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Drought tolerance in rice: morphological and molecular genetic consideration

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Abstract Rice is one of the most important food crop drastically affected by drought in lowland rice ecosystem. Dissecting out the traits of importance and genomic regions influencing the response of drought tolerance and yield traits on grain yield will aid the breeders to know the genetic mechanism of drought tolerance of rice leads to the development of drought tolerant varieties. Grain yield and its components on drought situation of recombinant inbred population (IR 58821/IR 52561) were investigated under lowland managed stress situation in 2003 and 2004 by given importance to the relative water content. Water deficit resulted in significant effect on phenology and grain yield. Best lines were selected for further varietal development programme. Variability studies showed the traits viz., days to 70% relative water content, leaf rolling, leaf drying, harvest index, biomass yield and grain yield offer high scope for improvement for drought tolerance by way of simple selection technique. Correlation and path analysis indicated that, to harness high yielding combined with drought tolerance breeders should give selection pressure on relative water content, panicle length, grains per panicle, harvest index, biomass yield, root/shoot ratio and root length in positive direction, and low scores of leaf rolling, leaf drying and drought recovery rate. Analysis of quantitative trait loci for drought tolerance, yield and its components allowed the identification of 38 regions associated with both drought tolerant and yield traits. Out of these, 18 were closely linked with DNA markers could be used for marker assisted selection in breeding for drought tolerance in rice. Pleiotropism and $G \times E$ effects interaction were noticed in some of the traits. Parent IR 58821 contributed favorable alleles for the entire drought related and most of the yield component traits. Identification of traits of

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importance and their nature of relationship by morphological and molecular level under lowland condition will be useful to improve drought tolerance of rice.

Abbreviations

G × E	Genotype × environmental interaction
QTL	Quantitative trait locus
RIL	Recombinant inbred line

Introduction

Rice is the principle food crop for more than half of the world's population. It is grown widely under rainfed lowland conditions in Asia, and about 45% of the total rice area is estimated to have no irrigation input (Crosson 1995). Yield of rainfed lowland rice, which occupies about 25% of the world's rice areas, are drastically reduced by drought due to unpredictable, insufficient and uneven rainfall during the growing period. To reduce yield losses of rice crops in rainfed lowland areas and to increase overall rice production, new rice varieties with greater adaptation to drought are essential. Hence, the development of drought resistant cultivars with a higher yield potential is one of the main objectives of rainfed lowland rice breeding programmes.

Genetic improvement of adaptation to drought is addressed through the conventional approach by selecting for yield and its stability over locations and years. Such selection programs are slow in attaining progress because of the low heritability of yield under stress, the inherent variation in the field, and the limitation that there is usually only one experimentally droughted crop per year (Ribaut et al. 1997). 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 program. The effectiveness of selection for secondary traits to improve yield under water-limiting conditions has been demonstrated in maize (*Zea mays* L.) (Chapman and

Edmeades 1999), wheat (*Triticum aestivum* L.) (Richards et al. 2000), and sorghum [*Sorghum bicolor* (L.) Moench]) (Tuinstra et al. 1998).

Many studies have been undertaken to find genetic variation in traits that are expected to influence the response of rice to water deficit, including deeper and thicker roots (Yadav et al. 1997); root pulling resistance (Pantuwan et al. 2002); greater root penetration (Clark et al. 2000; Ali et al. 2000); osmotic adjustment (Lilley et al. 1996); membrane stability (Tripathy et al. 2000); leaf rolling score and leaf relative water content (Courtois et al. 2000).

Drought screening is complicated by difficulties in field management, variation in phenology, and unexpected rainfall events. For this type of screening to be useful in the context of a breeding program, it must provide additional information that cannot be obtained in an unstressed control plot, and which predicts how the line will perform under natural stress in the target environment. Information on the repeatability of traits measured in stress experiments, the heritabilities of yield and secondary traits, and the genetic correlations among these traits are needed to decide whether or not such nurseries are useful (Fukai and Cooper 1995). Studies with mapping populations can help to provide this information. A difficulty with evaluating yield in many rice mapping populations, however, is that the parental lines are usually chosen to maximize polymorphism, so parents often have very different adaptations (Lafitte et al. 2004). It is, therefore, desirable to use a population derived from an *indica/indica* cross to identify genes controlling agronomic traits for the improvement of rainfed lowland rice.

Breeding varieties with drought tolerance and other root traits is very difficult. This is because screening numerous genotypes under field conditions is laborious and time-consuming, and no easy and efficient techniques have yet been developed (O'Toole and Chang 1979; Mambani and Lal 1983; Ekanayeke et al. 1986). Secondly, soil compaction is not uniform and consistent throughout rice fields, which makes the evaluation of root length and dry root ratio is difficult. To develop new varieties with improved traits, molecular marker technology could be used as an alternative strategy

(Nguyen et al. 1994, 1997). Drought tolerance characters are quantitative traits, and so dissection of these complex traits into component genetic factors is a prerequisite to manipulate the traits. Genome mapping using molecular genetic markers offers an excellent opportunity to locate genes or QTLs controlling quantitative characters (Paterson et al. 1988; Lander and Botstein 1989; Tanksley 1993). Markers linked with genes controlling a trait of interest could be used in the selection of genotypes in a breeding program. Hence the present study was aimed to know the drought tolerance in rice both under morphological and molecular level.

Materials and methods

Plant population

The plant population for this experiment consisted of 148 out of 166 RILs (F_7 generation) derived from a cross between two advanced breeding lines viz., IR 58821-23-B-1-2-1 (abbreviated as IR 58821) and IR 52561-UBN-1-1-2 (abbreviated as IR 52561). The RILs were developed from the F_2 generation by single seed decent to F_7 generation at International Rice Research Institute (IRRI), Philippines. Both parental lines are of *indica* types and suited to rainfed lowland condition. IR 58821 possesses thicker roots with high root penetration ability than IR 52561 (Ali et al. 2000).

Field experiments

Phenotyping of RIL population were conducted both in managed stress and fully irrigated conditions in the farm premises of Agricultural College and Research Institute, Maduari (latitude: 9°54′ E; longitude: 78°8′ N; altitude: 147 m MSL) during summer (May–July) and the fall (Sep–Dec), 2003. The experiments were laid out in a randomized block design (RBD) with three and four replications, in the respective season. Seeds were sown and transplanted in a clay loamy soil (Madhukur series) in May and September, 2003. Each RIL was raised in two rows (60 plants) with a row of 3 m length and adopting a spacing of

20×10 cm. In drought plot, IR 50 the susceptible variety for drought was raised along the borders to indicate the drought. The experiment was conducted in rainfed conditions with supplementary irrigation as needed. At peak tillering phase, irrigation was withheld in order to impose drought. IR 50, the stress indicator started to show stress symptoms within 2–4 days. Relative water content (RWC) was previously demonstrated to be a relevant screening tool of drought tolerance in cereals, as well as good indicator of plant water status (Teulat et al. 2003). In rice, once the plants attain 70% RWC, it indicates the real physiological stress of the plant irrespective of the environment. Hence the RWC was taken at regular intervals using the method suggested by Kramer (1969) in all RILs to measure in which day it reach 70% RWC. When most of the RILs attained the 70% level, then the scoring of leaf rolling (LR) and leaf drying (LD) was taken. At mid day, the canopy temperature (CT) was recorded using infrared thermometer with an 8° field of view and equipped with a 10.5–12.5 μm band bass filter. Then the field was reirrigated and drought recovery rate (DRR) was observed after 10 days of irrigation. At physiological maturity, the selected plants were uprooted by giving deep dig near the base after watering and dry it in the oven at 80°C for 48 h. The drought related root traits viz., root length (RL), dry root weight (DRW) and root/shoot ratio (RS) were recorded in five plants of each RILs. The yield components traits viz., days to flowering (DF), plant height (PH), number of productive tillers per plant (PT), panicle length (PL), grains per panicle (GP), 100 grain weight (HGW), biomass yield (BMY), harvest index (HI) and grain yield per plant (GY) were recorded on 10 plants at random in each RIL. In both the cropping season the same set of RIL population was raised under fully irrigated condition as control and only yield and its component traits viz., DF, PH, PT, PL, GP, HGW, BMY, HI and GY were recorded.

