



# Increasing Rice Grain Yield Under Abiotic Stresses: Mutagenesis, Genomics and Transgenic Approaches

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## Abstract

Rice is a main source of food to millions of people across the world, and hence increase in its production/yield is vital to feed the rapidly growing population. However, the yield of rice is decreased to a large extent due to the adverse effects of several kinds of abiotic stresses such as drought, salinity, heat stresses, etc. Different traditional and modern breeding approaches have been used to mitigate the damaging effects of different abiotic stresses on the rice production. Traditional breeding strategies such as hybridisation and selection have resulted in the development of few stress-tolerant varieties, but such strategies are laborious and time-consuming. The modern biotechnological approaches such as mutagenesis, transgenics and genomics have been effective in the identification, cloning and characterisation of genes that govern tolerance to different abiotic stresses. Insertion of such genes into the rice plants have decreased the yield loss caused by various abiotic stresses. Modern biotechnological tools have brought landmark achievements by developing varieties with enhanced tolerance to various abiotic stresses. The role of mutagenesis, genomics and transgenic approaches in the creation of rice varieties with improved yield under different abiotic stress has been reviewed in this chapter.

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**Keywords**Drought · Heat · Salinity · Mutagenesis · Transgenics · Genomics

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**1 Introduction**

*Oryza sativa* L. is commonly known as rice with chromosome complement  $2n = 2x = 24$ , a member of Poaceae family with a huge diversity comprising of more than 40,000 cultivated varieties. Rice is an ancient staple food with the origin of centre in southern and south-western tropical Asia and origin of domestication in India and China (Vavilov 1926). *Oryza sativa* is the main species of rice cultivated across the world. To date, 23 species and ten kinds of genomes of rice including AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ and HHKK have been reported ([gramene.org](http://gramene.org)). About one in three persons on Earth consumes rice, and it is believed that more than 50% of total human population is dependent on rice for their food requirements. According to FAO forecasts, the food production must be double to feed the rapidly growing human population which is likely to rise to nine billion in 2050. In addition to sky high population; shrinking arable land, depleting natural resources, erratic rainfalls and drastic climate change further reduces the rice production. This will create a huge demand on the food production and will exceed the food supply by a greater mark. Further, the overall yield of rice is sternly reduced by several environment induced abiotic stresses (Ansari et al. 2015; Manju et al. 2017). Increasing population and economic development have been posing a growing pressure for increase in food production (Zhang 2007). All these challenges can be met by the development of rice varieties with improved yield, resistance to abiotic stresses and improvement in grain quality via the use of modern biotechnological breeding approaches (Fahad et al. 2016a, b).

**1.1 Abiotic Stresses**

The occurrence of global warming, depleting rice lands, exhausted water resources, erratic rainfalls, expanding urbanisation and climate-induced abiotic stresses lead to significant reduction in the production of crops including rice (Pandey et al. 2015, b). Among the abiotic stresses, drought, salinity and heat have been reported to cause substantial yield loss in various agro-economically important crops (Ahmad and Samiullah 2019; Ahmad et al. 2019). In the current scenario, it is imperative to employ breeding approaches both conventional and modern with the main aim of increasing tolerance to abiotic stresses (Leonforte et al. 2013). However, with the complex nature of inheritance of tolerance to abiotic stress and meagre understanding, it will be quite difficult to enhance tolerance in existing rice varieties (Lafitte et al. 2006). The main abiotic stresses that limit the rice production are discussed below.

## 1.2 Drought Stress

As compared to other cereals, rice requires a huge quantity of water to complete its life cycle (Pandey and Shukla 2015). The drought reduces the yield, and the degree of reduction depends on the variety and the timing of drought occurrence (Wassmann et al. 2009; Dixit et al. 2014a, b). In addition to yield reduction, the drought stress affects various morpho-physiological and biochemical traits in rice plants (Basu et al. 2010). The significant decline in crop yield has been attributed to the negative impact of drought on plant growth, physiology and reproduction. Nahar et al. (2016) reported that drought induced low seed germination and decreased seedling growth could be the probable reason for substantial yield drop. Drought also disrupts the regulation of stomatal opening and closing by making stomatal closure at higher rate, reduces leaf water potential and consequently leads to decrease in cell dimensions and overall plant growth. The drought stress also causes a reduction in leaf dimensions and turgor pressure within leaf cells which in turn result in leaf rolling and quick senescence. An observation of reduced cell division and root elongation on the onset of drought may be attributed to the lesser growth and yield of the plant (Singh et al. 2012). Furthermore, severe drought stress results in drop in photosynthetic and respiration rate, translocation and ion uptake and carbohydrate and nutrient metabolism and consequently leads to stunted growth (Jaleel et al. 2008; Razmjoo et al. 2008). In addition to the abovementioned effects, drought stress also causes disturbance in assimilate partitioning and photosynthetic rate which eventually lead to a considerable reduction in overall yield (Praba et al. 2009). A shrink in the photosynthetic rate also results in reduced activity of chlorophylls a and b, PSI, PSII and photosynthetic enzymes such as Rubisco and PEPcase, thus reducing the rate of carbon dioxide fixation and overall production (Asharf and Harris 2013; Banerjee and Roychoudhury 2018). In order to combat the devastating effects of drought on plant growth and development, it is imperative to have broader understanding of drought stress and its tolerance mechanism (Nahar et al. 2016).

