield and biomass of plants (Ashraf and Harris, 2013; Fahad *et al.*, 2017; Hassan *et al.*, 2020).

To develop the drought tolerant genotypes, it is necessary to know how plants handle with drought stress issues. Drought stress can be categorized into two types, terminal and intermittent (Polania *et al.*, 2017) drought stress. The terminal drought stress is activated by the absence of water available to plant, causing a stress if it is prolonged for a long time and can lead to plant death. On the other hand, intermittent drought stress causes retardation in plant growth during the time of inadequate rainfall (Oladosu *et al.*, 2019). The ability of a plant to survive under the low moisture level in the cytoplasm is termed as DT. Mechanisms of DT including, cellular adjustment, morphological and physiological adaptations and it is directed by genes (Sahebi *et al.*, 2018). Morphological adaptations include a rise in root length and thickness, delay in leaf senescence, while physiological adaptations comprise of stomatal closure, condensed transpiration rate, relation among flowering and maturing stages of parents, as well as partitioning of biomass and yield. Improvement in chlorophyll content (CC), harvest index and osmotic potential (Ntuli, 2012; Khan *et al.*, 2018) are essential for cellular adjustment of DT. Knowledge about root response to drought stress in very crucial to improve DT in rice (Kim *et al.*, 2020).

Now a day's drought stress has emerged as an essential part of research and improvement of DT in plants is challenging task due to the complexity of these traits. Genetic variation among the rice cultivars is a substantial factor in the development of resistant cultivar as they react contrarily to drought stress. Genotypes that showed maximum DT are often used to investigate DT and are best source of DT genes used for the development of tolerant crop cultivars. For the development of drought-tolerant cultivars it is necessary to know the mechanism by which plant tackle with drought stress. DT mechanism in rice has been studied broadly, which can help to explore mechanisms of drought stress and improve DT (Pandey and Shukla, 2015; Sahebi *et al.*, 2018). Rice yield can increase under drought stress by developing DT cultivars. Therefore, this method needs detailed information to understand the mechanism of DT in rice (Dien *et al.*, 2019). Investigating DT in rice is an urgent need by identifying putative genes, QTL, and other factors. Our current review focuses on the effects of drought stress on rice plant, novel approaches to develop tolerant varieties and complete evidences about candidate genes, putative QTL for drought traits, and yield and new approaches to enhance DT in rice.

Effect of drought stress on rice

Drought stress has multidimensional effects, and ultimately it becomes complex in mechanistic action (Iqbal *et al.*, 2020). Drought stress inhibits seed germination in rice by reducing water content in seed necessary for seedling emergence and thus lowering the rate of germination (Pirdashti *et al.*, 2003; Khan *et al.*, 2018). Seasonal drought is a main stress that reduces rice production largely; nevertheless, rice sensitivity to drought at diverse growth stages is unclear (Yang *et al.*, 2019). Drought stress results in the closure of stomata leading to a reduction in the gaseous exchange rate. Stomatal closure is controlled by phytohormones like abscisic acid and cytokinins (Daszkowska-Golec and Szarejko, 2013;Yang *et al.*, 2019). Drought stress reduces cell size, leaf area, and intercellular volume and leads to leaf rolling and leaf death. Drought stress induces a reduction in meristematic activity, arrest root enlargement, damage root systems (Singh *et al.*, 2012a), and reduces the water content in rice plants by restricting the water uptake from the soil (Zain *et al.*, 2014). The consequences of drought stress on rice at different stages are presented in Figure 1.

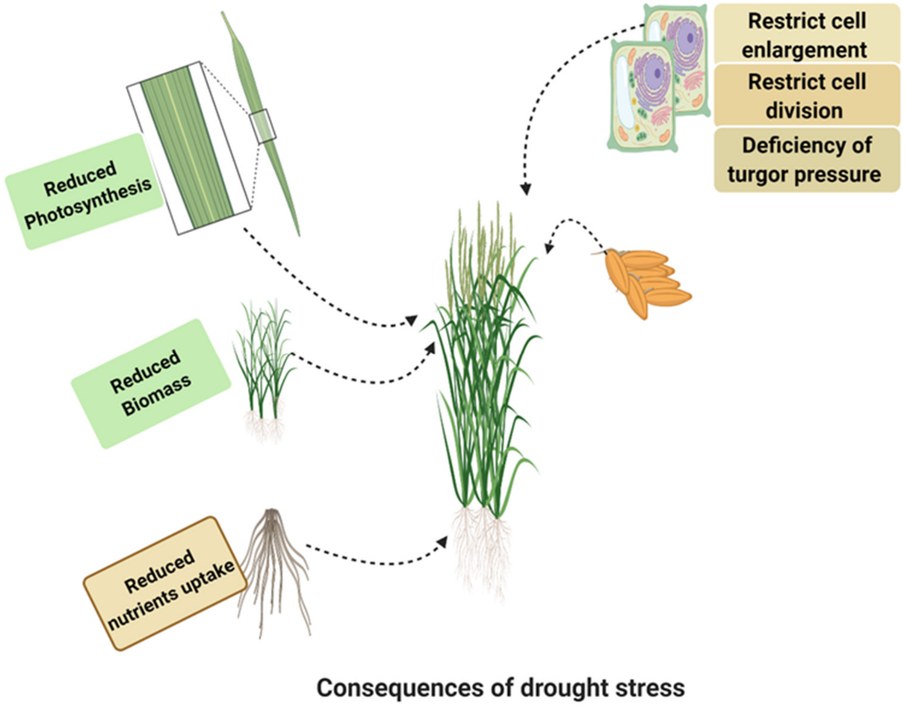

Figure 1. Effect of drought stress at various parts of rice leading to the decline in photosynthesis, biomass, nutrients uptake, cell division, turgor pressure and ultimately reduce yield

Drought stress reduces photosynthesis rate by damaging photosynthetic enzymes and photo-systems, thus disturbs numerous phases in the photosynthetic pathway (Ashraf and Harris, 2013; Khan *et al.*, 2018) eventually decreased plant biomass and yield. Another harmful effect of water stress is the production of reactive oxygen species (ROS), leading to the oxidative damage in plant and ultimately affect growth and yield (Ahmad *et al.*, 2014; Hussain *et al.*, 2018). Drought stress also induces many biochemical and physiological alterations during different developmental stages (Kim *et al.*, 2020). The effect of drought stress on growth stages in rice are shown in Table 1.

Drought stress reduces the concentration of many essential nutrients like, phosphorous (P) and nitrogen (N) and reduces their uptake from soil (Cramer *et al.*, 2009). This usually occurs due to a decline in the nutrients supply chain via mineralization, diffusion and mass flow in soil (Chapin III, 1991). Drought stress reduces the uptake of essential nutrients like, Ca, Cu, Zn, Mn, and alters many biochemical and physiological pathways in rice (Upadhyaya and Panda, 2019). Drought stress restricts their movement, which causes a decline in plant growth (Upadhyaya and Panda, 2019). Drought stress causes zinc deficiency, which damages plant cell by preventing the growth, and development of rice plants (Upadhyaya *et al.*, 2017).

Drought stress brings remarkable changes in the antioxidant defence system of plants (Todaka *et al.*, 2017). Drought stress leads to the production of ROS, which causes oxidation and disturbs rice growth. The imbalance between the ROS production and their scavenging is common in rice crop (Lum *et al.*, 2014). These oxidative species include singlet oxygen, hydroxyl free radicals, which cause denaturation of rice protein, peroxidation of lipid, and mutations in DNA (Sahebi *et al.*, 2018). Drought is the primary stress which badly affects rice growth and biomass and causes a serious decline in yield by affecting the grain filling stage (Nahar *et al.*, 2016). Drought stress impact on rice yield depends on stages of growth, flowering, and panicle formation (Kim *et al.*, 2020). Traits influencing drought stress in rice are presented in Table 2.

Table 1. Influence of drought stress at various growth stages of rice

	Stage	Effects	Reference
Rice	Flowering	23.2%	(Yang *et al.*, 2019)
	Water use efficiency	39%	(Yang *et al.*, 2019)
	Plant height	49.31%	(Singh *et al.*, 2018)
	Shoot length	mild	(Zhang *et al.*, 2018)
	1000 grain weight	13.71%	(Moonmoon and Islam, 2017)
	Photosynthesis	Decreased	(Fahad *et al.*, 2017)
	Panicle development	Reduced	(Wei *et al.*, 2017)
	Leaf area and biomass	Reduced	(Upadhyaya *et al.*, 2017)
	Reproductive (mild)	53 to 92%	(Lafitte *et al.*, 2007)
	Reproductive (severe)	48 to 94%	(Lafitte *et al.*, 2007)
	Stage of reproduction	24 to 84%	(Venuprasad *et al.*, 2007)
	Grain filling (mild)	30 to 55%	(Basnayake *et al.*, 2006)
	Grain filling (severe)	60%	(Basnayake *et al.*, 2006)

Table 2. Important factors to induce drought tolerance in rice

Traits	Function	Reference
Proline contents	Highly accumulated under drought	(Dien *et al.*, 2019)
Sugar contents	Increased under drought	(Dien *et al.*, 2019)
Starch contents	Increases and protect the plant	(Dien *et al.*, 2019)
Leaf strach regulation	Improved osmotic stress tolerance	(Thalmann *et al.*, 2016)
Spikelets fertility	Improved under drought stress	(Moonmoon and Islam, 2017)
Root dragging resistance	Root infiltration into deeper soil layers	(Pantuwan *et al.*, 2002)
Superior root infiltration capability	To sightsee a larger soil volume	(Ali *et al.*, 2000)
Membrane stability	Allows the plants leaves to effective at high temperature	(Tripathy *et al.*, 2000)
Leaf rolling score	Decrease transpiration	(Courtois *et al.*, 2000)
Relative water contents in leaf	Directs preservation of promising plant water status	(Courtois *et al.*, 2000)
Deeper and thicker roots	To explore a larger soil volume	(Yadav *et al.*, 1997)
Osmotic adjustment	To allow turgor conservation at a low plant water potential	(Lilley *et al.*, 1996)

Plant strategies to counter drought stress

DT is the plant capability to produce more yield under drought stress (Moonmoon and Islam, 2017). DT is a polygenic trait whose consequences depend on the action and relation of diverse morphological, biochemical as well as physiological responses (Mitra, 2001). The rice mostly reacts to drought stress by closing stomata , leaf rolling, and enhanced abscisic acid (ABA) production (Price *et al.*, 2002a). DT in rice generally depends on water use efficiency that permits lowest water usage for osmotic adjustment that enables the plants to retain turgor and protect meristem tissues (Nguyen *et al.*, 2004).

Drought escape

It involves to complete plants life cycle before the severity of drought increases (Kumar e*t al.*, 2017).It includes two mechanisms like, quick developmental plasticity and phonological development. In phonological development, plants are capable to produce flowers with lower vegetative growth, which allows them to produce seeds on a restricted water supply. In developmental plasticity, plants can produce higher vegetative growth, flowers as well as seeds in a season of high rainfall (Kumar *et al.*, 2008).

Drought avoidance

Avoidance from drought stress is termed as the plant's capability to retain comparatively higher tissue water potential regardless of water scarcity (Kumar *et al.*, 2017). The plant tissue has two ways to retain a higher water level in a period of high evaporative need and increasing soil water scarcity, either to decrease water loss or to retain the source of water. Rice cultivars that can retain water via biosynthesis of ABA or have extensive root system can or have extensive root systems can minimize the yield losses caused by drought (Singh *et al.*, 2012b). These plants usually have a deep root system capable of branching and soil infiltration, larger root to shoot ratio, efficient stomatal closure and higher cuticular wax (Wang *et al.*, 2006).

Drought tolerance

The plant's ability to survive under lower water content in tissue is called DT (Fleury *et al.*, 2010; Zhang *et al.*, 2018). DT is a complex process in rice controlled by several genetic factors and complicated morpho-physiological mechanisms (Li and Xu, 2007), including retention of turgor pressure via osmotic regulation, improved cell elasticity, reduced cell size as well as DT via protoplasmic resistance. The reaction of the plant to tissue water potential defines its level of DT (Mitra, 2001) and the characters related to these phenomena are classified as secondary traits like osmotic adjustment, leaf rolling and stomatal conductance used as selection criteria for DT (Kato *et al.*, 2006).

To trigger DT mechanism, the plant must sense an imbalance amid the water loss and availability. This perception is changed into an indicator of cellular stress. Plants have developed a complex chain of signals transmitted via several primary and secondary signalling corridors. Grouping of hormonal signals along with metabolites like ROS, proteins, as well as osmolytes are essential for variable expression of genetic factors. The plant may manufacture these compounds, or actively added due to cell injury (Hu and Xiong, 2014). The signalling cascades are produced in response to DT and cause further changes in gene expression, which resultantly leads to DT. Plant response to drought stress is demonstrated in Figure 2. A decrease in cytoplasmic osmotic potential is an outcome of an increase in solutes (organic or inorganic), which contributes to maintaining turgor pressure during stress. This osmotic adjustment depends on the level of stress. Osmotic adjustment is the result of the aggregation of proline, glycine betaine, and solutes, facilitating water absorption. Proline is a commonly studied osmolyte because of its significance in reducing stress under unfavourable conditions (Liang *et al.*, 2013). Proline accumulation is an imperative indictor of DT that can develop DT cultivars (Dien *at al.*, 2019).

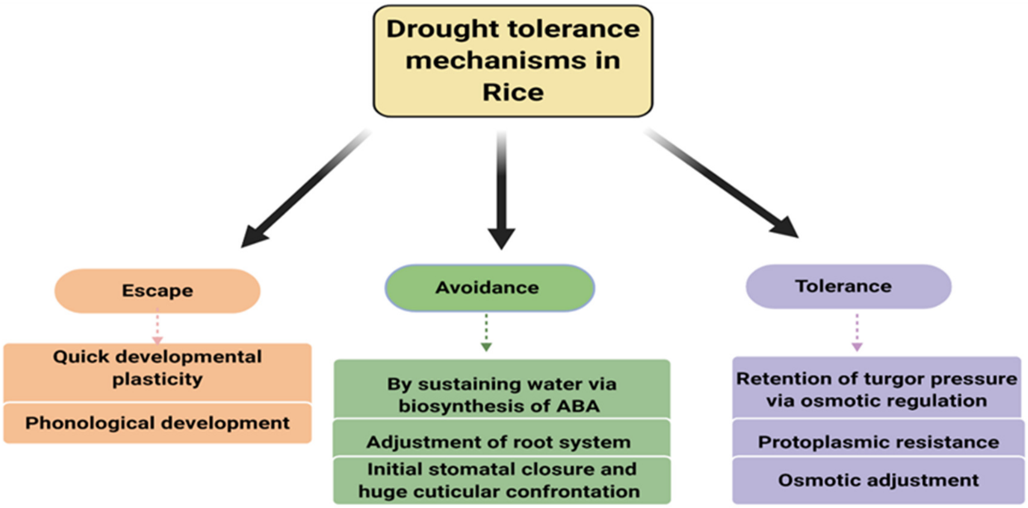

Figure 2. Plant response to drought stress via avoidance, escape, and tolerance mechanism. This shows that the rice plant uses several ways to cope with drought stress and which could be targeted to maintain rice yield under abiotic stress

Role of polyamines and proline

Polyamines and proline

Polyamines (PAs) are positively charged molecules produced under drought stress in rice *(Capell et al.*, 2004). The PAs include spermidine (spm) and spermine (spd) acting together in diverse signalling systems to control membrane stability, osmotic potential, and homeostasis. An increase in PAs content in drought stress is associated with enhanced photosynthesis ability, reduced loss of water and enhanced osmotic adjustments. PAs' controls gene expression, facilitates transcription factors in binding DNA, stabilizes membrane, scavenge free radicals, and avoids senescence of leaf through translation of genetic material and post translational modification of protein (Sahebi *et al.*, 2018). Rice synthesize high level of putrescine in stress, promotes the synthesis of spd and exogenous spm and eventually protects plants under drought stress (Capell *et al.*, 2004).

