

Quantitative trait loci linked to plant production traits in rice (*Oryza sativa*) under drought stress in a target environment

Kanjivavila Raghavan Biji^a, Paramasivam Jeyaprakash^b, Siruthaiyur Krishnamoorthy Ganesh^c, Alagaraswamy Senthil^a, Ranganathan Chandra Babu^{d,*}

^a Department of Plant Molecular Biology and Biotechnology, Tamil Nadu Agricultural University, Coimbatore, India

^b Agricultural College and Research Institute, Tamil Nadu Agricultural University, Madurai, India

^c National Pulses Research Centre, Tamil Nadu Agricultural University, Vamban, India

^d Dean, School of Post Graduate Studies, Tamil Nadu Agricultural University, Coimbatore, India

* Corresponding author, e-mail: chandrarc2000@yahoo.com

Received 17 Aug 2007

Accepted 24 Jun 2008

ABSTRACT: Drought stress is the major constraint to rice (*Oryza sativa*) production and yield stability in rainfed ecosystems. Identifying genomic regions contributing to drought resistance will help to develop rice cultivars suitable for rainfed regions through molecular marker-assisted breeding. Quantitative trait loci (QTLs) linked to plant production traits under drought stress were mapped by evaluating 155 F7 recombinant inbred (RI) lines of IR58821-23-B-1-2-1/IR52561-UBN-1-1-2 under rainfed and irrigated conditions in the target environment. The RI lines were subjected to water stress during grain filling by natural rainfall failure events in two successive seasons. The RI lines showed significant variation in plant phenology, plant biomass, yield, and yield components under rainfed and irrigated conditions. Grain yield under rainfed condition had a positive correlation with harvest index and negative correlations with spikelet sterility and the number of days to 50% flowering. A total of 11 QTLs, identified for various plant phenology and production traits under rainfed and irrigated conditions, accounted for 9.3–23.4% of the phenotypic variation. A genomic region identified on chromosome 2 harboured a large effect QTL for grain yield (23.4%) under rainfed conditions. The region C499-PC11M1 on chromosome 2 identified for grain yield under rainfed conditions was collocated with QTLs associated with root traits.

KEYWORDS: rice, drought resistance, heritability, phenotypic variation, quantitative trait loci mapping, collocation

INTRODUCTION

Rice (*Oryza sativa* L.) is grown on more than 150 million hectares¹ in a wide range of ecosystems under varying temperatures and water regimes. About 45% of the global rice area occurs in rainfed ecosystems, which frequently experience severe water deficit due to uncertain and uneven rainfall distribution patterns. It is estimated that 18 million tons of rice valued at US\$ 3.6 billion is lost annually to drought². Drought stress is the major constraint to rice production and yield stability in rainfed regions³. Developing high-yielding drought-tolerant rice cultivars will considerably improve rainfed rice production and/or yield stability. Genetic improvement of adaptation to drought is conventionally done by selecting for yield and its stability over locations and years. The progress is slow because of inherent variation in the field, year to year variation in rainfall, and the fact that there is only one crop per year⁴. Alternatively, yield improvements in water limited environments could be achieved by identifying secondary traits contributing

to drought resistance and selecting for those traits in a breeding programme^{5,6}. The effectiveness of selection for secondary traits to improve yield under water-limiting conditions has been demonstrated in sorghum⁷, maize⁸, and wheat⁹.

Several putative traits contributing to drought resistance in rice have been reviewed^{10,11}. Since phenotypic selection for these traits involves complex, labour intensive protocols and cost demanding experimental conditions, these traits are rarely selected for in crop improvement programmes. Considering these limitations to efficient selection, molecular marker technology is a powerful tool for selecting such traits. Quantitative trait loci (QTLs) have been identified for several drought resistance traits in rice^{12,13}. A significant proportion of the phenotypic variability of several of these drought resistance traits is explained by the segregation of relatively few genetic loci, thus leading to the possibility of indirect selection of these complex traits by means of a marker assisted selection (MAS) strategy⁶. Although QTL analysis indicates the map positions of QTLs

associated with drought resistance traits, the effects of those traits on plant production under drought is unknown. Thus there is a need to determine whether the QTLs linked to drought resistance traits also have an impact on the yield under stress. By comparing the coincidence of QTLs for specific traits and QTLs for plant production under drought, it is possible to test whether a particular constitutive or adaptive response to drought stress is of significance in improving field level drought resistance¹⁴.

