

Review Article

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Identification and Mapping of QTLs for Drought Resistance in Rice

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ABSTRACT

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Rice (*Oryza sativa* L.) is one of the most important staple foods for more than half the world's population and influences the livelihoods and economies of several billion people. Drought stress is the major constraint to rice production and yield stability in rainfed ecosystems. Efforts have been made to identify putative traits, which can confer drought resistance in rice grown under rainfed lowland. However, little progress has been made in incorporating tolerance to abiotic stresses such as drought, since the fundamental mechanisms of drought resistance in rice are poorly understood. Efforts have been made for identifying putative traits encoding different drought resistance traits. The results are being used in marker assisted selection (MAS) for the development of drought resistant varieties. Recent trends in climate change have predicted a further increase in drought intensity, making the development of new drought-tolerant rice cultivars critical to sustain rice production in this ecosystem.

Introduction

Rice has been feeding the world for over 4000 years and is the staple food of about 557 million people (Manzanilla *et al.*, 2011). In 2016-17, the average annual consumption per capita in India was about 102.72 million tonnes (Rice Commodity Profile, 2017). According to IRRI (2000) the global rice production should increase by 800 million tonnes by 2025 in order to feed the growing population. As a semi-aquatic crop, rice faces various abiotic stresses among which, drought is the most prominent.

Drought is a major limitation for rice production in rainfed ecosystems (Kamoshita *et al.*, 2008). Millions of hectares of lowland rainfed rice areas are affected by drought in

years with very low rainfall and it reduces rice productivity by 13–35% (Jongde, 1998.) The drought vulnerability scenarios are likely to worsen in the future with predicted climate change scenarios, which will also lead to more complex interactions of drought with other abiotic and biotic stresses (Wasmann *et al.*, 2009).

Despite drought having been a focus of agricultural research for several decades, progress in delivering drought adapted rice varieties and technologies has been relatively slow as the genetic mechanisms behind drought tolerance is still merely understood. The various methods used for developing a drought tolerant variety are listed in figure 1.

Effect of drought on rice

The effect of drought in rice varies with the variety, degree and duration of stress and its coincidence with different growth stages (Lanceras *et al.*, 2004). Water deficit at the vegetative stage seems to be the least detrimental to yield (Chang *et al.*, 1982). Water deficit at the reproductive stage is most damaging to rice yield (O'Toole, 1982). Grain yield is affected, particularly when drought coincide with reproductive growth. Bradford (1982) reported that water deficit during flowering resulted in the reduction of grain yield and harvest index by 60 percent. It was also noted that stress at flowering inhibited pollination and resulted in sterile spikelets, the deleterious effects of water deficit stress at the flowering stage on yield could be due to reduced number of filled spikelets, reduced effective sink capacity and indirectly leads to reduced photosynthesis.

Drought tolerance

Drought tolerance has been considered as a target for breeding in order to partially compensate for the yield loss. Drought tolerance involves mechanisms that allow plants to maintain their metabolism and limit the harm caused by prolonged drought periods. These mechanisms involve different metabolic pathways in the cell, all of which results in the activation of stress response genes. These can be groups in to five categories: the osmoprotectants, ion exclusion, ion export, cell membrane modifications and antioxidant enzymes.

Plant responses that help in drought tolerance

Rice plant uses less than 5 percent of the water absorbed through roots from the soil. The rest is lost through transpiration, which helps to maintain leaf energy balance of the

crop. The effect of water stress may vary with variety, growth stage of the crop, degree and duration of the stress. There may be two kinds of traits: constitutive and adaptive traits, which confer drought resistance in rice (Kamoshita *et al.*, 2002). Constitutive traits are expressed under anaerobic, non-water stressed conditions, don't require water stress for their expression and may demonstrate variation that is subsequently modified by adaptive traits. Adaptive traits can be defined as those, such as osmotic adjustment (OA), which are expressed in response to water deficit. Identifying traits of importance in drought resistance is difficult due to the complexity of climatic variation in precipitation and evapotranspiration, the diversity of the rice hydrological environments, the relationship between soil moisture status and nutrient availability and differential plant interactions with this environment. The problem of adaptation to drought conditions in rice is complex and unique as compared with most other crops.

Selection and breeding strategies for drought resistance

Conventional breeding has been based on empirical selection for yield (Atlin and Lafitte, 2002). However, this approach is far from being optimal, since yield is quantitative trait and characterized by a low heritability and is highly affected by environmental factors (Babu *et al.*, 2003). It is assumed that understanding the physiological and molecular basis may help target the key traits that limit yield. Such an approach may complement conventional breeding programs and hasten yield improvement (Cattivelli *et al.*, 2008). Screening under natural drought stress conditions in the target environments is difficult because of the irregular and erratic drought response. But screening under controlled stress environments and rain-out shelters is more manageable. Selection

response in the target population of environments under natural stress can be considered as a correlated response to selection in the managed stress environment (Venuprasad *et al.*, 2007).