Proline plays a significant role in numerous adverse conditions (Tran *et al.*, 2007). Proline accumulation in rye grass significantly increases under drought (Miao *et al.*, 2006). Proline is an osmotolerant and a source of nutrition (Chun *et al.*, 2018). Accumulation of Proline is believed to play a key role in rice response to drought stress. This molecule has been considered as a compatible osmolyte and acts as a way of storage of carbon and nitrogen (Heuer, 2010). It performs three functions by acting as a signalling molecule, an antioxidant molecule, and a metals chelator (Hayat *et al.*, 2012). Proline helps in maintenance of osmotic and leaf water potential and thus facilitates the plant to avoid dehydration by maintaining turgor pressure (Kandowangko *et al.*, 2009).

When the rice was exposed to drought stress it showed an elevated level of proline content (Hu *et al.*, 1992), contributing to DT. Proline accumulation under drought stress could minimize damage by enhancing antioxidant activity (Fahramand *et al.*, 2014). Drought-tolerant varieties accumulate more proline and maintained higher root water content (RWC) than susceptible genotypes (Heuer, 2010). Abdula *et al.* (2016) revealed that the increasing biosynthesis of proline improved drought stress tolerance in rice genotypes. Proline accumulation capability of varieties can be used as a useful criterion for DT potential in rice crop (Dien *at al.*, 2019). Proline also plays role in DT by promoting activity for cellular synthesis, stabilization of membrane, scavenging of ROS, and osmoregulation. Proline synthesis, its degradation as well as transport obligingly regulates its endogenous level in plants in reaction to water stress (Heuer, 2010). Therefore, proline could be utilized as an indicator of DT in rice.

Role of plant hormones in drought tolerance

Plant hormones work in conjugation to control plant growth and development against various environmental stresses (Kohli *et al.*, 2013). ABA, ethylene, and cytokinins (CK) are major plant hormones that are important against drought stress tolerance. Several plant hormones have an essential role in boosting DT in rice (Kumar *et al.*, 2017); however, we have discussed five essential hormones and their DT mechanism.

Abscisic acid (ABA)

The ABA concentration usually increases to transmit the signals of drought stress. At the same time, other hormones like cytokinin (CK) may be reduced by downward regulation of genes action, and finally degraded by oxidase enzyme. Some hormones work together, demonstrated by ABA indirect function in drought stress signalling by hindering ethylene production (Oladosu *et al.*, 2019). An increase in ABA under drought can quickly restrict transpiration via stomatal closure, which prevents the occurrence of deficiency at plant reproductive stages. Improving rice grain yield (GY) via ABA remains a significant challenge due to reductions in carbon fixation following stomatal closure and pollen sterility caused by ABA (Ji *et al.*, 2011). Besides, enhanced ABA can cause abortion of pollen during reproductive drought by suppressing source sink relation. The role of AB can be exploited to increase GY in rice during the drought at the reproductive stage.

ABA may also increase osmotic conductivity by improving the functioning of aquaporin and controlling osmotic potential leading to sustained growth even under drought at the reproductive stage (Tardieu *et al.*, 2010; Travaglia *et al.*, 2010). Additionally, ABA has been demonstrated to play a positive role during post-anthesis phase. A study showed that drought stress significantly increased ABA content at the late grain filling stage while partitioning fixed carbon was strongly correlated with ABA content. ABA was positively correlated with pre-stored carbon's remobilization under drought in leaves, stem, and roots (Yang and Zhang, 2010). Many studies demonstrated that increase in DT via homeostasis of ABA is possible by changing ABA's biosynthetic and catabolic pathways. These studies did not find good plant output under terminal drought, which largely disturbs GY. Various ABA-signalling genes have increased yield under drought stress at the reproductive stage. For example, senescence-associated and ABA-dependent genes such as *OsNAP* and *OsNAC5* enhanced yield under drought (Liang *et al.*, 2014). The role of ABA in DT could be further investigated in rice to increase DT.

Cytokinin (CK)

Cytokinin is a primary plant hormone that slows the leaf senescence and controls plants cell proliferation. This trait is beneficial during drought stress at the reproductive stage. CK content has been shown to increase quickly at an early stage of grain filling, with rapid induction at the late stage of grain filling, indicating its role in regulating grain production in rice (Yang *et al.*, 2001). Application of 6-benzylaminopurine, a synthetic CK, improved the GY and quality of two -hybrid rice genotypes at the heading stage (Pan *et al.*, 2013). The expression of the isopentenyl transferase (IPT) gene involved in CK biosynthesis improved plant stress tolerance (Rivero *et al.*, 2007). The IPT expression in rice under drought stress increased GY under pre and post-anthesis drought stress by delaying response to stress (Peleg and Blumwald, 2011). Transgenic plants have revealed a higher expression of brassinosteroid-related genes and reduced expression of jasmonate-related genes, suggesting that CK suppresses JA's negative effects resulting in increased yield. Earlier studies indicated that CK content was reduced; as a result, CK enhanced the response of the plant to increasing ABA, which includes closure of stomata and preventing photosynthesis (Rivero *et al.*, 2010). In another study, it was found that synthesis of CK induced by stress protected the plant against harmful effects of drought stress on photosynthesis and increased yield (Reguera *et al.*, 2013). Likewise, in another study, Reguera *et al.* (2013) proposed that the synthesis of CK promotes carbon and nitrogen regulation and increased DT in rice. Some of the earlier results recommended that variations in hormone homeostasis brought the alteration in source/sink relations in transgenic plants, resulting higher grain yield under drought (Peleg *et al.*, 2011). Therefore, CK could be targeted to enhance DT in rice.

Ethylene

Ethylene is recognized for its role in leaf senescence and abscission caused by drought stress (Fukao *et al.*, 2006; Perata and Voesenek, 2007). However, the increased ethylene content under drought stress has been shown to inhibit photosynthesis and growth and roots development (Sharp, 2002). Ethylene production directly affects yield, increasing embryo abortion, increasing rate of grain filling and plant senescence (Wilkinson *et al.*, 2012; Tamaki *et al.*, 2015). Under drought, ethylene's concentration has been shown to increase in the rice grain at early grain-filling stage and decrease during grain development (Yang *et al.*, 2004). The ethylene concentration is negatively correlated with the grain-filling rate. It has been proposed that ethylene and ABA work antagonistically and their effect on grain filling depends on their concentration and balance between ABA and ethylene (Yang and Zhang, 2006; Zhu *et al.*, 2011). In rice a sharp reduction in ABA in submerged rice shoots is governed by ethylene-induced expression of gene *OsABA8x1* and ethylene independent suppression of gene function responsible for ABA synthesis (Saika *et al.*, 2007). Ethylene has a key role in plant response to water deficiency by enhancing gene expression related to several pathways like, aerenchyma formation, fermentation, and glycolysis pathways (Salazar *et al.*, 2015). Its content increase under drought stress leading to several changes in plant growth, increase response to drought stress, and maintain plant yield (Oladosu *et al.*, 2019). Therefore, ethylene could be used as a physiological indicator for improvement of DT in rice.

Auxin and gibberellins

Auxin plays a key role in rice response to drought stress, and it induces stomatal opening and may modify the effect of ABA on the aperture of stomata (Tanaka *et al.*, 2006). Auxin reduces resistance against water flow. Hence, plant adaptation to drought stress may include an enhanced concentration of auxin in root and a decline in the concentration of auxin in a leaf to reduce water loss. These phytohormones play a key role in rice tolerance to drought stress. CK induce breaking of root apical dominance, which results in auxin induce new roots formation. Auxin has a crucial role in prolific root system against DT. However, auxin concentration decreases under drought stress when ethylene increases (Upadhyaya and Panda, 2019). Gibberellins is a crucial plant hormone (Urbanova and Leubner-Metzger, 2016), which play a crucial role against abiotic stresses (Serret *et al.*, 2014). Hence auxin and GA can be used to improve physiological based DT in rice. The role of plant hormones in DT in rice is shown in Figure 3.

Strategies for improving drought tolerance

For breeding drought-tolerant genotypes, we mainly use rice grain yield as selection criteria. There are several classical breeding approaches to enhance DT, which include inter-generic and inter-specific crosses and induced mutation (Bolaños and Edmeades, 1993) to increase plant traits under drought (Briglia *et al.*, 2019). Now a day's rice breeders use physiological parameters as selection criteria because they require less time and depend on genetic variation in population. Main problem while studying drought stress is that, these characters cause more complications due to the lack of actual selection criteria, little genetic variability under drought conditions for yield and its related traits. The second factor is the difficulty between stress factors and numerous physiological, biochemical, and molecular processes that disturb growth and development (Atkinson and Urwin, 2012). Nevertheless, high-yielding variety is a primary goal in water deficit conditions in crop breeding (Dixit *et al.*, 2014). The classical breeding approaches are significant for conserving germplasm, hybridization among genetically divergent parents, and introducing new genetic characters. During the last thirty years, the International Rice Research Institute (IRRI) used classical breeding methods to develop several varieties that are tolerant to many stresses (Khush, 1984). Pedigree selection, backcrossing as well as induced mutation are the main approaches used in classical breeding.

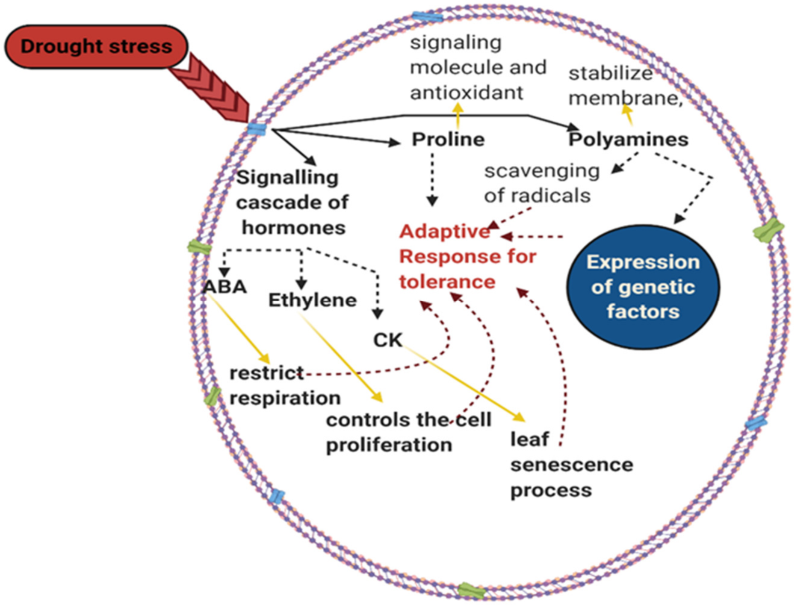

Figure 3. Role of plant hormones in drought tolerance in rice by scavenging of ROS, act as signalling pathway and control cell death

Pedigree selection

Pedigree selection is one of the classical methods broadly used in breeding rice to develop resistant cultivars if dominant genes control the trait. The advantage of pedigree selection include pyramiding genes that regulate biotic and abiotic factors (Khush, 1984). This method's limitations are that it is time consuming and requires regular assessment of many lines during planting seasons and need a record of selection criteria. This method needs a complete understanding of breeding material and the effects of abiotic factors on the trait of interest. This method is not appropriate for the characteristics because many genes influence it; hence, the diallel mating design is suitable for the selection (Khush, 1984). Usually recurrent method of selection is used for self-pollinated crops (Miah *et al.*, 2013).

Backcross method

The traditional backcross method is generally used in rice breeding to transfer favourable genes that control a particular character from donor to recipient parent, decrease the donor parent genome, and enhance the recovery rate of recurrent parent. This method gives a precise and accurate means for the development of numerous advanced breeding lines (Lafitte *et al.*, 2006). Backcross methods have led to the development of DT rice genotypes (Lafitte *et al.*, 2006).

Mutation breeding

Induced mutation breeding is widely used to develop resistant cultivars with improved GY (Oladosu *et al.*, 2014), seed quality, and insect and pest resistance (Oladosu *et al.*, 2015). This method reflects its significance because it leads to the formation of alleles that are not found naturally in genome. Induced mutation breeding technique has been discussed, and many cultivars have been developed using this technique (Oladosu *et al.*, 2016). 'Tarom Mahalli' is an Iranian variety of rice that was exposed to gamma radiation (230 Gy), and 11 rice lines having DT were picked at generation M4 (Hallajian *et al.*, 2014). Similarly, in Malaysia, two dominant lines ('MR219-9' and 'MR219-4') having DT and high yield traits were developed from common rice variety 'MR219' (Rahim *et al.*, 2012). Breeders are using this approach for introducing novel characters in rice cultivars.

Recurrent selection

This breeding method offers smaller breeding cycles, more accurate genetic improvements, and diverse breeding line development. This approach has been widely used in rice (Pang *et al.*, 2017), maize (Bolaños and Edmeades, 1993), and wheat (Rebetzke *et al.*, 2002). Pang *et al.* (2017) screened 12 DT lines using recurrent selection for higher grain yield. To sum up, this process's efficacy in improving agronomic characteristics and increasing DT, recurrent selection is more efficient than pedigree method. Recurrent selection methods have not been broadly useful in rice breeding experiments due to absence of male-sterility genes. Earlier scientists Reny *et al.* (2017) conducted research and evaluated 180 lines of rice for agronomic traits, result of recurrent selection at the seedling stage. They have selected 53 tolerant lines and concluded that selection of DT lines via recurrent selection would be more fruitful to improve DT in rice progenies. Singh *et al.* (2016) performed an experiment to assess the effect of recurrent selection on DT in wheat varieties. They have identified many tolerant lines showing higher yield and DT. Recurrent selection method along with some modifications like marker assisted recurrent selection method has been developed for improvement of DT in rice. An experiment was conducted in which population was developed using recurrent selection method for identification of QTL for DT in rice. Identified QTL enhanced yield of lines under drought stress which showed that use of marker assisted recurrent selection method is more useful than conventional method (Sandhu *et al.*, 2018).

With the advent of biotechnology, our awareness of plant reaction to drought at the entire plant and molecular level has steadily improved. Lots of genes showed expressions under drought stress were recognized, and some were cloned. Divergent strategies like the method of transgenic and gene expression is typically used to produce DT. Novel approaches like, proteomics, genome-wide association and stable isotopes helped to close the genotype-phenotype space. The key biotechnology methods are molecular biology and genetic manipulation that has resulted in the production of drought-resistant cultivars in rice. Generally, the development of genetic tolerance is a well-known and robust approach to decrease the influence of drought. These findings proved that the recurrent selection method along with some modifications could be used broadly for DT in rice.

Physiology and high throughout phenotyping

It is essential to develop techniques of screening that are simple, reproducible and predict success in targeted environments to classify causes of DT. Management of drought screening nurseries involves close consideration of the possible causes of non-genetic variability between plot, replication, repeated experiment, and protocol developed to mitigate these variables. Detailed knowledge of the spatial variation of various soil features within a field is important for enhancing phenotyping accuracy. New precision-farming devices and techniques can be used to monitor the soil using electrical and electromagnetic devices, depending on physical and chemical features (Adamchuk *et al.*, 2004). IRRI is now using such technologies (e.g., EM-38) to map the mechanical, physical, and chemical soil features of drought phenotyping fields at IRRI stations and multi-location selection sites in South Asia. The physiological processes of DT is still unclear, and only small portion of research is done in crop development by extreme stress plant survival approaches (Serraj and Sinclair, 2002). Process of dehydration avoidance is important as a technique to combat agricultural drought and sustain crop production. Kim *et al.* (2020) studied the high throughout phenotyping technique for DT in rice and concluded that this technique could be efficiently used for detection of tolerant and susceptible genotypes of rice.

For rice, the results gained from long term observations of drought stress at multiple sites showed that rainfed coastal rice is a drought avoider genotype. These cultivars showed maximum yield under drought and capable of sustaining good plant water status during the flowering and grain filling stage (Fukai *et al.*, 2009). IRRI uses many fields along with laboratory screening techniques for the phenotyping of germplasm of rice for drought tolerance with an emphasis on drought avoidance (Farooq *et al.*, 2010), including drip and line-source irrigation sprinkler systems (Centritto *et al.*, 2009), drained paddies and development of remote sensing techniques for irrigation, surveillance of field water status of plants (Jones *et al.*, 2009). Yoo *et al.* (2017) discovered a DT pathway OsPhyB in rice roots in response to drought stress. Detailed research work is required to define physiological causes in these screening techniques for variations in genotypic results and their relationship to drought tolerance's success under naturally occurring drought conditions of farmer's field. List of some drought-tolerant varieties of rice with different origin are shown in Table 3.