Previous studies indicated collocation of certain QTLs for root traits with those of the yield in the target environment^{6,15}. However, these studies involved rice lines derived from *indica/japonica* crosses. The necessity of QTL identification based on the variation from the crosses between rice lines belonging to the same subspecies has been emphasized^{16,17}. It is therefore desirable to use a population derived from an *indica/indica* cross to identify QTLs associated with drought resistance traits. Few studies reported mapping QTLs linked to drought resistance traits using *indica/indica* rice populations^{18,19}. QTLs associated with drought resistance traits and grain yield have been identified in an *indica/indica* population from a managed stress environment (MSE)²⁰, but there has been no corresponding study for populations from the target environment (TE). Hence, the present study was conducted with the objectives: (i) to identify genomic regions linked to plant production and drought resistance traits in *indica/indica* lines in the TE, (ii) to identify collocation of QTLs of drought resistance traits with those of plant production, and (iii) to identify a set of QTLs for marker assisted breeding for rainfed rice improvement.

MATERIALS AND METHODS

Plant materials

The rice breeding lines, IR58821-23-B-1-2-1 and IR52561-UBN-1-1-2, differ consistently for a range of drought resistance traits. These include gross root morphology, root penetration index, root pulling force, and osmotic adjustment²¹. A RI line population was developed by single-seed descent from a cross between IR58821-23-B-1-2-1 (abbreviated as IR58821, a lowland *indica* accession which has high root penetration index and thicker roots) and IR52561-UBN-1-1-2 (abbreviated as IR52561, a lowland *indica* line with low root penetration index and thinner roots) at the International Rice Research Institute, Philippines. Of the 166 F₇ recombinant inbred (RI) lines of the population, a subset of 155 lines was used in this study.

Field trials

Two separate field trials were conducted in experimental fields of Tamil Nadu Agricultural University at Paramakudi, India during the 2001–2 and 2002–3 wet seasons (September–February). In all the trials, the RI lines were evaluated under two water regimes, namely, rainfed and irrigated (nonstress) conditions, following randomized complete block design. The RI lines were replicated twice under rainfed and thrice under irrigated conditions in Trial 1, whereas both the treatments were replicated thrice in Trial 2. Experimental plots were 2.0 × 0.6 m² in size. The spacing between and within rows were 20 cm and 10 cm, respectively. Seeds were hand-dibbled into dry soil (100 kg/ha). NPK fertilizers were applied at 50:25:25 kg/ha. P and FYM (12.5 tons/ha) were applied in full as the basal dose during sowing, whereas N and K were applied in three splits as top dressing. Paddy micronutrient mixture was applied at 12.5 kg/ha during the early vegetative stage. Insect and weed control measures were applied periodically as required. The main soil and drought stress characteristics of the trials are summarized in Table 1.

Table 1 Site, soil, and drought stress characterization for the trials conducted in Paramakudi, India

Site	Trial 1	Trial 2
Elevation (metres above sea level)	40	40
Latitude and longitude	9° N, 70° E	9° N, 70° E
Soil texture	Clay loam	Clay loam
Soil pH	8.1	8.1
Characterization of the stress	Severe	Moderate
Timing of start of stress	101 DAE*	88 DAE
Duration of stress period (d)	21	33
Rainfall during stress period (mm)	0	0
Rainfall during crop period (mm)	435	460
Mean temperature (°C)		
Maximum	33.2	35.9
Minimum	20.1	21.8
Average relative humidity (%)		
Maximum	89.6	84.9
Minimum	65.4	67.5

* DAE = days after seedling emergence

Field measurements

Drought score (leaf rolling) was recorded at midday during peak stress using the 1–7 scale standardized for rice²². Data on days to 50% flowering, grain yield, straw yield, spikelet sterility, total biomass, and harvest index were recorded. Spikelet sterility was calculated as the ratio of unfilled spikelets to total spikelets per panicle. Relative grain yield under rainfed conditions, which was the ratio of the rainfed yield to the irrigated yield, was also computed.