## 1.3 Heat Stress

In the era of global warming due to continuous increase in the atmospheric temperatures, heat stress is considered as a potential abiotic stress that limits the overall yield of many agro-economically important crops including rice (Fahad et al. 2017). Rice is more sensitive to the heat stress occurring at grain filling stage that adversely affects many physiological and biochemical processes in crop plants, which result in reduced plant productivity (Zhang et al. 2016). Apart from various negative effects of heat stress on the grain filling stage, vegetative parts are also greatly impacted due to heat stress, and its impact depends on the variety grown and timing of occurrence. It also induces a series of morpho-physiological and biochemical variations, especially in enzyme activities with abnormal elevation or complete denaturation which consequently affects the overall growth. Heat stress also causes

reduction in pollen fertility, thereby disrupting the pollination rate, and hence reduced flower and seed set. This has been attributed to substantial decrease in yield in rice (Zhang 2007; Liu et al. 2013). Heat stress at the flowering stage resulted in the increase in the number of sterile and aborted spikelet that leads to a drop in yield, while heat stress at harvesting stage did not affect overall yield (Aghamolki et al. 2014). Fahad et al. (2016c) have reported that elevated temperature at night also results in a reduction in 100-grain weight, which is considered as one of the main yield-attributing traits of rice.

## 1.4 Salinity Stress

Globally, salinity stress is recognised as one of the most devastating abiotic stresses that limit the overall crop production of cereals (Mondini and Pagnotta 2015). It is considered as one of the main obstacles in achieving the desired goals of rice production as the rice varieties are more sensitive to the salinity stress that incurs more than 50% yield loss. Therefore, attention needs to be paid towards the genetic improvement of rice varieties with improved tolerance to salinity (Molla et al. 2015). All the main developmental stages including germination, vegetative, flowering and seed stages are influenced by the increase in salinity stress (Fujino et al. 2004). The effectiveness of employing a proper selection of rice seedlings for the development of rice varieties with improved salt tolerance and subsequent increase in the overall yield and yield-attributing traits has been reported by Cuartero et al. (2006). However, traditional breeding approaches such as selection is cumbersome, laborious and time-consuming and would require 8–9 years on an average for the development and official release of salt-tolerant rice varieties. Therefore, to speed up the development of elite varieties, it is important to have an in-depth understanding of mechanism underlying salinity tolerance at morpho-physiological and molecular levels (Roychoudhury et al. 2008; Horie et al. 2012). Baby et al. (2010) have reported that the development of salinity-tolerant genotypes is a challenging task as the salinity tolerance is polygenic trait with complex mode of inheritance; therefore, direct selection for tolerance trait is rarely effective. Hence, to create rice varieties with improved salt tolerance, deeper research that is based on identifying key genes that govern the inheritance of salt tolerance trait is required (Bizimana et al. 2017). Several morphological and molecular markers should be employed to screen and select the rice seedlings that display high tolerance to salt stress. After screening, the rice seedlings should be subjected to multi-location trials to check the stability of tolerance trait before official release of salt-tolerant rice varieties (Roychoudhury and Chakraborty 2013).

## 2 Modern Breeding Approaches for Improving Abiotic Stress Tolerance in Rice

At present, efforts are made to identify key genes that play a critical role in the abiotic stress tolerance with the main objective of creation of rice varieties with improved stress tolerance. For this, several approaches have been used from time to time, and some of the main approaches include mutagenesis, genomics, transgenics, etc. (Kim et al. 2014; De Leon et al. 2017; Okazaki and Saito 2016; Manju et al. 2017). However, transgenics and genomics were more successful in developing the varieties with improved tolerance to a wide range of abiotic stresses and are discussed in detail in following subsections.

### 2.1 Mutagenesis

Induced mutations by chemical and/or physical agents were employed by several plant breeders to create rice varieties with high yielding potential and better tolerance to abiotic stress (Raina et al. 2016; Khursheed et al. 2019). The continuous use of traditional breeding approaches in the past several decades led to narrowing of genetic variation in several crops including rice. Among the various breeding approaches used to date, mutagenesis has proven relatively effective tool for enhancing the genetic variation and improving resistance to abiotic stresses. Mutagenesis equips the plant breeders to make the efficient selection of the genotype for the desired traits including resistance to abiotic stresses (Raina et al. 2018a; Raina and Danish 2018). Several researchers have employed different mutagens in different doses for creating varieties with desired traits in crops such as chickpea (Laskar et al. 2015; Raina et al. 2017, Raina et al. 2019), lentil (Laskar et al. 2018a, b), cowpea (Raina et al. 2018b), mung bean (Goyal et al. 2020a, b; Wani et al. 2017), faba bean (Khursheed et al. 2018a, b, Khursheed et al. 2018c), fenugreek (Hassan et al. 2018) and black cumin (Amin et al. 2016, 2019; Tantray et al. 2017). Mutagenesis has played a vital role in improving characters such as plant yield, earliness, adaptability and tolerance to a wide range of abiotic stresses (Khursheed et al. 2015, 2016; Laskar et al. 2019; Goyal et al. 2019a, b; Raina and Khan 2020; Raina et al. 2020).

