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. 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
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 causal 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          |
|-------------------|---------|--------------------|
| 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 starch 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 et 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 morphophysiological 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 resultanty 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 indicator of DT that can develop DT cultivars (Dien et 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 *et 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 in 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 Voeseke, 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.

**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.

| 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.
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  | 7               | (Zheng et al., 2008) |
| Root length and thickness           | IR58821 × 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(qDTY2.5)        | 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 | 1.2 to 18.5 | (Price et al., 2002b) |
| Panicle number /plant          | 14                | All excluding | 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; AFLP, restriction fragment length polymorphism; ABLP, amplified fragment length polymorphism; RILs, recombinant inbred lines; 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$_2$O$_2$ (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       | Dular × IR62-21         | 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    | MRQ74 cultivar          | GY         | (Shamsudin et al., 2016)    |
| qDTY2.2 | 2    |                   | MRQ74 cultivar          | GY         | (Shamsudin et al., 2016)    |
| qDTY3.1 | 3    |                   |                         |            |       |                             |
| 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 | Teqing × Lemont BILs    | GY         | (Zhao et al., 2008)         |
| QDS_9.1 | 9    | IR453–RM491      | IR64 × IR77298-5-6-18(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 and BC1F3:6) | 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×Kongyu131 | RILs (F2:7) | GY    | (Xing et al., 2014)         |
| qDTY3.4 | 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 LEA 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 transgenic rice, the overexpression of OsRD4 gene showed DT by controlling root traits (Ramanathan et al., 2018).

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.

### Table 7. Candidate engineered genes for drought tolerance in rice

| Function                     | Gene name     | Promotor     | Transformation | Phenotyping                                  | Reference                  |
|------------------------------|---------------|--------------|----------------|----------------------------------------------|----------------------------|
| Drought adaptive traits      | OsARD4        |              | Drought tolerance | (Ramanathan et al., 2018)                     |
| Shoot and root growth        | SaVHAc1       | Agrobacterium| Drought tolerance | (Biradar et al., 2018)                      |
| High 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) |
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)             |
| AG01        | AT1G48410        | Arabidopsis  | Governing proteins, microRNAs                      | (Li et al., 2012)              |
| ABCG22      | AT5G06530        | Arabidopsis  | transporters/Channels                              | (Kuromori et al., 2011)        |
| CIPK12      | LOC Oo01g55450   | Rice         | Regulatory Proteins and protein Kinases            | (Xiang et al., 2007)           |
| CIPK03      | LOC Oo07g48760   | Rice         | Regulatory proteins and protein Kinases            | (Xiang et al., 2007)           |
| CDPK7       | LOC Oo03g03660   | 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)           |
| GhRLK       | LOC Oo04g56130   | Cotton       | Protein kinases                                    | (Zhao et al., 2013)            |
| GhMKK1      | Solyc12g090920   | Cotton       | Regulatory proteins                                | (Lu et al., 2013)              |
| GhNPR3      | Solyc09g063070   | Soyabean     | Transcription factors                              | (Zhang et al., 2009)           |
| GGF1P1      | Glyma10g041610   | Soyabean (Wild) | Zinc Fingers                      | (Tang et al., 2013)           |
| MIR166A     | 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        | AT5G65110        | 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 16.1 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](image_url)

**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 greenhouse 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. All authors read and approved the final manuscript.

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Conflict of Interests

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

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