Statistical analysis

Analysis of variance was done using the general linear model procedure of the SAS 9.1 program²³ in order to check the genetic variance among the RI lines for all the traits. Broad sense heritabilities (H) were then computed from the estimates of genetic (σ_G^2) and residual (σ_e^2) variances using $H = \sigma_G^2 / (\sigma_G^2 + \sigma_e^2/k)$, where k is the number of replications. The frequency distribution of all the traits was tested for skewness. The Pearson correlations among the traits within a trial were computed using the genotypic means²³.

Linkage map and QTL analysis

The genotypic data of the 155 RI lines provided by Dr. Henry T. Nguyen, Department of Agronomy, University of Missouri, Columbia, USA were used to map QTLs linked to various traits from the trials conducted in the present study. The genetic linkage map consisted of 399 marker loci including 303 RFLPs and 96 AFLPs with a total map length of 2022 cM¹⁸. Using the genetic linkage map, QTLs linked to plant production and drought resistance traits and their phenotypic effects were identified using MAPMAKER/QTL version 1.1b^{24,25}. The threshold LOD score used to declare the presence of QTLs

was 3.0 which was derived on the basis of the total map distance and average distance between markers according to Lander and Botstein (1989)²⁶. Putative QTLs with LOD 3.03–4.16 were used to construct the QTL map.

RESULTS AND DISCUSSION

Variation in drought resistance and plant production traits

The phenotypic means and range for the various traits along with broad sense heritabilities from the two trials are given in Table 2. Water stress occurred in both trials, although the severity of the stress differed as indicated by the mean values of drought score (leaf rolling) and days to heading under rainfed conditions for RI lines. Water stress was terminal but severe in Trial 1 with a continuous stress period of 21 days (without rain from 101 to 121 days after seedling emergence) coinciding with flowering and grain filling phases. The average drought score (leaf rolling) across the RI lines was 4.3. The average leaf drying was 4.8 under rainfed conditions in rice doubled haploid lines⁶. Mean heading date was delayed by 18 days under rainfed conditions as

Table 2 Trait mean values for 155 rice recombinant inbred (RI) lines tested under rainfed and irrigated conditions.

Trait	Trial	RI lines		SD ^a	H
		Mean	Range		
Drought score (leaf rolling)	1	4.3	1.0–7.0	1.6	0.43
	2	1.9	1.0–4.3	0.8	0.34
Days to heading-rainfed	1	104	83–130	15.1	0.64
	2	85	79–92	3.3	0.88
Days to heading-irrigated	1	86	76–98	4.7	0.75
	2	88	78–100	4.6	0.80
Plant height (cm)-rainfed	2	88.7	66.3–109	7.7	0.44
Plant height (cm)-irrigated	2	106.1	74.8–134	10.5	0.43
Grain yield (kg/ha)-rainfed	1	249	0.0–1017	300	0.84
	2	204	0.0–1067	241	0.29
Grain yield (kg/ha)-irrigated	1	1995	0.0–4644	1021	0.37
	2	2054	0.0–4783	854	0.27
Biomass (kg/ha)-rainfed	1	5811	1536–13591	2056	0.71
	2	6515	1100–12056	1932	0.35
Biomass (kg/ha)-irrigated	1	6313	1888–15432	2780	0.68
	2	10699	2375–22983	4493	0.55
Spikelet sterility (%)-rainfed	1	38.9	10.1–95.5	16	0.64
Spikelet sterility (%)-irrigated	1	20.7	4.1–52.9	8.7	0.41
Harvest index-rainfed	1	0.1	0.01–0.2	0.05	0.61
	2	0.08	0.01–1.0	0.13	0.49
Harvest index-irrigated	1	0.3	0.10–0.5	0.07	0.33
	2	0.25	0.11–1.0	0.10	0.18
Relative yield (%)	1	28	4–91	17	-