At present, continuously rising global warming along with drastic climate change has led to increased occurrence of drought which is affecting the overall production of important crops such as rice (Hallajian 2016). The International Rice Functional Genomics Consortium maintains 0.2 million mutant lines of rice, with mutations in about 50% of mapped genes to date (Krishnan et al. 2009). The FAO/IAEA Mutant Variety Database (MVD) maintains information about 3322 officially released mutant varieties which include 829 rice mutant varieties ([www.mvd.iaea.org](http://www.mvd.iaea.org) accessed March 2020). Recently in April 2019, a mutant variety of rice named as 'Trombay Chhattisgarh Dubraj Mutant-1' has been developed and released in Chhattisgarh, India. This variety has short stature and early maturity which improved its resistance to lodging and the grain yield. Several drought-tolerant rice varieties

have been created all over the world. In 2015, two drought-tolerant rice mutant varieties named as NMR 151 and NMR 152 have been developed by irradiation of popular Malaysia rice variety MR 219 (breeding line developed by MARDI) using gamma rays at dose 300 Gy ([mvd.iaea.org](http://mvd.iaea.org) accessed March 2020).

Up to now, nine drought-tolerant varieties of rice, viz. 202 in 1973 at China, Azmil mutant in 1976 at Philippines, RD 15 in 1978 at Thailand, CNM 6 in 1982 at India, Danau atas in 1988 at Indonesia, IACuba 23 in 1995 at Cuba, NMR 151 in 2015 at Malaysia, NMR 152 in 2015 at Malaysia and Binadhan-19 in 2017 at Bangladesh, have been developed (Table 1). Researchers at Vienna promote creation of more sustainable rice varieties with the main aim to improve the tolerance to abiotic stresses such as drought, heat and salt stress (Kaskey 2013). India made a landmark achievement by developing a mutant variety of rice, viz. CNM 6 (Lakshmi), by irradiating IR8 with 300 Gy X-rays under real field conditions at different geographical sites with improvement in tolerance to drought, reduction in maturity and stature and enhancement in aroma and yield ([mvd.iaea.org](http://mvd.iaea.org) accessed March 2020). Researchers at Australia were successful in developing rice varieties with improved tolerance to abiotic stresses and enhanced grain yield. Another mutant Nagina 22 (N22) was developed by treating the parent variety with ethyl methanesulfonate; the mutant variety displayed improvement in a deep-rooted system and enhanced tolerance to drought and heat stress (Panigrahy et al. 2011).

Heat stress is also one among the major abiotic stresses that restricts plant growth, metabolism and overall production of plants worldwide (IPCC 2007). Heat stress influences all growth stages of rice and incurs a huge loss in rice grain quality and yield (Nakagawa et al. 2003; Matsui et al. 1997). Mutagenesis is used to increase the overall genetic variability of rice that enables the rice breeders to make selection for the heat stress-tolerant lines. Physical mutagens such as gamma rays have broadened the scope of increasing genetic variability in various agro-economic traits. Gamma radiations were employed by rice breeders to improve genetic variations and to render them more yielding and tolerant to heat stress (Luzy-Kihupi et al. 2009). The rice mutant varieties may involve heat resistance mechanism that is linked with increased synthesis and build-up of heat shock proteins. However, the molecular mechanism making rice plant cells survive from heat stress is very complicated, and hence more information is needed. The heat-resistant mutant variety, namely, Zaoyeqing, was developed by irradiation of seeds with 200 Gy gamma rays and officially approved in 1980. Another mutant variety named as Binadhan-14 was developed in 2013 by Bangladesh. This variety had improved tolerance to high temperature, shorter height and long fine grains ([mvd.iaea.org](http://mvd.iaea.org) accessed March 2020). The mutant rice lines were developed using 150 and 200 Gy gamma rays with the main aim of enhancing tolerance to heat stress. Recently, Targeting Induced Local Lesions in Genome (TILLING), a reverse genetic method, has been used for the characterisation of putative heat-tolerant (HT) mutant upland rice lines from gamma ray-induced mutation and target mutation in genes linked with heat stress tolerance. Although originally TILLING was developed for use with *Arabidopsis* only, now the technique has been applied to a wide range of plants, including rice (Till et al. 2006). McCallum et al. (2000) reported its use for detection of mutations

**Table 1** Role of mutagenesis in the development of rice varieties with enhanced tolerance to abiotic stresses (MVD 2019)

