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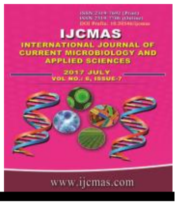

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Physiological, Morphological and Molecular Mechanisms for Drought Tolerance in Rice

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ABSTRACT

Rice is the most widely consumed staple food in India and a large part of the world's human population, especially in Asia. In this review we discussed about the Morphological and molecular mechanisms for drought tolerance in rice. Rice requires high temperature above 20^0C but not more than 35 to 40^0C. The lots of work have been done in this area to find out the cultivars, resistance to drought. Production of rice is decreasing day by day due to many biotic and abiotic stresses. Among them drought is one of the most common abiotic stress which affect yield and any other phenotypic factor of rice. There are three mechanisms are involved in drought resistance namely drought escape, drought avoidance and drought tolerance. Drought affect on the rice grain yield, chlorophyll content, plant height and no. of tillers per plant. During drought stress, proline and many other proteins provide defense against drought. It has also been discussed that how breeders improved these traits in rice by using a QTL mapping approach. Different approaches like AB-QTL analysis, gene pyramiding and association mapping can also be used for the improvement of rice. Transgenic approach have also been adopted for rice to over-express transcription factors involved in the regulation of stress-inducible genes such as CBF/DREB1, DREB2, RD29B, RD22, and ICE1. Transgenic rice plants have been produced to over-express several candidate genes, such as *Adc, P5CS, HVA1, TPS and TP, RWC3.*

Keywords

Rice, Drought, Phenotypic, QTL and Molecular markers.

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Introduction

Rice is (*Oryza sativa* L.*)* is the most widely consumed staple food for a large part of the world's human population, especially in Asia. More than 90% of the world's rice is grown and consumed in Asia where 60% of the earth's people and about two-thirds of the world's poor live (Khush and Virk, 2000). Rice requires high temperature above 20^0C but not more than 35 to 40^0C. Optimum temperature is around 30^0C (Tmax) and 20^0C (Tmin). In India rice is cultivated in an area of about 43.50 million hectares with an annual production of about 159.20 million tones with average productivity of 3659.8 kg per hectare (Anonymous, 2013a). In Uttar Pradesh the area of rice is about 59.78 million hectares and production is 153.02 million tones of 2532 kg per hectares (Anonymous, 2013b).

Production of rice is decreasing day by day due to many biotic and abiotic stresses, in which the abiotic stresses are prime important. Abiotic stress is defined as the negative impact of non-living factors on the living organisms in a specific environment. The non-living variable must influence the environment beyond its normal range of variation to adversely affect the population performance or individual physiology of the organism in a significant way (Vinebrooke and Rolf, 2004). On an average, the lowland stress reduced grain yield to75% of the control value (Lafitte *et al.*, 2006). Abiotic stresses curtail production and lower the quality and nutritional value of the grain in cereal crops world-wide. Among all abiotic stresses, drought is the most important from the economic standpoint. Drought tolerance in plants is one of the most interesting phenomena in all of biology (Wood, 2007).

Drought- the major problem for rice

Drought stress is a serious limiting factor to rice production and yield stability in rainfed areas. Breeding for drought tolerance is a challenging task because of the complexicity of the component traits, screening technique, environmental factors and their interaction. Rice is most susceptible to drought stress at the reproductive stage (Pantuwan *et al.*, 2002). Genetically, drought tolerance is a quantitatively inherited trait, controlled by several genetic loci (QTL). Furthermore, crop performance under drought conditions is a highly complex phenomenon because of unpredictable factors in the environments and the interaction with other abiotic and biotic factors (Reynolds *et al.*, 2006). Tolerance to drought involves a complex of mechanisms working in combination to avoid or tolerate water deficits.