^a SD = standard deviation

compared to irrigated conditions across RI lines. Heading delay is a common drought response observed in rice under drought stress²⁷. Late-maturing cultivars suffered greater yield reduction than earlier ones since the stress occurred late in the crop growth. The water stress caused an average reduction of 87.5% in grain yield. Lafitte et al¹³ tested 166 rice germplasm accessions under mild terminal drought in lowland conditions which on average reduced grain yield to 84% of the control. The tested varieties showed a wide range of yield response to the stress. Some lines produced up to 150% as much grain yield under stress as in the control, while others suffered a yield reduction of over 90%. In the present study, there was a 54% reduction in spikelet fertility under stress across the RI lines. Similar results were reported in rice DH lines under stress in Thailand²⁸. There was a 67% reduction in mean harvest index under rainfed condition in the present study. The relative yield under drought stress ranged from 4–91% with a mean of 28% across the RI lines. Similar variation in morpho-physiological, plant phenology, and production traits under rainfed conditions was reported in several rice populations^{29,30}. Transgressive segregation in both directions was observed for most traits. The frequency distribution of phenotypes for the traits evaluated in this study approximately fitted a normal distribution. Broad sense heritability of days to heading, spikelet sterility percentage, and total biomass under rainfed conditions was high (0.64, 0.64, and 0.71, respectively).

There was a continuous stress period of 33 days from 88 to 120 days after seedling emergence coinciding with flowering and grain filling phases in Trial 2. However, water stress was moderate. The average drought score (leaf rolling) was only 1.9 across the RI lines (Table 2). Stress delayed days to heading by only 4 days on average, while mean plant height was reduced by 17 cm (16%) across the RI lines as compared to the control. Average biomass, yield, and harvest index were reduced by 39%, 90%, and 68%, respectively, under rainfed conditions as compared to the control. Harvest index is a primary determinant of grain yield under rainfed conditions³¹, and the genetic improvement of the harvest index would increase grain yield^{32,6}. The broad sense heritability was low to medium for most traits except days to heading under stress (0.88). Babu et al⁶ reported high heritability for days to heading under rainfed conditions. The frequency distribution of phenotypes for the traits evaluated approximately fitted a normal distribution.

In summary, there was a significant genotypic variation for most traits under rainfed conditions in

both trials. Significant differences for plant production and drought resistance traits have been reported among a subset of 148 of these RI lines from an MSE²⁰.

Correlations among drought resistance traits and plant production

The correlation coefficients (r) among various traits are presented for Trial 1 (Table 3) since water stress was severe with an average yield reduction of 87.5% under rainfed conditions as compared to the irrigated conditions. A yield reduction of more than 50% under stress is considered critical for the expression of drought resistance potential in rice³³. Grain yield had a positive correlation with harvest index ($r = 0.77$). The positive relation between yield and harvest index in IR58821/IR52561 rice RI lines under stress has been reported²⁰. Significant negative correlations between grain yield and days to 50% flowering ($r = -0.47$) and spikelet sterility ($r = -0.28$) under rainfed condition were noticed. Negative correlations between grain yield and days to flowering and spikelet sterility under stress were reported in rice³¹. This suggests that RI lines flowering late due to drought suffered more yield loss³². Drought stress affected spikelet fertility in rice³³. Spikelet sterility had a negative correlation with harvest index ($r = -0.34$) under stress.

Although the stress was relatively moderate in Trial 2, drought score (leaf rolling) was negatively correlated with grain yield ($r = -0.33$) and grain yield showed positive correlation with harvest index ($r = 0.86$).

Table 3 Correlation coefficients among drought score (DS), days to heading (DH), biomass (BM), grain yield (GY), spikelet sterility (SS) and harvest index (HI) under rainfed condition in the field in Trial 1 in RI line population.

	DS	DH	BM	GY	SS	HI
DS	1.00	-0.15	0.11	0.02	0.11	-0.07
DH		1.00	0.03	-0.47**	0.36**	-0.41**
BM			1.00	0.11	0.16	-0.46**
GY				1.00	-0.28**	0.77**
SS					1.00	-0.34**
HI						1.00

** ($p < 0.01$)

QTLs linked to plant production and drought resistance traits

A total of 11 QTLs, significant at a logarithm of odds (LOD) score of ≥ 3.00 , were identified for various plant production and drought resistance traits under rainfed conditions from the trials (Table 4). The number of QTLs identified for each trait within

Table 4 QTLs detected with $\text{LOD} \geq 3.00$ for drought score (leaf rolling), days to heading (days after sowing), number of productive tillers, grain yield (kg/ha) and biomass (kg/ha) by interval mapping via MAPMAKER/QTL version 1.1b in RI line population of 155 lines from IR58821 and IR52561 from two trials. Individual QTLs are designated with the italicized abbreviation of the trait and chromosome number. When more than one QTL affects a trait on the same chromosome, they are distinguished by decimal numbers.