Name	Country	Year	Mutagen (dose)	Traits improved
202	China	1973	Gamma rays (200 Gy)	Small leaves, large panicle and tolerance to drought
CNM 6	India	1980	X-rays (300 Gy)	Early maturity, increased tillering, 10% higher yield, long grain size, resistance to drought, dwarf (85 cm), long bold grains
Danau atas	Indonesia	1988	Gamma rays (400 Gy)	Resistance to drought, high yield
RD 15	Thailand	1978	Gamma rays (150 Gy)	Early maturity and tolerance to drought
Azmil mutant	Philippines	1976	Gamma rays (200 Gy)	High yield, drought resistance
IACuba 23	Cuba	1995	Fast neutrons (20 Gy)	Resistance to drought and high amylose content
Binadhan-19	Bangladesh	2013	Physical mutagen	Shorter height, shorter duration, uniform plant growth, long and slender grains with golden colour, higher yield
NMR 151	Malaysia	2015	Gamma rays (300 Gy)	Minimal water requirement and high yield
NMR 152	Malaysia	2015	Gamma rays (300 Gy)	Minimal water requirement, high yield and longer panicle length
Zaoyeqing	China	1980	Gamma rays (200 Gy)	Large panicle and tolerance to high temperature
Fuxuan 1	China	1968	Gamma rays (300 Gy)	Early maturity, tolerance to salinity and good adaptability
Liaoyan 2	China	1992	Gamma rays	Tolerance to salinity, high yield, multiple resistance, high quality, good adaptability
Rasmi	India	1976	Gamma rays (220 Gy)	Awnless, high yield, tall plant type and tolerance to salinity
Mohan	India	1983	Gamma rays	Salt tolerance
Atomita 2	Indonesia	1983	Gamma rays (200 Gy)	Tolerance to salt, early maturity, higher protein content
Shadab	Pakistan	1987	0.5% EMS	High yield, improved grain quality, resistance to salinity
Shua 92	Pakistan	1993	Gamma rays	Resistance to salinity and high yield
NIAB-IRRI-9	Pakistan	1999	Fast neutrons (15 Gy)	Salt tolerance
A-20	Viet Nam	1990	0.015% MNH	Early maturity and high tolerance to salinity
DT17	Viet Nam	1999	NA	High yield and tolerance to salinity
VND 95-19	Viet Nam	1999	Gamma rays (200 Gy)	Strong tolerance to acid sulphate soil, sturdy stem, high yield (5–10 t/ha)

(continued)

**Table 1** (continued)

Name	Country	Year	Mutagen (dose)	Traits improved
VND 95-20	Viet Nam	1999	Gamma rays (200 Gy)	Short duration (90–95 days), stiff stem, high yield, amylose content, tolerant to salinity
Lunisree	India	1992	NA	Long slender grain for coastal saline areas, high yield
GINES	Cuba	2007	The mutant variety protons (20 Gy)	Tolerance to salinity and good quality
Wonhaebyeo	Korea, republic of	2007	Gamma rays (50 Gy)	Tolerance to salinity

in rice genomes; TILLING method can be used to screen genes for specific mutations using a PCR assay and then enzymatic digestion of PCR products by CEL I (Till et al. 2006). Among the 64 putative rice lines screened for heat tolerance, 34 mutant rice lines were recognised to have mutations in heat-tolerant genes (HSP genes) and reflected enhanced tolerance to high temperatures (Yona 2015).

Mutagenesis technique also played a vital role in developing crop varieties with improvement in tolerance to salinity stress. To date, about 15 mutant varieties with enhanced tolerance to salt stress have been developed. Moreover, there are several other elite mutants that showed promising results for heat tolerance and are subjected to multi-location trials as a prerequisite for the official registration and release. The rice mutant, viz. Shu-92, developed in Pakistan showed substantial increase in yield by 40–49% margins against standard salt-tolerant checks (Balooch et al. 2003). Another rice mutant, GINES, has been developed in 2007 by Cuba which have reflected high tolerance to saline soils and higher yielding potential. Bangladesh Institute of Nuclear Agriculture (BINA) in collaboration with International Rice Research Institute (IRRI) has been successful in developing two salt-tolerant rice varieties, namely, BINA dhan 8 and BINA dhan 10, which showed substantial improvements in tolerance to salt stress ([bina.gov.bd](http://bina.gov.bd)). The collaborative mutagenesis research between the IAEA and IRRI aimed at the genetic improvement of rice with the focus on improving salt tolerance in the backdrop of increased salt concentration in rice lands. A major breakthrough was the development of salt-tolerant variants from IR29, a variety which is highly sensitive to salt stress. The salt-tolerant mutant lines derived from IR29 with improved traits will play a major role in addressing the scourge of salinity in rice agriculture in Southeast Asia (Mba et al. 2007). Further attention has been paid towards the improvement for the overall plant growth and development and grain quality and quantity of wild rice species, Pokkali (Lee et al. 1996; Gregorio et al. 2002).



