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Integrated Approaches to Develop Drought-Tolerant Rice: Demand of Era for Global Food Security

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Abstract

Rice (*Oryza sativa* L.) is an important food crop that belongs to family *Gramineae* and needs a larger amount of water to complete its life cycle as compared to other crops. Hence, rice production is severely affected by water stress. Drought is an important issue in rainfed areas across the globe which limits rice production. Several morphological characters like germination, plant height, plant biomass, number of tillers, various root and leaf traits, physiological characters like photosynthesis, stomatal conductance, transpiration, water use efficiency, relative water content, chlorophyll content, photosystem-II activity, carbon isotope discrimination, membrane stability, and abscisic acid content of rice are reduced under drought conditions. Drought also induces the accumulation of several biochemical osmoprotectants like proline, polyamines, sugars, antioxidants and alters the expression of several genes including transcription factors and defense-related proteins, hence thereby affects the yield of rice crop. Drought escape, drought avoidance, and drought tolerance are the mechanisms that prevent plant from harmful effects of drought. Thus, this review is focused mainly on recent information about the morphological, physio-biochemical, and molecular effects, responses, and adaptation mechanisms of rice under drought stress. Here we also discussed that how we can improve the rice for drought tolerance using various molecular tools and techniques.

Keywords Rice (*Oryza sativa* L.) · Morphological · Physiological · Biochemical · Molecular effects · Drought stress · Abiotic stress

Introduction

Rice is an important food crop that belongs to the genus *Oryza* of *Gramineae* family. Globally, it provides 23% per capita energy which accounts for 65% of caloric intake (Khush 1996). It ranks second among cereal in the world (Farooq et al. 2009a, b) and most widely consumed staple food (Pirdashti et al. 2009). Rice occupied 197.59 million hectares area in the world with 996.07 million tons production (FAOSTAT 2018–19). India is second largest producer of rice with an annual production of over 172.58 million tons and has 44.5 million hectares area under rice cultivation (FAOSTAT 2018–19). Globally, with the increasing population, the demand for rice and other staple food grains is going to be increased day by day. Hence, to meet the global rice demand in the coming years, its production needs to be significantly increased from the current level. Globally, rice production is constrained by a number of biotic and abiotic factors. Among these abiotic stresses like drought, high temperatures, salinity, and oxidative stress are often interrelated, and may cause similar changes in plants (Szekeres 2003). In the past decades, drought has become frequent due to increasing aberrations in rainfall patterns. It limits crop production and is becoming a more severe problem in many regions of the globe (Passioura 1996, 2007). Drought refers to a situation where demand of water is more than water supply to plants and it becomes a limiting factor for biomass accumulation. Drought affects water relations both on the cellular level as well as a whole plant like other abiotic

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stresses (Beck et al. 2007). It influences several physiological, biochemical, and molecular processes in plants, like ion uptake, translocation, photosynthesis, respiration, carbohydrates, nutrient metabolism, harmonic balance, and expression level of several genes (Farooq et al. 2009c).

Since rice is an aquatic plant, it is very sensitive to drought stress for almost all its growth phases which cause poor expression of yield component traits (Hsiao et al. 1984; O'Toole 1982; Venuprasad et al. 2008, Bouman et al. 2005). Drought stress reduces cell division, cell elongation and thus restricts overall plant growth which is reflected from reduced height and lesser biomass. Drought at booting and seed setting stages caused decreased grain size and grain number (Zhang et al. 2018a, b). Breeding for drought tolerance has been a very challenging task, due to the complex genetic and molecular regulation of this trait. The production of varieties of drought tolerance will need to put together many features of drought tolerance along with high yield capacity under non-drought conditions, but progress in breeding for drought tolerance has been very slow (Kumar et al. 2008). Nevertheless, attempts by the International Rice Research Institute (IRRI) in this direction have contributed to the production of certain genotypes of drought-tolerant rice. These include IR 74371-46-1-1, IR 74371-54-1-1, and IR 74371-70-1-1. In addition, in various regions of South Asia, several drought-tolerant rice lines have been released (for example, DRR 42, 44 in India, SukhaDhan 4, 5 in Nepal, and BRRI Dhan 66, 71 in Bangladesh). In different countries, a conventionally bred line IR74371-70-1-1 was released with various names: in India as SahbhagiDhan, in Nepal as SukhaDhan 3, and in Bangladesh as BRRI 56 Dhan. This suggests the suitability of this line for a wide variety of environments to demonstrate improved results. But conventional breeding is costly, laborious, and takes a long time to develop a new variety for cultivation. Therefore, it is extremely important to have a comprehensive understanding of physiological and molecular basis of drought tolerance and associated morphological changes to facilitate designing of efficient breeding strategies for development of drought-tolerant varieties. In this review, we have discussed the morphological, physiological, and molecular responses of the rice plant under drought stress.

Drought-Induced Economic Losses

Droughts have a significant impact on agricultural production, but there is no agreement on how to measure and characterize them, which has ramifications for drought research and policy (Fontes et al. 2020). The cost–benefit analysis is frequently used to shape the right policy response to drought, particularly with respect to the costs of mitigation and climate adaptation in the agriculture sector (Mechler et al. 2008; Fontes et al. 2020). Recently, Kim et al. (2019) reported global patterns of drought-induced yield losses and associated national economic losses for the major cereals including rice, wheat and maize from 1983 to 2009. They applied empirical relationships among crop yields, a drought index, and annual precipitation to calculate production losses which was then translated into economic losses for these crops due to drought. The worldwide aggregated total economic loss of rice for the period 1983 to 2009 was estimated to be approximately $37Billion (Kim et al. 2019). More such studies are needed for evaluation of drought-induced economic losses in rice which will help design policy measures and technological development for effectively mitigating the drought in the most vulnerable regions.

Drought Categorization of Soils

Hsiao (1973) categorized drought stress based on the soil water potential (SWP) and reduction in leaf relative water content (RLWC) into three main categories; mild stress (SWP: − 0.1MPa; reduction in RLWC: 8-10%), moderate stress (SWP: − 1.2 to − 1.5; reduction in RLWC: 10-20%) and severe stress (SWP: < − 1.5; reduction in RLWC: > 20%). The US drought monitor map uses a range of indicators to measure intensity of drought and categorizes it into five categories; abnormally dry, moderate drought, severe drought, extreme drought and exceptional drought (https://droughtmonitor.unl.edu/About/AbouttheData/DroughtClassification.aspx). Although, drought is the most significant constraint to rainfed rice productivity; there are few papers which characterize the soil parameters in relation to the intensity of drought stress in the area. It has been reported that rice fields in similar locales that are totally rainfed are likely to have varying soil water potential and water table depth values (Singh et al. 2017). Other drought stresses that occur at the seedling and vegetative stages also provide considerable problems to rainfed rice growers, and can lead to varied crop performance and soil characteristics (Pandey and Bhandari 2008; Singh et al. 2017).

Evapotranspiration and Soil Moisture

Monitoring and modeling of land surface and vegetation processes is a critical component in determining the water and carbon dynamics of terrestrial ecosystems. In drought-related studies, the appropriate assessment of evapotranspiration (ET) and soil moisture content (SMC) is very crucial (Verstraeten et al. 2008). Controlling water stress levels and timing is critical for proper phenotyping for drought tolerance. Guimarães et al. (2016) determined the upland rice plant water use and its association with grain output during periods of irrigation withholding in order to improve the effectiveness of drought phenotyping. Such experiments are required for evaluating soil condition, which is directly linked with crop productivity.

Crop-Specific Drought Sensitivity Assessments

To combat drought stress, new rice cultivars with greater drought resistance should be developed. It is desirable to create a simple and accurate approach for evaluating rice drought tolerance for breeding reasons, particularly for producing highland rice (Zu et al. 2017). It is necessary to evaluate drought sensitivity of crop during their life in different time for understanding their need for water. Zu et al (2017) explained a new method that can be utilized to assess efficiently the drought tolerance degree (DTD) of upland rice varieties. The DTD is defined as the mean value of the relationships between the length of the green leaf and the total length of the three upper leaves in each rice shoot after the drought treatment and therefore takes values from zero to one. There is a need to develop such type of methods for crop-specific drought sensitivity assessments in near future.