Traits	QTL	Chromosome number	Interval	LOD	Effect ^a	R^{2b}
Drought score (leaf rolling)	<i>ds4.1</i>	4	PC11M4 - PC21M8	3.19	0.5450 (IR2)	9.7
	<i>ds5.1</i>	5	PC34M5 - RG229	3.59	0.5686 (IR2)	10.5
	<i>ds5.2</i>	5	PC38M8 - PC35M14	3.93	0.5898 (IR2)	11.1
Days to heading - irrigated	<i>dhi5.1</i>	5	PC38M8 - PC35M14	3.54	3.0644 (IR2)	10.3
Number of productive tillers- irrigated	<i>npti3.1</i>	3	PC26M1 - PC20M2	4.16	-0.7927 (IR1)	12.2
	<i>gyr5.1</i>	5	PC27M3 - RZ225	3.31	-199.49 (IR1)	10.8
Grain yield - rainfed	<i>gyr6.1</i>	6	PC48M2 - PC31M1	3.09	-183.71 (IR1)	9.3
	<i>gyr1.1</i>	1	PC26M7 - PC3M12	3.03	163.86 (IR2)	11.1
	<i>gyr2.1</i>	2	C499 - PC11M1	4.04	237.57 (IR2)	23.4
	<i>gyr6.1</i>	6	PC31M1 - PC28M15	3.32	-168.48 (IR1)	11.8
Biomass -rainfed	<i>bmr6.1</i>	6	PC28M3 - PC31M9	3.30	-1182.9 (IR1)	9.4

^a Letters IR1 and IR2 in parentheses indicate that positive alleles for the effects are from IR58821 and IR52561, respectively.

^b Relative contribution of the detected putative QTLs to the phenotypic variation.

a trial varied from one to three with the proportion of phenotypic variation (R^2) ranging from 9.3–23.4%. QTLs linked to various plant production traits under drought stress were located in chromosomes 1, 2, 3, 4, 5, and 6. QTLs for different traits were mapped to similar chromosomal locations between trials. For example, *ds5.2* and *dhi5.1* were mapped to the PC38M8 – PC35M14 region on chromosome 5 in Trials 1 and 2, respectively. Colocation of QTLs for days to 50% flowering and drought score index on chromosome 3 in Bala/Azucena RI lines were reported earlier in rice¹⁵. In both the trials, for traits related to plant production under rainfed conditions, the majority of favourable alleles came from IR58821, the *indica* parental line with a high root penetration index. However, alleles from IR52561 also contributed to plant production under rainfed conditions.

Colocation of QTLs for plant production and root traits

Understanding the genetic basis of drought resistance in crops is fundamental for enabling breeders and molecular biologists to develop new cultivars with drought resistance. Physiological studies have

indicated that the ability of a root system to provide for evapotranspirational demand from deep soil moisture and the capacity for osmotic adjustment are major drought resistance traits in rice¹¹. Information on genomic regions associated with grain yield and its components under drought stress in field conditions is limited in rice. A few QTLs linked to yield under drought stress were reported earlier using CT9993/IR62266 doubled haploid lines^{6,31} and Bala/Azucena RI lines¹⁵ but these lines received favourable alleles from the *japonica* ecotype. There was a single report on QTLs for plant production traits using *indica/indica* lines from MSE in IR58821/IR52561 RI lines²⁰. The present study identified five QTLs for grain yield under rainfed conditions in TE, namely, two QTLs on chromosomes 5 and 6 explaining 10.8% and 9.3%, respectively, of phenotypic variation in Trial 1, and three QTLs on chromosomes 1, 2, and 6 explaining, 11.1%, 23.4% and 11.8%, respectively, of phenotypic variation in Trial 2.