Timing of drought

Early season, midseason, or terminal stage has a major influence on how much yield loss occurs. Therefore, poverty reduction strategies in drought prone areas must focus on stabilizing yields, that is, on breeding varieties with improved yield under drought stress as well as good response to irrigated conditions. The identification and introgression of QTL leading to high grain yield under drought have been considered to be the preferred breeding strategy to improve drought tolerance in rice. The lots of work have been done in this area to develop the cultivars resistance to drought. The most affected states in India are Rajasthan, Gujarat, Haryana, Andhra Pradesh and U.P. Most of the crops are sensitive to water deficits, particularly during flowering to seed development stage (Salter *et al.*, 1967).

Plant response to drought

Plant response to stress conditions occurs through a number of changes at physiological and developmental levels, brought about by altering the expression of stress inducible genes (Philippe *et al.*, 2010). In general, genes associated with drought resistance are numerous and have been shown to interact with the environment, and thus the networks involved in drought tolerance are quite complex in nature. Therefore, progress in improving the drought tolerance of rice is slow (Lin *et al.*, 2007). Mannitol, a member of sugar alcohols, is an osmotic adjustment chemical to control osmotic potential in the culture media or nutrient solutions in order to induce water deficit conditions for protein expression or proteomic studies.

Mechanism of drought resistance

Plants acquired various mechanisms during the course of their evaluation to avoid drought as they do not have the ability to move and avoid drought. Responses to drought stress are commonly dependent on plant genotypes, plant species, age of plant, its developmental stage and the severity of drought (Ali *et al.*, 2011; Gall *et al.*, 2015). Three mechanisms, namely drought escape, drought avoidance and drought tolerance are involved in drought resistance. Various morphological, physiological and biochemical characters confer drought resistance.

Drought resistance

Drought resistance refers to the ability of a crop to produce its economic product with minimum loss in a water-deficit environment relative to the water constraint free management. Drought resistance is a complex trait whose expression depends on action and interaction of different morphological, physiological and biochemical characteristics. Rice crop responds to drought condition by stomatal closure, leaf rolling, enhanced root growth, enhanced ABA production etc., to minimize water deficit (Price *et al.,* 2002).

Drought escape

Drought escape is defined as the ability of a plant to complete its life cycle before serious soil and plant water deficits develop. This mechanism involves rapid phenological development (early flowering and early maturity), developmental plasticity (variation in duration of growth period depending on the extent of water deficit) and remobilization of pre-anthesis assimilates to the grain (Turner, 1979). In drought-prone upland areas of eastern India and Bangladesh, drought escape is an important mechanism that allows rice to produce grain despite limited water availability (Bernier *et al.*, 2008).

Drought avoidance

Drought avoidance is the ability of plants to maintain relatively high tissue water potential despite a shortage of soil moisture. Rice varieties which cope with drought using their root systems to maintain their plant water status comes under drought avoidance category. Such varieties therefore minimize the yield losses caused by drought (Singh *et al.*, 2012). Mechanisms for improving water uptake, storing it in plant cell and reducing water loss confer drought avoidance. Rice varieties which avoid drought usually have deep, coarse roots with a high ability of branching and penetration, higher root to shoot ratio, elasticity in leaf rolling, early stomatal closure and high cuticular resistance (Wang *et al.,* 2006).

Effect of drought stress on phenotypic traits in rice

To improve rice production under drought condition, firstly understand the changes of phenotypic traits of plant responses and secondly understand the mechanism and changes of biochemical and molecular components of plant under stress condition. Low-yielding lines under stress included Calcag, Nipponbare, and Haoannong, also identified in the control treatments, along with AP423, Phalguna, and Swarna (India), TB154E-TB-2 (Indonesia), Ilmibyeo (Korea), and Tai-Nong67 (Taiwan). Important yield components under lowland stress were percentage of fertile spikelets and grains per panicle. As in the control treatment, biomass and HI were also significantly correlated with grain yield (Lafitte *et al.,* 2006).