Geographical Location of Drought Resistance

India and Bangladesh provided the majority of the reproductive stage drought-tolerant accessions (Rahman and Zhang 2018). Nearly 40,000 germplasms (accessions and breeding lines) were screened for the finest drought-tolerant germplasm between 1978 and 1985; nevertheless, breeding lines made up the bulk of the top 20 excellent germplasms. India has slightly more tolerant accessions than Bangladesh, although the majority of Indian accessions came from Bangladesh's neighboring states. Furthermore, suggested cultivars for drought stress breeding such as Kataktara Da2, Dular, Shada Shaita, and DA 28 originated in Bangladesh, and the majority of these are still planted in large regions of the country (de Datta et al. 1988; Torres et al. 2013; Rahman and Zhang 2018).

Survival Mechanism of Plants Under Drought Stress

There are three ways by which plants can survive under drought conditions, i.e., drought escape, drought avoidance, and drought tolerance. The drought escape can be defined as the process in which a plant can complete its life cycle before developing the critical water deficiency in soil (Basu et al. 2016; Osmolovskaya et al. 2018). It consists of two different mechanisms like rapid phenological development and developmental plasticity. When the plants can produce flowers and seeds with minimum vegetative growth under limited water supply is known as rapid phenological development. When the plants can complete their proper vegetative growth, flowering and seed production during abundant rain seasons are known as developmental plasticity. This allows desert ephemerals to both survive long periods without rain and escape drought. Drought escape is an important process that allows rice to grow in a well manner and also to produce the grains while limited water availability (Kumar et al. 2008). Drought avoidance is referred as the ability of plants to maintain high water potential in tissues in spite of less moisture in soil. Rice genotype that shows the drought avoidance may follow ABA biosynthesis and other biochemical mechanisms or adaptation by a root system, to maintain the water status in plants. These drought avoidance rice genotypes can reduce the loss of yield which leads to drought stress (Singh et al. 2012). Drought avoidance can be also improved by improving water use efficiency (WUE) and minimizing the loss of water from plant. The rice genotypes that circumvent drought have several characteristics like, deep root system which has higher branching ability and soil penetration, high root–shoot ratio, less leaf rolling, early closure of stomata, and higher cuticle resistance (Blum et al. 1989; Samson et al. 2002; Wang et al. 2006). Likewise, drought tolerance is referred to as the ability of plants to survive under low water content in the tissues (Turner 1979; Delphine et al. 2010). Drought tolerance is one of the complex characters which is governed by polygenic effects and also includes complex morphological and physiological mechanisms (Li and Xu 2007), like maintenance of turgor pressure with the help of osmotic adjustment, increased cell elasticity, decreased cell size, and desiccation resistance with help of protoplasmic resistance (Sullivan and Ross 1979). The degree of drought tolerance can be determined by tissue water potential of plants and the traits involved in this phenomenon are appraised as secondary traits. Several secondary traits have been used for improvement of drought tolerance are leaf rolling, relative water content, osmotic adjustment and stomatal conductivity (Nguyen et al. 1997; Babu et al. 2001; Kato et al. 2006).

Effects of Drought on Rice Plants

The effects of drought on the plants can appear at all phenological stages at any stage of growth and development of plant, when the water deficiency occurs in the field. Plants respond to drought by a range of changes at morphological, physiological, and molecular levels. A description of various changes in plants during the drought is given in Fig. 1.

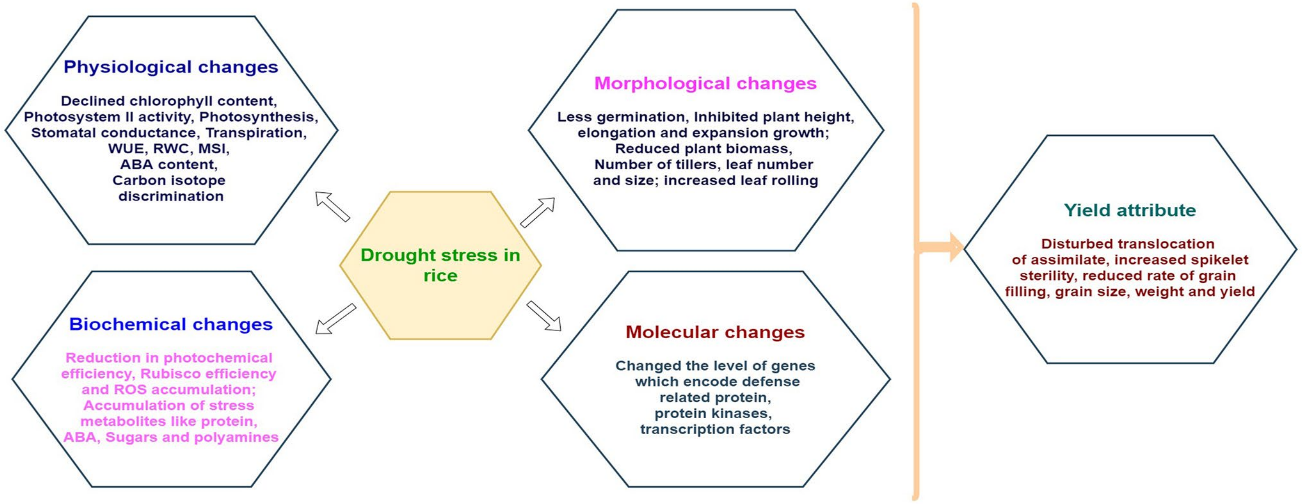

Fig. 1 Physiological, morphological, biochemical and molecular changes in rice under drought stress condition leads to yield decline

Morphological Responses Under Drought

Growth

Growth is an important factor that is governed by several events (such as morphological, physiological, ecological, biochemical and genetic) and their complex interactions. It is established by cell division, cell elongation and cell differentiation and involves two main parts of a plant that participate in the event of growth, i.e., root and shoot system of the plant. Water stress critically impacts plant growth and development than any other environmental stress effects. The quality and quantity of the plant growth depends on the complex interactions of the events during the water stress. During the water stress, growth of the cell is inhibited due to reduction in the turgor pressure (Taiz and Zeiger 2006) and cell elongation can be inhibited because of the interruption of water flow from xylem to surrounded elongating cells (Nonami 1998; Farooq et al. 2009a, b). Drought impaired he cell division, cell elongation and cell expansion which ultimately resulted in a reduction of the growth and development of a plant (Nonami 1998; Kaya et al. 2006; Hussain et al. 2008) (Fig. 2). It also reduces the germination, establishment (Harris et al. 2002) and severely enabled the sprouting of the seeds (Kaya et al. 2006).

Responses of Leaf, Root and Other Plant Characters

Water stress severely affects the growth and development of the leaves and roots and these are the important component which play important role in rice adaptation to drought stress. Since plants obtain the water and mineral nutrients from soil via, roots, so growth, development, proliferation, and size of the root are important factors for water stress resistance (Yoshida and Hasegawa 1982). Shallow rooting cultivars are more sensitive to drought than deep-rooting cultivars (Nemoto et al. 1998; Farooq et al. 2009e) because the deep root system of a plant allows obtaining the water from the depth of soil profile (Kondo et al. 2003). It has been found in several studies that rice varieties which have longer and thicker roots were found more drought resistant than other varieties those having short and thin root system (O'Toole and Chang 1979). In another study, the rice varieties which have deep root were found better adaptive during dry conditions (Boyer 1996). Drought reduces the number of leaves and new tillers decrease leaf elongation, promotes leaf rolling and increase leaf death(Cutler et al. 1980; Hsiao et al. 1984; Turner et al. 1986) in rice plants which results in reducing the photosynthetically active radiation (PAR) (Inthapan and Fukai 1988). The leaf expansion rate was decreased when 20 days of drought stress was given

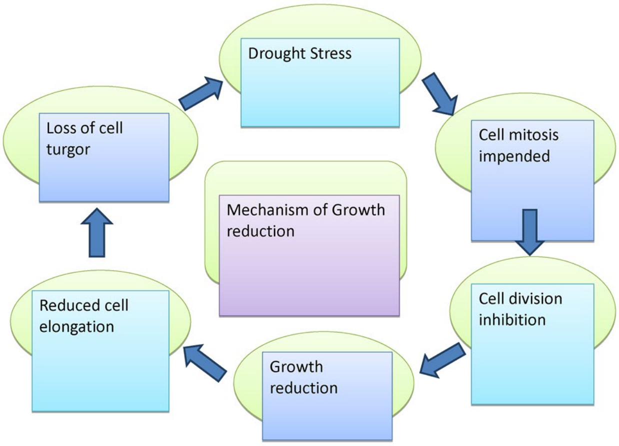

Fig. 2 Mechanisms of growth inhibition in rice due to drought stress

at vegetative phase in rice. Stomata are sensitive to water stress (Farooq et al. 2009d). When the leaf water potential decreases, it reduces the leaf conductance (O'Toole et al. 1984), which results in to decrease in the photosynthetic rate and radiation use efficiency (Inthapan and Fukai 1988). Several other responses of the plant have been observed during the water stress like reduction in height, leaf area and biomass production, decreasing the number of tillers and their abortion and changing in dry matter of roots and depth of root. According to recent studies water stress impact seedling and it significantly reduces the fresh and dry weight of seedlings (Farooq et al. 2008, 2009c).

