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Original Paper

Drought tolerance improvement for grain yield of a modern rice variety based on morphological and physiological response

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Abstract

Growth of rice (*Oryza sativa* L.) is severely affected by drought stress, which leads to decreased rice production in rainfed ecosystems worldwide. Particularly, modern rice varieties are more susceptible to drought stress rather than traditional rice varieties. In the present study, a modern short-term rice variety, ADT37, abundantly cultivated in the Cauvery delta region of the southern part of India, was improved for grain yield by introducing qDTY1.1 through the conventional backcross method. Positive F_1 progenies were identified using RM431 linked with qDTY1.1 in PCR amplification. In phenotypic selection, rice progenies with suitable plant height to avoid linkage drag as well as high degree of drought tolerance to manage the drought stress were selected and advanced through the backcrossing process up to the BC_3 generation. Finally, two near isogenic lines with equal plant height to the recurrent parent and high degree of drought tolerance were selected. A positive effect of qDTY1.1 on plant height and fertile seeds was revealed. In the future, the selected superior near isogenic lines would be useful to rice researchers and farmers facing unexpected water crises. Moreover, the morphological marker associated with the performance of crops according to the intensity of stress will support climate resilient agriculture.

Key words: ADT37, backcross, drought tolerance, qDTY1.1, rice.
Abbreviations: NIL, near isogenic lines; QTL, quantitative trait loci.

Introduction

Rice (*Oryza sativa* L.) is a semi-aquatic crop and it is an important food crop around the world. Unfavourable water level conditions cause reduced metabolic activity of rice and it gives poor or no grain-yield due to the intensity of drought, which depends on frequency of rainfall, evaporation and soil moisture (Hao et al. 2018; Oladosu, et al. 2019). This situation raises a question for food security of the increasing population. Nowadays, this condition has become familiar in some parts of the world frequently due to climate change. It is also important to note that seasonal drought stress in rain-fed regions poses a significant risk to rice agriculture from the stage of seed germination to the flowering stage. Therefore, over the past two decades, rice breeders have continued their efforts in identification of new sources from rice genotypes of landrace and wild rice, which are able to withstand drought. At the same time, they evaluate the existing genetic sources from different locations throughout the year for maintaining their efficiency under changing climate. As a result, a large number of effective quantitative trait loci (QTL) have been registered for drought tolerance all over the world. Particularly, many QTLs such as DTY1.1, DTY3.1, DTY2.1, etc. for drought tolerance at the reproductive stage have been reported (Bernier et al. 2007; Venuprasad et al. 2009; Sandhu et al. 2010; Vikram et al. 2011; Ghimire et al. 2012; Mishra et al. 2013; Swamy et al. 2013; Yadav et al. 2013; Dixit et al. 2014a, Dixit et al. 2014b; Dixit et al. 2014c; Palanog et al. 2014). These QTLs have been reported to have ability to withstand drought during the reproductive stage in many popular high-yielding rice cultivars all over the world (Venuprasad 2009; Vikram et al. 2011; Kumar et al. 2014; Chakraborty et al. 2023).

In the southern part of India, the rate of paddy cultivation is significant in the Cauvery delta region (Parasuraman et al. 2008; Araving et al. 2023). However, this region is highly prone to drought stress or flooding. Here, drought stress occurs at seedling stage or reproductive stage of rice crop due to lack or delay of the monsoon. In this region already, severe drought stress was reported between the years 1974 and 2014 (Parasuraman et al. 2008). Also, in 2016 this region received a total of only 168 mm precipitation, which is much less than the annual average of 1000 mm.

Several traits at morphological, physiological and molecular levels, such as plant height, panicle number, root volume, fertile spikelets, plant biomass, leaf area development, root/shoot ratio, grain yield, and chlorophyll, starch, soluble sugar and proline content have been used for selection of drought tolerant rice genotypes (Misura et al. 2014). Moreover, morphological markers are cheaper and an easy way to identify prominent characteristics of a specific crop plant. Hence, in the present study, keeping above considerations in mind, a popular high-yielding short-duration rice variety, ADT37, was improved for drought tolerance at the flowering stage by incorporation of qDTY1.1 through backcrossing, using plant height and drought tolerance degree as morphological markers.