Statistical analysis

The mean data of 148 RILs for all the characters both under water stress and fully irrigated condition were subjected to analysis of variance

appropriate to RBD. The broad sense heritabilities were then computed from the estimates of genetic (σ^2G) and residual (σ^2e) variances derived from the expected mean squares of the analysis of variances as H = (σ^2G/σ^2G + σ^2e/K), where K was the number of replications. Phenotypic correlations among the traits within a trial were computed using the genotypic means.

QTL analysis

The genetic linkage map for this RIL population constructed by Ali et al. (2000) was used as the base map for QTL analysis. It consisted of 399 molecular marker with 96 RFLPs and 303 AFLPs and a total map length of 2,022 cM with a average distance of 5.1 cM between adjacent markers. Despite a large number of markers mapped in the linkage map, there were several large gaps on the map. No marker could be mapped in these gap regions because of the monomorphic genetic make-up commonly shared by the closely related *indica* parents. Generally, monomorphic regions are expected in the genome of a population derived from intervarietal crosses or closely related parents. However, AFLP markers in conjunction with RFLP markers produced good coverage of the genome with desired resolution, making the map quite suitable for QTL analysis. Mapmaker/ QTL 1.1 version software was used to identify the QTLs for drought tolerant, yield and its component traits under both water stress and fully irrigated conditions using the phenotypic data of present investigation and, genotypic data and genetic linkage map which was already constructed by Ali et al. (2000). Phenotypic data from repeated experiments were pooled together and the means for each trait were used to identify QTLs for both drought and irrigated conditions. The threshold likelihood odd (LOD) score used for declaring the presence of QTLs was 2.0 and it was derived based on the total map distance and the average distance between markers (Lander and Botstein 1989). Tests for independence of QTLs were also conducted when two or more QTLs of a trait were located on the same chromosome (Paterson et al. 1988). Best multiple QTL models were worked out to find the exact

variance of a trait when more than one QTL contributed for that trait.

Results

Genetic potentiality

The analysis of variances of RILs under stress condition revealed that the mean squares values for RILs were significant for all the traits studied. Check varieties showed significance for all the traits except root length. Under controlled condition also significant difference was observed among genotypes for all the traits studied. The mean performance of RILs was worked out to know their genetic potentialities. Days to attain 70% RWC gave the correct prediction of occurrence of physiological stress in the plants. It varied from 10 days to 19 days in RILs with an average of 15.80 days (Table 1). At this stage, the scoring of LR and LD showed transgressive segregation data. The LD was ranged from 0.8 to 7.69 score. All the scales of DRR were observed in the present study. Surprisingly there was no significant deviation observed for DF between stress and irrigated plots. The PH differed 30 cm between stress and controlled condition showed the effect of stress on the phenology. The stress explodes its vigor in PT, in stress it was only 5.12 tillers, whereas in control it was around 12.16 tillers. There was no much difference in PL between the conditions. Another yield trait, GP also affected by drought around 20%. The drastic reduction of biological yield was observed in stress BMY (58.90 g) compared to control (90.31 g). The two year average yield of RILs in well watered and water stress conditions was 27.92 and 18.62 g, respectively. The performance of root traits under stress condition showed that, a maximum root length of 24.45 cm was measured in RILs. The DRW was ranged from 2.23 cm to 17.48 cm. In an average 0.30 RS ratio was observed in this population. In breeders selection points of view, among the 148 RILs studied, six viz., RIL # 31, 229, 251, 418, 475 and 500 showed significantly superior mean performance for drought tolerant traits as well as yield traits in both the conditions (data not shown) lead to large

Table 1 Genetic potentiality and variability parameters in RILs under both stress and irrigated condition

		Mean			Range	PV	GV	PCV (%)	GCV (%)	h^2 (%)	GA (%)
		P_1	P_2	RILs	RILs						
RWC	(S)	16.02	11.06	15.80	10–19	46.25	20.84	11.15	7.49	45.07	10.35
LR	(S)	4.26	5.65	5.22	2.12–8.97	2.15	1.64	22.42	19.56	76.15	35.16
LD	(S)	3.28	4.98	3.94	0.84–7.69	2.86	1.96	43.00	35.60	68.51	60.69
CT	(S)	30.53	38.58	35.75	31.95–39.05	62.35	52.22	5.47	5.01	83.75	9.43
DRR	(S)	3.28	5.42	5.34	1–9	3.12	1.76	51.42	38.62	56.41	59.76
DF	(S)	95.00	98.00	99.62	84–108	10.50	2.40	5.26	2.52	22.83	2.47
	(I)	92.00	94.00	96.95	83–105	9.22	6.25	5.54	5.5	61.15	11.24
PH	(S)	91.25	96.28	86.83	53.65–124.35	185.64	38.97	17.63	8.08	20.99	7.62
	(I)	112.47	116.63	116.24	85.20–144.5	250.65	200.63	20.56	20.53	80.04	42.24
PT	(S)	7.13	6.48	5.12	2.20–10.15	12.65	7.43	38.62	29.60	58.73	46.72
	(I)	11.03	9.19	12.16	4.00–17.00	6.23	3.34	28.31	27.29	53.61	54.1
PL	(S)	23.65	21.47	22.29	14.05–28.95	24.24	2.69	11.03	3.67	11.08	2.52
	(I)	25.47	22.34	23.84	16.70–29.30	10.28	6.17	20.11	19.9	60.02	40.56
GP	(S)	95.48	90.12	90.22	84.84–98.70	925.64	525.65	22.16	16.72	56.79	25.96
	(I)	115.68	100.11	112.10	83.66–143.9	753.36	324.25	22.16	16.96	44.09	18.55
HGW	(S)	2.75	2.46	2.68	1.86–3.91	0.41	0.31	23.89	20.78	75.61	55.41
	(I)	2.75	2.46	2.68	1.86–3.91	0.23	0.18	17.89	15.83	78.26	42.95
BMY	(S)	80.47	56.13	58.90	17.00–128.67	265.48	50.57	26.10	11.40	19.05	10.24
	(I)	104.78	90.11	90.31	37.11–160.30	400.56	325.67	20.09	19.85	81.30	40.39
RL	(S)	18.47	12.14	13.65	7.70–24.45	16.98	6.48	25.77	15.93	38.19	20.27
DRW	(S)	12.78	8.46	7.12	2.23–17.48	42.15	13.77	48.51	27.74	32.68	32.66
RS	(S)	0.41	0.22	0.30	0.09–0.70	1.36	0.30	52.74	24.74	22.01	23.91
HI	(S)	0.45	0.29	0.29	0.12–0.75	1.23	0.12	35.73	11.19	9.80	7.22
	(I)	0.58	0.31	0.45	0.23–0.87	0.42	0.18	34.6	32.74	42.86	63.82
GY	(S)	26.22	19.75	18.62	4.60–36.76	16.45	4.68	34.72	18.51	28.43	20.33
	(I)	47.48	31.46	27.92	10.50–56.98	12.35	6.67	33.83	33.44	54.01	68.11

P_1—IR 58821, P_2—IR 52561

(S)—Stress condition (I)—Irrigated condition

scale testing/multilocation trails both under water stress and irrigated condition.