Yield and Related Traits

Yield is the ultimate trait that is severely affected by water stress. There are several yield regulating factors that are affected by water stress. Many of these factors are responsible for the yield of a plant in several complex manners. Water stress effects yield by halting the leaf gas exchange which may adversely affect several processes and reduce the tissue size of source and sink, loading of phloem and assimilate translocation, etc. (Farooq et al. 2009a, b). In short, water stress decreases the growth and development of the crop plants that in turn causes inhibition of the grain filling process and flower developments. The reduction in grain filling process in plants occurs due to the decreasing of assimilate partitioning and starch and sucrose synthesizing enzymes. Under drought stress, the yield of rice plants depends on the drought timing and growth stages of the plant (Garrity and O'Toole 1994). Drought affects the yield component at different growth stages of plant, like vegetative stage (Guan et al. 2010; Sarvestani et al. 2008),Reproductive stage (Singh et al. 2018; Lafitte et al. 2007; Venuprasad et al. 2007; Dixit et al. 2012, 2014a, b; Guan et al. 2010; Swamy et al. 2017),flowering stage (Puteh et al. 2013; Sarvestani et al. 2008; Shamsudin et al. 2016a, b; Lanceras et al. 2004; Yang et al. 2019),anther dehiscence stage (Ekanayake et al. 1989) and Grain filling stage (Basnayake et al. 2006; Lanceras et al. 2004), Heading stage (Lafitte et al. 2006), panicle exertion stage (O'Toole and Namuco 1983). For example, water stress before 12 days of anthesis makes a severe impact on spikelet fertility with a higher reduction in the grain yield (Cruz and O'Toole 1984; Ekanayake et al. 1989) and water stress at reproductive phase leads to an increase in the number of unfilled grain on a spike and reduced grain weight thus ultimately reduce the grain yield of plants (Wopereis et al. 1996). Several other scientists also reported the reduction in yield of rice under drought stress condition (Jongdee et al. 2006; Kumar et al. 2008; Jian-Chang et al. 2008; Atlin et al. 2006; Carrijo et al. 2017; Daryanto et al. 2017; Zhang et al. 2018a, b) (Table 1).

Physiological Responses Under Drought

Drought induces various physiological changes in plants that may be critical for their survival under moisture deficit conditions. Some of the physiological responses to water stress in rice are described below.

Leaf Water Potential

During water stress, leaf water potential of rice plants decreases significantly in comparison to control plants (Hu et al. 2004; Farooq et al. 2009c; Parent et al. 2010). The net photosynthetic rate of a leaf is also decreased with the decreasing of leaf water potential when the water content or soil water potential reached at threshold level. In a study, the leaf water potential was decreased with the increased period of water stress induced by the supplying 20% PEG in all rice varieties. A significant difference was observed at 14 days after water stress treatment (Larkunthod et al. 2018). Liu et al. (2007a, b, c) found that upland rice cultivars decline the leaf water potential in comparison to lowland rice cultivars.

Stomatal Conductance

Stomatal conductance decreases the rate of transpiration and plays an important role to regulate the water balance of plants. The closing of stomata decreases the growth rate and expansion of cells thus significantly reduced the yield and biomass of the plants (Nemeskari et al. 2015; Rauf et al. 2015; Pirasteh-Anosheh et al. 2016). Several researchers believed that closing of the stomata is the first reaction given by the plants to prevent them during water stress for saving the water loss by transpiration (Torres-Ruiz et al. 2013; Clauw et al. 2015; Nemeskeri et al. 2015). Ouyang et al. (2017) reported the significant variation in stomatal conductance among species of rice. They observed that lowland rice showed much higher stomatal conductance than other cultivars. Stomatal conductance was found to decrease in all cultivars during the water stress treatments.

Phenology and Ontogeny or Leaf Area and Leaf Area Index

Leaf area also plays an important role during water stress. Rice plants reduce their leaf area under water stress to save themselves from drought (Kramer 1969). It has been observed that rice plants with reduced leaf areas use less water and are found less productive (Blum 2007). Plants with reduced leaf area can fight during water stress conditions but their growth rate and biomass production are relatively low than the normal irrigated plants (Henson 1985).

Table 1 Yield reduction in rice under drought stress condition

Stage of growth	Level of stress	Reduced yield (%)	References
Vegetative stage	Severe stress	50.6	Guan et al. (2010)
Vegetative stage	Water stress	21	Sarvestani et al. (2008)
Flowering stage	Severe stress	76.7–83.7	Puteh et al. (2013)
Flowering stage	Water stress	50	Sarvestani et al. (2008)
Flowering stage	Severe stress	> 70	Shamsudin et al. (2016a, b)
Flowering	Short severe stress	54%	Lanceras et al. (2004)
Tillering and reproductive stage	7 days at reproductive stage	19.71–46.07	Singh et al. (2018)
Reproductive	Mild stress	53.92%	Lafitte et al. (2007)
Reproductive	Severe stress	94.48%	Lafitte et al. (2007)
Reproductive	Severe stress	24–84%	Venuprasad et al. (2007)
Reproductive stage	Moderate stress	51–57	Dixit et al. (2014a, b)
Reproductive stage	Severe stress	70	Dixit et al. (2014a, b)
Reproductive stage	Moderate stress	90.6	Dixit et al. (2012)
Reproductive stage	Severe stress	63.1	Dixit et al. (2012)
Reproductive stage	Severe stress	74.5	Guan et al. (2010)
Reproductive stage	Moderate to severe stress	51–60	Swamy et al. (2017)
–	Severe stress	45–50%	Jongdee et al. (2006)
–	Mild stress	15–20%	Jongdee et al. (2006)
Reproductive stage	Severe stress	87–75%	Kumar et al. (2008)
Reproductive stage	Very severe stress	95%	Kumar et al. (2008)
Reproductive stage	Mild stress	35–56%	Kumar et al. (2008)
–	Mild stress	15–54%	Jian-Chang et al. (2008)
Reproductive stage	Mild stress	10–38%	Atlin et al. (2006)
Reproductive stage	Severe stress	56–76%	Atlin et al. (2006)
Grain filling	Mild stress	30–55%	Basnayake et al. (2006)
Grain filling	Severe stress	60%	Basnayake et al. (2006)
Grain filling	Mild stress	19%	Lanceras et al. 2004)
Grain filling	Prolonged severe stress	84%	Lanceras et al. (2004)
Grain filling	Prolonged mild stress	52%	Lanceras et al. (2004)
Heading	Severe stress	23%	Lafitte et al. (2006)
–	Drying, soils dried beyond − 20 kPa	22.6	Carrijo et al. (2017)
–	Drought, water stress (40% water deficit)	> 50	Daryanto et al. (2017)
–	Mild	17%	Zhang et al. (2018a, b)
–	Moderate	27.8%	Zhang et al. (2018a, b)
–	Severe	32%	Zhang et al. (2018a, b)

Kamaruddin et al. (2018) observed that flag leaf area had a significant reduction in rice genotypes as compared to control plants under drought. Decreased flag leaf area results in small leaf size, senescence of leaf, and decreased emergence rate of a leaf (Solomon et al. 2007).