QTL mapping and marker assisted selection for genetic improvement of drought tolerance

QTL mapping is a tool to separate the complex phenotypic traits into their components and is a source of understanding the genetic basis of plant traits under diversification selection during crop evolution (Bo *et al.*, 2015). The identification of QTLs affecting drought tolerance is a major step to understand the genetic basis of plant response to water deficit conditions and for the development of drought tolerant cultivars. Through indirect manipulation of quantitative trait loci, improvement in crop yield is possible because QTLs can be used to control the heritable variability of the traits and physiological mechanisms that determine biomass production and partitioning (Nicholas *et al.*, 2008).

Lang and Buu (2010) were identified Five QTLs for DT (Drought Tolerance), two QTLs for root length, and two QTLs for root dry weight. The proportion of phenotypic variation explained by each QTL ranged from 20.73% to 30.77% for drought, and from 6.23 to 3.39% for morphological characters related to drought at flowering. The role of bioinformatics software are prime important for QTL analysis. The list of different software for QTL analysis is given in table 1.

Molecular markers

Molecular markers have been used to identify many drought tolerant associated QTLs in the past decade. Loci affecting root systems, osmotic adjustment, leaf rolling, leaf drying, and relative water content have also been reported. Root-related traits under drought stress were mapped in several studies including root penetration ability, root thickness, root dry weight, pulling force, and root length (Zhang *et al.,* 2001; Nguyen *et al.*, 2004).A total of 15 alleles for 10 SSR loci were detected among 34 rice genotypes (10 parents and 24 hybrids). Two specific DNA bands, the first with 100 bp molecular size appearing by RM201 marker and the second with molecular size of 80 bp appearing by RM451 marker, may play an important role in drought response in the used rice genotypes.

The polymorphism among parental genotypes and 75 BC_2F_2 families were tested using 40, 98 and 400 different TRAP, SRAP and SSR primer combinations, respectively. Mapping analysis produced 14 QTLs, in which a single QTL explained 9-39% of the phenotypic variation. These QTLs distributed on eight chromosomes. The results also showed that the regression analysis for the relationship between the TRAP, SRAP and SSR markers and the phenotypes of BC_2F_2 families for the four physiological traits was highly significant. Therefore, the TRAP, SRAP and SSR markers linked to the QTL for the drought tolerance can be further used in breeding for drought tolerance in wheat (Barakat *et al.*, 2015).

Expression of drought induced genes

In most of the cases the over expression of *DREB1A* is obtained by using constitutive (CaMV 35S) promoter or the dehydration inducible (rd29A) promoter. In transgenic *Arabidopsis* plants Kasuga *et al.*, (1999) found that over expression of *CBF3*/*DREB*1A accompanied by constitutive promoter CaMV 35S greatly improved plant’s tolerance to abiotic stresses including drought stress. Different results indicate that backcross breeding combined with direct selection for yield in stressed nurseries may be a highly effective way to improve drought tolerance in rice. The timing of stress relative to the sensitive flowering stage has a tremendous effect on the yield reduction caused by a drought event (Garrity and O’Toole, 1994; O’Toole, 1982).

Genes encoding LEA proteins and heat shock proteins have also been used to improve drought tolerance in transgenic plants. A gene encoding galactinol synthase (GolS), a key enzyme involved in raffinose family oligosaccharide biosynthesis, was introduced to improve drought-stress tolerance in transgenic Arabidopsis (Taji *et al.*, 2002). Prior analyses demonstrate that GolS genes are induced by drought, cold, and ABA. Moreover, expression of the gene encoding raffinose synthase is also induced by drought stress. Additionally, recent metabolome analysis indicated significant accumulation of both galactinol and raffinose under drought stress. Not only metabolites, but also some stress-responsive proteins such as LEAs, have also been implicated in detoxification and alleviation of cellular damage during dehydration. Other studies demonstrate that overexpression of some LEA class genes results in enhanced tolerance to dehydration, although the precise mechanism is still unknown. LEA proteins may also function as chaperone-like protective molecules to combat cellular damage (Umezawa *et al.*, 2006). The functional classification of drought tolerance gene is illustrated in figure 2.