Variability

Coefficient of variation for drought, yield and its component traits revealed that, high phenotypic and genotypic coefficient of variation were exhibited for LD, DRR, PT, HGW, DRW and RS. The traits viz., LR, GP, RL, BMY, HI and GY showed high phenotypic and moderate genotypic coefficient of variation. Moderate PCV and low GCV was exhibited by the following traits viz., RWC, PH and PL. Two traits viz., DF and CT recorded low phenotypic and genotypic coefficients of variation. Heritability in broad sense ranged from 9.80% to 83.75%. High heritability was expressed by CT, LR, HGW and LD. The characters viz., PT, GP, DRR, RWC, RL and DRW exhibited moderate heritability. Low

heritability was observed in seven traits viz., GY, DF, RS, PH, BMY, PL and HI. Genetic advance as percent of mean ranged from 2.47 to 60.69. Leaf drying, DRR, HGW, PT, LR, DRW, GP, RS, RL and GY expressed high genetic advance. Low genetic advance was noticed in the traits viz., RWC, BMY, CT, PH, HI, PL and DF (Table 1).

Controlled condition

In controlled condition, high PCV and GCV were noticed in HI, GY, PT and PH. Three traits viz., GP, PL and BMY showed high genotypic and moderate phenotypic coefficients of variation. Hundred grain weight expressed moderate phenotypic and genotypic coefficients of variation. Only one trait (DF) registered low phenotypic and genotypic coefficients of variation. Heritability in broad sense ranged from 42.86% to 81.30%. High heritability was recorded in BMY,

PH, HGW, DF and PL. The traits viz., GY, PT, GP and HI exhibited moderate heritability. Genetic advance as percent of mean ranged from 11.24 to 68.11. High genetic advance was showed by GY, HI, PT, HGW, PH, PL and BMY. The remaining traits viz., GP and DF registered moderate heritability (Table 1).

Phenotypic correlation

The present study is oriented towards breeding for drought tolerance, much emphasize was given to understand the association between drought tolerant traits with yield and its components. Along with the correlation coefficient analysis, the path coefficient analysis suggested by Dewey and Lu (1959) provides a view into the interrelationships by further partitioning the correlation coefficients into direct and indirect effects. The drought tolerant and yield traits of RILs under stress condition resulted that, most of the traits viz., RWC, DF, PH, PT, PL, GP, HGW, BMY, RL, HI and RS showed significant positive correlation with grain yield. Studies on the same RIL population under fully moisture regime condition only for yield and its components showed that, the traits viz., PT, GP, HGW, BMY and HI registered significant relation with grain yield. Interrelationship among the traits under stress condition showed that, most of the above said traits were interlinked well with each other. Among these traits, BMY was intercorrelated with DF, PL, GP, HGW, RL, DRW and RS. Panicle length showed significant correlation with DF, PT, BMY, DRW, HI and RS. Root/ shoot ratio exhibited significant relation with DF, PH, PL, BMY, RL and DRW. Under controlled condition, the five yield components viz., PT, GP, HGW, BMY and HI expressed significant correlation with grain yield (Table 2). In overall view, the traits viz., RWC, BMY, PL, RL, GP, HI and RS under stress condition, the traits viz., GP, HGW and BMY under controlled condition showed interrelationship with each other besides positive correlation with grain yield. Hence improvement of any one of these traits will enhance the effect of other traits and finally improving the grain yield. Partitioning of correlation coefficient into direct and indirect

effect resulted that (Table 3), the traits viz., RWC, PT, PL, GP, HGW, BMY, DRW, HI and RS showed high direct effect on grain yield under stress condition. The traits viz., GP, HGW and HI also expressed indirect contribution of grain yield through root length. In controlled condition, GP, BMY and HI showed high direct effect on grain yield. Hence, the traits viz., RWC, PT, PL, GP, BMY, HI and RS showed positive effect on grain yield. Negative association of some components with grain yield in RIL population under stress condition showed that, the traits viz., LR, LD and DRR had significant negative correlation with grain yield. Interrelationship among the traits revealed that, the two traits viz., LR and LD showed significant negative relation with PL, HGW, BMY and RL. In path analysis, all the above mentioned traits showed high negative direct effect on grain yield. Meanwhile the traits viz., RWC, PH, PT, PL and BMY revealed indirect effect on grain yield through drought recovery rate. Therefore, selection of these traits in negative direction will influence the grain yield.

QTL mapping

A total of 38 putative QTLs were identified for various quantitative traits under both stress and fully irrigated conditions (Table 4; Fig. 1). An overall study of the QTL analysis indicated the distribution of QTLs on all over the segments of all chromosomes except those of chromosomes 11 and 12.

Drought related traits

Days to 70% RWC is the best indicator for studying the drought stress and for this trait only one QTL was detected on chromosome 7, flanked by two AFLP markers PC73M2 and PC20M7. Leaf rolling, LD and DRR are classically used by rice breeders as a way to estimate drought avoidance for their material because they are generally associated with deterioration of plant water status. In the present study, the QTL segment on chromosome 7 flanked by the AFLP markers PC75M7 and PC12M9, regulated the genes responsible for these traits. For canopy

Table 2 Correlation coefficients between grain yield and all other traits in RILs under both water stress and controlled condition

	RWC	LR	LD	CT	DRR	DF	PH	PT	PL	GP	HGW	BMY	RL	DRW	HI	RS	GY
RWC	1.00	-0.67*	-0.55*	0.11	-0.77*	0.23*	0.46*	0.14	0.30*	-0.04	0.04	0.04	-0.03	0.08	0.69*	0.11	0.32*
LR		1.00	0.89*	0.26*	0.83*	-0.22*	-0.70*	-0.09	-0.38*	0.03	-0.15*	-0.42*	-0.30*	0.08	0.21*	0.28*	-0.30*
LD			1.00	0.31*	0.90*	-0.06	-0.87*	-0.24*	-0.48*	0.03	-0.15*	-0.47*	-0.41*	0	-0.09	0.19*	-0.40*
CT				1.00	0.09	-0.02	0.49*	0.47*	0.58*	0.06	0.03	-0.29*	-0.29*	0.20*	0.46*	0.38*	0.07
DRR					1.00	0.03	-0.58*	-0.31*	-0.62*	0.05	-0.12	-0.22*	-0.04	0.13	0.22*	0.34*	-0.17*
DF						1.00	0.16*	-0.53*	0.49*	-0.03	-0.04	0.41*	0.11	0.48*	-0.18*	0.35*	0.18*
(C)						1.00	0.15*	-0.04	0.13	-0.1	-0.03	0.04	-	-	-0.1	-	-0.15*
PH							1.00	0.85*	-0.18*	0.03	-0.23*	0.09	0.54*	0.29*	0.03	0.24*	0.23*
(C)							1.00	-0.06	0.49*	-0.06	-0.07	0.16*	-	-	-0.15*	-	-0.1
PT								1.00	0.32*	0.1	-0.34*	-0.1	0.03	0.03	0.20*	0.03	0.18*
(C)								1.00	-0.15*	0.23*	0.17*	0.23*	-	-	0.03	-	0.31*
PL									1.00	-0.02	-0.02	0.52*	-0.1	0.27*	0.19*	0.24*	0.48*
(C)									1.00	-0.03	-0.04	0.20*	-	-	-0.08	-	0.05
GP										1.00	0.54*	0.40*	0.11	0.16*	0.66*	0.13	0.88*
(C)										1.00	0.31*	0.23*	-	-	0.44*	-	0.75*
HGW											1.00	0.26*	-0.01	0.09	0.31*	0.09	0.85*
(C)											1.00	0.28*	-	-	0.27*	-	0.41*
BMY												1.00	0.62*	0.79*	-0.31*	0.51*	0.73*
(C)												1.00	-	-	-0.33*	-	0.27*
RL													1.00	0.79*	-0.31*	0.51*	0.37*
DRW														1.00	-0.21*	0.94*	0.06
HI															1.00	-0.38*	0.62*
(C)															1.00	-	0.52*
RS																1.00	0.16*