Previous studies have mapped QTLs for various root traits^{18,19}, days to 70% relative water content, canopy temperature, and plant production under an MSE²⁰ in IR58821/IR52561 RI lines. On comparing

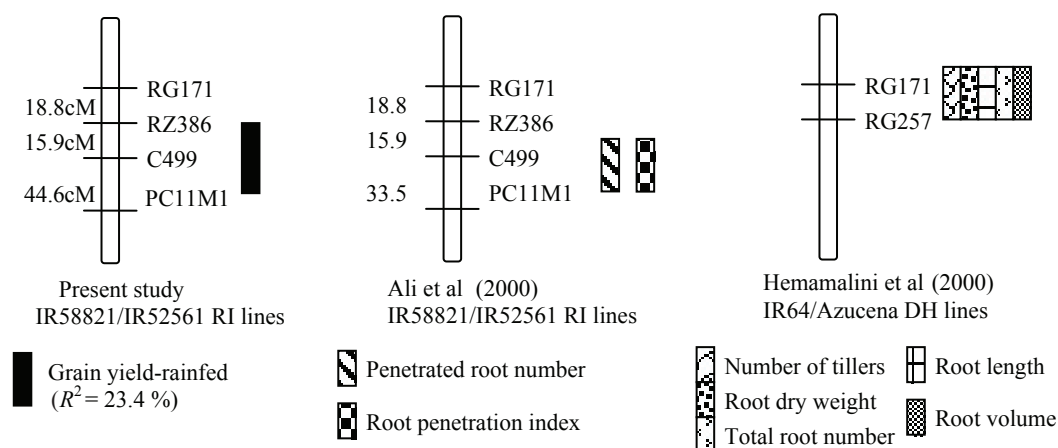


Fig. 1 Colocation of QTLs associated with grain yield under drought stress and root related traits in IR58821/IR52561 RI and other rice lines.

the genomic locations, colocation of QTLs for various drought resistance and plant production traits was noticed in these RI lines. For instance, the region C499-PC11M1 on chromosome 2 was found to carry the QTL *gyr2.1* associated with grain yield under drought stress explaining 23.4% of the phenotypic variation in the present study. This region harboured QTLs for root penetration index and penetrated root number in these RI lines¹⁸ (Fig. 1).

Comparison of QTLs across genetic backgrounds

To identify QTLs common across genetic backgrounds, the results of the present study were compared with QTLs for physio-morphological and plant production traits under stress reported in other rice populations. The linkage map developed by McCouch et al³⁴ served as a bridge to compare maps between different populations. The genomic region PC27M3-RZ225 on chromosome 5 was significant in terms of drought resistance in IR58821/IR52561 RI lines. QTL for grain yield under drought stress (Trial 1) was mapped to this region in the present study. Price et al³⁵ reported QTLs for the ratio of penetrated roots to total roots and the number of penetrated roots in this region in Bala/Azucena RI lines. Yue et al³⁶ identified QTLs for maximum root depth under stress in the field conditions in Zhenshan97/IRAT109 RI lines in the same region. Another QTL (PC48M2-PC31M1) for grain yield under drought stress (Trial 1) was mapped on chromosome 6 and Nguyen et al³⁷ identified QTLs for penetrated root thickness in CT9993/IR62266 DH lines in the same region. Another QTL, PC31M1-PC28M15 was linked to grain yield on chromosome 6 under moderate stress (Trial 2). This chromosomal

region was linked to penetrated root thickness in CT9993/IR62266 doubled haploid lines³⁷ and root dry weight and root branching index in Akihikari/IRAT109 RI lines of rice³⁸.

CONCLUSIONS

In summary, a subset of 155 rice RI lines derived from *indica* × *indica* ecotypes were subjected to drought stress during the reproductive phase due to a natural rainfall failure event under field conditions in the target environment. The RI lines showed significant variation in plant production traits under drought stress. QTLs linked to grain yield under rainfed conditions were identified. Colocation of QTLs for plant production traits under rainfed conditions and QTLs for root traits was observed in these RI lines. Consistent QTLs associated with drought resistance and plant production across genetic backgrounds were also detected and might be useful in marker assisted selection for rainfed rice improvement.

ACKNOWLEDGEMENTS

This research was supported by the Rockefeller Foundation, USA. We acknowledge sharing of genotypic data of RI lines by Dr. Henry T. Nguyen, Department of Agronomy, University of Missouri, Columbia, USA.