Transgenics

Transgenic rice plants have been produced to over-express several candidate genes. There are many candidate genes, play the key role against drought presented in table 2. Transgenic rice plants have also been produced to over-express transcription factors involved in the regulation of stress-inducible genes such as CBF/DREB1, DREB2, RD29B, RD22, and ICE1 (Shinozaki *et al.*, 2003), CDPK encoding Ca^{2+-}dependant protein kinase (Saijo *et al.*, 2000), ABF3 and CBF3 (Oh *et al.*, 2005), and SNAC1 encoding stress-responsive NAC 1 (Hu *et al.*, 2006).

Candidate genes for drought include DREB2a, ERF3, sucrose synthase, actin depolymerizing factor, and trehalose-6-phosphate phosphatase, among others. Most of the CBF/DREB1 target genes contain the DRE motif with a conserved (A/G)CCGACNT sequence in their promoter regions. The target gene products of these proteins are consequently involved in establishing stress tolerance. The DREB2 genes are induced by dehydration stress and may activate other genes involved in drought stress tolerance (Liu *et al.*, 1998). Over expression of OsDREB1 or Arabidopsis DREB also improved drought and chilling tolerance in rice (Ito *et al.*, 2006).

Trancription factors involved in drought tolerance and adaption

Madabula *et al.*, (2016) were evaluated 4 genes related to auxin response and root modifications (*OsGNOM1/ CRL4, OsIAA1, OsCAND1* and *OsRAA1)*. The expression of these genes were analyzed in stressed rice using public available microarray data and then through real-time quantitative polymerase chain reaction (RT-qPCR), in the 6 phenotypically evaluated Brazilian genotypes under standard conditions (absence of stress).Result showed that all genotypes lengthened its roots in response to drought, specially the 2 hybrids. The expression of these genes is modified in response to stress, and *OsRAA1* has a very special behavior, constituting a target for future studies.

Transcription factors (TFs), which can interact with *cis*-regulatory sequences and regulate a series of related genes expression, are critical components of the abiotic stress signal transduction pathway. Most of TFs fall into several large TF families, such as APETALA type2/ethylene responsive factors (AP2/ERF), basic region/leucine zipper motif (bZIP), NAM/ATAF/CUC transcription factor (NAC), myeloblastosis (MYB), myelocytomatosis (MYC), Cys2His2 zinc-finger proteins (ZFP) and domain binding transcription factor (WRKY) (Umezava *et al.*, 2006). The best characterized Transcription Factor groups are ABA responsive element binding protein 1 (AREB1), ABA responsive binding factor 2 (ABF2), dehydration responsive binding protein (DREB) genes, MYB genes, bZIP encoding genes and a protein kinase such as receptor like kinase 1, SNF1- related protein kinase 2C or guard cell expressing calcium dependant protein kinases (Choi *et al.*, 2000).

Stress-responsive rice SNAC genes such as SNAC1, OsNAC6/SNAC2 and OsNAC5 improve drought tolerance when over-expressed (Hu *et al.*, 2006; Takahashi *et al.*, 2010; Nakashima *et al.*, 2014). Many TFs have been used to produce transgenic rice lines with either constitutive or inducible promoters, such as HvCBF4, AP37 (Kim and Kim, 2009; Oh *et al.*, 2009), TaSTRG, OsDREB1A, OsDREB1B (Datta *et al.*, 2012), AtDREB1A (Hussain *et al.*, 2014; Ravikumar *et al.*, 2014), OsNAC6 (Rachmat *et al.*, 2014) (Fig. 1).