Materials and methods

Source of rice seeds

A small quantity of rice seeds of ADT37 were sourced from the Tamilnadu Rice Research Institute, Aduthurai, Tamilnadu state and CR Dhan 801 from the National Rice Research Institute, Cuttack, Odisha state. Rice varieties used were ADT37 as the female parent (recipient) for improving drought tolerance at the reproductive stage and CR Dhan 801 harboring qDTY1.1 as the male parent (donor). ADT37 is also a short duration variety (110 days) and its seed production is estimated to be 6.0 t ha^{-1}. This variety was developed from a cross between BG 280-12 and PTB 33. The rice seeds are bold and white in colour. The variety is resistant to many pests and diseases.

Genotypic selection

Genomic DNA was isolated from fresh leaves of ADT37 and CR Dhan 801 parental lines using the CTAB method with minor modifications (Murray et al. 1980). PCR was performed in a volume of 10 µL containing 20 to 30 ng template DNA, 5 pmol of each primer (forward 5'-tcctgcgaactgaagagttg-3' and reverse 5'-agagcaaaaccctggttcac-3') of SSR marker, RM431linked with qDTY1.1 (Vikram et al. 2011), 0.05 mM dNTPs, 10x PCR buffer (10 mM Tris, pH 8.4, 50 mM KCl and 1.8 mM $MgCl_2$) and 0.5 U of Taq DNA polymerase (Bangalore Genei, Bengaluru, India.

Phenotypic selection

For phenotypic selection of backcrossing progenies, plastic pots filled with rice field soil were used in a net house at Kandaswami Kandar's College (11.1202°N, 78.0031°E), Velur, Namakkal district, Tamil Nadu, India. Seedlings of backcrossing population grown for 21 days along with parental lines were transplanted to plastic pots. In each pot, five seedlings of the backcrossing population were planted along with its both parental lines. Seedlings were allowed to establish for 30 days and then drought stress was imposed for 5 days by withholding water irrigation. In the control, parental lines were grown under flooding. Plant height of the backcrossing progenies was measured from the ground level to the top of each plant after stress, and compared with the recurrent parent (Venuprasad et al. 2009; Vikram et al 2011). For selection of drought tolerant progenies based on the rate of leaf drying, total length of three leaves from top of the plant of each progeny minus with the length of the dried part of the leaf was measured and drought tolerance degree was scored according to Zu et al. (2017) and IRRI's scale for leaf drying (IRRI 2002).

Development of near isogenic lines

Hybridization was performed between ADT37 and CR Dhan 801 in a nethouse during Kharif season, 2019. The derived F1 seeds were subjected to foreground selection using RM431 linked with qDTY1.1 and positive plants were used for backcrossing with their recurrent parent during Kharif (monsoon) of 2020 to produce BC_1F_1 seeds. Similarly, BC_2F_1 and BC_3F_1 generations were produced during Kharif of 2021 and 2022, respectively. Selected BC_3F_1 progenies were allowed for selfing to derive BC_3F_2 seeds during Rabi (dry, winter to spring season) of 2022 to 2023.

Evaluation of near isogenic lines

For evaluation of near isogenic lines (NILs), seedlings of NIL-1 and NIL-2 along with the parental line (ADT37) were raised in the nursery and transplanted into plots of the rice field with 10 × 15 cm gaps between seedlings of four replications. Each replication consisted of three plants. Drought stress was imposed on rice plants at the time of flag leaf initiation by withholding water irrigation and another set of the isogenic and parental lines was maintained under flooding. After harvesting of seeds, the seed setting percentage (SS%) in NILs was calculated.

Statistic analysis

Mean value, range, standard deviation and standard error were calculated for seed setting percentage (SS%).

Results and discussion

Drought stress reduces the rice growth through limited leaf growth (Zhu et al. 2020), reduced leaf area, leaf rolling, leaf drying, thickened leaf size, early senescence, stomatal closure and development of a cutinized layer on the leaf surface (Mishra, Panda 2017; Hussain et al. 2018; Panda et al. 2021). Particularly, the flowering stage of rice crop is highly sensitive to water stress and it results in poor or no seed setting due to spikelet sterility, depending on the intensity of drought stress (Yang et al. 2019). In this study, we found polymorphism between varieties ADT37 and CR Dhan 801 at phenotypic as well as genotypic levels. Rate of seed setting of CR Dhan 801 and ADT37 according to IRRI's scale was registered as score 1 and 7, respectively, under water limited conditions. In PCR screening, the size of the PCR band using RM431 was 250 and 260 bp in CR Dhan 801 and ADT37, respectively (Fig. 1).