Table 3. List of some drought tolerant genotypes with diverse origins

Varieties	Origin	Subspecies	Drought index
Nephuong	Vietnam	Indica	1.89
Maniangu	China	Indica	1.62
IR45	Philippines	Indica	1.43
IAC1	Brazil	Japonica	1.34
IAC47	Nigeria	Japonica	1.15
LAC23	Liberia	Japonica	1.11
DINALAGA	Thailand	Japonica	1.06
CICA4	Colombia	Indica	1.04
AUS454	Bangladesh	Aus	1.88
Zhonghang 3	China	Indica	1.04
PR325	Puerto Rico	Indica	1.37

Molecular techniques for drought tolerance (DT)

The DT is a complex process; however, several QTL regulate the drought traits (Fleury *et al.*, 2010) have been identified. Plant response to drought stress is complicated and hard to recognize unless a deep investigation is directed towards the physiological and genetic background. Traditional and modern breeding techniques cannot effectively enhance DT in rice (Sinclair, 2011; Dormety *et al.*, 2020). The classical crop breeding approaches use old methods and routine natural processes that need broad field (Dormety *et al.*, 2020). Advancement in physiology, phenotyping, and genomics of plants resulted in novel findings in tolerance to drought. With the detection of these novel genes breeders will be able to increase yield under drought stress (Gosal *et al.*, 2009). The knowledge of plant physiology increases our understanding of the nature of the drought-tolerant system and its relationship to specific characteristics. Selection efficacy using molecular and genomic methods can contribute to the discovery of QTL. Selection efficacy using molecular and genomic methods can contribute to the discovery of QTL trait-linked genes. Identifying the genes of interest accountable for plant tolerance in response to diverse abiotic stresses is necessary for the development of transgenic genotypes with increased tolerance for drought (Gosal *et al.*, 2009). There are numerous new reviews published on molecular techniques (for reference, see Gouda *et al.*, 2020). The development of DT genotypes using advanced breeding methods, is shown in Figure 4.

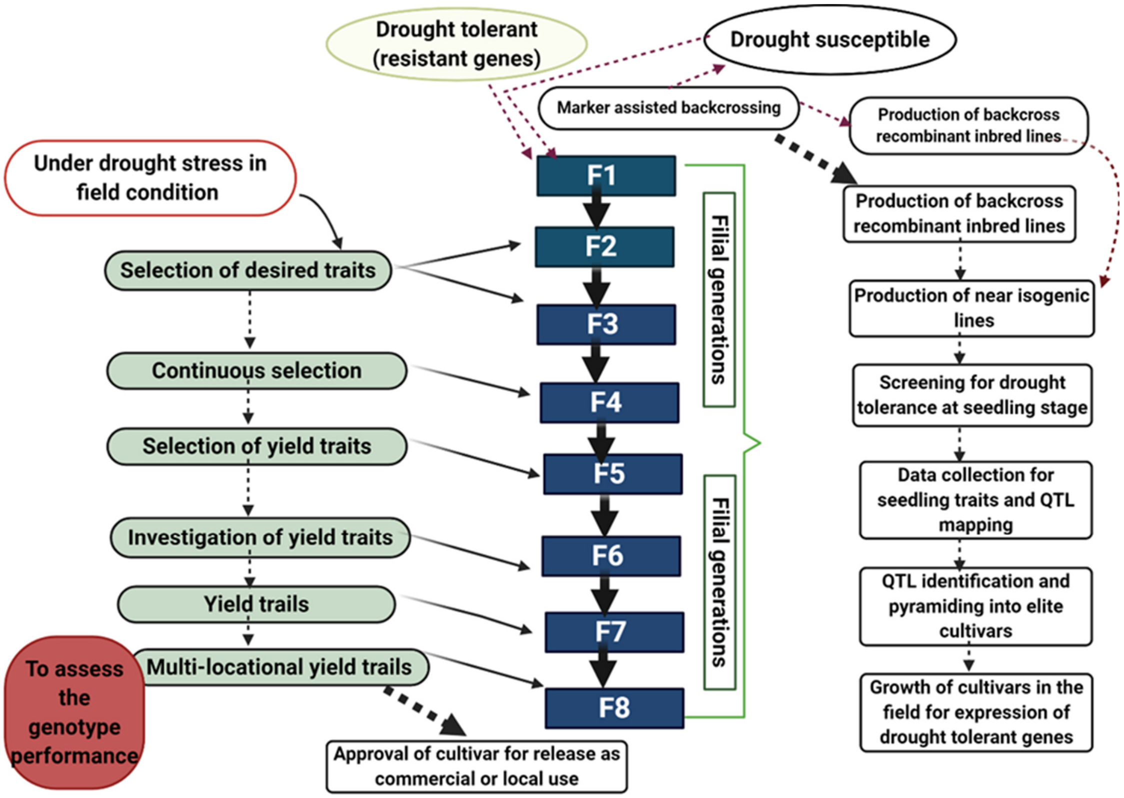

Figure 4. Development of drought-tolerant genotypes using advanced breeding methods mainly aims to develop varieties adapted to multiple environments, near isogenic lines, backcross recombinant inbred lines for sustainable rice production under water shortage conditions

Putative QTL for DT in rice

Identification of QTL regulating characteristics in drought stress requires a sequence of operations like mapping progenies in which desired characters associated with dehydration tolerance are separated; discovery of polymorphic markers, genotyping of the population with polymorphic markers; creation of linkage maps; precise phenotyping based on DT. Several mapping results have been reviewed regarding drought stress tolerance in many crops by (Sahebi *et al.*, 2018). Li *et al.* (2017) reported 262 QTL for root traits in rice mapping population under drought conditions. Mapping populations have several limitations such as, lack of heritability and association of genotype with the environment. For this reason, QTL mapping based on linkage analysis cannot give more precise information about the QTL position. These drawbacks include isolation of connected QTL for the same trait in various mapping populations and insufficient phenotypic variability for the mapping's desired trait (Liu *et al.*, 2012). Association mapping is the most effective mapping technique to overcome this difficulty. Cetolos *et al.* (2017) identified two QTL for seedling traits in rice mapping population under drought stress, which showed that these traits could minimize the effect of drought stress in rice. Sabar *et al.* (2019) identified two QTL for seedling traits and showed that these traits might be used to improve drought tolerance in rice. Yun *et al.* (2019) used RILs population and identified two QTL for shoot length and shoot dry weight under drought stress.

The benefits of association mapping over bi-parental association mapping include better accuracy due to recombination events in the evolutionary history of crop specie. This includes avoiding the development a particular specific population and using the crops with natural germplasm to reduce the time needed for QTL mapping. Several QTL linked to root and shoot based DT in rice are shown in Table 4. It uses genotypic data and group of association mapping to map QTL for complicated trait markers. This technique is cost-effective and more useful. This can also be used to eliminate the recombinant inbred lines (RIL) which are developed accidentally and showing an inadequate form of population structure and secondly, it can be used to analyse more alleles per locus compared to the sampling of the method (survey of just two alleles) (Rafalski, 2010).

Nevertheless, only a rare study has been reported for GY. The majority of the QTL in rice were defined based on a broad array of significant features comprising root and shoot reactions, osmotic modification, hormonal response, photosynthesis as well as DT at whole plant response. Table 5 shows the list of some QTL related to drought-related traits in rice.

Table 4. QTL for root and shoot traits under drought stress

Plant traits	Mapping population	Marker	Type	Genomic regions	References
Shoot length	M-203 × M-206	SNP	RILs	1	(Yun *et al.*, 2019)
Shoot dry weight	M-203 × M-206	SNP	RILs	1	
Root dry weight	Dular × IR62-21			1	(Cetolos *et al.*, 2017)
Root length	Dular × IR62-21			1	(Cetolos *et al.*, 2017)
Root parameters	IR1552 × Azucena	SSR	RILs	23	(Zheng *et al.*, 2003)
Deep roots	3 populations	SSR, SNP	RILs	6	(Lou *et al.*, 2015)
Osmotic adjustment	CT9993 × IR62266	RFLP	DH	5	(Zhang *et al.*, 2001)
Drought avoidance	Bala × Azucena	RFLP	RIL	17	(Price *et al.*, 2002b)
Grain yield heritability	CT9993 × IR62266	AFLP	DH	1	(Kumar *et al.*, 2007)
Grain yield over localities and years	Apo/2 × Swarna	SSR	RILs	1	(Venuprasad *et al.*, 2009)
Grain yield under drought	Two population	SSR	BS	18	(Vikram *et al.*, 2012)
Seedlings drought tolerance	Indica × Azucena	AFLP & SSR	RILs	7	(Zheng *et al.*, 2008)
Root length and thickness	IR58821 x IR52561	RFLP	RIL	28	(Ali *et al.*, 2000)

Table 5. QTL for some drought-related traits in rice

Trait	QTL	Chr	PVE%	Ref
Vegetative stage	*qTWU3-1*	3	9.96	(Sabar *et al.*, 2019)
Leaf area	*qLA3*	3	17.12	(Sabar *et al.*, 2019)
Root traits	264	1-12		(Li *et al.*, 2017)
Grain yield under drought stress	1(*qDTY2.3*)	2	9.0	(Palanog *et al.*, 2014)
Plant production	24	1,6	14 to 20.9	(Prince *et al.*, 2015)
Osmotic adjustment	1 (OA70)	8	Major	(Lilley *et al.*, 1996)
Drought avoidance	17	All excluding 9	1.2 to 18.5	(Price *et al.*, 2002b)
Panicle number /plant	14	All excluding 1, 3, 8	33.8	(Wang *et al.*, 2014)
1000-grain weight	21	All except 12	50.3	(Wang *et al.*, 2014)
Physio-morphological	9	4	36.8	(Prince *et al.*, 2015)
Grain yield	7	1, 2, 3, 9, 12	31-77	(Singh *et al.*, 2016)

QTL, quantitative traits loci: SSR, single sequence repeat: SNP, single nucleotide polymorphism: AFRLP, restriction fragment length polymorphism: AFLP, amplified fragment length polymorphism: RILs, recombinant inbredlines: DH, double haploid population: BS, bulk segregant: Ref, references.

Putative QTL for rice yield under drought stress

The grain yield of rice is a complex polygenic trait influenced by the environmental factors (Kumar *et al.*, 2017). Hence identification of QTL for yield under drought stress is always a primary objective of rice breeders. Numerous studies have been conducted under water-limited conditions in rice for significant and independent QTL linked to GY and its components. Some QTL have a positive effect on GY, but others negatively affect alleles acquired from female parent. The QTL, *qDTY12.1*, the first QTL with large effect, was identified for GY under drought stress conditions in a population of 436 random F3 lines from a cross between 'Vandana' and 'Way Rarem' upland rice cultivars (Mishra *et al.*, 2013). The recurrent parent Way Rarem contributed this QTL, and the other two QTL, *qDTY2.3* and *qDTY3* were shared by 'Vandana' parent. These genomic regions showed digenic interaction. From these findings, it was concluded that rice lines that have a mixture of these QTL showed more DT as compared to those who have individual (Dixit *et al.*, 2012). The QTL, *qDTY3.1* was recognized in a mapping population (BC1) of the high yielding lowland rice variety ('Swarna') and upland variety ('Apo') and QTL, *qDTY6.1* was mapped in high yielding lowland rice variety ('Swarna') and upland rice variety ('Apo'). These QTL have a complementary impact under conditions of drought stress (Dixit *et al.*, 2014). A large-scale experiment with F3 populations produced from crosses between drought-tolerant donor N22 and high-yielding mega-varieties 'Swarna', 'IR64', and 'MTU1010' identified one the most robust QTL, *qDTY1.1*, which had a significant impact on GY under drought (Vikram *et al.*, 2011). Sandhu *et al.* (2018) identified a yield QTL, *qDTY7-1* under drought stress in a pyramided population developed from a cross of recurrent selection and marker-assisted recurrent selection methods. Likewise, two primary yield-related QTL *qDTY2-2* and *qDTY3-1* were identified in Malaysian high-yielding rice variety significantly showed higher yield under drought stress (Sahmsudin *et al.*, 2016). Cetolos *et al.* (2017) identified two yield QTL, *qDTY8-1* and *qDTY3-1* in rice mapping population under drought stress, which showed improved population yields. Two significant genetic effects were reported, QTL, *qDTY8.1,* and *qDTY10.1,* in a population derived from a cross between 'Basmati 334'/ 'Swarna' (Vikram *et al.*, 2012) and 'Aday Sel'/*4 'IR64 BIL' (BP *et al.*, 2013). A list of some yield-related QTL detected under drought stress is given in Table 6.

Candidate genes for drought tolerance in rice

Plants have developed pathways for stress response by producing different proteins including transcriptional factors, enzymes, and molecular chaperones (Usman *et al.*, 2017). By using various genomic methods, numerous genes have been identified. In rice, these genes were inserted into the genome to study their effect on the improvement of drought by suppression and overexpression. Various transcription factors in rice encoded by *WRKY* genes regulate different biological processes. The zinc finger proteins are widely distributed in plants, particularly those that control stress responses. The *WRKY* genes have a positive or negative role in regulating plant reactions to numerous stresses (Sahebi *et al.*, 2018). Rice zinc-finger protein, for example, demonstrated increased drought and salt resistance by decreasing stomatal density and enhancing the closure of stomata. DST non-mutants, however, function adversely on the closure of stomata by altering homeostasis of H_2O_2 (Huang *et al.*, 2009). The overexpression of Zinc finger protein (*OsZFP252*) demonstrated 74 to 79% increase in survival by improving resistance to drought. It also enhances the concentration of soluble sugar and proline (Xu *et al.*, 2008). Sahebi *et al.* (2018) improved the DT in rice by identifying 89 genes and concluded that *WRKY* genes could be engineered to develop transgenic crops with DT.