## 2.2 Transgenics

The abiotic stresses incurred a huge loss to the overall productivity of rice, and common transgenic approaches are employed to address the issues of abiotic stress (Table 2). As the understanding of mechanisms involved in tolerance to abiotic stresses increases, the identification and characterisation of multiple genes that govern the stress tolerance is becoming easier. In response to salinity, drought and heat stress plants regulate the expression of genes that control the synthesis of low molecular weight compounds, viz. GB (glycine betaine), proline, trehalose, amphoteric quaternary amines and LEA (late embryogenesis abundant) proteins to combat the effects of abiotic stresses (Roychoudhury et al. 2011; Roychoudhury et al. 2015; Roychoudhury and Banerjee 2016). Shirasawa et al. (2006) reported the increased synthesis of GB that imparted resistance to salinity and heat stress in transgenic rice overexpressing spinach choline monoxygenase. Kumar et al. (2009) have reported mutagenised gene P5CS ( $\Delta^1$ -pyrroline-5-carboxylate synthase) with phenylalanine substituted for an alanine at 129-amino acid position, hence named as P5CSF129A gene in transgenic rice that leads to the increased synthesis of proline in response to exposure to salinity stress. Similarly, another gene in transgenic rice that plays a vital role in imparting tolerance to abiotic stress is OsTPS1 (trehalose-6-phosphate synthase) and results into manifold increase in the synthesis of osmoprotectant solute, proline and trehalose (Li et al. 2011). Xiao et al. (2007) and Duan and Cai (2012) have reported that overexpression of OsLEA3-2 (rice late embryogenesis abundant), OsLEA3-H and OsLEA3-S genes in genetically engineered rice imparted much better resistance to drought and salt stress. The role of polyamines in combating the abiotic stresses is not much known and is at very initial stage; however, the functional genomics have brought few significant insights into the role of polyamine synthesising genes in abiotic stress tolerance. Although no genetically engineered rice with increased polyamine synthesis have been developed, however, preliminary research has reflected that genes OsPUT1 (rice polyamine uptake transporter) and AdoMetDC (*S*-adenosylmethionine decarboxylase) are the potential candidate genes that confer the tolerance to abiotic stresses via regulating the synthesis of polyamine (Mulangi et al. 2012). To date, a huge number of transcription genes have been isolated and characterised that confer resistance to drought, heat and salinity (Kumar et al. 2013). Many genes isolated from different plants or even rice varieties that show tolerance to abiotic stresses have been introduced into widely cultivated rice varieties through genetic modification with the objective to enhance the tolerance to a wide range of abiotic stresses. Some of the noteworthy examples include the following: The transgenic rice showing overexpression of HvCBF4, ZmCBF3, OsDREB1F and OsDREB2A isolated from barley, maize and rice, respectively, introduced and overexpressed showed an increased survival under salinity and drought stress (Wang et al. 2008, b; Mallikarjuna et al. 2011). Research has shown that different transcription factors (TFs) in transgenic rice play a pivotal role in modulating the expression of genes that govern the tolerance to a wide range of abiotic stresses (Todaka et al. 2012).

**Table 2** Role of transgenics in the development of rice varieties with enhanced tolerance to abiotic stresses

Gene(s)	Traits improved	References
<i>AtHsp101, OsHsp101</i>	Heat tolerance	Agarwal et al. (2003)
<i>OsPIP1;3</i>	Cold tolerance	Lian et al. (2004)
<i>Choline monoxygenase</i>	Salt and heat tolerance	Shirasawa et al. (2006)
<i>SsNHX1, AVP1</i>	Salt tolerance	Zhao et al. (2006a, b)
<i>OsSBPase</i>	Heat tolerance	Feng et al. (2007)
<i>HvPIP2;1</i>	Salt tolerance	Katsuhara (2007)
<i>OsGSK1</i>	Heat tolerance	Koh et al. (2007)
<i>KatE</i>	Drought tolerance	Nagamiya et al. (2007)
<i>HvCBF4</i>	Cold, drought and salt stress	Oh et al. (2007)
<i>OsLea1-3</i>	Drought tolerance	Xiao et al. (2007)
<i>ZFP245</i>	Cold tolerance	Huang et al. (2009)
<i>RWC3</i>	Drought tolerance	Matsumoto et al. (2009)
<i>OsWKRY11</i>	Heat and drought tolerance	Wu et al. (2009)
<i>OsTPS1</i>	Cold, drought and salt stress	Li et al. (2011)
<i>OsNAC5</i>	Cold, drought and salt stress	Song et al. (2011)
<i>ZmCBF3</i>	Cold, drought and salt stress	Xu et al. (2011)
<i>ZmCBF3</i>	Cold, drought and salt stress	Xu et al. (2011)
<i>OsMYB55</i>	Heat tolerance	El-kereamy et al. (2012)
<i>OsCam1-1</i>	Salt tolerance	Saeng-ngam et al. (2012)
<i>OsMYB48-1</i>	Drought and salt stress	Xiong et al. (2014)
<i>GS2</i>	Salt and cold tolerance	Hoshida et al. (2000)
<i>OsCDPK7</i>	Salt and drought tolerance	Saijo et al. (2000)
<i>Adc, Samdc</i>	Salt and drought tolerance	Capell et al. (2004)
<i>HVA1</i>	Salt and dehydration tolerance	Babu et al. 2004
<i>OtsA</i>	Salt, drought and cold tolerance	Jung et al. (2004)
<i>pdcl, adc</i>	Submergence tolerance	Rahman et al. (2001)
<i>AGPAT, SGPAT</i>	Cold-tolerant	Ariizumi et al. (2002)
<i>Cat</i>	Cold-tolerant	Matsumura et al. (2003)
<i>spl7</i>	Tolerance to heat stress	Yamanouchi et al. (2002)
<i>OsPYL3 and OsPYL9</i>	Drought and cold tolerance	Tian et al. (2015)
<i>SOD2</i>	Salt tolerance	Zhao et al. (2006a, b)
<i>P5CS</i>	Salt tolerance	Karthikeyan et al. (2011)
<i>MnSOD</i>	Drought tolerance	Wang et al. (2005)
<i>pENAI</i>	Salt tolerance	Jacobs et al. (2011)
<i>miR319</i>	Cold, salt and drought tolerance	Khraiweh et al. (2012)