Effect of Drought on Root–Shoot Signaling

During stress environments, plants can regulate the signals positively or negatively between shoots and roots to maintain their growth and development. Root–shoot signaling reduced the growth and distribution of roots, growth, and functions of shoots during environmental stress (Novak and Lipiec 2012). Several molecules and factors act as signal molecules to regulate the physiological processes of a plant during the environmental stress such as Auxin, Cytokinin, Abscisic acid, Gibberellins, Ethylene and pH (Schachtman and Goodger 2008). Abscisic acid has been recognized as a stress hormone and plays an important role in root–shoot signaling during stress (Schachtman and Goodger 2008). During the water stress, plant roots synthesizes abscisic acid and transport it in the shoots via xylem, where it reduces the expansion of leaves and closes the stomata (Wang et al. 2000). Closing of stomata caused by the efflux of potassium ions from the guard cells resulting in loss of turgor pressure, which is promoted by the abscisic acid. Stomatal closure is an important process for plant adaptation under water stress conditions in the field. The level of abscisic acid has been found 50-folds increased due to loss of the turgor pressure of the cell (Guerrero and Mullet 1986). A series of signals from roots to shoots are responsible for the physiological changes in plants and determines the adaptation level of plants during the stress condition.

Photosynthesis

Photosynthesis is an important metabolic process that is directly altered by the drought. It determines the production of a crop. Plants respond to water stress by closing their stomata (Cornic and Massacci 1996; Hu et al. 2004; Farooq et al. 2009a, b), reducing the CO_2 entrance into plant leaves, lipid peroxidation and in balancing of water status (Allen and Ort 2001). The amount of heat dissipated by the plant declines with the decreasing transpiration rate (Condon et al. 2002). Higher temperature and water pressure make a negative impact on plant and reduce the leaf photosynthesis and WUE thus ultimately reduce the photosynthesis rate and transpiration rate of the plant. These effects can be partially balanced by the increasing atmospheric CO_2 concentration. The lower rate of transpiration for saving the water status can be managed by maintaining the optimal concentration of CO_2 in sub stomatal chamber at a lower level of stomatal opening (Condon et al. 2002). Water stress inhibits the gas exchange in plants and this may have resulted in decreased leaf expansion, alteration in photosynthesis system, premature leaf senescence, chloroplast lipid oxidation and changed structure of proteins and pigments (Menconi et al. 1995). In several studies, the net photosynthetic rate of rice plants has been found to increase by 20–30% under the drought stress (Farooq et al. 2009c). It has been also found in several studies that stressful condition affects on photoassimilates (sink strength) (Sharkey 1990; Tezara et al. 1999; Paul and Foyer 2001; Von Caemmerer 2003; Zhou et al. 2007). Sink strength decreases the process of photosynthesis under a stressful environment. Photosynthetic capacity of rice plants has been found a decreased cause of early stomatal closure in response to drought stress resulted to decrease in the assimilation rate and yield of plants (Yang et al. 2019). It has been investigated that when the plants were in gradually stress condition, the distribution of assimilates between roots and shoots was not affected. However, roots were found to have additional biomass in such conditions.

Rice is a C_3 cereal and has well defined grain (sink). Flag leaf of the plants has maximum contribution toward photosynthesis process and stores 62–90% carbon for grain development (Yoshida 1981). Tolerant plants maintain their assimilate export from source (leaves) to sink (storage organs) under the unfavorable environment and maintain their growth, development and yield during changed environments. Rubisco activity is reduced under drought conditions and it is responsible for decreasing the photosynthetic activity of a plant (Bota et al. 2004). During the drought, cell shrinks thus reduce the cell volume. At this time, the concentration of solutes in cell increased which may become toxic for the activity and function of the several important enzymes which are required for the photosynthetic process of the plants (Hoekstra et al. 2001).

Effect of Drought Stress on Pigment Composition

Photosynthetic pigments are an essential component of plants that plays an important role in light harvesting and in generating reducing power. Water stress affects both chlorophyll-A and chlorophyll-B (Farooq et al. 2009a, b). However, carotenoids may help to plant to stand against water stress. The changes in chlorophyll and carotenoids under the drought stress condition can be summarized as follows.

Chlorophyll Content

Chlorophyll is a major component of photosynthesis in green plants and has a positive relationship with photosynthetic rate. During the drought stress, chlorophyll degradation and oxidation of pigments occurs and this is considered as a typical symptom of oxidative stress and responsible for decreasing the chlorophyll content of the plant. Drought affects both chlorophyll-A and chlorophyll-B (Farooq et al. 2009a, b). The leaves of plant become old and yellow while losing chlorophyll and decreased the power of photosynthesis during the stress condition (Ahmadi 1985). Stress tolerance of plants is associated with high chlorophyll content (Kraus et al. 1995; Pastori and Trippi 1992). The measurement of chlorophyll fluorescence helps to understand the involvement of chlorophyll during the environmental stress (Brestic and Zivcak 2013; Jedmowski and Bruggemann 2015; Guidi et al. 2019). Stress has a negative impact and decreases chlorophyll content of plant. However, it has an important role in plant adaptation and maintaining the growth and development under the drought condition (Munne-Bosch and Alegre 1999; Sarani et al. 2014).Khan et al. (2017) observed the reduced chlorophyll content in drought stressed plants than normal plants (Nahakpam 2017).They reported the reduction in chlorophyll content of two rice cultivars under drought. The reduction was more pronounced in Super-7 (approx. 14.28%) in compare to PR-115 (approx. 7.04%) variety under drought. Whereas, Prasad et al. (2019) reported reduced chlorophyll content (SPAD value) in five rice genotypes Nagina 22 (approx 3% reduction), Swarna sub1 (approx 30% reduction), NDR 97(approx. 10% reduction), Shusk Samrat (approx 12% reduction) and NDR 9830102 (approx 20% reduction) at reproductive stage. Drought decreased chlorophyll-a content by 11.2 to 61.6% from 3 to 12 days of treatment and chlorophyll-b content by 21.4% at 6 days and it decreased the chlorophyll-a/b ratio by 18.2 to 58.5% from 3 to 12 days of treatment. It also decreased total chlorophyll content by 9.01 to 66.2% from 3 to 12 days of drought stressed condition (Nasrin et al. 2020).

Carotenoids

All photosynthetic and several non-photosynthetic organisms synthesize the carotenoids by de novo method of synthesis. Carotenoids are the molecules that belong to isoprenoid class(Andrew et al. 2008).Carotene plays an important role in the antioxidant defense system of plants but having much susceptibility to oxidative stress. Chloroplast is present in all green plants and contains Beta-carotene which is bound to the core of PSI and PS II complex (Havaux 1998). The concentration of both carotenoids and chlorophyll is decreased under the water stress condition (Kiani et al. 2008) because of ROS production in thylakoids(Reddy et al. 2004). Drought decreased the carotenoids content by 0.41 to 32.7% from 3 to 12 days of treatment (Nasrin et al. 2020). So the tolerance of the plants to drought can be improved by either inducing pigment synthesis or the modification in pathways that involves in pigment synthesis.

Osmolyte Accumulation

Under stressful conditions, different types of organic and inorganic substances are accumulated in the cytosol of the plants to reduce the osmotic potential by which they maintain their cell turgor (Rhodes and Samaras 1994). Several substances like Proline, Sucrose, soluble carbohydrates and others are accumulated under drought stress and improve the water uptake of plants from drying soil. The accumulation process of such substances under water stress conditions is called osmotic adjustment. The accumulation of proline occurs firstly in the plants under water stress condition to decrease the cells injury. Glycine betaine is also an important substance that improves the resistance of plants to several abiotic stresses. It has been suggested by several scientists to introduce the gene of glycine betaine in non-glycine betaine producing plants because it helps to improve the resistance of plant to abiotic stress (Chen and Murata 2002; Sakamoto and Murata 2002; Kumar et al. 2004). However, glycine betaine is not produced by rice plants in stress or non-stress condition (Rhodes and Hanson 1993). So, the transgenic plant of rice with overexpression of glycine betaine gene will increase the production of glycine betaine and shows resistance to water stress (Rhodes and Hanson 1993).