Table.1 Software for QTL analysis

S.NO.	Software	Features
1.	MAPMAKER/QTL	Interval mapping (IM)
2.	QGene	Single Marker Analysis (SMA), IM and multiple-trait analysis
3.	MapQTL	IM, Composite Interval Mapping (CIM), non-parametric mapping with the kruskal-Wallis rank sum test per marker (for non-normally distributed data), permutation tests, etc.
4.	PLABQTL	Simple Interval Mapping (SIM), CIM, also analysis for QTL x Environment (QE) interactions
5.	MQTL	SIM, CIM, also analysis for main effect, QE interactions, and can perform permutation tests
6.	MapManager	QTXSMA, SIM, CIM, searches for interacting QTLs, etc.
7.	QTL Cartographer	SMA, SIM, CIM, Bayesian Interval Mapping (BIM), Multiple Interval Mapping (MIM), multiple trait analysis, permutation tests, etc.
8.	QTLMapper	Mapping QTL with epistatic effects, QE interaction effects etc.
9.	QTLNetwork	Mapping QTL with epistatic effects, QE interaction effects etc

Table.2 Candidate genes and their properties

S.No	Candidate gene	Properties	Reference
1.	*Adc*	Encoding arginine decarboxylase, which modulates the plant polyamine content	Capell *et al.*, 2004
2.	*P5CS*	Encoding pyrroline-5-carboxylate synthetase involved in proline biosynthesis	Zhu *et al.*, 1998
3.	*HVA1*	Encoding late embryogenesis abundant (LEA) proteins	Xu *et al.*, 1996; Cheng *et al.*, 2002; Rohila *et al.*, 2002
4.	*TPS and TP*	Encoding trehalose-6-phosphate synthase and trehalose-6-phosphatase, involved in trehalose biosynthesis	Garg *et al.*, 2002; Lee *et al.*, 2003
5.	*RWC3*	Encoding the water channel protein aquaporin	Lian *et al.*,2004
6.	*OCPI1*	(*Oryza sativa* chymotrypsin inhibitor-like 1), a stress responsive proteinase inhibitor gene	Huang *et al.*, 2007

Table.3 Genetic engineering of transcription factors for enhancing drought tolerance in rice

Gene/protein	Name	Source	Promoter	phenotype	Reference
NAC family genes					
SNAC1	Stress responsive NAC1	*Oryza sativa*	CaMV35S	Drought and salinity tolerance	Hu *et al.*, 2006
NAC6/SNAC2	Stress responsive NAC2	*Oryza sativa*	OsNAC6, LIP9	Tolerance to cold, salt stress	Nakashima *et al.*, 2007
NAC045	NAC045 transcription factor	*Oryza sativa*	CaMV35S	Drought and salt stress	Zheng *et al.*, 2009
NAC10	NAC10 transcription factor	*Oryza sativa*	GOS2, RCc3	Tolerance to drought and low temperature	Jeong *et al.*, 2010
OsNAC6		*Oryza sativa*	CaMV35S	Drought tolerance	Rachmat *et al.*, 2014
Basic leucine zipper transcription factor					
ABF3	ABA responsive element binding protein/factor3	*Arabidopsis thaliana*	Ubiquitin	Drought tolerance	Oh *et al.*, 2005
bZIP23	Basic leucine zipper 23	*Oryza sativa*	Ubiquitin	ABA sensitive, salinity and drought tolerance	Xiang *et al.*, 2008
bZIP46	Basic leucine zipper 46	*Oryza sativa*	Ubiquitin	Drought and osmotic stresses tolerance	Tang *et al.*, 2012
bZIP72	Basic leucine zipper 72	*Oryza sativa*	CaMV35S	ABA hypersensitivity, drought tolerance	Lu *et al.*, 2008
HD-Zip	Homeodomain leucine zipper	*Oryza sativa*	CaMV35S	Plant development and drought stress adaptation	Agalou *et al.*, 2008
MYB-Type transcription factor					
MYB2	MYB-Type transcription factor	*Oryza sativa*	Ubiquitin	Salt, cold and dehydration tolerance	Yang *et al.*,2012
Zinc finger transcription factors					
ZFP252	C-repeat DRE element binding factors	*Oryza sativa*	CaMV35S	Tolerance to salt and drought stresses	Xu *et al.*, 1996
ZFP245	Zinc finger protein 245	*Oryza sativa*	CaMV35S	Cold, drought and oxidative stresses tolerance	Huang *et al.*, 2009
Ethylene-responsive factors					