Abscisic acid (ABA) is popularly known as stress hormone due to its critical role in mitigation of a wide range of abiotic stresses. In rice varieties with improved stress tolerance, ABA-synthesising gene is unregulated and led to increased synthesis of ABA under stress conditions, and hence it is evident that ABA production is directly

related to enhanced stress in rice (Roychoudhury and Paul 2012). With the increasing understanding of ABA-mediated signalling pathways, several bZIP TFs have been discovered to play a key role in drought stress tolerance, thereby improving the yield substantially (Banerjee and Roychoudhury 2017; Kumar et al. 2019). Saeng-ngam et al. (2012) have reported that MAPK (mitogen-activated protein kinase) and  $\text{Ca}^{2+}/\text{CaM}$  (calcium/calmodulin)-mediated pathways play a crucial role in stress signalling response. Several novel genes have been isolated and characterised by working on these pathways. For instance, OsCam1-1 (rice calmodulin gene) can sense the severity of salt stress and upregulate the ABA synthesising gene to build up more ABA which in turn impart increased tolerance to salinity (Saeng-ngam et al. 2012). Another gene OsMAPK44 (rice mitogen-activated protein kinase) has been shown to play a critical role in the mitigation of various abiotic stresses, particularly salinity and drought (Jeong et al. 2006). Lee et al. (2011) while studying the role of genes in stress signalling reported that downregulation of OsMAPK33 resulted in the improvement of tolerance to salinity stress in rice plants. Nagamiya et al. (2007, b) and Gu et al. (2013) have reported that several genes such as KatE (*E. coli* catalase), OsIRL (rice isoflavone reductase-like gene), PPK (maize pyruvate orthophosphate dikinase) and PEP carboxylase (maize phosphoenolpyruvate carboxylase) introduced and overexpressed increased the survival of rice plants exposed to drought and salt stress. Several workers have postulated different underlying mechanisms that confer tolerance to salinity stress, and one such mechanism has been attributed to the upregulation of Na/H (sodium proton pump) gene that led to rapid and effective extrusion of sodium ions across the cell membranes. Another gene, viz. SOD2, (superoxide dismutase) isolated from fission yeast and introduced and overexpressed into rice imparted substantial increase in the rate of photosynthesis, increased grain yield and improved salt tolerance (Zhao et al. 2006a, b). The genetically engineered rice with overexpressed ( $\text{Na}^+$  pumping ATPase gene) PpENA1 isolated from moss *Physcomitrella patens* revealed enhanced potential to withstand salt stress (Jacobs et al. 2011). Similarly, the OsECS ( $\gamma$ -glutamylcysteine synthetase) gene overexpression in genetically engineered rice showed enhanced seed germination and seedling survival in rice exposed to abiotic stress, and this has been attributed to improved redox homeostasis (Choe et al. 2013). In addition to the genes, several micro-RNAs, for instance, miR160, have been reported to play a critical role in mitigation of adverse effects of drought stress in rice (Nadarajah and Kumar 2019).

Apart from the transcription factors and signalling pathways, aquaporins, members of the major (membrane) intrinsic protein (MIP) family, have been reported to play a role in improving the ability to tolerate salt and drought stress. For instance, transgenic rice harbouring and/or overexpressing HvPIP2;1 (barley aquaporin gene), OsPIP1;1 (rice aquaporin gene) and RWC3 (rice water channel protein) plays an important role in imparting tolerance towards salinity and drought, respectively (Kapilan et al. 2018). Zhao et al. (2006a, b) while studying salt tolerance in rice reported that co-expression of SsNHX1 (vacuolar  $\text{Na}^+/\text{H}^+$  antiporter gene) and AVP1 (vacuolar  $\text{H}^+$ -PPase) isolated from *Suaeda salsa* and *Arabidopsis*, respectively, introduced in transgenic rice seedlings revealed improved tolerance

to salinity with increased grain yield. Genetically engineered rice plants harbouring and overexpressing *ZFP245* displayed substantial increase in tolerance to drought and other abiotic stresses (Huang et al. 2009). Further, the increased stress tolerance has been attributed to augmented proline content and upregulation of P5CS and proline transporter genes. Likewise, another gene PgNHX1 (vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter) isolated from *Pennisetum glaucum* and introduced in transgenic rice showed enhanced plant yield in severe salt stress (Verma et al. 2007). The literature is scanty on identification, isolation and characterisation of transporter genes and underlying mechanism that impart stress tolerance in rice. More attention is required to pay toward this area to develop a broader understanding of the role of transporter genes in conferring tolerance to abiotic stress (Huang et al. 2009).

Several new genes such as Athsp101 (*Arabidopsis* heat shock protein), FAD7 (*Arabidopsis thaliana* fatty acid desaturase) and OsHSP101 (rice heat shock protein) governing the heat tolerance serve as a promising approach in developing transgenic rice plants with increased yield under heat stress. Transgenic rice revealed manifold increase in heat tolerance due to downregulation of FAD gene (Sohn and Back 2007). These genes required for acclimation to heat stress and their insertion into rice resulted into the development and official release of heat-tolerant rice varieties (Agarwal et al. 2003). The knockout mutants of OsGSK1 gene showed substantial increase in the ability to tolerate high temperature (Koh et al. 2007). Likewise, the upregulation of SBPase gene imparted heat tolerance along with the simultaneous increase in grain yield due to increased rate of carbon dioxide fixation in genetically engineered rice plants (Feng et al. 2007). Additionally, the upregulation of OsMYB55 (rice myb transcription factor 55) activates stress genes associated with increased heat tolerance, amino acid metabolism and grain yield in transgenic rice (Deeba et al. 2017).