* Significant at 5% level; (C)—Controlled condition

Table 3 Path coefficients between grain yield and all other traits in RILs under both water stress and controlled condition

	RWC	LR	LD	CT	DRR	DF	PH	PT	PL	GP	HGW	BMY	RL	DRW	HI	RS	Corr. with GY
RWC	**0.32**	−0.32	−0.12	−0.01	−0.49	−0.15	−0.23	0.21	0.24	0.04	−0.01	0.23	0.02	−0.29	0.3	0.58	0.32*
LR	1.58	**−0.98**	0.12	−0.02	0.23	0.14	−0.5	−0.14	−0.7	0.03	0.01	−0.59	0.22	−0.26	−0.09	0.66	−0.30*
LD	1.29	−1.23	**−1.02**	−0.19	0.61	0.22	0.46	−0.37	−0.89	0.03	0.03	−0.65	0.3	−0.01	0.04	0.97	−0.40*
CT	−0.25	−0.92	−0.49	**−0.08**	0.15	0.02	−1.16	0.74	1.08	0.06	0.06	−0.41	0.21	−0.7	−0.2	1.96	0.07
DRR	1.83	−1.02	−0.46	−0.01	**−0.56**	−0.02	0.74	−0.48	−1.15	0.05	−0.01	−0.31	0.03	−0.12	−0.1	1.42	−0.17*
DF	−0.55	0.69	0.1	0.01	0.05	**−0.66**	−0.37	−0.84	0.9	−0.03	0.12	0.57	−0.08	−1.02	0.08	1.21	0.18*
(C)	–	–	–	–	–	**−0.07**	−0.01	−0.01	0.02	−0.05	−0.01	0.01	–	–	−0.03	–	−0.15*
PH	−0.45	0.23	0.12	−0.04	−0.47	−0.1	**0.31**	0.33	−0.34	0.03	−0.01	0.18	−0.39	0.23	−0.01	1.23	0.23*
(C)	–	–	–	–	–	−0.01	**−0.09**	−0.01	0.06	−0.03	−0.01	0.04	–	–	−0.05	–	−0.1
PT	−0.32	0.31	−0.38	−0.23	−0.5	0.35	−1.01	**1.31**	0.3	0.31	−0.01	−0.14	−0.02	−0.12	0.22	0.14	0.18*
(C)	–	–	–	–	–	0.01	0.01	**0.14**	−0.02	0.11	0.01	0.05	–	–	0.01	–	0.31*
PL	−0.71	0.12	0.08	−0.05	−1.01	−0.32	0.43	0.5	**0.92**	−0.02	0.01	0.26	0.07	−0.96	−0.08	1.24	0.48*
(C)	–	–	–	–	–	−0.01	−0.04	−0.02	**0.13**	−0.02	−0.01	0.04	–	–	−0.03	–	0.05
GP	−0.12	−0.08	−0.05	−0.45	0.01	−0.13	−0.02	0.25	0.31	**0.86**	0.01	0.01	0.26	0.01	0.09	−0.08	0.88*
(C)	–	–	–	–	–	0.01	0.01	0.03	−0.01	**0.49**	0.02	0.05	–	–	0.15	–	0.75*
HGW	0.03	−0.05	−0.03	−0.12	−0.06	−0.21	−0.03	0.11	0.09	0.46	**0.33**	0.01	0.25	0.05	0.15	−0.13	0.85*
(C)	–	–	–	–	–	0	0.01	0.03	−0.01	0.15	**0.08**	0.06	–	–	0.1	–	0.41*
BMY	−0.08	1.47	0.74	0.02	−0.36	−0.27	−0.2	−0.15	0.96	0.41	−0.16	**0.67**	−0.45	−0.41	−0.13	−1.33	0.73*
(C)	–	–	–	–	–	−0.01	−0.01	0.03	0.03	0.11	0.02	**0.21**	–	–	−0.11	–	0.27*
RL	0.07	1.06	0.64	0.02	−0.06	−0.07	−1.27	0.04	−0.18	0.11	0.16	0.5	**−0.73**	−0.35	0.13	0.32	0.37*
DRW	−0.19	−0.26	−0.06	−0.02	0.06	−0.32	−0.7	0.05	0.5	0.16	−0.23	0.16	−0.58	**0.48**	0.11	0.91	0.06
HI	−0.46	−0.72	0.15	−0.56	0.35	0.12	−0.24	0.31	0.35	0.39	0.11	0.41	0.22	0.73	**0.44**	−0.98	0.62*
(C)	–	–	–	–	–	0.01	0.01	0.01	−0.01	0.21	0.02	−0.07	–	–	**0.35**	–	0.52*
RS	−0.26	−0.33	−0.3	−0.23	0.47	−0.23	−0.56	0.78	0.44	0.13	0.01	−0.36	−0.37	0.48	0.18	**0.32**	0.16*

Residual effect: 0.043, Diagonal values denote direct effects, (C)—Controlled condition

temperature, three QTLs were identified, each one on chromosome 8, 9 and 10 that explained 10.8%, 6.5% and 12.4% of phenotypic variation, respectively. Also it was established in the present study that 16.4% of the phenotypic variation for this trait would be exploited if three QTLs were combined together. Root traits were found to confer drought resistance under rainfed lowland conditions (Nguyen et al. 1997). Totally 10 QTLs were identified for three root traits, RL, DRW and RS. For root length, single QTL was detected on chromosome 8 flanked by PC75M12 and PC32M7 markers. Four QTLs were dissected out for DRW that located on chromosomes 1, 2, 4 and 5 and explained 9.8%, 10.1%, 7.5% and 6.4% of phenotypic variation, respectively. The best multiple QTL model accommodated with four QTLs for dry root weight explained 23.6% of phenotypic variation suggesting the relative

importance of these QTLs for breeding of drought tolerant genotypes. Five QTLs for root/shoot ratio, each one on chromosome 1, 4 and 5 and two on chromosome 2, were detected that exhibited 10.6%, 6.9%, 7.5%, 6.3% and 6.8% phenotypic variation, respectively. Five QTLs accommodated in the best multiple QTL model showed 26.5% phenotypic variation indicating the relative importance of these QTLs.