Seed Priming

When the metabolic processes for seed germination starts but the radical of seeds does not emerge cause of partial hydration of seeds is known as seed priming (Bradford 1986). It regulates the seed within lag phase (Taylor et al. 1998), so that seeds are not able to reach in log phase of growth. Primed seeds in rice usually show improved rate of germination, equal germination and percentage of total germination (Farooq et al. 2006; 2009d). It happens because of metabolic repair (Farooq et al. 2006; 2009d) during the process of seed imbibitions (Farooq et al. 2006).

Effects of Drought on Biochemical Characteristics

To maintain cell turgidity under water stressed conditions, plants accumulate several organic and inorganic compounds in the cytosol to maintain their osmotic potential (Rhodes and Samaras 1994). The process of biochemicals accumulation in cell is known as osmotic adjustment. Sucrose, glycine betaine, Proline, and several other solutes when accumulates in cytoplasm, osmotic adjustment is achieved which improves water uptake by a plant from drying soil. Among these compounds, due to its large importance in the stress tolerance, proline is most widely studied (Mostajeran and Rahimi-Eichi 2009; Chutia et al. 2012). The accumulation of soluble sugars is also induced by drought (Usman et al. 2013; Maisura et al. 2014). At molecular level, reactive oxygen species (ROS) is produced by the cell as a result of drought, which causes oxidative stress in cell. In terms of thiobarbituric acid (TBA) and thiobarbituric acid reactive substances (TBARS), the level of superoxide radical (O_2) and lipid peroxidation (LPO) have been found increased, and on the other hand, the concentration of total soluble proteins and thiols have been found decreased in rice plants under drought. Several other experiments showed enhanced antioxidant enzymes like superoxide dismutase (SOD), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR) and dehydroascorbate reductase (DHAR) activity in the rice crop when subjected to drought stress (Sharma and Dubey 2005). Rice plants activate the antioxidants defense mechanism and increase the level of these enzymes during oxidative stress by drought. Better antioxidant production was observed in drought-tolerant varieties as compared to susceptible ones (Lum et al. 2014). Also, the drought tolerance varieties shows increased proline level and higher soluble sugars production under drought stress (Mostajeran and Rahimi-Eichi 2009; Chutia et al. 2012).

Role of Proline Under Drought

Proline plays an important role in plants when the plant suffered by various stress (Verbruggen and Hermans 2008). In rye grasses, Kemble and Mac-Phersonin (1954) firstly reported the accumulation of free proline due to water stress. Due to its osmolytic properties, proline accumulation contributes to drought tolerance and better performance to plant (Vajrabhaya et al. 2001). Under drought stress condition in rice, the variation in proline concentration has been observed (Sheela and Alexallder 1995; Mostajeran and Rahimi-Eichi 2009; Bunnag and Pongthai 2013; Kumar et al. 2014; Lum et al. 2014; Maisura et al. 2014).Proline accumulation in the leaf of rice was increased by 1.3- to 10.2-folds from 9 to 18 days of drought treatment (Nasrin et al. 2020).Likewise, Swapna and Shylaraj (2017) imposed the drought by15% PEG6000 with osmotic potential (OP) of − 2.35 to − 2.95 MPa for 5 days at (28 ± 2) °C and observed the increased proline content by 31.81-folds in Swarnaprabha variety under drought with compare to control plants. Proline has an osmolytic activity and plays three important roles, i.e., as a defense molecule (saves the cell by oxidative stress), as a metal chelator and a signaling molecule during drought stress (Hayat et al. 2012). The accumulation of proline under drought stress increases the antioxidants activity which improves the damage repairing ability of plants. Proline can be used as a biochemical marker for screening the varieties for drought-tolerant under drought stress condition (Fahramand et al. 2014).

Role of Polyamines Under Drought

Polyamines are the important molecule involved in plant response to drought (Calzadilla et al. 2014). Polyamines like Putrescine, spermine and spermidine are mostly present in plants. They act as antioxidant, help in membrane stabilization and controls ionic and osmotic homeostasis. Higher polymer content is seen by the water-tolerant plant and this is attributable to increased photosynthesis ability, decreased water loss and improved osmotic responses. Many scientists suggested the role of polyamines, like it improves the binding activity of TFs (Panagiotidis et al. 1995) to DNA thus regulates action of gene, ionic maintenance, senescence inhibition, preventing free radical formation and helps to stabilizing membranes (Bouchereau et al. 1999), involved in protein phosphorylation and conformational changes of DNA (Martin-Tanguy 2001). Under the drought condition in rice, the instant response of polyamines accumulation has been observed (Yang et al. 2007; Basu et al. 2010). It has been suggested in several studies that rice plants have higher capacity to biosynthesis of PAs especially spermidine and spermine under the drought condition (Yang et al. 2007). Thus rice plants can enhance their tolerance to drought. Several events, mechanisms and components such as photosynthesis, WUE, synthesis of Proline, phenolics and anthocyanins respectively can be improved by the application of polyamines (Farooq et al. 2009c). The foliar application has been found more efficient than seed priming in several studies and spermidine is found more effective among polyamines to enhance tolerance in rice plant under drought (Farooq et al. 2009c; Do et al. 2013).Genetic engineering technology can be used to modify the Polyamines level of a plant. A gene, Datura adc, encodes arginine decarboxylase has been introduced in rice. These transgenic rice plants produce higher level of putrescine under drought, enhance the synthesis of spermidine and spermine and resulted plants save themselves by drought stress (Capell et al. 2004).Thus, the drought-tolerant plants can be produced by overexpression of the polyamines synthesizing gene in transgenic plants (Calzadilla et al. 2014).

Role of Plant Growth Regulators Under Drought

Plant growth regulators are the substances that can regulate the growth and development of plants. They act as chemical messengers for intracellular communication (Fishel 2006). It has been found that PGRs improve the plant tolerance to drought. Rice plants accumulate ABA under drought (Wang et. al. 2007; Ye et al. 2011; Ashok et al. 2013). ABA reduces the water stress effects and helps to better growth and development of plants under the stress condition. ABA reduces loss of water through transpiration by stomatal closure (Zhu 2002; Wang and Song 2008) and induces the expression of several genes whose products are involved in providing strength to plant under drought. ABA significantly increases the level of antioxidant enzymes (Latif 2014; Li et al. 2014), improves protein transport, inducing the carbon metabolism and resistance proteins expression, resulted plant shows tolerance to drought (Zhou et al. 2014; Pandey and Shukla 2015). It has been found in several studies that cytokines regulates the cell differentiation, leaf senescence and other important processes of plant growth and development (Sakakibara et al. 2006; Reguera et al. 2013). It has been found to regulate the assimilate partitioning (Ronzhina et al. 1994), sink strength (Kuiper 1993) and relationship of source/sink (Roitsch 1999). The increased level of cytokines improves the survival rate of plants under drought (Rivero et al. 2007). It has been found that synthesis of cytokinins in rice improves the drought tolerance (Peleg and Blumwald 2011; Reguera et al. 2013).