DREB1A/CB3	C-repeat/DRE element binding factors	*Arabidopsis thaliana*	Ubiquitin	Drought, Salt, and freezing tolerance	Oh *et al.*, 2005
HARDY	AP2/ERF like transcription factor	*Arabidopsis thaliana*	CaMV35S	Drought, Salt, and freezing tolerance	Karaba *et al.*, 2007
TERF1	Tomato ethylene responsive factor	*Lycopersium esculatum*	CaMV35S	Drought and salinity tolerance	Gao *et al.*, 2008
DREB1F	DREB class1 protein	*Oryza sativa*	CaMV35S	Salt, drought and low temperature tolerance	Wang *et al.*, 2008
OsDREB1G, OsDREB2B	DREB class 1 and 2 protein	*Oryza sativa*	CaMV35S	Water deficit stress tolerance	Chen *et al.*, 2008
JERF3	Ethylene response factor		CaMV35S	drought and osmotic stress tolerance	Zhang *et al.*, 2010
AP37	AP2/ERF domain containing transcription factors	*Oryza sativa*	OsCc1	Drought and high salinity **tolerance**	Oh *et al.*, 2009
TSRF1	Tomato ethylene responsive factors	*Oryza sativa*	CaMV35S	Drought stress tolerance	Quan *et al.*, 2010
ARAG1	ABA-responsive DREB gene	*Oryza sativa*	CaMV35S	Seed germination and drought tolerance	Zhao *et al.*, 2010
SUB1A	ERF transcription factor	*Oryza sativa*	Ubiquitin	Drought and oxidative stress tolerance	Fukao *et al.*, 2011
DERF1	Drought and ethylene-responsive factor	*Oryza sativa*	CaMV35S, Actin1	drought sensitive	Wan *et al.*, 2011
OsWR1	Rice wax synthesis regulatory gene	*Oryza sativa*	CaMV35S, Actin1	Drought tolerance	Wang *et al.*, 2011
DREB2A	DREB class2 protein	*Oryza sativa*	4XABRC	Drought and salt tolerance	Cui *et al.*, 2011
DREB2A	DREB class2 protein	*Oryza sativa*	RD29	Dehydration and salt stress tolerance	Mallikarjuna *et al.*, 2011
AtDREB1A		*Oryza sativa*	CaMV35S	Drought tolerance	Hussain *et al.*, 2014

Fig.1 Associations between primary, secondary, and integrative drought-resistance traits, and plant-type traits and phenology. Primary traits are further divided into constitutive traits and induced traits. Traits in the lower part of the diagram (primary traits, plant-type traits, and phenology) are presumed to be controlled with fewer genes/ QTLs compared with traits in the upper part of the diagram (grain yield, integrative traits, and secondary traits). Traits on the left-hand side (phenology, plant-type traits, some secondary traits [e.g., leaf death score]) were more easily measured for selection compared with traits shown on the right-hand side (primary traits, some secondary traits [e.g., leaf water potential] (Kamoshita *et al.*, 2008)