Table 6. List of some yield-related QTL under drought stress in rice

QTL	Chr	Marker	Parent	Population	Trait	References
qDTY7-1	7		MAS × MARS	PLs	GY	(Sandhu *et al.*, 2018)
qDTY8-1	8		Dular IR62-21	Dular × IR62-21		(Cetolos *et al.*, 2017)
qDTY1-3	1		Dular IR62-21	Dular × IR62-21		(Cetolos *et al.*, 2017)
qDTY2-2	2			MRQ74 cultivar	GY	(Shamsudin *e/* al., 2016)
qDTY3-1	3			MRQ74 cultivar	GY	(Shamsudin *e/* al., 2016)
qgy3.1	33	RG348/ RM22–RZ329	CT9993-5-10-1-M × IR62266-42-6-2	DH	GY	(Lanceras *et al.*, 2004)
qgy4.3	4	RM120–RZ675/ RM274	CT9993-5-10-1-M × IR62266-42-6-2	DH	GY	(Lanceras *et al.*, 2004)
qDTY1.1	1	EM11–RG109	CT9993-5-10-1-M × IR62266-42-6-2	DH	GY	(Kumar *et al.*, 2007)
qGY-2b	2	RM526–RM525	Zhenshan 97B × IRAT109	RILs (F9)	GY	(Zou *et al.*, 2005)
qDTY12.1	12	RM201–RG667	Way Rarem × Vandana	F3 derived lines	GY	(Bernier *et al.*, 2007)
qGy10	10	RM242–RM278/ RZ12	Tequing × Lemont	BILs	GY	(Zhao *et al.*, 2008)
QDS_9.1	9	RM453–RM491	IR64 × IR77298-5-6-B-18(Aday Sel)	BILs (BC2F2:3)	GY	(BP *et al.*, 2013)
qDTY3.1	3	RM275–RM340	TDK1 × IR55419-04	BILs (BC1F3:4)	GY	(Dixit *et al.*, 2014)
qDTY6.1	6	RM168–RM468	TDK1 × IR55419-04	BILs (BC1F3:4)	GY	(Dixit *et al.*, 2014)
qPDL1.2	1	RM488–RM237	Appo × Moroberekan	BILs (BC1F3:4 And BC1F3:6)	GY	(Sellamuthu *et al.*, 2015)
qHI3	3	RM545–RM186	Appo × Moroberekan	BILs (BC1F3:4 andBC1F3:6)	GY	(Sellamuthu *et al.*, 2015)
qPSS8.1	2	RM547–RM978	IR64 × IRAT177	RILs(F6)	GY	(Trijatmiko *et al.*, 2014)
qGPP8.2	8	RM339–RM223	IR64 × IRAT177	RILs(F6)	GY	(Trijatmiko *et al.*, 2014)
qPN-6-2	6	RM589–RM402	Xiaobaijingzi×Kongyu 131	RILs(F2:7)	GY	(Xing *et al.*, 2014)
qDTY 3.4	3	RG191–RM546	Danteshwari× Dagaddeshi	RILs (F11)	GY	(Verma *et al.*, 2014)

The abundant late embryogenesis (LEA) proteins are mainly found in plants and contain many intrinsically unstructured proteins (IUPs). Throughout the maturation drying phase of embryo development, these minor proteins fluctuating from 10 to 30 kDa and act as chaperones (Yadira *et al.*, 2011). Drought causes a cellular water shortage that leads to the production of LLE proteins. Many studies confirmed that these proteins provided strong resistance against different water stress levels (Duan and Cai, 2012). *OsLEA3* in rice and improved DT in field conditions (Xiao *et al.*, 2007). A gene *HVA1*from barley was over-expressed in wheat and rice, increases water use efficiency and growth under drought (Sivamani *et al.*, 2000). LEA encoding gene *OsLEA3-1* in rice has been reported to play an essential role in controlling drought stress (Xiao *et al.*, 2007). Recently, *OsLEA3-2* over-expressed in rice also showed a strong drought resistance pattern, and yield loss was lower when compared with water sufficient situations (Duan and Cai, 2012). A lot of DT genes have been identified in rice. A list of some DT genes is given in Table 7. Likewise, Li *et al.* (2017) reported 11 root related genes contributing DT including *DRO1* and *OsPID*. In the same way Rahman *et al.* (2016) identified a DT gene *EcNAC67* for leaf and root trait. In trangeneic rice, the overexpression of *OsRD4* gene showed DT by controlling root traits (Ramanathan *et al.*, 2018).

Table 7. Candidate engineered genes for drought tolerance in rice

Function	Gene name	Promotor	Transformation	Phenotyping	Reference
Drought adoptive traits	*OsARD4*			Drought tolerance	(Ramanathan *et al.*, 2018)
Shoot and root growth	*SaVHAc1*		Agrobacterium	Drought tolerance	(Biradar *et al.*, 2018)
Hgih levels of proline	*OsGS1*		Agrobacterium	Drought tolerance	(James *et al.*, 2018)
Root related gene	*DRO1*			Tolerance to drought	(Li *et al.*, 2017)
Leaf related gene	*EcNAC67*				(Rahman *et al.*, 2016)
Scavenging of ROS	*OsSRO1c*	*Ubi1*	Agrobacterium	Tolerance to oxidative stress and regulation of stomatal closure	(You *et al.*, 2013)
Synthesis of proline	*P5CS*	*Act1*	Agrobacterium	Confrontation to salinity and water stress	(Su and Wu, 2004)
Digestion of amino acids	*OsOAT*	*Ubi1*	Agrobacterium	Increase in drought tolerance and seeds setting ratio	(You *et al.*, 2012)
Protoporphyrinogen oxidase	*PPO*	*Ubi1*	Agrobacterium	Decrease in oxidative stress and increase drought tolerance	(Phung *et al.*, 2011)
LEA protein gene	*OsLEA3-1*	*RiceLEA3-1*	Agrobacterium	Drought tolerance for grain yield in field circumstances	(Xiao *et al.*, 2007)
LEA protein gene	*HVA1*	*Actin 1*	Biolistic	Improved drought, salinity tolerance.	(Xu *et al.*, 1996)
LEA protein gene	*OsLEA3-2*	*CaMV35S*	Agrobacterium	Drought tolerance and enhance grains/panicle	(Duan and Cai, 2012)
Transcription factor (TF)	*DREB2*	*rd29A*	Agrobacterium	Enhanced grain yield over drought	(Bihani *et al.*, 2011)
TF	*OsbZIP72*	*CaMV35S*	Agrobacterium	Drought tolerance & sensitivity to ABA	(Lu *et al.*, 2009)
Jasmonate as well as ethylene responsive factor 1	*JERF1*	*CaMV35S*	Agrobacterium	Drought tolerance	(Zhang *et al.*, 2010)

The stability of membrane structure can be sustained by the accumulation of osmolytes. Several earlier studies showed that plants are more resistant to drought stress, which favours the process of osmotic adjustment (Ahmed *et al.*, 2009). The variations in the level of proline accumulated under drought and normal conditions have been reported in rice (Lum *et al.*, 2014). Proline plays three basic roles during stress, i.e. proline serves as a signalling molecule, antioxidant agent and involves in chelation of metals (Liang *et al.*, 2013). This amino acids accumulated in higher concentrations under drought stress and minimize the damage by increasing antioxidant activity (Fahramand *et al.*, 2014). Proline involves in scavenging of ROS and acts as an antioxidant agent. The maize plants under drought stress increase their proline level to maintain osmotic adjustment (Köşkeroğlu and Tuna, 2010). The concentration of the proline accumulation depends on level of water scarcity and plant species (Ahmed *et al.*, 2009). The proline can also be used as a marker to estimate the drought resistance in rice. In transgenic rice, overexpression of a proline gene (*P5CS*) showed significant development in DT (Zhu *et al.*, 1998). In brief, these findings demonstrated DT can be achieved by transformation of these genetic factors into elite rice genotypes.

Drought tolerance genes for rice, main crops, and model plants

Many candidate genes governing DT have been recognized in plants by genetic modelling (Sahebi *et al.*, 2018). The genomes of several model plants and higher plants have been sequenced (Feuillet *et al.*, 2011). The plant faces several abiotic stresses that lead to a decline in plant growth and ROS production (Begum *et al.*, 2019; Kosar *et al.*, 2020). Studies of genome annotation, functional genomics, and molecular biology were performed in multiple models crops to identify candidate genes involved in resistance to drought. These genes have been transferred into a population with a broad genetic base and conferred DT. Candidate genes can be confirmed by many methods, such as expression processing, qRT-PCR, integration into QTL maps, linkage modelling, and allele mining, and previously tested applications of these methods (Varshney *et al.*, 2005). Many transcriptomic and functional genomics studies have been performed in recent years, using several crops to investigate the drought stress mechanism. A popular method that isolates the candidate genes responsible for drought stress in drought-resistant genotypes is the production of transmitted sequence tags (ESTs) from (normalized or non-normalized) cDNA libraries of tissues collected under drought stress. To date, many crop plants have been reported having several drought-responsive genes. Therefore, the use of near-isogenic lines (NILs) will produce novel results because of the differentially expressed genes related to the targeted characters (Kulcheski *et al.*, 2011). There are various techniques for transcriptional profiling, including PCR-based differential view PCR (DDRT-PCR) (Liang and Pardee, 1992), cDNA-amplified fragment length polymorphism (cDNA-AFLP) (Bachem *et al.*, 1996), cDNA, and suppression subtractive hybridization (SSH) (Sahebi *et al.*, 2015). Li *et al.* (2019) transferred the gene *GME+GMP* into tomato and revealed that this gene increased the ascorbic acid contents in tomato conferred DT. In the same way another researcher, Fan *et al.* (2019) studied the function of engineered gene *SOS1+AHA1* in Arabidopsis and found a decrease in death rate of leaves under drought stress.

Super-serial gene expression analysis (super-SAGE) is another useful technique used successfully in different crops under stress conditions (Matsumura *et al.*, 2010). The generation sequencing (NGS) technology allows reliable automated and real-time analysis of sequence-based transcriptomes. Other approaches, such as microarrays, are likely to be replaced soon with NGS. The use of NGS in the study of gene expression has contributed to innovative techniques such as Deep SAGE (Nielsen *et al.*, 2006), Virtual Gene-TAG (DGE-TAG) (Nielsen *et al.*, 2008), and RNA-Seq (Nagalakshmi *et al.*, 2008). The transcriptional profile of drought resistant and susceptible cultivars may recognize candidate genes responsible for DT and may serve as "genic molecular markers" combined with genetic/QTL maps (Hiremath *et al.*, 2011). The findings of recent NGS (transcriptome) research on screening and defining novel genes involved in Malaysia's most drought tolerant variety of rice detected thousands of up and down-regulated novel genes involved in more than one hundred various pathways. Transcriptional NGS-based profiling would be used to recognize candidate genes of DT from major crop species and used in molecular breeding, genetics, and genomics. There are numerous genes discovered in many model plants for DT, however we have enlisted some of them in Table 8.

Table 8. List of some drought tolerance genes in rice, main crops, and some models' plants

Gene	Accession number	Model plants	Role	Reference
GME+GMP		Tomato	Increase ascorbic acid content	(Li *et al.*, 2019)
SOS1+AHA1		Arabidopsis	Reduce death rate of leaves	(Fan *et al.*, 2019)
AGO1	AT1G48410	Arabidopsis	Governing proteins, microRNAs	(Li *et al.*, 2012)
ABCG22	AT5G06530	Arabidopsis	transporters/Channles	(Kuromori *et al.*, 2011)
CIPK12	LOC Os01g55450	Rice	Regulatory Proteins and protein Kinases	(Xiang *et al.*, 2007)
CIPK03	LOC Os07g48760	Rice	Regulatory proteins and protein Kinases	(Xiang *et al.*, 2007)
CDPK7	LOC Os03g03660	Rice	Regulatory proteins and protein Kinases	(Saijo *et al.*, 2000)
CBF4	MLOC 54227	Barley	Regulatory Proteins and transcription factors	(Oh *et al.*, 2007)
BnPIP1	AT3G53420	Mustard	Ion and osmotic homeostasis	(Oh *et al.*, 2007)
CAP2	Solyc05g052410	Chickpea	Regulatory proteins	(Xiang *et al.*, 2007)
GbRLK	LOC Os04g56130	Cotton	Protein kinases	(Zhao *et al.*, 2013)
GhMKK1	Solyc12g009020	Cotton	Regulatory proteins	(Lu *et al.*, 2013)
GmERF3	Solyc06g063070	Soyabean	Transcription factors	(Zhang *et al.*, 2009)
GsZFP1	Glyma10g44160	Soyabean (Wild)	Zinc Fingers	(Tang *et al.*, 2013)
MIR168A	AT4G19395	Arabidopsis	Regulatory proteins	(Lee *et al.*, 2009)
CML9	AT3G51920	Arabidopsis	Signal transduction	(Jossier *et al.*, 2010)
AnnAt1	AT1G35720	Arabidopsis	Regulation of growth	(Konopka-Postupolska *et al.*, 2009)
ERD1	AT5G51070	Arabidopsis	Involved in detoxification	(Tran *et al.*, 2007)
DOR	AT2G31470	Arabidopsis	Stomatal movement	(Lu *et al.*, 2013)
HDA6	AT5G63110	Arabidopsis	Modification of histone	(Tang *et al.*, 2013)

Application of marker-assisted selection for drought tolerance in rice

Using marker-assisted selection rice breeders use genes markers to increase qualitative and quantitative traits against abiotic stress such as drought, besides observing these complex traits at a time (Dormatey *et al.*, 2020). Nevertheless, it is problematic to trace targeted genes' existence, restraining the selection of desired offspring's (Malav *et al.*, 2016). This technique is used to transfer genes (Shamsudin *et al.*, 2016), and it is preferred over classical breeding as the complexity of traits is enhanced using classical breeding. It is used with three main objectives, (i) to combine favourable alleles by finding beneficial alleles, either dominant/recessive; (ii) to segregate desired plants of breeding lines depending on the whole genome of an allelic arrangement (iii) to introgressed favourable alleles by breaking the undesirable linkage. The most robust and reliable modern breeding strategies include, marker-assisted pedigree selection, marker-assisted selection, genomic selection, and marker-assisted backcrossing (MABC). MABC is the most effective and commonly used approach from the methods stated above (Usman *et al.*, 2018). The transfer of a gene from a donor parent to the recurrent parent responsible for considerable phenotypic variation will indicate a significant increase in that trait using this method has three main advantages over other breeding methods like (i) it improves the precision and efficiency of selection for polygenic attributes due to selection of linked marker with the allele of male parent at a locus near to targeted gene (ii) it increases the rate of introgression of a gene from male to recurrent parent while it maintains the original characteristics of recurrent parent (iii) additional selfing is not required in this method during the transfer of recessive gene as compared to classical breeding methods. Quantitative genetics theory shows that MAS's efficiency is inversely proportional to the heritability of desired traits as proposed by (Knapp, 1998) and (Lande and Thompson, 1990). Predictably, breeders working with the classical phenotypic selection method need additional breeding material (1.0 to 16.t more.). In contrast, breeders practicing MAS need one or more elite genotypes based on the heritability of traits, as well as genotypic dominance. Hence, MAS's application will reduce the time and cost necessary to reach a target for heritable characters with low to moderate values. MAS is most consistent, environmentally sustainable, rapid, and economical technique of developing elite genotypes of rice having DT. Several QTL have been identified and transferred in rice to create DT genotypes using different breeding methods.

Worldwide approaches for investigating the genetics of DR in the areas with low rice yield

The molecular and physiological techniques have not proved very fruitful and enable us to revisit our strategy. These limitations can be addressed by use of newly developed genomic approaches. There are three critical approaches for increasing DT in rice and other crops: (i) selecting high yielding rice genotypes under water deficit conditions. This method has been largely used, and the outstanding morphology of new genotypes is an indication of success of this method. However, several studies have shown that these genotypes grain yield may not be enough to meet commercial needs (Dixit *et al.*, 2014). Study of rice physiological ideo-types under drought situation to increase output, the documentation of source of deviation for these traits to transfer into particular varieties is critical (Mir *et al.*, 2012). The use of carbon isotopes to screen elite genotypes with high water usage efficiency is highly endorsed, and the use of MAS to test for QTL, including beneficial DT alleles, may be fruitful. A complete pathway towards successful DT in rice by novel strategies is given in Figure 5.