Role of Antioxidant Under Drought

Drought stress imparts disturbance between the production and quenching of reacting oxygen species (ROS) (Smirnoff 1998; Faize et al. 2011). ROS cause lipid peroxidation, proteins denaturation, DNA mutation, disturbance in cellular homeostasis and several other types of oxidative damages in a cell by the production of hydrogen peroxide, singlet oxygen, superoxide radical and hydroxyl free radical. The plant cell saves themselves from harmful effect of ROS by the use of complex antioxidation defense system. The antioxidant defense system maybe non-enzymatic as well as enzymatic. In the cell, SOD, MDHAR, GPX, DHAR, APX and GR are enzymatic antioxidants whereas ascorbate and glutathione are non-enzymatic antioxidants (Bors et al. 1989; Noctor and Foyer 1998). These antioxidants play an important role in ROS scavenging system and presence of these antioxidants in cell can improve the drought tolerance of rice plants. In rice, the action of ASA, APX, GSH (Selote and Khanna-Chopra 2004), SOD, MDHAR, DHAR, GR (Sharma and Dubey 2005), Phenyl ammonia lyase and CAT (Shehab et al. 2010) has been found increased with the increased level of drought stress. Catalase activity was found to be increased in the leaf of rice by 74.70% and also increased superoxide dismutase activity in the leaf of rice by 1.1-folds at 15 days of drought treatment (Nasrin et al. 2020). Nahar et al. (2018) found the increased level of CAT in shoots (approx 25%) and roots (approx. 28.57%), increased level of SOD in shoots (approx. 100%) and roots (approx. 111%), increased level of GPX in shoots (approx.100%) and roots (approx. 78%), increased level of APX in shoots (approx. 100%) and roots (approx. 150%), increased level of GR in shoots (approx. 155%) and roots (approx 140%) by comparing with control plants under drought stress applied by using PEG6000 using different varieties. In the tolerant cultivar, SOD enzymatic activity increased significantly only in the root tissue in the reproductive stage (268.00 Un/Mg), whereas in the sensitive cultivar, SOD increased in the leaf (112.17 Un/Mg) and root (172.56 Un/Mg) tissues during the reproductive stage (Deus et al. 2015). The increased level of these antioxidant enzymes protects the plants from oxidative damages under the drought stress in rice. SOD, POD and CAT are found to effectively reducing the ROS production and thereby saving the plants from negative effect of drought stress (Lum et al. 2014; Yang et al. 2014).Wang et al. (2019) reported the activity of SOD, POD and CAT which maintains the ability to scavenge hydrogen peroxide under drought condition, was increased with accumulation of time and intensity of drought stress in rice. Therefore, increasing the production of naturally occurring antioxidant enzymes can be a strategy to save the plants from oxidative damage and enhancing the drought resistance of plants (Hasanuzzaman et al. 2014).

Molecular Responses and Mechanism of Drought

Underpinning molecular basis of drought tolerance is very crucial for development of drought-tolerant varieties. Over the past two decades, extensive studies have been conducted to understand molecular basis of drought tolerance in rice (McCouch et al. 2003; Yue et al. 2006; Pandey and Shukla 2015). Transcriptomics analyses of rice genotypes under drought stress have shown differential expression of large number of genes associated with physiological, biochemical and signaling pathways to be critical for drought tolerance response (Rabbani et al. 2003). Among the main categories of genes differentially expressed under drought are (1) genes associated with biosynthesis of osmolytes, (2) genes involved in water uptake and transport; water channels and transporters, (3) genes encoding for detoxification enzymes and protective function proteins, (4) transcriptional control/signaling pathways associated genes (Yamaguchi-Shinozaki and Shinozaki 2005). Drought-induced intricate signaling network is a very critical component for activation molecular level responses that may determine adaptation of rice genotypes to low water regime. In rice, like any other plant species, drought stress is sensed at the level of plasma membrane level and transmitted through a range of signaling molecules (transducers) and thus finally regulate downstream genes encoding for protective proteins such as antioxidant enzymes, osmolyte biosynthesis pathway genes and stress associated proteins. Among the various transducers involved in drought signaling, receptor like kinases (RLKs) are the most important as these activate protein phosphorylation cascade needed for early stress responses (Tena et al. 2011; Ramegowda et al. 2014). RLKs are known to sense drought stress at the plasma membrane level by their extracellular domain which leads to dimerization followed by phosphorylation of the cytoplasmic domain that subsequently activates downstream signaling components. In rice two RLKs, *GROWTH UNDER DROUGHT KINASE* (*GUDK*) and S*TRESS INDUCED PROTEIN KINASE 1* (*OsSIK1*) are shown to be critical for drought tolerance response (Ouyang et al. 2010; Ramegowda et al. 2014). The GUDK phosphorylates a APETALA2/ETHYLENE RESPONSE FACTOR OsAP37 which then activates a range of drought stress responsive genes.

The drought responsive mechanisms in plant are broadly grouped into ABA-dependent and ABA-independent pathways (Liu et al. 2018). Water deficit causes enhanced ABA accumulation in vegetative parts leading to a range of morphological effects like stomata closure, accumulation of stress associated proteins and metabolites with protective function, and accumulation of H_2O_2 in guard cell. In a recent study, it was reported that early stage low water deficit treatment induced early flowering through ABA-dependent pathway and enabled rice plants escape drought (Du et al. 2020). Similarly, overexpression of *LOS5/ABA3*, which is involved in ABA biosynthesis was found to improve the grain filling and grain yield in rice under drought stress (Hu and Xiong 2014). The ABA-dependent responses essentially result from expression of ABA-responsive genes that contain a conserved ABA-responsive element (*ABRE*) in their promoter regions. On the other hand ABA- independent pathway involves drought-induced genes whose expression does not depend on accumulation of ABA and their promoter regions are.

Transcription factors (TFs) have also been implicated as major regulators of drought stress response in plants (Sahebi et al. 2018). TFs binds to the cis-elements located in the promoter region of their target downstream genes to regulate their expression and in turn responses to drought stress. Over the years many TF families such as AP2/ERF, MYB, NAC, WRKY, NF-Y and CAMTA have been demonstrated to have a role in abiotic stress tolerance (Mizoi et al. 2012, Puranik et al. 2012 and Lindemose et al. 2013). Notably, overexpression of some of the members of these TF genes under stress inducible or constitutive promoters conferred enhanced tolerance in rice against drought stress. Among these, AP2/ERF family TF, DREB that interacts with C-repeat/DRE (A/GCCGAC) elements have been most widely used to create drought-tolerant rice lines (Wang et al. 2008; Chen et al. 2008). Transgenic rice lines overexpressing*OsDREB1G* and *OsDREB2B* showed significantly higher level of tolerance to drought stress (Chen et al. 2008). Several members of NAC family also have role in drought tolerance. For example, a stress responsive NAC 1 (*SNAC1*), when overexpressed in rice, improved drought tolerance by regulating expression of its target gene *OsSRO1c* (You et al. 2013). Many other studies have demonstrated enhanced tolerance in rice lines expressing transcription factor genes such as *HVCBF4* (Oh et al. 2007), Ap37 (Kim and Kim 2009, Oh et. al. 2009), OsNAC045 (Zheng et al. 2009), *TSRF 1* (Quan et al. 2010), *JERF 3* (Zhang et al. 2010a, b), OsDREB2A (Cui et al. 2011), OsDREB2A (Mallikarjuna et al. 2011), SbDREB 2 (Bihani et al. 2011), Os5DIRI (Datta et al. 2012), *At DREB1A* (Hussain et al. 2014; Ravikumar et al. 2014), *OsNAC6* (Rachmat et al. 2014), and the BZIP family genes (Xiang et al. 2008; Liu et al. 2014a, b). Therefore, TFs have been considered as key targets to generate stress tolerance plants using genetic engineering approaches (Liu et al. 2014a, b).

Besides, signaling and transcription factor genes, there are many other proteins that play role in drought response. Accumulation of dehydrins and Late Embryogenesis Abundant (LEA) proteins in response to both low-temperature and water stress have been observed (Close 1997). LEA proteins are small proteins ranging from 10 to 30 kDa that are mostly present in plants that are produced during the embryo development maturation period and function as chaperons (Yadira and Reyes 2011). Overexpression of *OsLEA3* in rice enhanced drought tolerance in response to water stress. Similarly, overexpression of *HVA1* gene from barley which encodes LEA protein conferred enhanced tolerance in rice (Sivamani et al. 2000; Babu et al. 2004). Many studies reported changes in individual gene expression in rice under drought stress condition. These include glutathione reductase (Kaminaka et al. 1998), a translation elongation factor (Li and Chen 1999), an endo-1, 3-glucanase (Akiyama and Pillai 2001).

Drought Tolerance Associated Quantitative Trait Loci (QTLs)

A plant's drought tolerance system is very complex, regulated by several genes known as Quantitative Trait Loci (QTLs) (Fleury et al. 2010). The use of genomic methods has contributed to the discovery of QTLs correlated with characteristics of drought tolerance. Some of the significant and consistent grain yield QTLs during reproductive stage have been successfully established and validated by the rice drought breeding program at IRRI (qDTYs) such as qDTY$_{12.1}$ (Bernier et al. 2007), qDTY$_{2.1}$ (Venuprasad et al. 2009), qDTY$_{3.1}$(Venuprasad et al. 2009), qDTY$_{1.1}$ (Vikram et al. 2011; Ghimire 2012), qDTY$_{3.2}$ (Vikram et al. 2011), qDTY$_{2.2}$ (Swamy et al. 2013), qDTY$_{6.1}$ (Dixit et al. 2014a, b)using molecular markers. A variety of mapping experiments on drought stress in rice have been published. A list of QTLs listed for rice under drought is shown in Table 2.