REFERENCES

1. FAO (Food and Agricultural Organization) (2006) <http://www.fao.org>.

2. O' Toole JC (1999). Molecular approaches for the genetic improvement of cereals for stable production in water limited environments. In: a strategic planning workshop. (Ribaut JM, Poland D, eds). CIMMYT, El Batan, Mexico. 21–25 June 1999.
3. Evenson R, Herdt RW, Hossain M (1996) Rice research in Asia: progress and problems. CAB International, Wallingford, UK.
4. Ribaut JM, Jiang C, Gonzalez-de-Leon D, Edmeades GO, Hoisington DA (1997) Identification of quantitative trait loci under drought conditions in tropical maize. 2. Yield components and marker-assisted selection strategies. *Theor Appl Genet* **94**, 887–96.
5. Lafitte R, Blum A, Atlin G (2003) Using secondary traits to help identify drought-tolerant genotypes. In: Breeding rice for drought-prone environments. (Fischer KS, Lafitte R, Fukai S, Atlin G, Hardy B, eds) pp 37–48, IRRI, Philippines.
6. Babu RC, Nguyen BD, Chamarek V, Shanmugasundaram P, Chezian P, Jeyaprakash P, Ganesh SK et al (2003). Genetic analysis of drought resistance in rice by molecular markers: association between secondary traits and field performance. *Crop Sci* **43**, 1457–69.
7. Uptmoor R, Wenzel W, Ayisi K, Donaldson G, Gehringer A, Friedt W, Ordon F (2006) Variation of the genomic proportion of the recurrent parent in BC₁ and its relation to yield performance in sorghum (*Sorghum bicolor*) breeding for low-input conditions. *Plant Breed* **125**, 532–4.
8. Tuberosa R, Salvi S (2007) From QTLs to genes controlling root traits in maize. In: Scale and complexity in plant systems research: Gene-Plant-crop Relations, (Spiertz JHJ, Struik PC, van Laar HH, eds), pp 15–24, Springer.
9. Mathews KL, Chapman SC, Trethowan R, Singh RP, Crossa J, Pfeiffer W, van Ginkel M et al (2006) Global adaptation of spring bread and durum wheat lines near-isogenic for major reduced height genes. *Crop Sci* **6**, 603–13.
10. Fukai S, Cooper M (1995) Development of drought-resistant cultivars using physio-morphological traits in rice. *Field Crops Res* **40**, 67–86.
11. Nguyen HT, Babu RC, Blum A (1997). Breeding for drought resistance in rice: physiology and molecular genetics considerations. *Crop Sci* **37**, 1426–34.
12. Babu RC, Pathan MS, Shanmugasundaram P (2003) Improving water productivity in cereal crops under rainfed ecosystem: progress in molecular genetics and genetic engineering approaches. In: Transitions in agriculture for enhancing water productivity. Sep 23 – 25, 2003, Agricultural College and Research Institute, Killikulam, Tamil Nadu Agricultural University.
13. Lafitte HR, Li ZK, Vijayakumar CHM, Gao YM, Shi Y, Xu JL, Fu BY et al (2006) Improvement of rice drought tolerance through backcross breeding: Evaluation of donors and selection in drought nurseries. *Field Crops Res* **97**, 77–86.
14. Lebreton C, Lazić-Jančić V, Steed A, Pekić S, Quarrie SA (1995) Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. *J Exp Bot* **46**, 853–65.
15. Gomez SM, Kumar SS, Jeyaprakash P, Suresh R, Biji KR, Boopathi NM, Price AH et al (2006) Mapping QTLs linked to physio-morphological and plant production traits under drought stress in rice (*Oryza sativa* L.) in the target environment. *Am J Biochem Biotechnol* **2**, 161–9.
16. Redona ED, Mackil DJ (1996) Mapping quantitative trait loci for seedling vigor in rice using RFLPs. *Theor Appl Genet* **92**, 395–492.
17. Yano M, Sasaki T (1997) Genetic and molecular dissection of quantitative traits in rice. *Plant Mol Biol* **35**, 145–53.
18. Ali ML, Pathan MS, Zhang J, Bai G, Sarkarung S, Nguyen HT (2000) Mapping QTLs for root traits in a recombinant inbred population from two *indica* ecotypes in rice. *Theor Appl Genet* **101**, 756–66.
19. Kamoshita A, Wade LJ, Ali ML, Pathan MS, Zhang J, Sarkarung S, Nguyen HT (2002) Mapping QTLs for root morphology of a rice population adapted to rainfed lowland conditions. *Theor Appl Genet* **104**, 880–93.
20. Manickavelu A, Nadarajan N, Ganesh SK, Gnanamalar RP, Chandra Babu R (2006) Drought tolerance in rice (*Oryza sativa* L.): morphological and molecular genetic consideration. *Plant Growth Regul* **50**, 121–38.
21. Babu RC, Shashidhar HE, Lilley JM, Thanh ND, Ray JD, Sadasivam S, Sarkarung S, et al (2001) Variation in root penetration ability, osmotic adjustment and dehydration tolerance among accessions of rice adapted to rainfed lowland and upland ecosystems. *Plant Breed* **120**, 233–8.
22. IRRI (International Rice Research Institute) (1996) International network for genetic evaluation of rice: Standard evaluation system for rice. IRRI, Los Banos, Philippines.
23. SAS Institute Inc (1990) SAS/STAT user's guide,