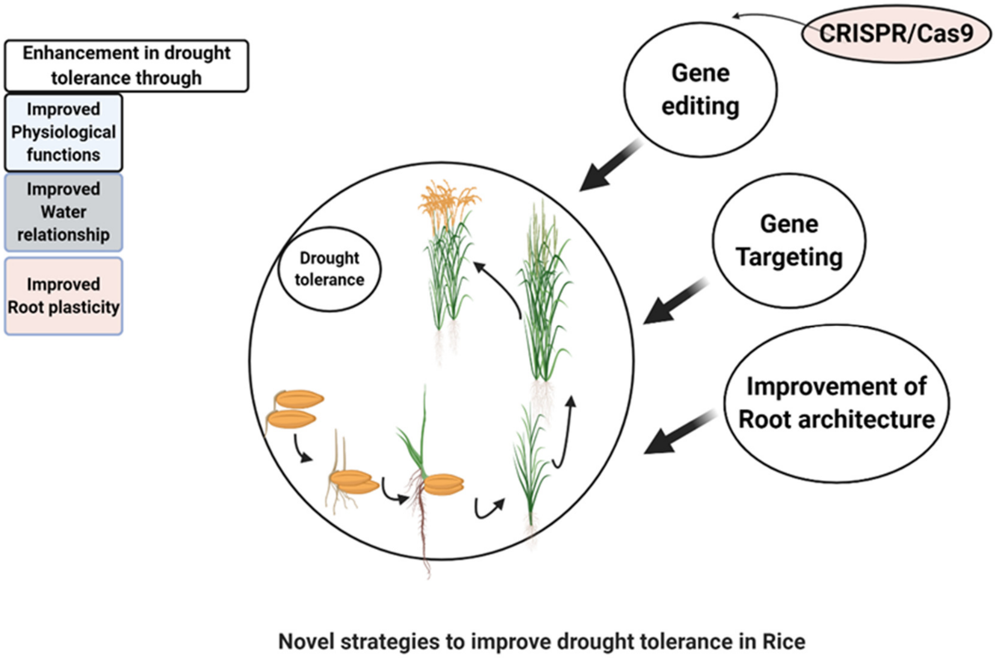

Figure 5. A complete pathway towards successful drought tolerance in rice by adopting gene editing, gene targeting, root architecture improvement, improvement of root plasticity to maintain rice production under drought stress conditions

Conclusions

DT is a very complex trait and to improve the DT, the investigation of the genetic basis of DT is essential. Environmental factors strongly influence the drought stress in the areas where rice is grown. Investigation of rice response to other abiotic factors like heat stress and salinity stress in very important to study the level of DT in rice. Screening of ideal mapping population is critical to identify the putative QTL and to dissect the gene of interest which could be transferred in the development of tolerant varieties. Recent studies on genomics demonstrate that detection of novel QTL, influencing DT makes it possible to use QTL pyramiding via marker-assisted selection for development of cultivars tolerant to drought stress. A lot of glasshouse studies have been conducted to identify genes but are not effective for the improvement of DT. Field trails should be conducted to check these genes stability before using them in any breeding scheme. Most of the studies on DT have been conducted using above ground parts so, studies can also be undertaken using below-ground parts. Therefore, root plasticity and architecture should be studied regarding DT, as they play a key role in closure of stomata and growth improvement under drought stress. Annotation of WRKY gene in rice may help to improve DT by transferring in elite cultivars. These genetic studies did not need the actual separation of plant reactions to drought circumstances and did not ponder on conditions of drought stress. Current studies in production of markers, genome sequencing, and genomic analysis have generated a way for reconsideration of the techniques of making suitable progenies and find, and genomic analysis has generated a way for reconsideration of the techniques of making suitable progenies and finding the actual factor behind drought tolerance. Rate limiting and costly phenotyping stage is a significant challenge to study DT in rice. Developing fast and cost-effective ways to identify the mechanisms of the drought response would boost the genetic resolution.

Improvement of drought DT can be achieved by QTL pyramiding, the development of near-isogenic lines, the use of backcross recombinant inbred lines (BRILs), and the adjustment of the root system to investigate the nature of drought stress. Role of plant hormones is not fully investigated and should be further studied for achieving novel results in DT. Effective management of field conditions can help to reduce drought stress in crops. Until now complete genetic understanding of DT is not understood. The use of CRISPR/Cas9 technique will be an ideal choice for targeted gene cloning to develop tolerant cultivars in rice. Use of newly developed novel technique, CRISP/Cas12 would be highly recommended for genetic editing to enhance DT. At the same time, we recommend that use of BRILs population could give more reliable results if we screen the lines for DT at seedling stage. It led to production of NILs which will be used to develop variety with complete fixation of desired traits. Use of hormones with different levels would give a slightly different results in a population tested for DT. We strongly recommend to conduct field experiments for DT instead of lab experiment as plants develop in green house could not face harsh environmental condition when tested in field. Transfer of gene from genetically divergent crops would increase the possibility of transfer of more alleles for DT. Genetic mechanism of DT is not fully understood, so more studies are required for comprehensive understanding of the genetic background of DT.

Prospects of drought tolerance

The use of classical breeding methods is not effective when compared to modern breeding approaches because they are time-consuming and costly. The accurate, efficient, and high throughput phenotyping has developed to find the restrictions of genotype-phenotype studies and it can be helpful in simultaneous selection of numerous genotypes. Plant genomics helps to bridge the gap among phenotyping and high-throughput marker recognition (Großkinsky *et al.*, 2015), thus helping in plant breeding targeting higher yield and abiotic stress tolerance (Yang *et al.*, 2013). In genetically different crops, drought response has been studied but only few studies have been conducted on genotypic variation in water use efficiency and drought tolerance. Use of genome editing technology has revolutionized the breeding program and started a new period of development of high tolerant varieties.

CRISPR/Cas9 is one of the best and novel gene editing techniques in plant breeding (Weeks *et al.*, 2016). This technique has high accuracy, adaptability and usability and it has been used broadly in many crops (Xu *et al.*, 2016). Rice response to drought stress has been improved due to over-expression of *OsNAC14* during the vegetative stage (Shim *et al.*, 2018). Likewise, field assessment exhibited that over-expression of

OsNAC14 in transgenic rice caused a higher grain filling rate and enhanced the number of panicles as compared to non-transgenic rice under drought stress. This study showed that *OsNAC14* gene induced by CRISPR-Cas9 technique directly governs the expression of *OsRAD51A1* and controls additional downstream genes for defence related DNA repair, and rice response to drought stress that together confirm DT in rice. The suitable methods for determining drought stress include peak stress and length of stress within a targeted area. In many experiments on drought stress, rice breeders and physiologists performed field evaluations of rice for phenotypic studies, whereas molecular biologists are focused on studies in glasshouse conditions. A fruitful DT method can be studied from biological, physiological and breeding perception of the individual plant species (Volaire *et al.*, 2014). Plant hormones like CK, auxin, GA, Prolines, polyamines, and ethylene could be used as biochemical indicators to improve drought tolerance in rice. The increase in the concentration of these hormones under drought stress would provide an initiative to develop tolerant cultivars to mitigate drought stress. Therefore, it is necessary to apply these hormones at a different concentration under different water deficit conditions. Here are some of the valuable tips which can be used to improve DT in rice (i) traits of interest should be aerial and root parts, mostly those that influence plant-water relationship (ii) several field experiments under drought stress should be conducted to judge if transgenic plants are capable of avoiding and tolerating dehydration conditions (iii) measurement of the rate of photosynthesis during drought stress is very critical and can be calculated to study their correlation with entire plant growth (iv) screening of rice genotypes should be done in laboratory to examine the level of DT in rice population to make effective selection based on data obtained after drought stress.

Authors' Contributions

AR conceptualized and prepared the draft; MUH and MA reviewed the manuscript; MB improved the scientific figures; SF has provided technical assistance; ZW supervised the study and HL provided funding.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

Rahim HA, Zarifth SK, Bhuiyan MAR, Narimah MK, Wickneswari R, Abdullah M, Abdullah MZ, … Rusli I (2012). Evaluation and characterization of advanced rice mutant line of rice (*Oryza sativa*), MR219-4 and MR219-9 under drought condition. R and D Seminar 2012: Research and Development Seminar 2012, Malaysia.

Abdula SE, Lee HJ, Ryu H, Kang KK, Nou I, Sorrells ME, Cho Y (2016). The overexpression of the BrCIPK1 gene enhances abiotic stress tolerance by increasing proline biosynthesis in rice. Plant Molecular Biology Reporter 34:501-511.

Adamchuk VI, Hummel J, Morgan M, Upadhyaya S (2004). On-the-go soil sensors for precision agriculture. Computers and Electronics in Agriculture 44:71-91. *https://doi.org/10.1016/j.compag.2004.03.002*

Ahmad P, Jamsheed S, Hameed A, Rasool S, Sharma I, Azooz M, Hasanuzzaman M (2014). Drought stress induced oxidative damage and antioxidants in plants. In: Oxidative damage to plants. Elsevier, pp 345-367.

Ahmed CB, Rouina BB, Sensoy S, Boukhris M, Abdallah FB (2009). Changes in gas exchange, proline accumulation and antioxidative enzyme activities in three olive cultivars under contrasting water availability regimes. Environmental and Experimental Botany 67:345-352. *https://doi.org/10.1016/j.envexpbot.2009.07.006*

Ali M, Pathan M, Zhang J, Bai G, Sarkarung S, Nguyen H (2000). Mapping QTLs for root traits in a recombinant inbred population from two indica ecotypes in rice. Theoretical and Applied Genetics 101:756-766. *https://doi.org/10.1007/s001220051541*

Ashraf M, Harris PJ (2013). Photosynthesis under stressful environments: an overview. Photosynthetica 51:163-190. *https://doi.org/10.1007/s11099-013-0021-6*

Atkinson NJ, Urwin PE (2012). The interaction of plant biotic and abiotic stresses: from genes to the field. Journal of Experimental Botany 63:3523-3543. *https://doi.org/10.1093/jxb/ers100*

Bachem CW, Van Der Hoeven RS, De Bruijn SM, Vreugdenhil D, Zabeau M, Visser RG (1996). Visualization of differential gene expression using a novel method of RNA fingerprinting based on AFLP: analysis of gene expression during potato tuber development. The Plant Journal 9:745-753. *https://doi.org/10.1046/j.1365-313x.1996.9050745.x*

Briglia N, Montanaro G, Petrozza A (2019). Drought phenotyping in *Vitis vinifera* using RGB and NIR imaging. Scientia Horticulturae 256:108555. *https://doi.org/10.1016/j.scienta.2019.108555*

Basnayake J, Fukai S, Ouk M (2006). Contribution of potential yield, drought tolerance and escape to adaptation of 15 rice varieties in rainfed lowlands in Cambodia. In: Proceedings of the Australian Agronomy Conference, Australian Society of Agronomy, Birsbane, Australia.

Bernier J, Kumar A, Ramaiah V, Spaner D, Atlin G (2007). A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. Crop Science 47:507-516. *https://doi.org/10.2135/cropsci2006.07.0495*

Begum N, Ahanger MA, Su Y, Lei Y, Mustafa NSA, Ahmad P, Zhang L (2019). Improved drought tolerance by AMF inoculation in maize (*Zea mays*) involves physiological and biochemical implications. Plants 8(12):579. *https://doi.org/10.3390/plants8120579*

Bihani P, Char B, Bhargava S (2011). Transgenic expression of sorghum DREB2 in rice improves tolerance and yield under water limitation. The Journal of Agricultural Science 149:95. *https://doi.org/10.1017/S0021859610000742*

Biradar H, Karan R, Subudhi PK (2018) Transgene pyramiding of salt responsive protein 3-1 (sasrp3-1) and savhac1 from spartina alterniflora l. enhances salt tolerance in rice. Frontiers in Plant Sciences 9(7):1-14. *https://doi.org/10.3389/fpls.2018.01304*

Bolaños J, Edmeades G (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. Field Crops Research 31:253-268. *https://doi.org/10.1016/0378-4290(93)90064-T*

BP MS, Ahmed HU, Henry A, Mauleon R, Dixit S, Vikram P, ... Mandal NP (2013). Genetic, physiological, and gene expression analyses reveal that multiple QTL enhance yield of rice mega-variety IR64 under drought. PloS One 8:e62795. *https://doi.org/10.1371/journal.pone.0062795*

Capell T, Bassie L, Christou P (2004). Modulation of the polyamine biosynthetic pathway in transgenic rice confers tolerance to drought stress. Proceedings of the National Academy of Sciences 101:9909-9914. *https://doi.org/10.1073/pnas.0306974101*

Centritto M, Lauteri M, Monteverdi MC, Serraj R (2009). Leaf gas exchange, carbon isotope discrimination, and grain yield in contrasting rice genotypes subjected to water deficits during the reproductive stage. Journal of Experimental Botany 60:2325-2339. *https://doi.org/10.1093/jxb/erp123*

Chapin III FS (1991) Integrated responses of plants to stress: a centralized system of physiological responses. Bioscience 41:29-36. *https://doi.org/10.2307/1311538*

Courtois B, McLaren G, Sinha P, Prasad K, Yadav R, Shen L (2000). Mapping QTLs associated with drought avoidance in upland rice. Molecular Breeding 6:55-66. *https://doi.org/10.1023/A:1009652326121*

Catolos M, Sandhu N, Dixit S, Shamsudin NAA, Naredo MEB, McNally KL, … Kumar A (2017). Genetic loci governing grain yield and root development under variable rice cultivation conditions. Frontiers in Plant Sciences *https://doi.org/10.3389/fpls.2017.01763*

Cramer MD, Hawkins HJ, Verboom GA (2009). The importance of nutritional regulation of plant water flux. Oecologia 161:15-24. *https://doi.org/10.1007/s00442-009-1364-3*

Chun SC, Paramasivan M, Chandrasekaran M (2018). Proline accumulation is influenced by the osmotic stress in arbuscular mycorrhizal symbiotic association with plants. Frontiers in Microbiology 29. *https://doi.org/10.3389/fmicb.2018.02525*

Daszkowska-Golec A, Szarejko I (2013). Open or close the gate–stomata action under the control of phytohormones in drought stress conditions. Frontiers in Plant Science 4:138. *https://doi.org/10.3389/fpls.2013.00138*

Dormatey R, Sun C, Ali K, Coulter JA, Bi Z, Bai J (2020) Gene pyramiding for sustainable Crop improvement against biotic and abiotic stresses. Agronomy 10(9):1255. *https://doi.org/10.3390/agronomy10091255*

Dien DC, Mochizuki T, Yamakawa T (2019). Effect of various drought stresses and subsequent recovery on proline, total soluble sugar and starch metabolisms in rice (*Oryza sativa* L.) varieties. Plant Production Science 22:530-545. *https://doi.org/10.1080/1343943X.2019.1647787*

Dixit S Singh A, Kumar A (2014). Rice breeding for high grain yield under drought: a strategic solution to a complex problem. International Journal of Agronomy 2014:1-16. *https://doi.org/10.1155/2014/863683*

Dixit S, Swamy BM, Vikram P, Bernier J, Cruz MS, Amante M, … Kumar A (2012). Increased drought tolerance and wider adaptability of qDTY 12.1 conferred by its interaction with qDTY 2.3 and qDTY 3.2. Molecular Breeding 30:1767-1779.

Duan J, Cai W (2012). OsLEA3-2, an abiotic stress induced gene of rice plays a key role in salt and drought tolerance. PLoS One 7:e45117. *https://doi.org/10.1371/journal.pone.0045117*

Fahramand M, Mahmoody M, Keykha A, Noori M, Rigi K (2014). Influence of abiotic stress on proline, photosynthetic enzymes and growth. International Research Journal of Applied and Basic Sciences 8:257-265.

Farooq M, Kobayashi N, Ito O, Wahid A, Serraj R (2010). Broader leaves result in better performance of indica rice under drought stress. Journal of Plant Physiology 167:1066-1075. *https://doi.org/10.1016/j.jplph.2010.03.003*

Feuillet C, Leach JE, Rogers J, Schnable PS, Eversole K (2011). Crop genome sequencing: lessons and rationales. Trends in Plant Science 16:77-88. *https://doi.org/10.1016/j.tplants.2010.10.005*

Fleury D, Jefferies S, Kuchel H, Langridge P (2010). Genetic and genomic tools to improve drought tolerance in wheat. Journal of Experimental Botany 61:3211-3222. *https://doi.org/10.1093/jxb/erq152*

Fukai S, Basnayake J, Makara O (2009). Drought resistance characters and variety development for rainfed lowland rice in Southeast Asia. In: Drought frontiers in rice: crop improvement for increased rainfed production. World Scientific pp 75-89.

Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, Ihsan MZ (2017). Crop production under drought and heat stress: Plant responses and management options. Frontiers in Plant Sciences 8:1147. *https://doi.org/10.3389/fpls.2017.01147*

Fan Y, Yin X, Xie Q, Xia Y, Wang Z, Song J, Jiang X (2019). Co-expression of SpSOS1 and SpAHA1 in transgenic *Arabidopsis* plants improves salinity tolerance. BMC Plant Biology 19(1):1-13. *https://doi.org/10.1186/s12870-019-1680-7*

Fukao T, Xu K, Ronald PC, Bailey-Serres J (2006). A variable cluster of ethylene response factor–like genes regulates metabolic and developmental acclimation responses to submergence in rice. The Plant Cell 18:2021-2034. *https://doi.org/10.1105/tpc.106.043000*

Gosal SS, Wani SH, Kang MS (2009). Biotechnology and drought tolerance. Journal of Crop Improvement 23:19-54. *https://doi.org/10.1080/15427520802418251*

Gouda G, Gupta MK, Donde R, Mohapatra T, Vadde R, Behera L (2020). Marker-assisted selection for grain number and yield-related traits of rice (*Oryza sativa* L.). Physiology and Molecular Biology of Plants 26(5):885. *https://doi.org/10.1007/s12298-020-00773-7*

Großkinsky DK, Svensgaard J, Christensen S, Roitsch T (2015). Plant phenomics and the need for physiological phenotyping across scales to narrow the genotype-to-phenotype knowledge gap. Journal of Experimental Botany 66:5429-5440. *https://doi.org/10.1093/jxb/erv345*

Hallajian M, Ebadi A, Mohammadi M, Muminjanov H, Jamali S, Aghamirzaei M (2014). Integration of mutation and conventional breeding approaches to develop new superior drought-tolerant plants in rice (*Oryza sativa*). Annual Research & Review in Biology 1173-1186. *https://doi.org/10.9734/ARRB/2014/5935*

Hassan MU, Muhammad A, Muhammad UC, Tang H, Babar S, Lorenzo B, Muhammad N, Adnan R, Aniqa A, Ying L, Huang G. (2020). The critical role of zinc in plants facing the drought stress. Agriculture 10:396. *https://doi.org/10.3390/agriculture10090396*

Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A (2012). Role of proline under changing environments: a review. Plant Signaling and Behavior 7:1456-1466. *https://doi.org/10.4161/psb.21949*

Heuer B (2010). Role of proline in plant response to drought and salinity. Handbook of plant and crop stress. CRC Press, Boca Raton pp 213-238.

Hussain HA, Hussain S, Khaliq A, Ashraf U, Anjum SA, Men S, Wang L (2018). Chilling and drought stresses in crop plants: Implications, cross talk, and potential management opportunities. Frontiers in Plant Science 9:393. *https://doi.org/10.3389/fpls.2018.00393*

Hijmans RJ, Serraj R (2009). Modeling spatial and temporal variation of drought in rice production. In: Drought frontiers in rice: Crop improvement for increased rainfed production. World Scientific pp 19-31.

Hadiarto T, Tran LSP (2010). Progress studies of drought-responsive genes in rice. Plant Cell Reports 30(3):297-310. *https://doi.org/10.1007/s00299-010-0956-z*

Hiremath PJ, Farmer A, Cannon SB, Woodward J, Kudapa H, Tuteja R, ... Gujaria N (2011). Large-scale transcriptome analysis in chickpea (*Cicer arietinum* L.), an orphan legume crop of the semi-arid tropics of Asia and Africa. Plant Biotechnology Journal 9:922-931. *https://doi.org/10.1111/j.1467-7652.2011.00625.x*

Hu C, Delauney AJ, Verma D (1992). A bifunctional enzyme (delta 1-pyrroline-5-carboxylate synthetase) catalyzes the first two steps in proline biosynthesis in plants. Proceedings of the National Academy of Sciences 89:9354-9358. *https://doi.org/10.1073/pnas.89.19.9354*

Hu H, Xiong L (2014). Genetic engineering and breeding of drought-resistant crops. Annual Review of Plant Biology 65:715-741. *https://doi.org/10.1146/annurev-arplant-050213-040000*

Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX (2009). A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. Genes and Development 23:1805-1817. *https://doi.org/10.1101/gad.1812409*

Iqbal MS, Akhilesh Singh K, Ansari MI (2020). Effect of drought stress on crop production. New Frontiers in Stress Management for Durable Agriculture pp 35-47.

Islam MT (2017). Effect of drought stress at different growth stages on yield and yield components of six rice (*Oryza sativa* L.) genotypes. Fundamental and Applied Agriculture 2:285-289. *https://doi.org/10.5455/faa.277118*

James D, Borphukan B, Fartyal D, Ram B, Singh J, Manna M, Reddy MK (2018) Concurrent overexpression of OsGS1;1 and OsGS2 genes in transgenic rice (*Oryza sativa* L.): Impact on tolerance to abiotic stresses. Frontiers in Plant Sciences 9:1-19. *https://doi.org/10.3389/fpls.2018.00786*

Ji X, Dong B, Shiran B, Talbot MJ, Edlington JE, Hughes T, ... Dolferus R (2011). Control of abscisic acid catabolism and abscisic acid homeostasis is important for reproductive stage stress tolerance in cereals. Plant Physiology 156:647-662. *https://doi.org/10.1104/pp.111.176164*

Jones HG, Serraj R, Loveys BR, Xiong L, Wheaton A, Price AH (2009). Thermal infrared imaging of crop canopies for the remote diagnosis and quantification of plant responses to water stress in the field. Functional Plant Biology 36:978-989. *https://doi.org/10.1071/FP09123*

Jossier M, Kroniewicz L, Dalmas F, Le Thiec D, Ephritikhine G, Thomine S, ... Leonhardt N (2010). The *Arabidopsis* vacuolar anion transporter, AtCLCc, is involved in the regulation of stomatal movements and contributes to salt tolerance. The Plant Journal 64:563-576. *https://doi.org/10.1111/j.1365-313X.2010.04352.x*

Kandowangko NY, Suryatmana G, Nurlaeny N, Simanungkalit RDM (2009). Proline and abscisic acid content in droughted corn plant inoculated with Azospirillum sp. and Arbuscular mycorrhizae fungi. HAYATI Journal of Biosciences 16:15-20.

Kato Y, Abe J, Kamoshita A, Yamagishi J (2006). Genotypic variation in root growth angle in rice (*Oryza sativa* L.) and its association with deep root development in upland fields with different water regimes. Plant and Soil 287:117-129. *https://doi.org/10.1007/s11104-006-9008-4*

Kosar F, Akram NA, Ashraf M, Ahmad A, Alyemeni MN, Ahmad P (2020). Impact of exogenously applied trehalose on leaf biochemistry, achene yield and oil composition of sunflower under drought stress. Physiology of Plants *https://doi.org/10.1111/ppl.13155*

Khan A, Pan X, Najeeb U, Tan DKY, Fahad S, Zahoor R, Luo H (2018). Coping with drought: stress and adaptive mechanisms, and management through cultural and molecular alternatives in cotton as vital constituents for plant stress resilience and fitness. Biological Research 47:1-17. *https://doi.org/10.1186/s40659-018-0198-z*

Kim Y, Chung, YS, Lee E, Tripathi P, Heo S, Kim KH (2020). Root response to drought stress in rice (*Oryza sativa* L.). International Journal of Molecular Sciences 21:1-22. *https://doi.org/10.3390/ijms21041513*

Kim SL, Kim N, Lee H, Lee E, Cheon KS, Kim M, … Kim KH (2020). High-throughput phenotyping platform for analyzing drought tolerance in rice. Planta 252:38. *https://doi.org/10.1007/s00425-020-03436-9*

Khush GS (1984). IRRI breeding program and its worldwide impact on increasing rice production. In: Gene manipulation in plant improvement. Springer pp 61-94.

Knapp SJ (1998). Marker-assisted selection as a strategy for increasing the probability of selecting superior genotypes. Crop Science 38:1164-1174. *https://doi.org/10.2135/cropsci1998.0011183X003800050009x*

Kohli A, Sreenivasulu N, Lakshmanan P, Kumar PP (2013). The phytohormone crosstalk paradigm takes center stage in understanding how plants respond to abiotic stresses. Plant Cell Reports 32:945-957. *https://doi.org/10.1007/s00299-013-1461-y*

Konopka-Postupolska D, Clark G, Goch G, Debski J, Floras K, Cantero A, … Hennig J (2009). The role of annexin 1 in drought stress in *Arabidopsis*. Plant Physiology 150:1394-1410. *https://doi.org/10.1104/pp.109.135228*

Köşkeroğlu S, Tuna AL (2010). The investigation on accumulation levels of proline and stress parameters of the maize (*Zea mays* L.) plants under salt and water stress. Acta Physiologiae Plantarum 32:541-549. *https://doi.org/10.1007/s11738-009-0431-z*

Kulcheski FR, de Oliveira LF, Molina LG, Almerão MP, Rodrigues FA, Marcolino J, … Marcelino-Guimarães FC (2011). Identification of novel soybean microRNAs involved in abiotic and biotic stresses. BMC genomics 12:307. *https://doi.org/10.1186/1471-2164-12-307*

Kumar A, Basu S, Ramegowda V, Pereira A (2017). Mechanisms of drought tolerance in rice. Burleigh Dodds Science Publishing Limited 131-63. *https://doi.org/10.19103/AS.2106.0003.08*

Kumar A, Bernier J, Verulkar S, Lafitte H, Atlin G (2008). Breeding for drought tolerance: direct selection for yield, response to selection and use of drought-tolerant donors in upland and lowland-adapted populations. Field Crops Research 107:221-231. *https://doi.org/10.1016/j.fcr.2008.02.007*

Kumar R, Venuprasad R, Atlin G (2007). Genetic analysis of rainfed lowland rice drought tolerance under naturally-occurring stress in eastern India: heritability and QTL effects. Field Crops Research 103:42-52. *https://doi.org/10.1016/j.fcr.2007.04.013*

Kuromori T, Sugimoto E, Shinozaki K (2011). *Arabidopsis* mutants of AtABCG22, an ABC transporter gene, increase water transpiration and drought susceptibility. The Plant Journal 67:885-894. *https://doi.org/10.1111/j.1365-313X.2011.04641.x*

Lafitte H, Li Z, Vijayakumar C, Gao Y, Shi Y, Xu J, … Domingo J (2006). Improvement of rice drought tolerance through backcross breeding: evaluation of donors and selection in drought nurseries. Field Crops Research 97:77-86. *https://doi.org/10.1016/j.fcr.2005.08.017*

Lafitte H, Yongsheng G, Yan S, Li Z (2007). Whole plant responses, key processes, and adaptation to drought stress: the case of rice. Journal of Experimental Botany 58:169-175. *https://doi.org/10.1093/jxb/erl101*

Lanceras JC, Pantuwan G, Jongdee B, Toojinda T (2004). Quantitative trait loci associated with drought tolerance at reproductive stage in rice. Plant Physiology 135:384-399. *https://doi.org/10.1104/pp.103.035527*

Lande R, Thompson R (1990). Efficiency of marker-assisted selection in the improvement of quantitative traits. Genetics 124:743-756.

Lee SJ, Kang JY, Kim SY (2009). An ARIA-interacting AP2 domain protein is a novel component of ABA signaling. Molecules and Cells 27:409-416. *https://doi.org/10.1007/s10059-009-0058-3*

Li W, Cui X, Meng Z, Huang X, Xie Q, Wu H, … Liang W (2012). Transcriptional regulation of *Arabidopsis* MIR168a and argonaute1 homeostasis in abscisic acid and abiotic stress responses. Plant Physiology 158:1279-1292. *https://doi.org/10.1104/pp.111.188789*

Li ZK, Xu JL (2007). Breeding for drought and salt tolerant rice (*Oryza sativa* L.): progress and perspectives. In: Advances in molecular breeding toward drought and salt tolerant crops. Springer pp 531-564.

Li X, Guo Z, LV Y, Cen X, Ding X, Wu H, Li X, Huang J, Xiong L (2017). Genetic control of the root system in rice under normal and drought stress conditions by genome-wide association study. PLoS Genetics 1:24. *https://doi.org/10.1371/journal.pgen.1006889*

Li X, Ye J, Munir S, Yang T, Chen W, Liu G, Zhang Y (2019). Biosynthetic gene pyramiding leads to ascorbate accumulation with enhanced oxidative stress tolerance in tomato. International Journal of Molecular Sciences 20(7):1-17. *https://doi.org/10.3390/ijms20071558*

Liang C, Wang Y, Zhu Y, Tang J, Hu B, Liu L, Ou S, Wu H, Sun X, Chu J (2014). OsNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. Proceedings of the National Academy of Sciences 111:10013-10018. *https://doi.org/10.1073/pnas.1321568111*

Liang P, Pardee AB (1992). Differential display of eukaryotic messenger RNA by means of the polymerase chain reaction. Science 257:967-971. *https://doi.org/10.1126/science.1354393*

Liang X, Zhang L, Natarajan SK, Becker DF (2013). Proline mechanisms of stress survival. Antioxidants & Redox Signaling 19:998-1011. *https://doi.org/10.1089/ars.2012.5074*

Lilley J, Ludlow M, McCouch S, O'Toole J (1996). Locating QTL for osmotic adjustment and dehydration tolerance in rice. Journal of Experimental Botany 47:1427-1436.

Liu W, Reif JC, Ranc N, Della Porta G, Würschum T (2012). Comparison of biometrical approaches for QTL detection in multiple segregating families. Theoretical and Applied Genetics 125:987-998. *https://doi.org/10.1007/s00122-012-1889-4*

Lou Q, Chen L, Mei H, Wei H, Feng F, Wang P, Xia H, Li T, Luo L (2015). Quantitative trait locus mapping of deep rooting by linkage and association analysis in rice. Journal of Experimental Botany 66:4749-4757. *https://doi.org/10.1093/jxb/erv246*

Lu G, Gao C, Zheng X, Han B (2009). Identification of OsbZIP72 as a positive regulator of ABA response and drought tolerance in rice. Planta 229:605-615. *https://doi.org/10.1007/s00425-008-0857-3*

Lu W, Chu X, Li Y, Wang C, Guo X (2013). Cotton GhMKK1 induces the tolerance of salt and drought stress, and mediates defence responses to pathogen infection in transgenic *Nicotiana benthamiana*. PLoS One 8:e68503. *https://doi.org/10.1371/journal.pone.0068503*

Lum M, Hanafi M, Rafii Y, Akmar A (2014). Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice. Journal of Animal and Plant Sciences 24:1487-1493.

Matsumura H, Yoshida K, Luo S, Kimura E, Fujibe T, Albertyn Z, ... Schroth GP (2010). High-throughput SuperSAGE for digital gene expression analysis of multiple samples using next generation sequencing. PloS One 5:e12010.

Miah G, Rafii M, Ismail M, Puteh A, Rahim H, Asfaliza R, Latif M (2013). Blast resistance in rice: a review of conventional breeding to molecular approaches. Molecular Biology Reports 40:2369-2388. *https://doi.org/10.1007/s11033-012-2318-0*

Moonmoon S, Islam MDT (2017). Effect of drought stress at different growth stages on yield and yield components of six rice (*Oryza sativa* L.) genotypes. Fundamental and Applied Agriculture 2(3):1. *https://doi.org/10.5455/faa.277118*

Malav AK, Chandrawat I, Chandrawat KS (2016). Gene pyramiding: an overview. International Journal of Current Research in Bioscience and Plant Biology 3:22-28. *http://dx.doi.org/10.20546/ijcrbp.2016.307.004*

Thalmann M, Pazmino D, Seung D, Horrer D (2016). Regulation of leaf starch degradation by abscisic acid is important for osmotic stress tolerance in plants. The Plant Cell 28(8). *htpps://doi.org/10.1105/tpc.16.00143*

Miao Y, Lv D, Wang P, Wang XC, Chen J, Miao C, Song C-P (2006). An Arabidopsis glutathione peroxidase functions as both a redox transducer and a scavenger in abscisic acid and drought stress responses. The Plant Cell 18:2749-2766. *https://doi.org/10.1105/tpc.106.044230*

Mir RR, Zaman-Allah M, Sreenivasulu N, Trethowan R, Varshney RK (2012). Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. Theoretical and Applied Genetics 125:625-645. *https://doi.org/10.1007/s00122-012-1904-9*

Mishra KK, Vikram P, Yadaw RB, Swamy BM, Dixit S, Cruz MTS, ... Kumar A (2013). qDTY 12. 1: a locus with a consistent effect on grain yield under drought in rice. BMC Genetics 14:12. *https://doi.org/10.1186/1471-2156-14-12*

Mitra J (2001). Genetics and genetic improvement of drought resistance in crop plants. Current Science 758-763. *https://www.jstor.org/stable/24105661*

Miyan MA (2015). Droughts in Asian least developed countries: Vulnerability and sustainability. Weather and Climate Extremes 7:8-23. *https://doi.org/10.1016/j.wace.2014.06.003*

Nagalakshmi U, Wang Z, Waern K, Shou C, Raha D, ... Snyder M (2008). The transcriptional landscape of the yeast genome defined by RNA sequencing. Science 320:1344-1349. *https://doi.org/10.1126/science.1158441*

Nahar S, Kalita J, Sahoo L, Tanti B (2016). Morphophysiological and molecular effects of drought stress in rice. Annals of Plant Science 5:1409-1416. *https://doi.org/10.21746/aps.2016.09.001*

Nguyen T, Klueva N, Chamareck V, Aarti A, Magpantay G, Millena A, ... Nguyen H (2004). Saturation mapping of QTL regions and identification of putative candidate genes for drought tolerance in rice. Molecular Genetics and Genomics 272:35-46. *https://doi.org/10.1007/s00438-004-1025-5*

Nielsen KL, Høgh AL, Emmersen J (2006). DeepSAGE-digital transcriptomics with high sensitivity, simple experimental protocol and multiplexing of samples. Nucleic Acids Research 34:e133-e133. *https://doi.org/10.1093/nar/gkl714*

Nielsen KL, Petersen AH, Emmersen J (2008). DeepSAGE-tag based transcriptome analysis beyond microarrays. In: Next Generation Genome Sequencing-Towards Personalized Medicine. Wiley-VCH.