### 2.3 Genomics

To feed the rapidly increasing human population, creation of varieties with high yielding potential and improved resistance towards abiotic stresses is prerequisite (Leonforte et al. 2013). Chee et al. (2005) have documented that conventional approaches of breeding such as mutagenesis are cumbersome and require a longer time span; modern breeding strategies such as marker-assisted breeding (MAB) have proven effective for creating varieties with enhanced yield and stress tolerance in a short span of time with better precision. MAB has been employed in several agricultural and horticultural important crops in rice with the objective to screen and isolate varieties with abiotic stress tolerance (Mondal et al. 2013). Molecular markers, viz. RFLP, RAPD, AFLP, SSRs and SNPs have played a vital role in marker-assisted breeding (MAB) for developing crops with improved tolerance to abiotic stress (Hussain 2006; Raina et al. 2019). QTL mapping has been employed to understand the underlying mechanism of abiotic stress tolerance in rice (Shanmugavadeivel et al. 2017).

**Table 3** Role of genomics in the development of rice varieties with enhanced tolerance to abiotic stresses

Gene(s)	Traits improved	References
<i>DSM1</i>	Dehydration tolerance	Ning et al. (2010)
<i>OsCPK12</i>	Salt tolerance	Asano et al. (2012)
<i>OsCPK4</i>	Salt and drought tolerance	Campo et al. (2014)
<i>OsSIK1</i>	Salt and drought tolerance	Ouyang et al. (2010)
<i>SIT1</i>	Salt tolerance	Li et al. (2014)
<i>OsPP18</i>	Osmotic and oxidative stress tolerance	You et al. (2014)
<i>OsANN1</i>	Drought tolerance	Qiao et al. (2015)
<i>Os SAPPK2</i>	Drought tolerance	Lou et al. (2017)
<i>Dro1</i>	Drought tolerance	Uga et al. (2011)
<i>Saltol</i>	Salt tolerance	Das and Rao (2015)
<i>qDTY2.2, qDTY3.1 and qDTY12.1</i>	Drought tolerance	Shamsudin et al. (2016)
<i>SKC1</i>	Salinity stress	Emon et al. (2015)
<i>DST</i>	Salinity stress	Emon et al. (2015)
<i>qSCT-11</i>	Chilling-tolerant	Chen and Li (2005)
<i>qPSST-3, qPSST-7, qPSST-9, qSCT1a and qSCT2</i>	Cold stress	Jena et al. (2010)
<i>qHTSF4.1</i>	Heat stress	Ye et al. (2015)
<i>ABO28184</i>	Drought tolerance	Khattab et al. (2014)
<i>AJ578494</i>	Drought tolerance	Khattab et al. (2014)
<i>OsNAC2</i>	Salt, drought, cold stress	Hu et al. (2006)
<i>OsDREB2A</i>	Salt, drought, cold stress	Chen et al. (2008)
<i>OsNAC5</i>	Salt, drought, cold stress	Hu et al. (2008)
<i>OsHOX24</i>	Salt, drought, cold stress	Bhattacharjee et al. (2017)
<i>OsCMO</i>	Salinity stress	Burnet et al. (1995)
<i>Erf68</i>	Salinity stress	Steffens (2014)

Increased salt concentration in the rice lands incurs a huge loss in overall yield and monetary loss worldwide. In order to improve the yield in rice, it is important to identify, isolate and characterise genes that improve acclimation to salt stress (Table 3). Therefore, global collaborative research has been initiated with the main objective of screening QTLs that govern improved salt stress tolerance in rice. Since the tolerance to salinity is polygenic trait, it is difficult to screen QTLs that are linked with salt tolerance and is at the central place in broadening the concept of stress responses in a wide range of crops. A landmark achievement was made by developing a set of introgression lines (ILs) from “Pokkali” which served as donor of genes that confer tolerance to salinity stress in a “Bengal” rice cultivar with better yield but sensitive to mild salt concentration in soil. These ILs were subjected to genotyping using SSRs and SNP markers and lead to the identification of 18 and 32 QTLs, respectively, that are linked with salt stress tolerance and can be used to transfer

salinity tolerances to other crops. They concluded that salt tolerance may be attributed sodium dilution and compartmentalisation and build-up of osmoprotectant compounds (De Leon et al. 2017). Similarly, molecular dissection of SST by means of a high-density rice genetic map was constructed using a cross between varieties Bengal and Pokkali that resulted into the development of 187 recombinant inbred lines (RILs). These RILs were evaluated for several morpho-physiological and biochemical characters associated with salt tolerance and were also genotyped with 9303 SNP markers. The study leads to the identification of 85 QTLs that govern several traits, viz. shoot  $\text{Na}^+$  and  $\text{K}^+$  concentration, shoot  $\text{Na}^+/\text{K}^+$  content, shoot length/root length, salt injury score, chlorophyll content and dry weight of shoots. Hence, construction of genetic linkage map provides new clues in understanding the mechanism of salinity tolerance and identification of novel genes that govern salt tolerance (De Leon et al. 2016). Cheng et al. (2012) reported isolation of salt-tolerant QTLs by employing two sets of reciprocal IL derived from a cross between Xiushui09 and IR2061-520-6-9 with former being salt-resistant and latter salt-sensitive rice variety. A total of 26 QTLs linked with salt toxicity symptoms (SST) and days to seedling survival (DSS) were identified and can be used to further improve the salt tolerance. Gregorio et al. (2002) were successful in isolating *Saltol* QTL that confers salinity stress tolerance in Pokkali by improving  $\text{Na}^+/\text{K}^+$  homeostasis. This QTL can be intergressed into salt-sensitive varieties through marker-assisted backcross breeding and will equip the plant breeders to create salinity-tolerant version of otherwise high yielding rice varieties (Singh et al. 2018; Valarmathi et al. 2019).