- Version 6. 4th edn, Vols. 1 and 2. SAS Institute Inc., Cary, North Carolina, USA.
24. Paterson AH, Lander E, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature* **335**, 721–6.
 25. Lincoln S, Daly M, Lander E (1992) Mapping genes controlling quantitative traits with MAPMAKER/EXP 3.0. Whitehead Institute Technical Report, 3rd edn, pp 213–224, Whitehead Institute, Cambridge, MA, USA.
 26. Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics* **121**, 185–99.
 27. Lilley JM, Fukai S (1994) Effect of timing and severity of water deficit on four diverse rice cultivars. II. Physiological responses to soil water deficit. *Field Crops Res* **37**, 215–23.
 28. Jongdee B, Pantuwan G, Fukai S, Fischer K (2004) Improving drought tolerance in rainfed lowland rice: an example from Thailand. In: New directions for a diverse planet. Proceedings of the 4th International Crop Science Congress, Sep 26 – Oct 1, 2004, pp 1–14, Brisbane, Australia.
 29. Price AH, Cairns JE, Horton P, Jones HG, Griffiths H (2002) Linking drought-resistance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. *J Exp Bot* **53**, 989–1004.
 30. Lanceras JC, Pantuwan G, Boonrat J, Toojinda T (2004) Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiol* **135**, 384–99.
 31. Fukai S, Pantuwan G, Jongdee B, Cooper M (1999) Screening for drought resistance in rainfed lowland rice. *Field Crops Res* **64**, 61–74.
 32. Jongdee B, Fukai S, Cooper M (2002) Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. *Field Crops Res* **76**, 153–63.
 33. Pantuwan G, Fukai S, Cooper M, Rajatasereekal S, O' Toole JC (2002) Yield response of rice genotypes to different types of drought under rainfed lowlands Part 1. Grain yield and yield components. *Field Crops Res* **73**, 153–68.
 34. McCouch SR, Teytelman L, Xu Y, Lobos KB, Clare K, Walton M, Fu B, et al (2002) Development and mapping of 2240 new SSR markers for rice. *DNA Res* **9**, 199–207.
 35. Price AH, Steele KA, Moore BJ, Barraclough PB, Clark LJ (2000) A combined RFLP and AFLP map of upland rice (*Oryza sativa*) used to identify QTL for root-penetration ability. *Theor Appl Genet* **100**, 49–56.
 36. Yue B, Xue W, Xiong L, Yu X, Luo L, Cui K, Jin D et al (2006) Genetic basis of drought resistance at reproductive stage in rice: separation of drought tolerance from drought avoidance. *Genetics* **172**, 1213–28.
 37. Nguyen TTT, Klueva N, Chamareck V, Aarti A, Magpantay G, Millena ACM, Pathan MS et al (2004) Saturation mapping of QTL regions and identification of putative candidate genes for drought tolerance in rice. *Mol Genet Genomics* **272**, 35–46.
 38. Horii H, Nemoto K, Miyamoto N, Harada J. (2006) Quantitative trait loci for adventitious and lateral roots in rice. *Plant Breed* **125**, 198–200.