Similarly, Nagina 22 (N22), the drought-tolerant donor,

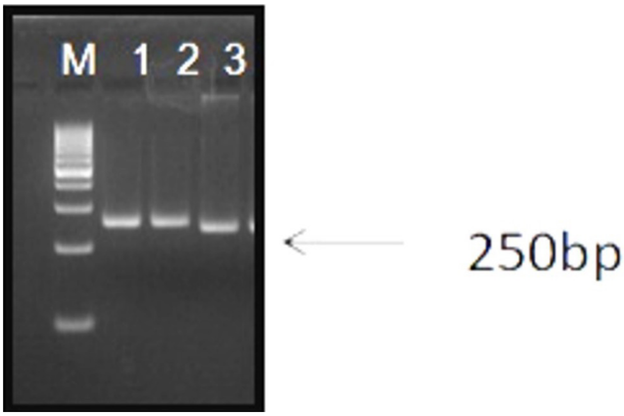

Fig. 1. Parental polymorphism between recipient (ADT37) and donor (CR Dhan 801) in PCR screening using RM 431 (qDTY 1.1). M, 100 bp DNA ladder; lane 1, ADT37; lane 2, ADT36; lane 3, CR Dhan 801.

harbouring qDTY1.1, was differentiated from drought intolerant popular mega rice varieties such as Swarna, IR64, and MTU1010 in a study using RM431 as a marker (Vikram et al. 2011). In PCR screening using RM431as a foreground marker, two plants (# F_1.13 and F_1.15) out of eight F_1 plants having heterozygous alleles for qDTY1.1 were detected (Fig. 2). Details of the seeds derived and used for phenotypic selection are given in Table 1.

As a result of backcrossing of these positive F_1 plants with ADT37, 82 seeds were produced for the BC_1F_1 generation. From these, 50% (41 seeds) of seeds were used for phenotypic selection, in which only 37 seedlings survived. In drought screening of the BC_1F_1 population, plant height of donor and recurrent parent were 34.6 and 38.0 cm, respectively, and plant height in 37 progenies ranged from 26.0 to 45.0 cm. After 5 days of drought stress, the drought tolerance degree value was higher in the donor line (0.61), with IRRI's scores 3, 5, and 9 for the 1st, 2nd and 3rd leaf of the plant, respectively, compared to scores 7, 5, and 9 for the recurrent parent (drought tolerance degree value 0.31) (Fig. 3).

This scoring pattern in three leaves of parental lines reflected in one progeny (F_1 15.2) for the donor and one progeny for the recipient (F_1 13.1), and the other 35 progenies showed variation from that of both parental lines. However, the drought tolerance degree was in the range of 0.27 to 0.74 among progenies. Here, the lower and higher drought tolerance degree values were observed to be associated with drought intolerance and tolerance of these progenies, respectively. Therefore, ten progenies (BC_1F_1 13.10 plants 12, 13, 15, 17, 18, and BC_1F_1 15.2 plants 10, 11, 13) were selected as drought tolerant, based on higher drought tolerance degree value than recurrent parent (0.31). Similarly, Zu et al. (2017) observed higher drought tolerance degree values in 13 rice cultivars, which showed the strongest drought tolerance in upland screening. The rate of drought tolerance in these selected plants increased from 21.0 to 59.45% when compared to the recurrent parent. The plant height in selected plants was higher (40.0 to 45.5 cm) than that of the recurrent parent (38.0 cm). Increased plant height was reported in the N22 drought tolerant variety and reduced growth in the drought susceptible rice variety, Swarna-Sub1 under drought conditions. In intolerant genotypes, reduced plant height hampers cell division and cell elongation activity due to drought stress (Panda et al. 2023). Supportively, qDTY1.1 showed a greater effect on plant height and higher grain-yield under drought stress at the reproductive stage since this QTL is tightly linked to the sd1 loci controlling plant height in rice (Vikram, et al., 2015). Similarly, many studies have been carried out with N22 (harboring qDTY1.1) under drought stress conditions (Rahman et al. 2002; Yang et al. 2019).

In earlier attempts to improve grain-yield under reproductive stage stress, selection of the best rice lines was based on root architecture, leaf water potential, panicle water potential, osmotic adjustment and relative water content, but did not give the expected results (Fukai et al. 1999; Pantuwan et al. 1999). Here, plant height was used for introgression of DTY1.1 into the ADT37 popular rice variety to improve grain yield at reproductive stage stress. In the screening, we considered only plant height, but not the character of day to flowering, since it did not affect grain yield under drought stress (Vikram et al. 2011). Thus, selected plants were backcrossed with ADT37 and produced