Yield and its components

The QTLs for yield and its component traits in both water stress and irrigated condition showed that, in DF, single QTL was identified between the RFLP markers R2280 and C1018 on chromosome 5. For PH, two different QTLs were identified on two different chromosomes viz., 7 and 2 for water stress and fully irrigated con-

Table 4 DNA markers linked to QTLs in both water stress and irrigated conditions

Trait (1)	Ch # (2)	Marker interval (3)	Peak position of QTL from AFLP/RFLP markers (cM) (4)	LOD (5)	R^2 (%) (6)	Effect (7)
Days to 70% RWC	7	PC73M2-PC20M7	0.0	3.16	9.4	1.095 (P_1)
Leaf rolling	7	PC75M7-PC12M9	4.0	3.91	13.1	1.278 (P_1)
Leaf drying	7	PC75M7-PC12M9	4.0	3.91	13.1	1.278 (P_1)
Drought recovery rate	7	PC75M7-PC12M9	6.0	5.32	18.3	1.569 (P_1)
Canopy temperature	8	G1073-RG598	16.0	2.13	10.8	1.338 (P_1)
	9	PC35M10-PC32M13	0.0	2.41	6.5	1.015 (P_2)
	10	BCD386-PC184M15	26.0	2.24	12.4	1.449 (P_1)
Best multiple QTL model R^2 = 16.4						
Root length	8	PC75M12-PC32M7	8.0	2.09	6.6	2.051 (P_1)
Dry root weight	1	PC32M5-PC31M10	10.0	2.54	9.8	1.724 (P_1)
	2	PC73M14-PC17M3	4.0	3.15	10.1	1.762 (P_2)
	4	PC28M11-CDO241	0.0	2.80	7.5	1.465 (P_1)
	5	PC17M7-PC18M6	0.0	2.34	6.4	1.353 (P_1)
Best multiple QTL model R^2 = 23.6						
Root/shoot ratio	1	PC32M5-PC31M10	14.0	2.68	10.6	0.078 (P_1)
	2	PC73M14-PC17M3	4.0	2.07	6.9	0.064 (P_2)
	2	PC180M2-RG188	10.0	2.04	7.5	0.065 (P_1)
	4	PC28M11-CDO241	0.0	2.34	6.3	0.059 (P_1)
	5	PC17M7-PC18M6	0.0	2.49	6.8	0.068 (P_1)
Best multiple QTL model R^2 = 26.5						
Days to flowering						
Water stress	5	R2289-C1018	18.0	2.16	8.5	3.169 (P_2)
Irrigated	5	R2289-C1018	20.0	2.18	8.1	3.208 (P_2)
Plant height						
Water stress	7	PC34M16-PC75M7	10.0	2.70	8.6	7.697 (P_1)
Irrrigated	2	PC79M6-RG83	4.0	2.19	7.0	6.612 (P_2)

Table 4 continued

Trait (1)	Ch # (2)	Marker interval (3)	Peak position of QTL from AFLP/RFLP markers (cM) (4)	LOD (5)	R^2 (%) (6)	Effect (7)
Productive tillers per plant						
Water stress	3	RG191-PC73M7	0.0	2.52	6.8	1.504 (P$_2$)
Irrigated	3	PC150M7-PC35M4	0.0	3.56	10.5	1.408 (P$_1$)
Panicle length						
Water stress	6	R2654-RG716	8.0	2.57	8.4	1.334 (P$_2$)
	9	PC26M5-RZ206	0.0	2.32	7.0	1.232 (P$_2$)
	Best multiple QTL model $R^2 = 13.9$					
Irrigated	3	RG191-PC73M7	24.0	2.15	8.4	1.310 (P$_1$)
Grains per panicle						
Water stress	3	R3226-RG558	0.0	2.64	7.2	4.202 (P$_1$)
Irrigated	6	PC73M6-PC184M1	0.0	2.14	5.8	5.354(P$_1$)
Hundred grain weight						
Water stress	4	PC48M9-PC47M4	0.0	2.17	5.9	0.186 (P$_1$)
Irrigated	4	PC48M9-PC47M4	0.0	2.38	6.5	0.199 (P$_1$)
Biomass yield						
Water stress	6	C1478-R2147	0.0	2.77	8.3	4.159 (P$_2$)
Irrigated	6	C1478-R2147	2.0	3.36	10.0	4.761 (P$_2$)
	6	PC17M4-PC180M12	0.0	2.40	6.5	3.854 (P$_2$)
	Best multiple QTL model $R^2 = 10.1$					
Harvest index						
Water stress	3	RG191-PC73M7	26.0	2.36	8.8	0.067 (P$_2$)
	3	R1925-RG1356	6.0	2.21	8.1	0.065 (P$_1$)
	Best multiple QTL model $R^2 = 10.1$					
Irrigated	6	PC32M6-PC31M6	0.0	2.10	6.4	0.083 (P$_1$)
Grain yield						
Water stress	3	R1925-RG1356	0.0	2.46	6.8	1.482 (P$_1$)
Irrigated	1	C49-PC11M10	0.0	2.36	6.7	2.083 (P$_1$)

P$_1$ and P$_2$ in parenthesis indicate positive or favorable alleles for the QTLs obtained from IR 58821 and IR 52561 parents, respectively

dition with 8.6% and 7.0% phenotypic variation, respectively. The major yield contributing and important trait in rice is PT. Dissecting out the genomic region controlling this trait will be more helpful for further breeding programmes. In the present study, two different QTLs were located in the same chromosome but in different regions for two different conditions. In stress condition, RG 191 and PC73M7 markers flanked the QTL which showed 8.6% of phenotypic variation for this trait, but in irrigated condition, the QTL was bracketed by PC150M7 and PC75M4 and 7.0% of phenotypic variation was shown by this QTL. For PL under stress condition, two QTLs were detected and located in chromosome 6 and 9, and explained 8.4% and 7.0% of phenotypic variation, respectively,

which in combination registered 13.9% of phenotypic variation, whereas, in irrigated condition, single QTL was identified on chromosome 3 that explained 8.4% of phenotypic variation. Single putative QTL was detected for GP one each for stress and irrigated condition. In stress condition, a single QTL was located on chromosome 3 flanked by R3226 and RG558 markers and showed 7.2% of phenotypic variation. In irrigated condition, the QTL was positioned on chromosome 6 between PC73M6 and PC184M11 markers and 5.8% of the phenotypic variation was showed by this QTL. In BMY, one QTL for stress and two QTLs for irrigated condition were dissected out on chromosome 6. Among these QTLs, one QTL was located between the markers C1487 and R2147 in both the

situations and elucidated 8.3% and 10.0% of phenotypic variation, respectively. Another QTL with 6.5% of phenotypic variation was flanked by PC17M4 and PC180M12 markers in irrigated condition. Shanmugasundaram et al. (2002) suggested that, while selecting superior genotypes for cultivation under rainfed situations, GY, HI and straw yield should be considered as