By evolving different protein classes including transcriptional factors, molecular chaperones, enzymes, and other functional proteins, plants have evolved stable stress mechanisms or signaling chain processes (Usman et al. 2017). These proteins maximize plants' tolerance or immunity to drought conditions. In fact, multiple genomic methods have detected a several number of these genes (regulatory part and protein). These genes have been introduced into the rice genome either by repression or by overexpressions (Table 3) to examine their effect on drought improvement.

miRNA and Drought Responses

miRNAs are 20–22 nt long molecules that serve as an important regulator of genes at the post-transcriptional level (Baldrich et al. 2015; Gebert and MacRae 2018). They have been implicated in multiple processes such as growth and development, photosynthesis, biotic and abiotic stress responses and hormone signaling. miRNAs work closely with target genes and TFs to regulate associated processes. Studies have shown the role for miRNA genes in shaping drought

Table 2 Reported Quantitative Trait Loci (QTLs) under drought for shoot and root responses

Name of trait	Name of population	Name of marker	Type of lines	Number of QTL	References
Cellular membrane stability	IR62266 × CT9993	AFLP, RFLP& SSR	Doubled haploid line	9	Tripathy et al. (2000)
Dehydration avoidance	Bala × Azucena	AFLP, RFLP & SSR	Recombinant inbred lines	17	Price et al. (2002)
Deep roots	3 Populations	SSR, SNP	Recombinant inbred line	6	Lou et al. (2015)
Grain yield	Cocodrie (drought-sensitive) × Nagina 22 (N22) (drought-tolerant	SSRs, Indel markers, genic SSRs and SNPs	190 F2:3 progeny lines	1	Baisakh et al. (2020)
Grain yield over years and location	Apo/2 × Swarna	SSR	Recombinant inbred lines	1	Venuprasad et al. (2009)
Grain yield under severe lowland drought over environments	R77298 × Sabitri	SSR	BC1 derived	1	Yadav et al. (2013)
Grain yield under drought	Two population	SSR	Bulk-segregant and Selective genotyping	–	Vikram et al. (2012)
Grain yield in aerobic environments	Three populations	SSR	Bulk-segregant	1	Venuprasad et al. (2012)
Heritability for grain yield	CT9993 × IR62266	AFLP	Doubled haploid lines	1	Kumar et al. (2007)
Leaf water relations and rolling	Azucena × Bala	AFLP, RFLP & SSR	Recombinant inbred line	13	Khowaja and Price (2008)
Morphological and physiological traits	IR64 × Azucena	RFLP	Doubled haploid Lines	15	Hemamalini et al. (2000)
Osmotic adjustment	CT9993 × IR62266	AFLP, RFLP & SSR	Doubled haploid line	5	Zhang et al. (2001)
Osmotic adjustment and Dehydration tolerance	CO39 × Moroberekan	RFLP	Recombinant inbred line	1	Lilley et al. (1996)
Root traits	IR1552 × Azucena	SSR	Recombinant inbred line	23	Zheng et al. (2003)
Root architecture and distribution	IR64 × Azucena	RFLP	Doubled haploid line	39	Yadav et al. (1997)
Root number, thickness, length, and penetration index	IR58821 × IR52561	AFLP & RFLP	Recombinant inbred line	28	Ali et al. (2000)
Root penetration, root number, and tiller number	CO39 × Moroberekan	RFLP	Recombinant inbred line	39	Ray et al. (1996)
Root penetration	Azucena × Bala	AFLP & RFLP	Recombinant inbred line	18	Price et al. (2000)
Seedling drought resistance	Indica × Azucena	AFLP, RFLP & SSR	Recombinant inbred line	7	Zheng et al. (2008)
Seed fertility, spikelet per panicle and grain yield	Teqing × Lemont	SNP	Introgression lines	5	Wang et al. (2014)
Total water uptake, drought resistance and yield-related parameters	IR55419-04 × Super Basmati	SSR	composite interval mapping	1&3	Sabar et al. (2019)
Yield and yield traits at the reproductive stage	IR64 × Cabacu	SNP	Recombinant inbred line	1	Trijatmiko et al. (2014)
Yield at reproductive stage over environments	Two populations	SSR	Bulk-segregant analysis	2	Palanog et al. (2014)

Table 2 (continued)

Name of trait	Name of population	Name of marker	Type of lines	Number of QTL	References
Yield improvement	Crosses between elite *Geng* variety, Jigeng88, and four donors from three different countries	SSR	Joint segregation distortion method	–	Cui et al. (2018)
Yield under reproductive stage stress over seasons	Swarna × WAB	SSR	Backcross inbred line	1	Saikumar et al. (2014)

responses of plants. Differential expression of miRNA genes has been observed under stress. Under drought stress, miRNA genes act by regulation of ABA induced signaling (Samad et al. 2017). There are several families of TFs implicated under drought stress that regulate auxin-induced changes in tissues and organs, such as auxin response factors (ARFs), the NAC domain and AGO1(Sorin et al. 2005). miR160 targets ARF10 and ARF16, while ARF6 and ARF8 are controlled by miR167 in rice (Huang et al. 2014a, b; Li et al. 2016). Both miR160 and miR167 were downregulated in rice roots under drought stress. MiR164 targeted NAC genes and was shown to negatively regulate the resistance of drought in rice (Fang et al. 2014a, b).

On the other hand, miR160 negatively controls ARF10, resulting in sensitivity to ABA, which suggests cross-talk between the two hormones (Liu et al. 2007a, b, c). In rice, the miR167-ARF8-GH3 pathway is strongly reserved (Yang et al. 2006). In rice (Zhao et al. 2007), miR397 was also induced under drought conditions. Up regulation of Auxin responsive genes are occurred by suppressing miR396, where OsGRF6 positively controls auxin signaling in rice(Hu et al. 2018; Liu et al. 2014a, b).MiR396 and miR397 cross-talk and co-expression networks provide evidence that brassinosteroid (BR) and auxin is involved in controlling rice growth and yield (Zhang et al. 2014). BR cross talks with auxin and or GA to monitor rice yield (Niu et al. 2017). In Arabidopsis and rice, miR156 was dramatically induced, where it negatively controls SPL9 to improve tolerance of abiotic stress such as salinity and drought (Cui et al. 2014). The knockdown of miRNA166 in rice resulted in morphological changes related to the resistance to drought, such as leaf rolling and xylem constriction (Zhang et al. 2018a, b). In addition, miR167, miR394 and miR399 control physiological changes to the adventitious root growth in drought stress during mineral deficiency in rice (Grewal et al. 2018). MiR408 cleaves OsUCL8 (plastocyanin-like protein) to positively control photosynthesis and grain yield in rice (Zhang et al. 2017). MiR397 is downregulated in rice under drought (Zhou et al. 2010; Fahad et al. 2017) while miR397b is upregulated in Arabidopsis by ABA and drought. Another modulator, miR398, controls rice respiration by targeting subunit V (COX5b) of cytochrome C oxidase, which functions as an electron transporter in respiration (Ding et al. 2013; Cheah et al. 2015).

Two zinc finger TFs are regulated by miR159 such as OsTZF1 (CCCH-tandem zinc finger protein 1) and OsDOS (delay of senescence protein onset) that negatively control senescence and thus provide immunity to abiotic stresses such as drought in rice (Kong et al. 2006; Pomeranz et al. 2010). MiR159, along with miR167 and miR172, mediates resistance to senescence in rice (Lim et al. 2003). In addition, miR164 was strongly expressed in rice leaves, where SIP19 (salicylic acid-induced protein 19) was negatively regulated by it, hence delayed senescence (Xu et al. 2014). NAC genes are also targeted to negatively control drought resistance by miR164 in rice (Fang et al. 2014a, b).