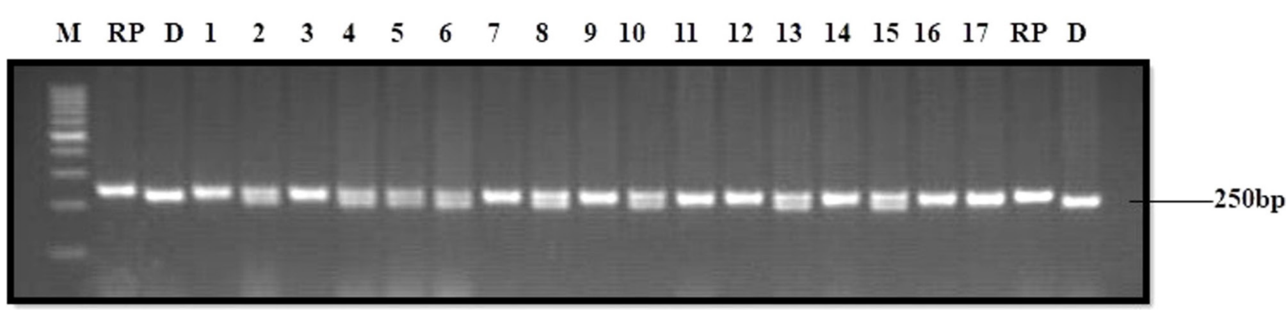

Fig. 2. PCR screening of F1 progenies derived from a cross between ADT37 and CR Dhan 801 to detect qDTY1.1 using RM431. M, 100 bp DNA ladder; RP, ADT36/ADT37; D, CR Dhan 801; lane 1 to 10, F_1 plants from a cross between ADT36 and CR Dhan 801; lane 11 to 17, F_1 plants from a cross between ADT37 and CR Dhan 801.

Table 2. Details of F_1 seeds produced in BC_1, BC2 and BC_3 generations and used for phenotypic selection

Progeny	BC progenies	Number of seeds derived through backcrossing	Number of seeds used for next generation	Number of seedlings survived
		BC_1F_1 generation		
1	BC_1F_1 13.10	5	2	2
2	BC_1F_1 13.12	10	5	4
3	BC_1F_1 13.13	7	3	2
4	BC_1F_1 13.15	2	1	1
5	BC_1F_1 13.17	4	2	2
6	BC_1F_1 13.18	12	6	4
7	BC_1F_1 15.2	16	7	4
8	BC_1F_1 15.10	11	5	2
9	BC_1F_1 15.11	5	3	1
10	BC_1F_1 15.13	2	1	1
		74	**35**	**23**
		BC_2F_1 generation		
1	BC_2F_1 13.10.1	8	4	3
2	BC_2F_1 13.10.2	6	5	0
3	BC_2F_1 13.12.1	3	1	0
4	BC_2F_1 13.12.2	0	0	0
5	BC_2F_1 13.15.1	7	4	1
6	BC_2F_1 13.15.2	10	4	1
7	BC_2F_1 15.2.2	7	3	2
8	BC_2F_1 15.11.1	7	4	2
		48	**24**	**9**
	BC_3F_1 generation		BC_3F_2 generation	
1	BC_3F_1 13.10.1.3	–	BC_3F_2 13.10.1.3	–
2	BC_3F_1 15.11.1.2	–	BC_3F_2 15.11.1.2	–

72 seeds for the BC_2F_1 generation. From these, half of the seeds (35 seeds) were used for phenotypic selection as mentioned above, but only 24 plants were survived. In drought screening of the BC_2F_1 population, plant height of donor and recurrent parent was 34.5 and 38.5 cm, respectively, and the plant height in 24 progenies ranged from 36.6 to 41.5 cm. In these progenies, drought tolerance degree varied in the range of 0.30 to 0.70, and from these, eight plants (BC_2F_1 13 plants 10.1, 10.2, 12.1, 12.2, 15.1, 15.2; and BC_2F_1 15 plants 2.2, 11.1) were selected as drought tolerant based on a higher drought tolerance degree. Moreover, these progenies showed drought tolerance at a 30 to 50% higher level than that of the recurrent parent and they had greater plant height, more or less similar to that of the recurrent parent. Following the backcrossing with the recurrent parent, 48 seeds were produced from these progenies for the BC_3F_1 generation and from these, 24 seeds were used for phenotypic selection, but only nine plants survived.