selection criteria. In the present study, for HI, two QTLs were located on chromosome 3 flanked by the markers RG191 and PC73M7 and R1925 and RG1356 under stress. For irrigated condition, one QTL was identified on chromosome 6 and flanked between PC32M6 and PC31M6 markers. For GY only one QTL was identified each in stress and irrigated
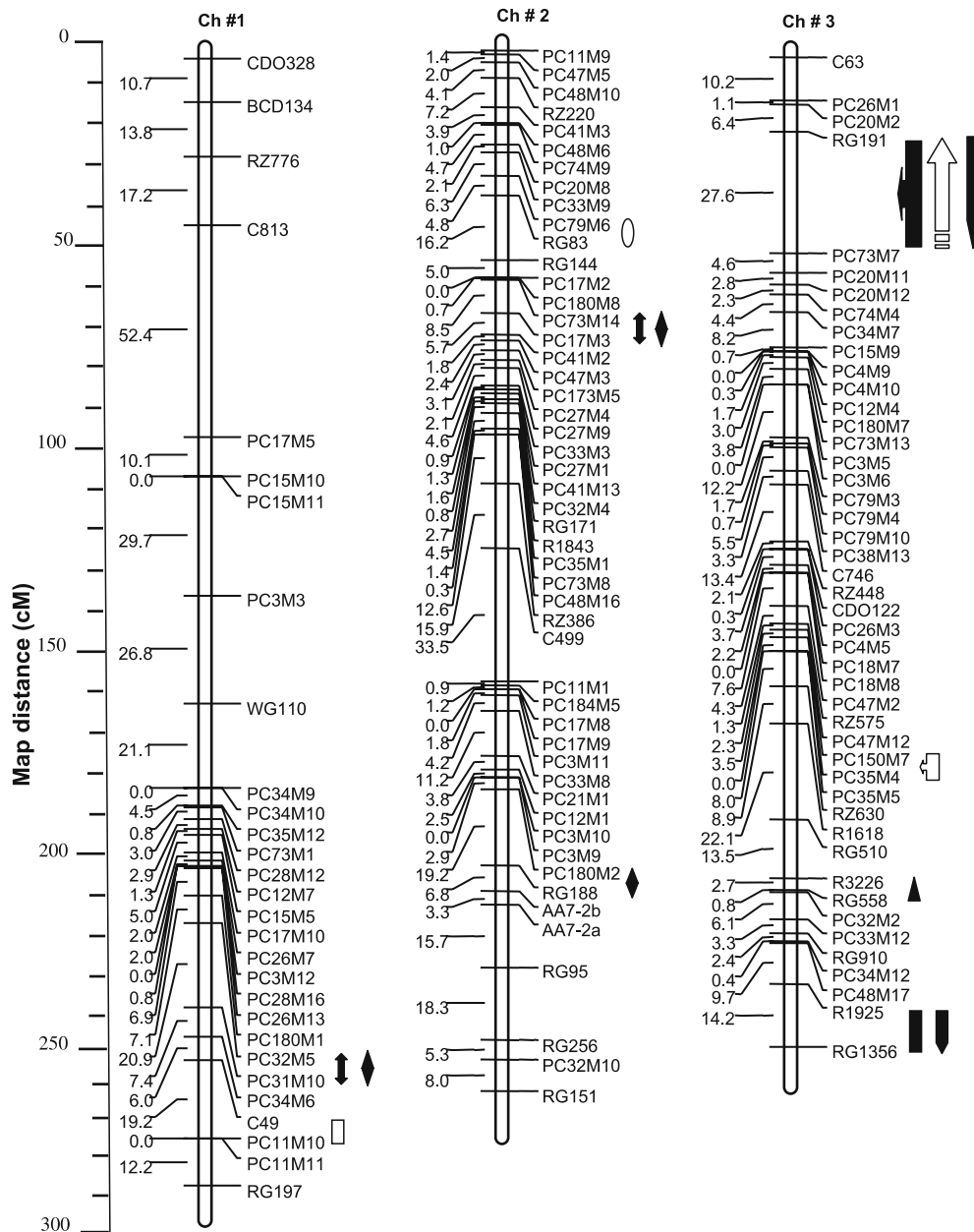
Fig. 1 Genetic linkage map showing QTLs under both conditions
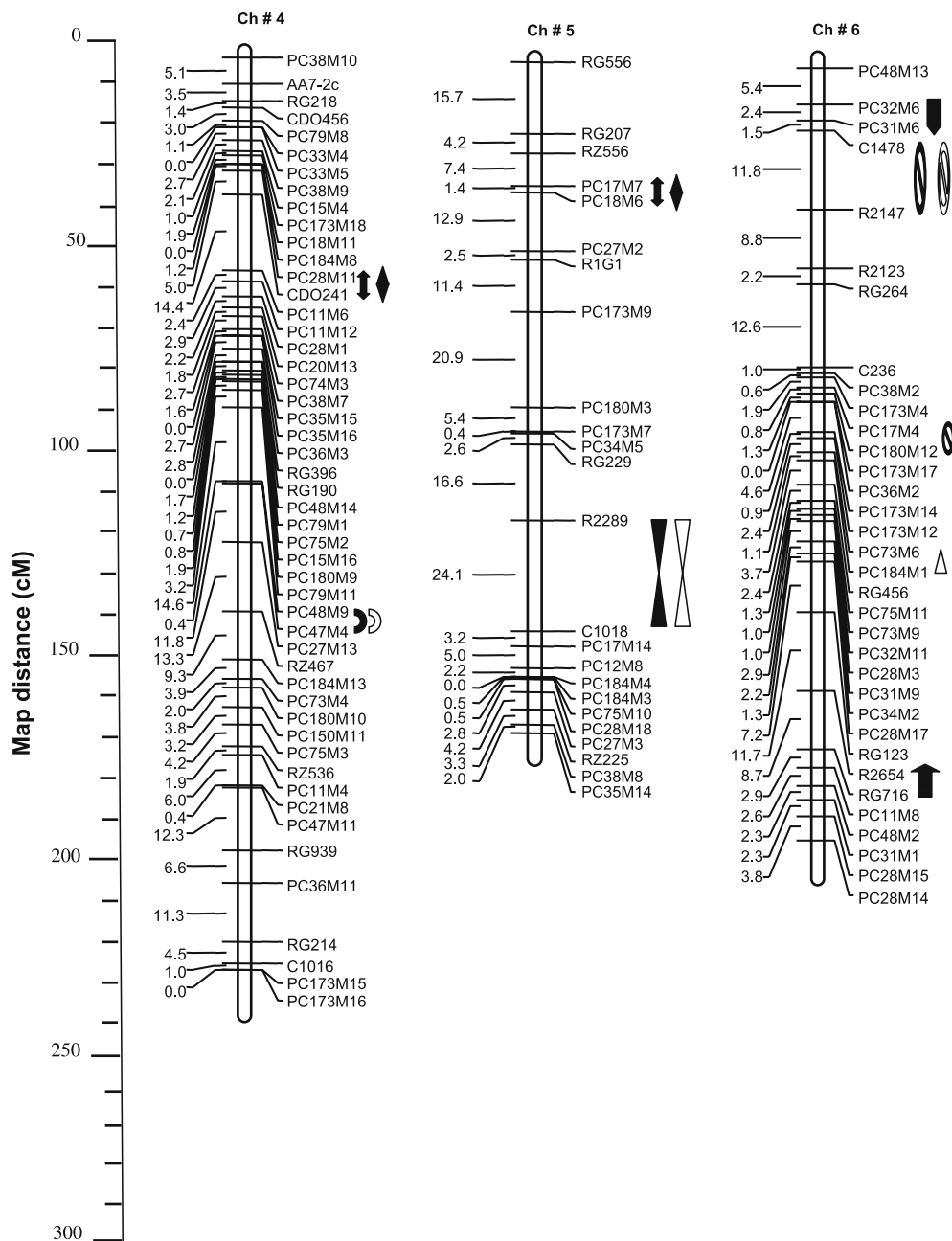
Fig. 1 continued

condition. In stress situation, the QTL with 6.8% of phenotypic variation was located in chromosome 3 flanked by R1925 and RG1356 markers, whereas in irrigated condition the QTL was positioned at chromosome 1 flanked by C49 and PC11M10 markers and explained 6.7% of phenotypic variation.