Seven miRNAs were identified by Li et al. (2011a, b) in rice during oxidative stress which was responsible for the regulation of H_2O_2 (miR169, miR319a.2, miR397, miR408-5p, miR528, miR827, miR1425). Many others like miR164 and miR169 (Andres-Colas et al. 2018), downregulation ofmiR159f, miR397a, miR398b, miR408-3p, miR528-5p, miR1871, and miR2878-5p was found to involve in antioxidant defense system.

Fertilizer Management

Fertilizers input play vital role in increasing crop productivity. Over the past five decades, productivity of rice in irrigated ecosystems has increased due to the combined use of modern semi-dwarf varieties and high inputs of nitrogen fertilizers (Banayo et al. 2021a, b). The improved fertilizer management system, known as “site-specific nutrient management,” has been developed for use in rice cultivation in tropical Asia, where fertilizer requirements of rice crop are estimated from the nutrient supply of the soil and the needs of plants (Dobermann et al. 2002). This approach has been extensively evaluated in farm studies over the past two decades (Buresh et al. 2019; Pampolino et al. 2007). Among the major plant nutrients, appropriately higher levels of nitrogen have been shown to alleviate drought stress

Table 3 Drought-tolerant gene tested in rice

Action of gene	Name of gene	Name of promoter	Technique of transformation	Response in plant	References
Abscisic acid Metabolism	CaM-V35SP	DSM2	Agrobacterium	Oxidative and drought stress resistance and increase of the xanthophylls and non-photochemical quenching	Du et al. (2010)
Amino acid metabolism	OsOAT	Ubi1	Agrobacterium	Improve drought tolerance and increase seed setting	You et al. (2012)
Arginine decarboxylase	ADC	CaMV35S	Biolistic	Reduction in chlorophyll loss under water deficiency	Capell et al. (1998)
Polyamine synthesis	ADC	Ubi1	Agrobacterium	Improved drought tolerance by producing higher levels of putrescine and spermine synthesis	Capell et al. (2004)
Protoporphyrinogen oxidase	PPO	–	Agrobacterium	Less oxidative damage, and drought tolerance	Phung et al. (2011)
Proline synthesis	P5CS	Act1	Agrobacterium	Resistance to water and salinity stress	Su and Wu (2004)
Proline synthesis	P5CS	AIPC	Biolistic	Increased biomass production under salinity and drought stresses	Zhu et al. (1998)
Reactive oxygen species scavenging	OsS-RO1c	Ubi1	Agrobacterium	Oxidative stress tolerance and stomata closure regulation	You et al. (2013)
Trehalose synthesis	OsTPS1	Actin1	Agrobacterium	Tolerance of rice seedling to drought, cold, and high-salinity	Li et al. (2011a, b)
Trehalose synthesis	TPSP	Ubi1	Agrobacterium	Cold, salt and drought tolerance expressed by chlorophyll fluorescence	Jang et al. (2003)
Genes associated to late embryogenesis abundant (LEA) protein					
LEA protein gene	HVA1	Actin1	Agrobacterium	Cell membrane stability, higher leaf relative water content (RWC) and increase in growth under drought stress	Babu et al. (2004)
	HVA1	Actin1	Agrobacterium	Drought and salinity tolerance	Rohila et al. (2002)
	HVA1	Actin 1	Biolistic	Increased drought tolerance and salinity stress	Xu et al. (1996)
	OsLEA3-1	Rice LEA3-1	Agrobacterium	Drought resistance for grain yield under field conditions	Xiao et al. (2007)
	OsLEA3-2	CaMV35S	Agrobacterium	Drought resistance and increase grain per panicle	Duan and Cai (2012)
Different regulatory genes					

Table 3 (continued)

Action of gene	Name of gene	Name of promoter	Technique of transformation	Response in plant	References
Transcription factor	ABF3	Ubi1	Agrobacterium	Improved salinity and drought tolerance	Oh et al. (2005a, b)
	AP37	OsCc1	Agrobacterium	Improve growth performance under drought stress	Oh et al. (2009)
	OsNAC9	GOS2 (constitutive promoter), RCc3 (root-specific promoter)		Under drought conditions (vegetative stage), RCc3:OsNAC9 plants showed an increased grain yield of 28%–72%, while the GOS2:OsNAC9 plants remained unchanged. Both transgenic lines exhibited altered root architecture involving an enlarged stele and aerenchyma	Redillas et al. (2012)
	OsNAC10	GOS2 (constitutive promoter), RCc3 (root-specific promoter)	–	Enhanced drought tolerance at the reproductive stage, increasing grain yield by 25% to 42%, root-specific overexpression of OsNAC10 enlarges roots	Jeong et al. (2010)
	OsNAC14	*OsRAD51A1*	Agrobacterium	Higher number of panicle and filling rate under drought	Shim et al. (2018)
	DREB1 or OsDREB1	CaMV 35S	Agrobacterium	Tolerance to water deficient, low-temperature and high-salt stresses	Ito et al. (2006)
	DREB2	rd29A	Agrobacterium	Improve grain yield under drought stress	Bihani et al. (2011)
	HvCBF4	Ubi1	Agrobacterium	Tolerance to drought, high-salinity, and low-temperature	Oh et al. (2007)
	OsbZIP23	Ubi1	Agrobacterium	Wide spectrum to salt and drought tolerance and improvement in yield	Xiang et al. (2008)
	OsbZIP72	CaMV35S	Agrobacterium	Drought resistance and ABA sensitivity	Lu et al. (2009)
Ethylene-responsive factor 1	TSRF1	–	Agrobacterium	Enhances the osmotic and drought tolerance	Quan et al. (2010)
Harpin	protein Hrf1	CaMV 35S	Agrobacterium	Drought resistance through ABA signaling and antioxidants, and stomata closure regulation	Zhang et al. (2011)
Jasmonate and ethylene-responsive factor 1	JERF1	CaMV35S	Agrobacterium	Drought resistance	Zhang et al. (2010a, b)
Protein degradation (E3 ubiquitin ligase)	OsRDCP1	CaMV35S	Agrobacterium	Improved tolerance to drought stress	Bae et al. (2011)
	OsSDIR1	Ubi1	Agrobacterium	Stomata regulation under drought stress	Gao et al. (2011)

Table 3 (continued)

Action of gene	Name of gene	Name of promoter	Technique of transformation	Response in plant	References
RING finger protein	OsCOIN	CaMV35S	Agrobacterium	Cold, salt and drought tolerance	Liu et al. (2007a, b, c)
Stress/zinc finger protein	OsiSAP8	–	Agrobacterium	Tolerance to salt, drought and cold stress	Kanneganti and Gupta (2008)

tolerance and reduce grain yield losses in rice as well as many other species. The plant supplied with appropriate level of nitrogen have better stomatal dynamic, maintain photosynthetic integrity, elasticity in root system development and have strong antioxidant capacity. A recent study by Du et al. (2020) suggests that heavy nitrogen application before start of the drought may be an important approach to improve grain yield in rice. However, too much of nitrogen application in rice nursery can produce seedling with weak stem that are easily damaged during transplanting. Further, rice varieties are also known to differ in their response to N fertilizer, therefore choosing fertilizer-efficient varieties in drought conditions appears to be the key to increasing rice productivity through better fertilizer management in the rainfed lowlands (Haefele et al. 2016; Banayo et al. 2021a, b).

Conclusions

Abiotic stress signaling is a significant area for augmenting plant productivity. Among the abiotic stress, drought is a major global problem, which severely reduced quality and crop production worldwide. Due of advances in omic-based integrated approaches and rice genome sequencing project provides the genetic and genomic information to the researchers for improving the trait against stress condition. Several novel molecular markers were investigated after genome sequencing project and being utilized for crop improvement. The responses of rice at genomic, transcriptomic and phenomics levels under drought stress are also decoded and this information can be utilized for improving drought tolerance in rice using integrated approaches. The integration of the multidisciplinary fields like genomics, transcriptomics and other omics with precise phenotyping can be used for the improvement of rice against drought stress in future and this can result in the higher production of rice for global food security.

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Declarations

Conflict of interest Authors declare no conflict of interest.

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