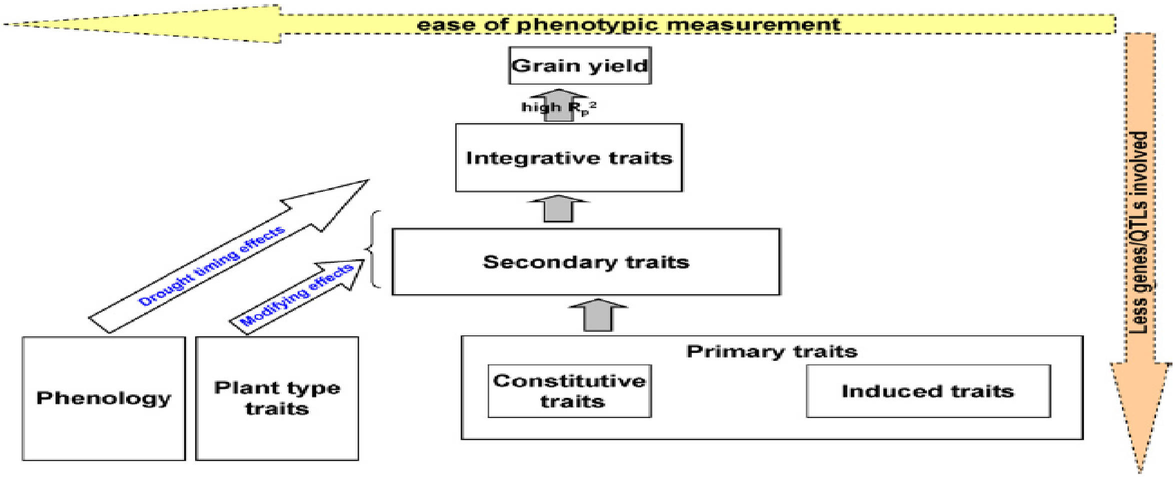
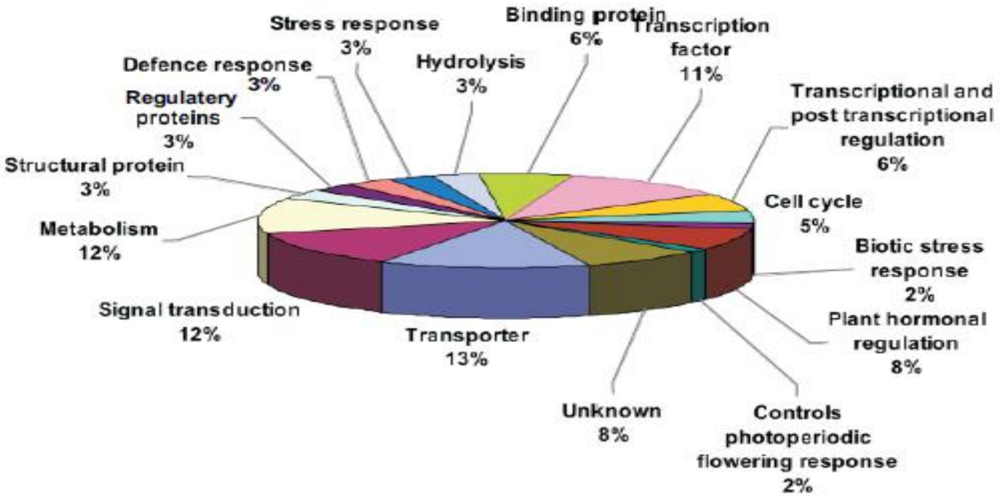


Fig.2 Functional classification of selected drought tolerance genes



TFHYR (higher yield rice) over expression in rice enhances photosynthesis leading to higher grain yields under drought conditions (Ambavaram *et al.*, 2014). Various type of abiotic stress response genes have been listed in table 3.

In conclusion, rice grow at high temperature above 20^{0}C but not more than 35 to 40^{0}C. Production of rice is decreasing day by day due to many biotic and abiotic stresses. Drought stress is a serious limiting factor to rice production and yield stability in rainfed areas. Rice grain yield, chlorophyll content, plant height and no. of tiller per plant decreased under drought condition. Proline and many other protein works as a defense induced in drought condition. Transgenic rice plants have also been produced to over-express transcription factors involved in the regulation of stress-inducible genes such as CBF/DREB1, DREB2, RD29B, RD22, and ICE1. Transgenic rice plants have been produced to over-express several candidate genes, such as *Adc, P5CS, HVA1, TPS and TP, RWC3.*

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