Discussion

Phenotypic effect

Growing rainfed lowland rice is a conservative strategy for drought avoidance (Fukai and Cooper 2002). The phenotypic values of the
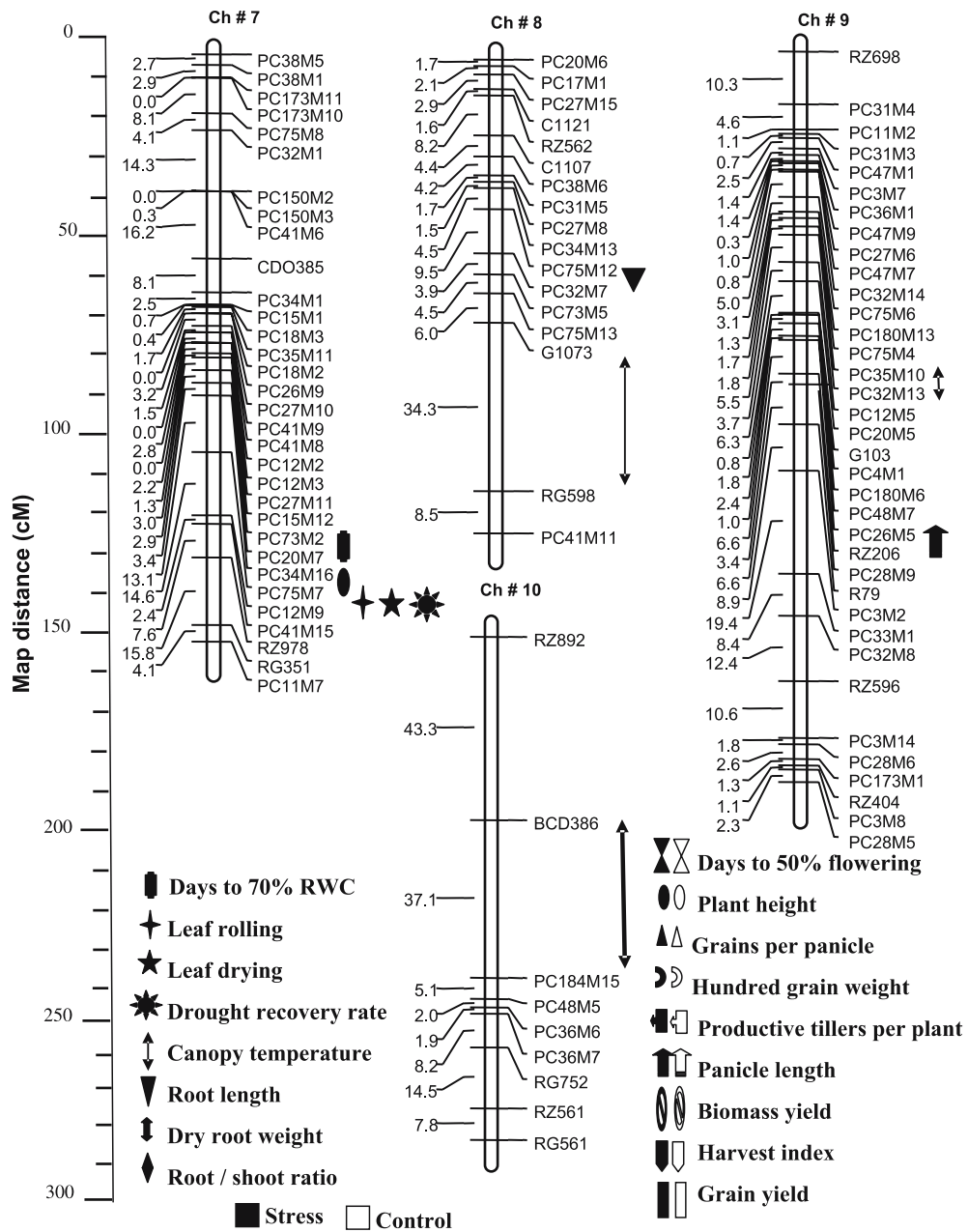
Fig. 1 continued

traits in the RILs have continuous distribution indicating that all measured traits were quantitatively inherited. Traits allowing the evaluation of plant water-status, and particularly relative water content, could give an idea of the level of the water deficit in the plant at a specific time-point (Teulat et al. 2003). As related water content is related to cell volume, when it is measured on the flag leaf, it may closely reflect the balance between water supply to the leaf and transpiration rate (Sinclair and Ludlow 1985). The potential value of relative water content for breeding under drought stress conditions has been demonstrated by Schonfeld

et al. (1988) in winter bread wheat. Hence in the present study importance was given to relative water content to screen the drought. The significant differences in plant phenology and production traits under stress and water stress conditions was observed showed the effect of stress on lowland rice population. Importantly 10 g yield reduction per plant gave the more impact in the over all yield of the crop. Among the yield component traits, the productive tillers per plant was reduced around 50% and grains per panicle was reduced in 20% between the treatments affects the overall performance. The root traits performance gave the way for drought tolerance in that population. The rainfed lowland rice genotypes adapted to drought prone areas should have the capacity to avoid development of severe internal water stress during the period of drought, and also have high potential. Hence the selected RIL lines could be used for further breeding programme.

Creation and utilization of genetic variability are the important factors for crop improvement. The potentiality of a breeding method is judged on the extent of variability generated in different quantitative traits (Allard 1960), as it indicates the extent of recombination for effective selection. Genetic variability studies on the characters related to drought tolerance and grain yield is much essential to know their inherent potential, and based on the capacity, the breeder should propose the suitable breeding methodology. Variability studies in homozygous population gives a clear picture about the variation present among a collection of genotypes, which will be useful to proceed further with the different breeding programmes. Coefficients of variation showed the existence of considerable amount of variability for most of the traits (except days to flowering, panicle length and plant height), which could enable selection of high yielding genotypes coupled with drought tolerance. Heritability serves as a good index for transmission of characters from one generation to next and it should be considered in terms of selection concept (Hanson 1959). The traits viz., days to 70% RWC, leaf rolling, leaf drying, harvest index, biomass yield and grain yield recorded high or moderate her-

itability along with high genetic advance. These characters also had high genotypic coefficient of variation. Hence, these characters offer much scope for improvement by way of simple selection techniques in lowland drought condition. This is in accordance with the finding of Lokaprakash et al. (1992). Therefore, these characters can be improved very easily.