In recent studies on unselected populations of doubled haploid lines, broad-sense heritability of grain yield under reproductive-stage drought stress was comparable with that of grain yield estimated in non-stressed conditions (Atlin and Lafitte, 2002; Babu *et al.*, 2003; Venuprasad *et al.*, 2007). Considerable efforts have been targeted at the genetic analysis of secondary traits such as root system architecture, leaf water potential, panicle water potential, osmotic adjustment and relative water content (Jongdee *et al.*, 2002). A suitable secondary trait is:

Genetically associated with grain yield under drought;

Highly heritable;

Stable and feasible to measure and

Not associated with yield loss under ideal growing conditions (Edmeades *et al.*, 2001).

However, such traits rarely have high broad-sense heritability like yield under drought stress and are often not highly correlated with it (Atlin and Lafitte, 2002).

Molecular markers

Recent advances in DNA marker technology together with the concept of marker assisted selection (MAS) offer solutions for improving complex traits such as drought resistance. Molecular markers linked to complex root and shoot traits would provide a new tool for selecting cultivars with greater drought resistance capacity and thereby improving rice productivity under rainfed conditions.

Molecular markers allow breeders to dissect complex traits without having to measure the phenotype, thus reducing the need for extensive field testing over time and space. Several molecular markers like Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), Amplified Fragment Length Polymorphism (AFLP), Sequence Tagged sites (STS), microsatellites or Single Sequence Length Polymorphism (SSLP), Simple Sequence Repeats (SSRs), Single Nucleotide Polymorphisms (SNPs) etc., are being used in mapping efforts. Upon identification of molecular markers tightly linked to drought resistance traits, MAS can be performed for developing high yielding cultivars suitable for water-limited environments.

Marker Assisted Selection

Molecular marker-assisted selection, often simply referred to as marker-assisted selection (MAS) involves selection of plants carrying genomic regions that are involved in the expression of traits of interest through molecular markers. With the development and availability of an array of molecular markers and dense molecular genetic maps in crop plants, MAS has become possible for traits both governed by major genes as well as quantitative trait loci (QTLs).

If the individual gene(s) or QTLs with significant influence on specific target trait(s) can be identified based on their linkage to molecular markers, the efficiency of incorporating the desired traits in elite germplasm could be greatly enhanced. While plenty of information is already available on different kinds of marker systems and gene-marker associations, the practicalities of designing an MAS strategy, increasing their chance of success and efficiency have not received adequate attention till now.

Fig.1 Different techniques for the development of a drought tolerant variety (Farooq *et al.*, 2009)