Ntuli T (2012). Drought and desiccation-tolerance and sensitivity in plants, botany. Tech, Rijeka, Croatia

Oh SJ, Kwon CW, Choi DW, Song SI, Kim JK (2007). Expression of barley HvCBF4 enhances tolerance to abiotic stress in transgenic rice. Plant Biotechnology Journal 5:646-656. *https://doi.org/10.1111/j.1467-7652.2007.00272.x*

Oladosu Y, Rafii M, Abdullah N, Abdul Malek M, Rahim H, Hussin G, ... Kareem I (2014). Genetic variability and selection criteria in rice mutant lines as revealed by quantitative traits. The Scientific World Journal. *https://doi.org/10.1155/2014/190531*

Oladosu Y, Rafii MY, Abdullah N, Hussin G, Ramli A, Rahim HA, ... Usman M (2016). Principle and application of plant mutagenesis in crop improvement: a review. Biotechnology & Biotechnological Equipment 30:1-16. *https://doi.org/10.1080/13102818.2015.1087333*

Oladosu Y, Rafii MY, Abdullah N, Malek MA, Rahim HA, Hussin G, ... Kareem I (2015). Genetic variability and diversity of mutant rice revealed by quantitative traits and molecular markers. Agrociencia 49:249-266.

Oladosu Y, Rafii MY, Samuel C, Fatai A, Magaji U, Kareem I, ... Kolapo K (2019). Drought resistance in rice from conventional to molecular breeding: a review. International Journal of the Molecular Sciences 20:3519. *https://doi.org/10.3390/ijms20143519*

Ozga JA, Kaur H, Savada RP, Reinecke DM (2017). Hormonal regulation of reproductive growth under normal and heat-stress conditions in legume and other model crop species. Journal of Experimental Botany 68:1885-1894.

Palanog AD, Swamy BM, Shamsudin NAA, Dixit S, Hernandez JE, Boromeo TH, ... Kumar A (2014). Grain yield QTLs with consistent-effect under reproductive-stage drought stress in rice. Field Crops Research 161:46-54. *https://doi.org/10.3390/plants8060186*

Pan S, Rasul F, Li W, Tian H, Mo Z, Duan M, Tang X (2013). Roles of plant growth regulators on yield, grain qualities and antioxidant enzyme activities in super hybrid rice (*Oryza sativa* L.). Rice 6:9. *https://doi.org/10.1186/1939-8433-6-9*

Pandey V, Shukla A (2015). Acclimation and tolerance strategies of rice under drought stress. Rice Science 22:147-161. *https://doi.org/10.1016/j.rsci.2015.04.001*

Pang Y, Chen K, Wang X, Xu J, Ali J, Li Z (2017). Recurrent selection breeding by dominant male sterility for multiple abiotic stresses tolerant rice cultivars. Euphytica 213:268. *https://doi.org/10.1007/s10681-017-2055-5*

Pantuwan G, Fukai S, Cooper M, Rajatasereekul S, O'toole J (2002). Yield response of rice (*Oryza sativa* L.) genotypes to drought under rainfed lowland: 3. Plant factors contributing to drought resistance. Field Crops Research 73:181-200. *https://doi.org/10.1016/S0378-4290(01)00195-2*

Peleg Z, Blumwald E (2011). Hormone balance and abiotic stress tolerance in crop plants. Current Opinion in Plant Biology 14:290-295. *https://doi.org/10.1016/j.pbi.2011.02.001*

Peleg Z, Reguera M, Tumimbang E, Walia H, Blumwald E (2011). Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. Plant Biotechnology Journal 9:747-758. *https://doi.org/10.1111/j.1467-7652.2010.00584.x*

Perata P, Voesenek LA (2007). Submergence tolerance in rice requires Sub1A, an ethylene-response-factor-like gene. Trends in Plant Science 12:43-46. *https://doi.org/10.1016/j.tplants.2006.12.005*

Phung TH, Jung HI, Park JH, Kim JG, Back K, Jung S (2011). Porphyrin biosynthesis control under water stress: sustained porphyrin status correlates with drought tolerance in transgenic rice. Plant Physiology 157:1746-1764. *https://doi.org/10.1104/pp.111.188276*

Pirdashti H, Sarvestani ZT, Nematzadeh G, Ismail A (2003). Effect of water stress on seed germination and seedling growth of rice (*Oryza sativa* L.) genotypes. Journal of Agronomy *https://doi.org/10.3923/ja.2003.217.222*

Polania J, Rao IM, Cajiao C, Grajales M, Rivera M, Velasquez F, Raatz B, Beebe SE (2017). Shoot and root traits contribute to drought resistance in recombinant inbred lines of MD 23-24× SEA 5 of common bean. Frontiers in Plant Science 8:296. *https://doi.org/10.3389/fpls.2017.00296*

Price AH, Steele K, Moore B, Jones R (2002a). Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes: II. Mapping quantitative trait loci for root morphology and distribution. Field Crops Research 76:25-43. *https://doi.org/10.1016/S0378-4290(02)00010-2*

Price AH, Townend J, Jones MP, Audebert A, Courtois B (2002b). Mapping QTLs associated with drought avoidance in upland rice grown in the Philippines and West Africa. Plant Molecular Biology 48:683-695. *https://doi.org/10.1023/a:1014805625790*

Prince SJ, Beena R, Gomez SM, Senthivel S, Babu RC (2015). Mapping consistent rice (*Oryza sativa* L.) yield QTLs under drought stress in target rainfed environments. Rice 8:25. *https://doi.org/10.1186/s12284-015-0053-6*

Rafalski JA (2010). Association genetics in crop improvement. Current opinion in Plant Biology 13:174-180. *https://doi.org/10.1016/j.pbi.2009.12.004*

Rasheed A, Fahad Shah, Hassan MU, Tahir MM, Aamer M, Wu ZM (2020a). A review on aluminum toxicity and quantitative trait loci maping in rice (*Oryza sativa* L). Applied Ecology and Environmental Research 18:3951-3961. *http://www.aloki.hu/pdf/1803_39513964.pdf*

Rasheed A, Fahad S, Aamer M, Hassan MU, Tahir MM, Wu ZM (2020b). Role of genetic factors in regulating cadmium uptake, transport and accumulation mechanisms and quantitative trait loci mapping in rice. Applied Ecology and Environmental Research 18(3):4005-4023.

Rasheed A, Hassan MU, Aamer M, Bian JM, Xu ZR, He XF, ... Wu ZM (2020c). Iron toxicity, tolerance and quantitative trait loci mapping in rice; a review. Applied Ecology and Environmental Research 18:7483-7498.

Rebetzke G, Condon AG, Richards R, Farquhar G (2002). Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat. Crop Science 42:739-745. *https://doi.org/10.2135/cropsci2002.7390*

Rivero RM, Gimeno J, Van Deynze A, Walia H, Blumwald E (2010). Enhanced cytokinin synthesis in tobacco plants expressing PSARK:IPT prevents the degradation of photosynthetic protein complexes during drought. Plant Cell Physiology 51:1929-1941. *https://doi.org/10.1093/pcp/pcq143*

Rathna Priya TS, Nelson ARLE, Ravichandran K, Antony U (2019). Nutritional and functional properties of coloured rice varieties of South India: a review. Journal of Ethnic Foods 6:1-11. *https://doi.org/10.1186/s42779-019-0017-3*

Ramanathan V, Rahman H, Subramanian S, Nallathambi J, Kaliyaperumal A, Manickam S, ... Muthurajan R (2018). OsARD4 encoding an acireductone dioxygenase improves root architecture in rice by promoting development of secondary roots. Scientific Reports 8:15713.

Rahman H, Ramanathan V, Nallathambi J, Duraialagaraja S, Muthurajan R (2016). Over-expression of a NAC 67 transcription factor from finger millet (*Eleusine coracana* L.) confers tolerance against salinity and drought stress in rice. BMC Biotechnology 16:35. *hpps://doi.org/10.1186/s12896-016-0261-1*

Reguera M, Peleg Z, Abdel-Tawab YM, Tumimbang EB, Delatorre CA, Blumwald E (2013). Stress-induced cytokinin synthesis increases drought tolerance through the coordinated regulation of carbon and nitrogen assimilation in rice. Plant Physiology 163:1609-1622. *https://doi.org/10.1104/pp.113.227702*

Reny H, Masdar M, Ganefianti DW (2017). Screening and identification of upland rice lines derived recurrent selection for drought tolerance. International Journal on Advanced Science Engineering Information Technology 7:1-6. *http://dx.doi.org/10.18517/ijaseit.7.6.2955*

Rivero RM, Kojima M, Gepstein A, Sakakibara H, Mittler R, Gepstein S, Blumwald E (2007). Delayed leaf senescence induces extreme drought tolerance in a flowering plant. Proceedings of the National Academy of Sciences 104:19631-19636. *https://doi.org/10.1073/pnas.0709453104*

Rohman A, Helmiyati S, Hapsari M, Setyaningrum DL (2014). Rice in health and nutrition. International Food Research Journal 21:13.

Sahebi M, Hanafi MM, Azizi P, Hakim A, Ashkani S, Abiri R (2015). Suppression subtractive hybridization versus next-generation sequencing in plant genetic engineering: challenges and perspectives. Molecular Biotechnology 57:880-903. *https://doi.org/10.1007/s12033-015-9884-z*

Sahebi M, Hanafi MM, Rafii M, Mahmud T, Azizi P, Osman M, ... Shabanimofrad M (2018). Improvement of drought tolerance in rice (*Oryza sativa* L.): Genetics, genomic tools, and the WRKY gene family. BioMed Research International 2018: 1-20. *https://doi.org/10.1155/2018/3158474*

Sabar M, Shabir G, Masood S, Shah SM, Aslam K, Naveed SA, Arif M (2019). Identification and mapping of QTLs associated with drought tolerance traits in rice by a cross between Super Basmati and IR55419-04. *Breeding* Science 69(1):169-178. *https://doi.org/10.1270/jsbbs.18068*

Saijo Y, Hata S, Kyozuka J, Shimamoto K, Izui K (2000). Over-expression of a single Ca2+-dependent protein kinase confers both cold and salt/drought tolerance on rice plants. The Plant Journal 23:319-327. *https://doi.org/10.1046/j.1365-313x.2000.00787.x*

Saika H, Okamoto M, Miyoshi K, Kushiro T, Shinoda S, Jikumaru Y, ... Ando M (2007). Ethylene promotes submergence-induced expression of OsABA8ox1, a gene that encodes ABA 8′-hydroxylase in rice. Plant and Cell Physiology 48:287-298. *https://doi.org/10.1093/pcp/pcm003*

Salazar C, Hernández C, Pino MT (2015). Plant water stress: Associations between ethylene and abscisic acid response. Chilean Journal of Agricultural Research 75:71-79. *http://dx.doi.org/10.4067/S0718-58392015000300008*

Salehi-Lisar SY, Bakhshayeshan-Agdam H (2016). Drought stress in plants: causes, consequences, and tolerance. In: Drought Stress Tolerance in Plants. Springer 1:1-16.

Sandhu N, Dixit S, Swamy BPM, Vikram P, Venkateshwarlu C, Catolos M, Kumar A (2018). Positive interactions of major-efect QTLs with genetic background that enhances rice yield under drought. Scientific Reports 8:1-13. *https://doi.org/10.1038/s41598-018-20116-7*

Sellamuthu R, Ranganathan C, Serraj R (2015). Mapping QTLs for reproductive-stage drought resistance traits using an advanced backcross population in upland rice. Crop Science 55:1524-1536.

Swamy BPM, Kumar A (2013). Genomics-based precision breeding approaches to improve drought tolerance in rice. Biotechnology Advances 31(8):1308-1318. *https://doi.org/10.1016/j.biotechadv.2013.05.004*

Serraj R, McNally KL, Slamet-Loedin I, Kohli A, Haefele SM, Atlin G, Kumar A (2015). Drought resistance improvement in rice: an integrated genetic and resource management strategy. Plant Production Science 14:1-14. *https://doi.org/10.1626/pps.14.1*

Shamsudin NAA, Swamy BPM, Ratnam W, Cruz MTS, Raman A, Kumar A (2016). Marker assisted pyramiding of drought yield QTLs into a popular Malaysian rice cultivar, MR219. BMC Genetics 17:30. *https://doi.org/10.1186/s12863-016-0334-0*

Serrat X, Cardona M, Gil J, Brito AM, Moysset L, Nogués S (2014). A Mediterranean japonica rice (*Oryza sativa*) cultivar improvement through anther culture. Euphytica 195:31-44. *https://doi.org/10.1007/s10681-013-0955-6*

Serraj R, Sinclair T (2002). Osmolyte accumulation: can it really help increase crop yield under drought conditions? Plant, Cell and Environment 25:333-341. *https://doi.org/10.1046/j.1365-3040.2002.00754.x*

Sharp R (2002). Interaction with ethylene: changing views on the role of abscisic acid in root and shoot growth responses to water stress. Plant, Cell & Environment 25:211-222. *https://doi.org/10.1046/j.1365-3040.2002.00798.x*

Shim JS, Oh N, Chung PJ, Kim YS, Choi YD, Kim JK (2018). Overexpression of OsNAC14 improves drought tolerance in rice. Frontiers in Plant Science 9:310. *https://doi.org/10.3389/fpls.2018.00310*

Sinclair TR (2011). Challenges in breeding for yield increase for drought. Trends in Plant Science 16:289-293. *https://doi.org/10.1016/j.tplants.2011.02.008*

Shamsudin NA, Swamy BPM, Ratnam W, Cruz MTS, Sandhu N, Raman AK, Kumar A (2016). Pyramiding of drought yield QTLs into a high quality Malaysian rice cultivar MRQ74 improves yield under reproductive stage drought. Rice 9:21. *https://doi.org/10.1186/s12284-016-0093-6*

Singh C, Binod K, Suhel M, Kunj C (2012a). Effect of drought stress in rice: a review on morphological and physiological characteristics. Trends in Biosciences 5:261-265.

Singh R, Singh Y, Xalaxo S, Verulkar S, Yadav N, Singh S, ... Rao PR (2016). From QTL to variety-harnessing the benefits of QTLs for drought, flood and salt tolerance in mega rice varieties of India through a multi-institutional network. Plant Science 242:278-287. *https://doi.org/10.1016/j.plantsci.2015.08.008*

Singh S, Prasad S, Yadav V, Kumar A, Jaiswal B, Kumar A, Khan NA , Dwivedi DK (2018). Effect of drought stress on yield and yield components of rice (*Oryza sativa* L.) genotypes. International Journal of Current Microbiology and Applied Sciences 7:2752-2759.

Singh PR, Jain N, Singh PK, Pandey MK, Sharma K (2016). Effect of recurrent selection on drought tolerance and related morpho-physiological traits in bread wheat. PLoS One 11(6):e0156869. *https://doi.org/10.1371/journal.pone.0156869*

Singh S, Pradhan S, Singh A, Singh O (2012b). Marker validation in recombinant inbred lines and random varieties of rice for drought tolerance. Australian Journal of Crop Science 6:606.