In breeding for drought tolerance, much emphasize was given to understand the association between drought tolerant traits with yield and its components. The relationship of a particular trait or drought tolerant trait with yield would be of immense use to the breeders when they exercise simultaneous selection for both drought tolerant and yield characters. The selection on the basis of single parameters could not provide the true picture of a genotype that response to stress and therefore at least two or three parameters should be used for identifying drought tolerant genotypes. As the drought occur intermittently among seasons and years, selection for yield potential in well watered condition and yield under drought in turn is appropriate for drought tolerance breeding program (Zou et al. 2005), hence the traits were recorded in irrigated condition also. Present study, the important yield contributing traits, productive tillers per plant, biomass yield, 100 grain weight and grains per panicle showed high correlation effect with grain yield in both the situation. The trait of importance relative water content significantly correlated with morphological and yield traits viz., plant height, days to flowering, panicle length and harvest index besides grain yield. Significant effect of stress was observed in panicle length and plant height in positive direction with grain yield in stress condition but there was no correlation in irrigated condition. Leaf rolling, leaf drying and drought recovery rate expressed significant negative correlation with grain yield showed the resistance mechanism involved in the early stage of the crop before it came to reproductive phase. Pantuwan et al. (2002) also observed negative correlation of leaf rolling and leaf drying with grain yield. As a whole, it was indicated by correlation and path analysis that in the RILs to harness high yield combined with drought tolerance, breeders should give selection pressure on

relative water content, panicle length, grains per panicle, harvest index, biomass yield, root/shoot ratio and root length in positive direction, and low scores of leaf rolling, lead drying and drought recovery rate. Singh et al. (1994) reported the effect of relative water content and dry root weight on grain yield. Rao and Saxena (1999) suggested that harvest index could be one of the major selection criteria for yield improvement in rice under water stress. These are candidates for further study to identify drought adaptive traits.

QTL mapping

Genetic dissection by means of QTL identification for various drought tolerant, yield and its component traits indicated that, totally 38 QTLs were responsible for the above traits both under water stress and fully irrigated conditions. Among 38 QTLs, position of 23 QTLs was found to be less than 10 cM from AFLP/RFLP markers. Out of these 23 QTLs, 18 were closely linked (0 cM) with DNA markers/markers themselves. These markers may be used for effective marker assisted selection (MAS) in breeding for drought tolerance in rice. Genetic markers that are associated with economically important traits such as drought resistance can be used as indirect selection tools (Beckman and Soller 1983; Darvasi and Soller 1992). Among these 18, only two were moderate QTLs, each one for days to 70% relative water content and productive tillers per plant in the markers PC73M2 and PC150M7, respectively. The QTL on chromosome 7, positioned between the AFLP markers PC75M7 and PC12M9 showed pleiotropism for leaf rolling and leaf drying. This region also flanks the QTL for drought recovery rate and plant height. Near to this region QTL for relative water content was identified showed the importance of this region for drought resistance breeding programme. It remains to be tested whether these genomic regions have pleiotropic effects or there are clusters of tightly linked genes for many related traits in these regions. Courtois et al. (2000) identified QTLs for relative water content, leaf rolling and lead drying in other population. The five QTLs on chromosomes 1, 2, 4 and 5 for dry

root weight and root/shoot ratio were located together confirmed the highly significant phenotypic correlation between the traits. The QTLs for traits viz., productive tillers per plant, panicle length, grains per panicle, biomass yield, harvest index and grain yield were located on two chromosomes viz., 3 and 6. All these traits also showed the significant correlation with grain yield. Therefore, introgression of these QTLs on chromosome 3 and 6 (with the help of respective markers) into any breeding line will help in grain yield improvement programmes. Two different QTLs were identified for two different environments viz., stress and controlled condition for the traits viz., plant height, productive tillers per plant, panicle length, grains per panicle, grains per panicle, harvest index and grain yield. This may be due to 'on' and 'off' mechanism of gene regulation, but it requires further study to confirm. For characters viz., days to flowering, 100 grain weight and biomass yield, though the QTLs were present in the same chromosome under stress and controlled conditions, there was difference in position and phenotypic variation showed by them between the two conditions. This may be due to G × E interaction. Such a G × E interaction was also reported by Chandrababu et al. (2003) for plant height in CT 9993/IR 62266 population. For grain yield, only two QTL were detected each one in stress and controlled condition. In stress condition, QTL was located along with harvest index confirmed the high phenotypic correlation between the traits. Whereas in control condition, QLT was located close to the root/shoot ratio trait confirmed the relationship between these traits. The Parent IR 58821 contributed favorable alleles for all the drought related and yield component traits except days to flowering and biomass yield. Hence, this parent could be used as a donor for drought tolerance breeding programme.

To determine if common QTLs across genetic background exists, the result of this study were compared to other similar studies (Fig. 2). The map developed by Temnykh et al. (2001) was used to serve as a bridge among the populations compared. The putative QTL identified for days to flowering on chromosome 5 that was flanked

between R2289 and C1018 RFLP markers in the present study was found to be positioned on the same chromosomal location in IR 64/Azucena population (Shashidhar et al. 2002). Similarly, two QTLs associated with root/shoot ratio on chromosome 2 and 5 in the present study were found to be localized in the similar genomic region of IR 64/Azucena population (Yadav et al. 1997). For dry root weight, QTL positioned on Chromosome

2 flanked between RG171 and PC73M14 markers in the present study was found to be similar in position in CT 9993/IR 62266 mapping population (Zhang et al. 2001). This result suggested that similarity existed among *japonica* and *indica* races for the control of these three traits in the present study. These consistent QTLs could be used for introgression into elite rainfall lowland rice in a marker assisted selection programme. However, further research is to be carried out to investigate the nature of these QTLs for their expression.

Fig. 2 Comparative mapping

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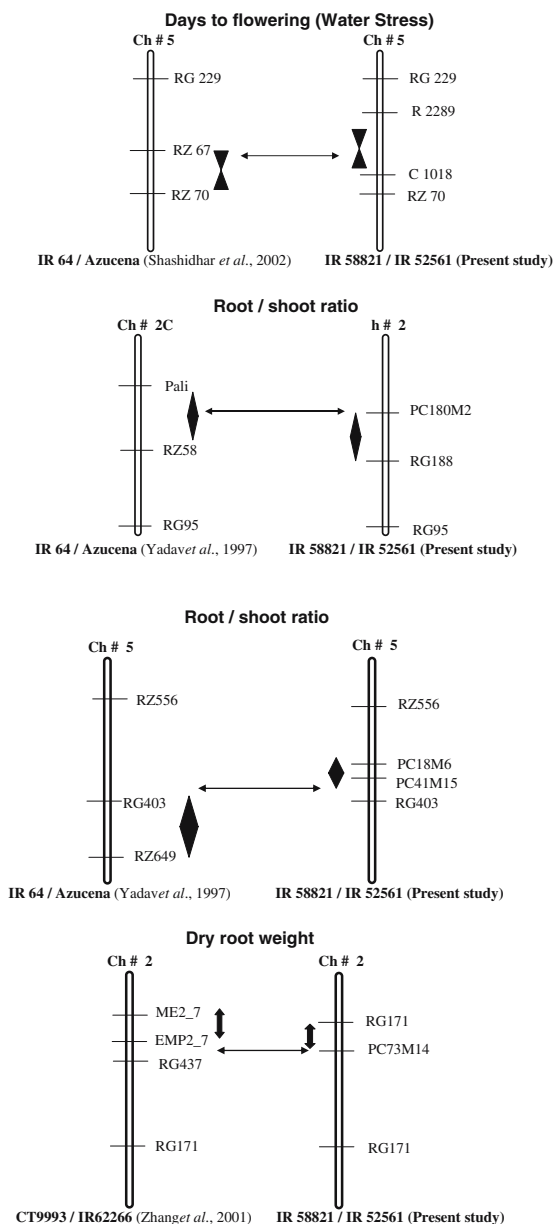
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