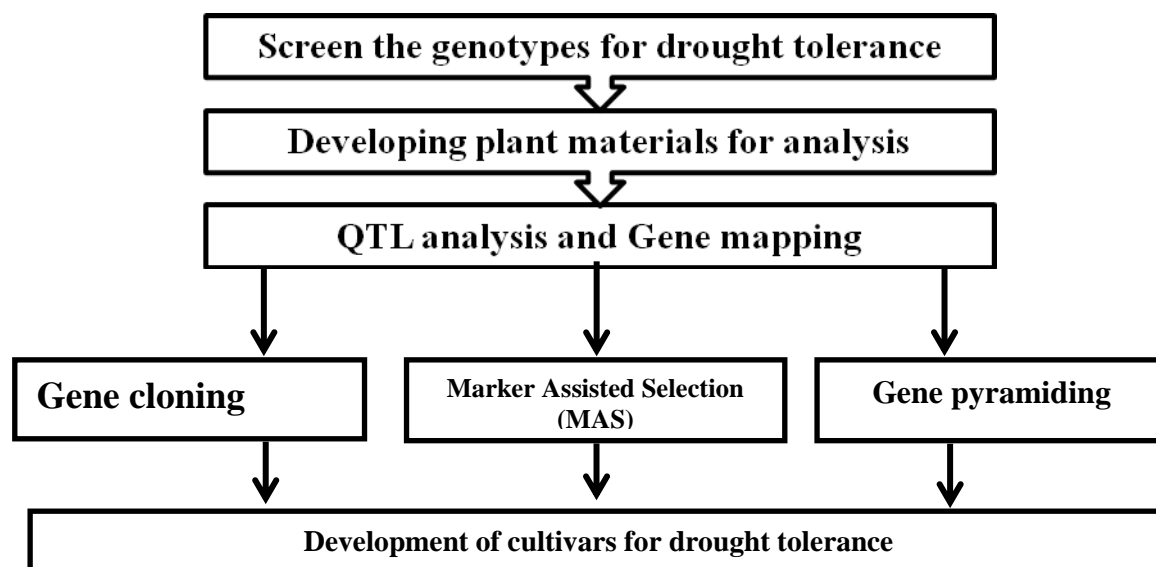


Table.1 QTLs identified for drought resistance in rice

Parents	Population	No. Of Markers	Traits	No. Of QTLs	Phenotypic Variance	Reference
IR64/Azucena	135 DH lines	175(RFLP,RAPD)	Plant height	4	29.2	Hemamalini <i>et al.</i> , 2000
			No. of tillers	11	25.7	
			Root length	5	15.4	
			Root thickness	5	26.7	
			Total root number	10	25.1	
Bala/Azucena	205 RI lines	135(RFLP,AFLP)	No. of penetrated roots	7	16.7	Price <i>et al.</i> ,2002
			Number of roots	3	10.3	
IR64/Azucena	135 DH lines	175 (RFLP,RAPD)	Root penetration index	4	13.5	Zhenget <i>et al.</i> , 2000
			Penetrated root number	2	9	
			Penetrated root thickness	4	16.4	
IR1552/Azucena	150 RI lines	207(RFLP,AFLP)	Seminal root length	2	11.2	Zhang <i>et al.</i> ,2001
IR58821/IR52561	166 RI lines	399(RFLP,AFLP)	Penetrated root number	7	27.2	Ali <i>et al.</i> ,2000
			Root penetration index	6	26.2	
			Penetrated root thickness	8	13.9	
			Total root number	2	12.2	
				2	12.2	
CT9993/IR62266	154 DH lines	315(RFLP,AFLP)	Penetrated root thickness	11	31.3	Zhang <i>et al.</i> , 2001
			Basal root thickness	6	37.6	
			Root pulling force	6	19.9	

Genetic linkage map in rice

Construction of linkage map is essentially the first step in QTL mapping. Such maps allow genetic dissection of QTL, facilitate high-resolution genetic mapping and positional cloning of important genes, assist in local comparisons of synteny within and across the species and provide an ordered scaffold on which complete physical maps can be assembled (Harushima *et al.*, 1998). Recent progress in DNA markers and their linkage maps have provided an efficient tool and methods for mapping individual loci conferring not only monogenic, but also polygenic traits (Tanksley, 1997). The rice genetic map is well covered by microsatellite markers (McCouch *et al.*, 2002) and rice researchers worldwide developed diverse mapping populations and related databases (Ware *et al.*, 2002). A comparative genetic linkage map was constructed with rice and maize for interpreting molecular, genetic, and breeding information between these two important species and to establish a framework for ultimately connecting the genetics of all grass species (Ahn and Tanksley, 1993). A universal core genetic map (UCGM) was constructed with different rice accessions to facilitate the comparison of low resolution genetic maps with evenly distributed markers in rice (Orjuela *et al.*, 2009). An integrated map of AFLP, SSLP and RFLP was constructed (Cho *et al.*, 1998) with a population derived from Milyang 23 and Gihobyeo in Korean Rice Genome Research Project (KRGRP). Another kind of marker, called as Amplified Fragment Length Polymorphism (AFLP) has been described (Vos *et al.*, 1995) and it was utilized in the genetic map construction along with previously mapped RFLP markers in rice (Causse *et al.*, 1994; Maheswaran *et al.*, 1997). Similarly, Random Amplified Polymorphic DNA (RAPD) markers have been integrated into the RFLP map in rice

(Subudhi and Huang, 1999). AFLP and RAPD markers offer several advantages like high frequency of polymorphism, rapidity, technical simplicity, use of fluorescence, requirement of a few nanograms of DNA, no requirement of prior information of the DNA sequence and feasibility of automation.

QTL mapping for drought resistance in rice

The availability of high density linkage maps is a valuable resource for studies that genetically dissect out the complex traits such as drought resistance. QTL mapping provides a potential tool for conducting physiological and genetics research to understand and improve drought resistance. It eases screening for traits that are difficult to quantify and influenced by environmental stimuli (Hanson *et al.*, 1990). Marker-assisted selection using consistent-effect QTL is an efficient approach for developing appropriate aerobic rice varieties. Trait selection is another important concern in molecular breeding for aerobic traits. Wild progenitors and landraces possess valuable drought-resistance traits (Kamoshita *et al.*, 2008). Traditional drought-tolerant donors such as Nootripathu (Gomez *et al.*, 2010) and Dhagaddeshi (Ghimire *et al.*, 2012) were used to identify major-effect QTLs for drought-tolerance traits. As in the case of drought, QTL for a number of physiological and morphological traits have been identified (Table 1) but they have limited implications in breeding drought-tolerant rice varieties.

In conclusion, to sum up, development of high yielding drought tolerant rice cultivars will considerably improve rice production, especially in rainfed areas. Identifying consistent QTLs for yield under stress with large effect and fine-mapping them will speed up MAB for drought tolerance in rice. QTLs with large intervals have the chance of getting undesirably linked genes; hence it is

important to fine-map the QTLs so as to introgress the precise genomic segment of interest.

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