Sivamani E, Bahieldin A, Wraith JM, Al-Niemi T, Dyer WE, Ho THD, Qu R (2000). Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively expressing the barley HVA1 gene. Plant Science 155:1-9. *https://doi.org/10.1016/s0168-9452(99)00247-2*

Su J, Wu R (2004). Stress-inducible synthesis of proline in transgenic rice confers faster growth under stress conditions than that with constitutive synthesis. Plant Science 166:941-948. *https://doi.org/10.1016/j.plantsci.2003.12.004*

Tamaki H, Reguera M, Abdel-Tawab YM, Takebayashi Y, Kasahara H, Blumwald E (2015). Targeting hormone-related pathways to improve grain yield in rice: a chemical approach. PLoS One 10:e013121. *https://doi.org/10.1371/journal.pone.0131213*

Tang L, Cai H, Ji W, Luo X, Wang Z, Wu J, ... Zhu Y (2013). Overexpression of GsZFP1 enhances salt and drought tolerance in transgenic alfalfa (*Medicago sativa* L.). Plant Physiology and Biochemistry 71:22-30. *https://doi.org/10.1016/j.plaphy.2013.06.024*

Tanaka Y, Sano T, Tamaoki M, Nakajima N, Kondo N, Hasezawa S (2006). Cytokinin and auxin inhibit abscisic acid-induced stomatal closure by enhancing ethylene production in Arabidopsis. Journal of Experimental Botany 57(10):2259-2266. *https://doi.org/10.1093/jxb/erj193*

Tardieu F, Parent B, Simonneau T (2010). Control of leaf growth by abscisic acid: hydraulic or non-hydraulic processes? Plant, Cell & Environment 33:636-647. *https://doi.org/10.1111/j.1365-3040.2009.02091.x*

Tran LSP, Nakashima K, Sakuma Y, Osakabe Y, Qin F, Simpson SD, ... Yamaguchi-Shinozaki K (2007). Co-expression of the stress-inducible zinc finger homeodomain ZFHD1 and NAC transcription factors enhances expression of the ERD1 gene in *Arabidopsis*. The Plant Journal 49:46-63. *https://doi.org/10.1111/j.1365-313X.2006.02932.x*

Travaglia C, Reinoso H, Cohen A, Luna C, Tommasino E, Castillo C, Bottini R (2010). Exogenous ABA increases yield in field-grown wheat with moderate water restriction. Journal of Plant Growth Regulation 29:366-374. *https://doi.org/10.1007/s00344-010-9147-y*

Trijatmiko KR, Prasetiyono J, Thomson MJ, Cruz CMV, Moeljopawiro S, Pereira A (2014). Meta-analysis of quantitative trait loci for grain yield and component traits under reproductive-stage drought stress in an upland rice population. Molecular Breeding 34:283-295. *https://doi.org/10.1007/s11032-013-0012-0*

Tripath, J, Zhang J, Robin S, Nguyen TT, Nguyen H (2000). QTLs for cell-membrane stability mapped in rice (*Oryza sativa* L.) under drought stress. Theoretical and Applied Genetics 100:1197-1202. *https://doi.org/10.1007/s001220051424*

Thalmann M, Pazmino D, Seung D, Horrer D (2016). Regulation of leaf starch degradation by abscisic acid is important for osmotic stress tolerance in plants. The Plant Cell 28:8. *https://doi.org/10.1105/tpc.16.00143*

Usman MG, Rafii MY, Martini MY, Yusuff OA, Ismail MR, Miah G (2017). Molecular analysis of Hsp70 mechanisms in plants and their function in response to stress. Biotechnology and Genetic Engineering Reviews 33:26-39. *https://doi.org/10.1080/02648725.2017.1340546*

Todaka D, Zhao Y, Yoshida T, Kudo M, Kidokoro S, Mizoi J (2017). Temporal and spatial changes in gene expression, metabolite accumulation and phytohormone content in rice seedlings grown under drought stress conditions. Plant Journal 90:61-78. *https://doi.org/10.1111/tpj.13468*

Usman MG, Rafii MY, Martini MY, Yusuff OA, Ismail MR, Miah G (2018). Introgression of heat shock protein (Hsp70 and sHsp) genes into the Malaysian elite chilli variety Kulai (*Capsicum annuum* L.) through the application of marker-assisted backcrossing (MAB). Cell Stress and Chaperones 23:223-234. *https://doi.org/10.1007/s12192-017-0836-3*

Upadhyaya H, Roy H, Shome S, Tewari S, Bhattacharya MK, Panda SK (2017). Physiological impact of Zinc nanoparticle on germination of rice (*Oryza sativa* L) seed. Journal of Plant Science. Phytopathology 1:62-70. *https://doi.org/10.29328/journal.jpsp.1001008*

Upadhyaya H, Panda SK (2019). Drought stress responses and its management in rice. Advances in Rice Research for Abiotic Stress Tolerance1-24. *https://doi.org/10.1016/B978-0-12-814332-2.00009-5*

Upadhyaya H, Shome S, Tewari S, Bhattacharya MK, Panda SK (2016). Zinc nanoparticles induced comparative growth responses in rice (*Oryza sativa* L.) cultivars. In: Paul S, Tewari S (Eds). Frontiers of Research in Physical Sciences. pp 71-77.

Urbanova T, Leubner-Metzger G (2016). Gibberellins and seed germination. Annual Plant Reviews 49. *https://doi.org/10.1002/9781119210436.ch9.*

Varshney RK, Graner A, Sorrells ME (2005). Genomics-assisted breeding for crop improvement. Trends in Plant Science 10:621-630. *https://doi.org/10.1016/j.tplants.2005.10.004*

Venuprasad R, Dalid C, Del Valle M, Zhao D, Espiritu M, Cruz MS, ... Atlin G (2009). Identification and characterization of large-effect quantitative trait loci for grain yield under lowland drought stress in rice using bulk-segregant analysis. Theoretical and Applied Genetics 120:177-190. *https://doi.org/10.1007/s00122-009-1168-1*

Venuprasad R, Lafitte HR, Atlin GN (2007). Response to direct selection for grain yield under drought stress in rice. Crop Science 47:285-293. *https://doi.org/10.2135/cropsci2006.03.0181*

Verma SK, Saxena RR, Saxena RR, Xalxo MS, Verulkar SB (2014). QTL for grain yield under water stress and non-stress conditions over years in rice (*Oryza sativa* L.). Australian Journal of Crop Science 8:916.

Vikram P, Swamy BM, Dixit S, Ahmed H, Cruz MS, Singh AK, Ye G, Kumar A (2012). Bulk segregant analysis: An effective approach for mapping consistent-effect drought grain yield QTLs in rice. Field Crops Research 134:185-192.

Vikram, P, Swamy BM, Dixit S, Ahmed HU, Cruz MTS, Singh AK, Kumar A (2011). qDTY 1.1, 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. *https://doi.org/10.1186/1471-2156-12-89*

Volaire F, Barkaoui K, Norton M (2014). Designing resilient and sustainable grasslands for a drier future: adaptive strategies, functional traits and biotic interactions. European Journal of Agronomy 52:81-89. *https://doi.org/10.1016/j.eja.2013.10.002*

Wang H, Inukai Y, Yamauchi A (2006). Root development and nutrient uptake. Critical Reviews in Plant Sciences 25:279-301. *https://doi.org/10.1080/07352680600709917*

Wang X, Pang Y, Zhang J, Zhang Q, Tao Y, Feng B, ... Li Z (2014). Genetic background effects on QTL and QTL× environment interaction for yield and its component traits as revealed by reciprocal introgression lines in rice. The Crop Journal 2:345-357. *https://doi.org/10.1016/j.cj.2014.06.004*

Weeks DP, Spalding MH, Yang B (2016). Use of designer nucleases for targeted gene and genome editing in plants. Plant Biotechnology Journal 14:483-495. *https://doi.org/10.1111/pbi.12448*

Wei H, Chen C, Ma X, Zhang Y, Han J, Mei H (2017). Comparative analysis of expression profiles of panicle development among tolerant and sensitive rice in response to drought stress. Frontiers in Plant Science 8:437. *https://doi.org/10.3389/fpls.2017.00437*

Wilkinson S, Kudoyarova GR, Veselov DS, Arkhipova TN, Davies WJ (2012). Plant hormone interactions: innovative targets for crop breeding and management. Journal of Experimental Botany 63:3499-3509. *https://doi.org/10.1093/jxb/ers148*

Xiang Y, Huang Y, Xiong L (2007). Characterization of stress-responsive CIPK genes in rice for stress tolerance improvement. Plant Physiology 144:1416-1428. *https://doi.org/10.1104/pp.107.101295*

Xiao B, Huang Y, Tang N, Xiong L (2007). Over-expression of a LEA gene in rice improves drought resistance under the field conditions. Theoretical and Applied Genetics 115:35-46. *https://doi.org/10.1007/s00122-007-0538-9*

Xing W, Zhao H, Zou D (2014). Detection of main-effect and epistatic QTL for yield-related traits in rice under drought stress and normal conditions. Canadian Journal of Plant Science 94:633-641. *https://doi.org/10.4141/cjps2013-297*

Xu DQ, Huang J, Guo SQ, Yang X, Bao YM, Tang HJ, Zhang HS (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. *https://doi.org/10.1016/j.febslet.2008.02.052*

Xu D, Duan X, Wang B, Hong B, Ho THD, Wu R (1996). Expression of a late embryogenesis abundant protein gene, HVA1, from barley confers tolerance to water deficit and salt stress in transgenic rice. Plant Physiology 110:249-257. *https://doi.org/10.1104/pp.110.1.249*

Xu R, Yang Y, Qin R, Li H, Qiu C, Li L, Wei P, Yang J (2016). Rapid improvement of grain weight via highly efficient CRISPR/Cas9-mediated multiplex genome editing in rice. Journal of genetics and genomics Yi Chuan Xue Bao 43:529. *https://doi.org/10.1016/j.jgg.2016.07.003*

Yadav R, Courtois B, Huang N, McLaren G (1997). Mapping genes controlling root morphology and root distribution in a doubled-haploid population of rice. Theoretical and Applied Genetics 94:619-632. *https://doi.org/10.1007/s001220050459*

Yadira O, Reyes J, Alejandra A (2011). Late embryogenesis abundant proteins. Plant Signaling Behaviour 6:586-589. *https://doi.org/10.4161/psb.6.4.15042*

Yang J, and Zhang J (2006). Grain filling of cereals under soil drying. New Phytologist 169:223-236. *https://doi.org/10.1111/j.1469-8137.2005.01597.x*

Yang J, Zhang J (2010). Crop management techniques to enhance harvest index in rice. Journal of Experimental Botany 61:3177-3189. *https://doi.org/10.1093/jxb/erq112*

Yang J, Zhang J, Wang Z, Xu G, Zhu Q (2004). Activities of key enzymes in sucrose-to-starch conversion in wheat grains subjected to water deficit during grain filling. Plant Physiology 135:1621-1629. *https://doi.org/10.1104/pp.104.041038*

Yang, J, Zhang J, Wang Z, Zhu Q, Wang W (2001). Hormonal changes in the grains of rice subjected to water stress during grain filling. Plant Physiology 127:315-323. *https://doi.org/10.1104/pp.127.1.315*

Yang W, Duan L, Chen G, Xiong L, Liu Q (2013). Plant phenomics and high-throughput phenotyping: accelerating rice functional genomics using multidisciplinary technologies. Current Opinion in Plant Biology 16:180-187. *https://doi.org/10.1016/j.pbi.2013.03.005*

Yang X, Wang B, Chen L, Li P, Cao C (2019). The different influences of drought stress at the flowering stage on rice physiological traits, grain yield, and quality. Scientific Reports 9:1-12

You J, Hu H, Xiong L (2012). An ornithine δ-aminotransferase gene OsOAT confers drought and oxidative stress tolerance in rice. Plant Science 197:59-69. *https://doi.org/10.1016/j.plantsci.2012.09.002*

You J, Zong W, Li X, Ning J, Hu H, Li X, Xiao J, Xiong L (2013). The SNAC1-targeted gene OsSRO1c modulates stomatal closure and oxidative stress tolerance by regulating hydrogen peroxide in rice. Journal of Experimental Botany 64:569-583. *https://doi.org/10.1093/jxb/ers349*

Yoo YH, Nalini Chandran AK, Park JC (2017). OsPhyB-mediating novel regulatory pathway for drought tolerance in rice root identified by a global RNA-seq transcriptome analysis of rice genes in response to water deficiencies. Frontiers in Plant Sciences 8:1-19. *https://doi.org/10.3389/fpls.2017.00580*

Yun YT, Kim HJ, Tai TH (2019). Identification of QTLs controlling seedling traits in temperate japonica rice under different water conditions. Plant Breeding and Biotechnology 7(2):106-122. *https://doi.org/10.9787/PBB.2019.7.2.106*

Zain NAM, Ismail MR, Puteh A, Mahmood M, Islam MR (2014). Impact of cyclic water stress on growth, physiological responses and yield of rice (*Oryza sativa* L.) grown in tropical environment. Ciência Rural 44:2136-2141. *http://dx.doi.org/10.1590/0103-8478cr20131154*

Zhang G, Chen M, Li L, Xu Z, Chen X, Guo J, Ma Y (2009). Overexpression of the soybean GmERF3 gene, an AP2/ERF type transcription factor for increased tolerances to salt, drought, and diseases in transgenic tobacco. Journal of Experimental Botany 60:3781-3796. *https://doi.org/10.1093/jxb/erp214*

Zhang J, Zheng H, Aarti A, Pantuwan G, Nguyen T, Tripathy J, ... Nguyen BD (2001). Locating genomic regions associated with components of drought resistance in rice: comparative mapping within and across species. Theoretical and Applied Genetics 103:19-29. *https://doi.org/10.1007/s001220000534*

Zhang Z, Li F, Li D, Zhang H, Huang R (2010). Expression of ethylene response factor JERF1 in rice improves tolerance to drought. Planta 232:765-774. *https://doi.org/10.1007%2Fs00425-010-1208-8?LI=true*

Zhang J, Li Y, Zahng H, Dong P, WE C (2018). Effects of different water conditions on rice growth at the seedling stage. Universidade Federal Rural do Semi-Árido 32:440-448. *http://dx.doi.org/10.1590/1983-21252019v32n217rc*

Zhao J, Gao Y, Zhang Z, Chen T, Guo W, Zhang T (2013). A receptor-like kinase gene (GbRLK) from *Gossypium barbadense* enhances salinity and drought-stress tolerance in *Arabidopsis*. BMC Plant Biology 13:110. *https://doi.org/10.1186/1471-2229-13-110*

Zhao XQ, Xu JL, Zhao M, Lafitte R, Zhu LH, Fu BY, ... Li ZK (2008). QTLs affecting morph-physiological traits related to drought tolerance detected in overlapping introgression lines of rice (*Oryza sativa* L.). Plant Science 174:618-625.

Zheng B, Yang L, Zhang W, Mao C, Wu Y, Yi K, ... Wu P (2003). Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. Theoretical and Applied Genetics 107:1505-1515. *https://doi.org/10.1007/s00122-003-1390-1*

Zheng BS, Yang L, Mao CZ, Huang YJ, Wu P (2008). Mapping QTLs for morphological traits under two water supply conditions at the young seedling stage in rice. Plant Science 175:767-776

Zhu B, Su J, Chang M, Verma DPS, Fan YL, Wu R (1998). Overexpression of a Δ1-pyrroline-5-carboxylate synthetase gene and analysis of tolerance to water-and salt-stress in transgenic rice. Plant Science 139:41-48.

Zhu G, Ye N, Yang J, Peng X, Zhang J (2011). Regulation of expression of starch synthesis genes by ethylene and ABA in relation to the development of rice inferior and superior spikelets. Journal of Experimental Botany 62:3907-3916. *https://doi.org/10.1093/jxb/err088*

Zou G, Mei H, Liu H, Liu G, Hu S, Yu X, ... Luo L (2005). Grain yield responses to moisture regimes in a rice population: association among traits and genetic markers. Theoretical and Applied Genetics 112:106-113. *https://doi.org/10.1007/s00122-005-0111-3*