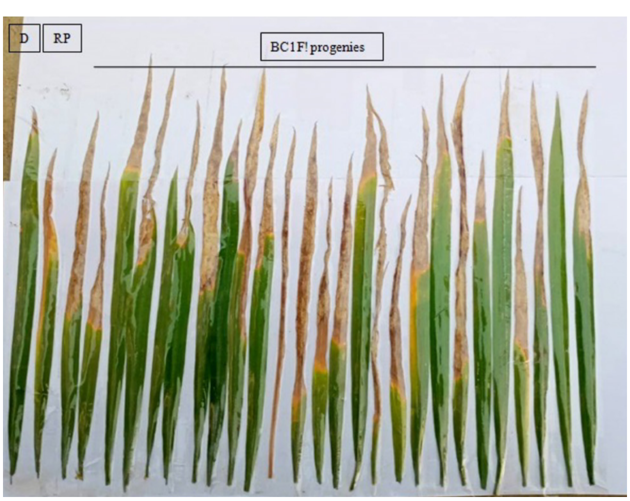

Fig. 3. Phenotypic selection of BC_1F_1 progenies based on leaf drying score under drought stress condition. D, donor; RP, recurrent parent (ADT37).

In drought screening of the BC_3F_1 population, plant height of donor and recurrent parent were 33.75 and 38.25

Table 2. Statistical analysis of NIL population for seed setting percentage under drought condition

Rice lines	Seed setting (%)			
	Mean	Range	Standard deviation	Standard error
NIL-1	71.23	57.6 – 83.6	3.30	6.6
NIL-2	70.18	67.7 – 83.0	2.96	5.92

cm, respectively, and the plant height in nine progenies ranged from 37.7 to 39.2 cm. In these progenies, the drought tolerance degree varied in the range of 0.48 to 0.61, and from these, two plants (plant BC_3F_1 13 10-1.3 and BC_3F_1 15 11-1.2) were selected as drought tolerant based on a higher drought tolerance degree value. Moreover, these progenies showed drought tolerance at a 31.25 to 45.9% higher level than that of the recurrent parent and they had plant height more or less similar to that of recurrent parent. These two progenies were allowed to self and BC_3F_2 seeds were derived. Under drought conditions, seed setting percentage was in the range of 57.6 to 83.6 in NIL-1 and 67.7 to 83.0 in NIL-2. Results of statistical analysis are presented in Table 2. The seed setting percentage in the ADT37 rice variety was 100 and 39.4% under control and drought conditions, respectively.

Hence, NILs selected based on plant height and drought tolerance degree increased the grain yield in ADT37 rice variety under drought conditions in the presence of DTY1.1. Similarly, many promising breeding lines linked with drought tolerance at the reproductive stage for rainfed lowlands and uplands have been reported and have been used for improvement of popular rice varieties at morpho-physiological and growth levels (Mandal et al. 2010; Verulkar et al. 2010; Vikram et al. 2011; Dixit et al. 2017; Vinod et al. 2019). Thus, identification of rice lines with superior morphological and physiological characters can enhance breeding programmes (Panda et al. 2023). Many studies have been carried out using direct selection for grain yield under drought stress based on a practical approach of combining high yield genetic sources for grain yield (Venuprasad et al. 2008). In this study, the rate of seed setting in ADT37 with DTY1.1 was increased to 30% under drought conditions, when compared to ADT37 with no DTY1.1. Interestingly, qDTY1.1 has been reported to consistently have a major positive effect on grain yield under control conditions in different genetic backgrounds of mega rice varieties (Vikram et al. 2011). Very recently, qDTY1.1 in N22 (drought tolerant) was reported to have a greater number of fertile seeds through increased levels of chlorophyll, total phenolics and proline, and antioxidant potential, lipid peroxidation and 5-methylcytosine under drought stress conditions (Nitin Kumar et al. 2019; Kumar et al. 2023).

Conclusions

Higher and lower plant height among backcrossing population is associated with drought tolerance and intolerance, respectively, under drought stress (Vikram et al. 2011). Thus, we could advance the breeding programme up to the BC3 generation using plant height as a morphological marker. In this study, modern rice variety, ADT37 was proven at phenotypic and genotypic level to have drought intolerance at the reproductive stage. In PCR screening, we could confirm the introgression of qDTY1.1 into progenies of ADT37 × CR Dhan 801 cross using RM431, which is closely linked with this locus. Moreover, we could advance the backcrossing process using positive progenies up to the BC3F2 generation through selection of rice progenies with equal or taller height than that of the recurrent parent, to avoid linkage drag as well as high degree of drought tolerance. Lastly, evaluation of NILs proved the linkage of plant height with greater number of fertile seeds than recurrent parent under drought conditions. Thus, introgression of QTL associated with the morphological character would be cheaper and more effective to address the problem for climate resilient agriculture.

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