Drought causes substantial reduction in the overall yield of rice crops and hence is considered main obstacle in achieving the desired goals of rice production. Hence, plant breeding programmes are required to plan with the main aim of developing drought tolerance in crops (Venuprasad et al. 2007). The isolation of QTLs that govern drought tolerance plants could be useful to enhance the survival of rice seedlings exposed to drought stress (Prince et al. 2015). Hence, MAB research is being carried out to have a broader understanding of mechanisms of drought tolerance and to quicken the progress of developing varieties with improved drought tolerance (Dixit et al. 2017a, b; Muthu et al. 2020). For instance, root length and density (RLD) play an important role in mitigation of adverse effects of drought stress, and hence indirect selection for drought tolerance through RLD is an emerging research area in stress studies. Due to severe drawbacks in traditional breeding, selection for RLD is cumbersome, time-consuming and laborious; hence, advanced breeding approaches such as MAB may prove effective in improving the drought tolerance (Siddique et al. 2015). With the advent of molecular marker techniques, a very minute details and a broader understanding of genetics involved in tolerance against drought in several crops including rice became available in data repositories. A global collaboration between stress-oriented research institutes such as IRRI, Philippines, initiated with the aim of mapping of drought-responsive QTLs in rice (Kumar et al. 2007; Bernier et al. 2007; Venuprasad et al. 2009; Vikram et al. 2011; Dixit et al. 2014a, b). Some of the noteworthy QTLs, viz. *qDTY<sub>1.1</sub>* and *qDTY<sub>2.1</sub>*, from the drought-resistant genotype, Apo, have been identified and are

suitable for improving the drought tolerance in drought-sensitive genotypes (Muthu et al. 2020). Recently, Uga et al. (2011) identified a key QTL (RDR Dro1) in rice on chromosome 9 that governs deep rooting/root growth angles, thereby playing a role in making water available under severe drought. Shamsudin et al. (2016) carried out MAS in Malaysian rice cultivar MR219 that leads to the identification of three drought yield QTLs, qDTY2.2, qDTY3.1 and qDTY12.1.

The QTL mapping strategy has been employed to unfold the complex genetic control of heat tolerance in rice which is also counted as one of the main stresses that limit the rice production to a great extent (Poli et al. 2013). In order to overcome the deleterious effects of continuous rise in atmospheric temperature, it is imperative to create rice varieties with improved heat tolerance (Chang-lan et al. 2005). Rice plants usually face the negative effects of high temperature at the reproductive stage, and hence it is very important to identify QTLs that are responsive to heat stress at this stage. The main effects include anomalous pollination, increased pollen sterility, reduced seed set and lower yield. Hence, the progress in breeding for heat resistance can be rapid by detection of QTLs and candidate genes governing heat stress tolerance at reproductive stage (Qingquan et al. 2008). A cross was made between IAPAR-9 (heat susceptible) and Liaoyan241 (heat resistant) that leads to the creation of RIL mapping population and identification of heat-stable QTLs viz., qNS1, qNS4, qNS6, qRRS1, qHTS4 and qRRS4 (Li et al. 2018). Similarly, two QTLs *qPF4* and *qPF6* were shown to affect the pollen fertility under high temperature (Xiao et al. 2011). Ye et al. (2015) identified heat tolerance QTL, viz. qHTSF1.2, qHTSF2.1, qHTSF3.1 and qHTSF4.1, at the reproductive stage in rice. Zhao et al. (2016) while investigating the key components of molecular mechanism for heat stress tolerance at flowering stage were successful in identifying 11 QTLs that are linked with spikelet fertility, flowering and pollen maturation timing. Among several QTLs, qPSLht4.1 was shown to control pollen attributes and is useful to improve the pollen maturation and pollen tube growth. Shanmugavadivel et al. (2017) investigated the mapping of heat tolerance QTLs and developed 272 recombinant inbred lines in the F8 generation by crossing Nagina22 (heat resistant) and IR64 (heat susceptible) rice varieties. This experimentation has resulted in the identification of two QTLs qSTIPSS9.1 and qSTIY5.1/qSSIY5.1 associated with heat tolerance at reproductive stage.

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### 3 Conclusion

Overall, the modern biotechnological tools such as mutagenesis, transgenics and genomics have led to the identification, cloning and characterisation of genes (from different organisms), followed by its insertion into the rice plants with the aim of decreasing the yield loss incurred by the different abiotic stresses. Such approaches have brought landmark achievements by developing varieties with improved tolerance to various abiotic stresses.



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