

Stability Analysis of Rice Root QTL-NILs and Pyramids for Root Morphology and Grain Yield

Grace Sharon Arul Selvi¹, Farhad Kahani² and Shailaja Hittalmani^{3*}

¹Department of Genetics and Plant Breeding, University of Agricultural Sciences, Bangalore-65, India

²Marker Assisted Selection Laboratory, Genetics and Plant Breeding, University of Agricultural Sciences, GKVK, Bangalore 560065, India

³University Head, Genetics and Plant Breeding, University of Agricultural Sciences, GKVK, Bangalore-560065, India

Abstract

Cultivation of rice in the rain fed conditions is threatened by frequent spells of water deficits and limits the productivity to a greater extent. Root system plays a major role in uptake of water and they contribute to drought tolerance in a major way. In this study, Root QTL were pyramided and evaluated under aerobic and drought conditions and the stable genotypes were identified. Two QTL and three QTL pyramid lines for roots were developed and evaluated under drought, aerobic and in different locations to study the performance. While qRT26-9 with 2 QTL pyramid performed better with respect to the root traits, qRT16-1+7 and qRT17-1+7 performed better for shoot morphology over the various growth water regimes. Among the pyramids, qRT11-7 × qRT18-1+7-17 recorded increased performance for plant height and seed yield while qRT11-7 × qRT18-1+7-32 recorded increased performance for total biomass and maximum root length. qRT24-9 × qRT11-7-32 recorded increased performance for root traits only across environments. Lines with high means and average stability were identified as suitable across growth niches, while those with low stability and high means were identified as suitable for growth under poor environments and for specific locations.

Keywords: Rice; Aerobic; Stability; Root QTLs; Environments

Introduction

Rice (*Oryza sativa* L), the second most important cereal of the world is traditionally grown under submerged anaerobic conditions. However, this cultivation is now foraying into the less traditional rain fed uplands and marginal lands with mounting pressure on land availability. This coupled with changes in the climate make cultivation in these delicate ecosystems rather intricate. Therefore, the development of genotypes that consistently perform under conditions of climate change with less moisture availability is a viable option. The constancy or preferably increase in yield potential under climate change scenario is fundamental for food sustainability in the near future, given the expected population growth projections. Cultivation in the rain fed uplands is threatened by frequent spells of water deficits being a major limiting factor directly affecting grain yields during reproductive phases. Several mechanisms that determine drought tolerance and or resistance have been outlined, of which manipulation of the root system to maintain the water status of a crop under conditions of increasing water deficits has been the choice breeding strategy for drought. Several QTLs governing root traits across populations have been identified in rice. Root studies have become very important now that there are several ways to study them [1-17].

Pyramiding of genes is conducted to develop a genotype that expresses the said genes appropriately, such that the phenotype is enhanced. It has been used extensively in major gene controlled rice blast, rice blight and against insect pests such as diamond back moth (Cao et. al., 2002). Pyramids enhance the phenotype effectively and can be used to analyse the effect of QTLs upon each other as they offer a common background for the QTLs to interact. Subsequently QTL pyramiding was attempted by several researchers. Consistent and quality performance of developed genotypes is always desired as it increases the longevity of the genotypes. In breeding exercises, stable and high performance of developed varieties in target growth environments or across different environments and or seasons is an important attribute. Stability of the lines is measured as a non-significant deviation from its regression coefficient and is stated with reference to its mean. Lines

with high means and average stability can be identified to suit in most environments [18-30].

Material and Methods

Plant material

A set of twenty-nine near-isogenic lines with Root QTL introgressions of IR64 (*indica*, high yielding) with QTL introgressions from Azucena (*japonica*, drought tolerant) controlling root morphology (QTL Introgressed Lines (QILs)) developed by [31] and fine mapped by [16] was used for the study. These QILs were used in a pairwise crossing programme to develop 2 and 3 QTL pyramids. The QILs, the generated pyramids along with parents: IR64, Azucena and checks: Buddha and Moroberekan were evaluated in RCBD design with 2 replications over the various growth regimes (Table 1) in 2011-2012 (Tables 2-4).

Phenotypic observations

Five plants with QTL pyramids were selected at random in each entry for recording observations. The average of these five plants was used for the statistical analysis. The individual plants were observed for plant height (cm) from the base to the tip of the panicle at harvest days to 50% flowering i.e., first flowering in 50 per cent of the plants, number of tillers per plant, number of panicles per plant, panicle length (cm) from collar to the tip, number of filled grains per panicle, number

*Corresponding author: Shailaja Hittalmani, Professor and University Head, Genetics and Plant Breeding, University of Agricultural Sciences, GKVK, Bangalore 560065, India, Tel: 91-8023624967; E-mail: shailajah_maslab@rediffmail.com

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Regression Coefficient	Stability	Mean yield	Remarks
b=1	Average	High	Well adopted to all environments
b=1	Average	Low	Poorly adopted to all environments
b>1	Below average	High	Specially adopted to favorable environments
b<1	Below average	High	Specially adopted to unfavorable environments

Table 1: Mean, yield and Regression Co-efficient (b) values.

Sl. No.	Genotype	QTL introgression on
1	qRT1-1	1
2	qRT2-1	1
3	qRT3-1	1
4	qRT4-2	2
5	qRT5-2	2
6	qRT6-2	2
7	qRT7-2	2
8	qRT8-2	2
9	qRT9-7	7
10	qRT10-7	7
11	qRT11-7	7
12	qRT12-7	7
13	qRT13-7	7
14	qRT14-7	7
15	qRT15-7	7
16	qRT16-1+7	1+7
17	qRT17-1+7	1+7
18	qRT18-1+7	1+7
19	qRT19-1+7	1+7
20	qRT20-1+7	1+7
21	qRT21-1+7	1+7
22	qRT22-1	1
23	qRT23-1	1
24	qRT24-9	9
25	qRT25-9	9
26	qRT26-9	9
27	qRT27-9	9
28	qRT28-9	9
29	qRT29-9	9

Table 2: List of QTL Introgressed Lines (QILs) used in the study (Vaishali,2003).

of chaffy grains per panicle, panicle weight (g) total grain weight per plant (g) root length (cm) from the crown to the tip of the longest roots, root thickness (mm), root number at 15cm root depth, total biomass (g) and test weight (g) was observed.

Statistical analyses

The data that was generated was subject to a series of statistical analyses to elucidate the relative effects of the presence of various QTLs in the rice genotypes and are presented here below:

Two way Analysis of variance: The data obtained was subjected to two way analysis of variance using the method outlined by [32] for each character in order to ascertain existence of genotype x environment interaction. If interaction was found to be significant, then the data was further subjected to stability analysis.

Stability analysis: The stability model proposed by [33] was adopted to analyze the data over the studied environments. The model considers three parameters: the mean (M), the regression co-efficient (bi) which

Sl. No.	Pyramids	Chro. Introgression on	No. Plants
1	qRT11-7 X qRT18-1+7	7+ (1+7)	35
2	qRT24-9 X qRT11-7	9 + 7	38
3	qRT6-2 X qRT11-7	2+ 7	32
4	qRT11-7 X qRT19-1+7	7 + (1+7)	36
5	qRT20-1+7 X qRT18-1+7	(1+7) + (1+7)	37
6	qRT11-7 X qRT6-2	7 + 2	38
7	qRT6-2 X qRT19-1+7	2+ (1+7)	32
	Total No.		248

Table 3: List of two and three QTL pyramids generated for the study.

is the regression of the mean of environmental index and deviation for regression (s^2_{di}), which is a measure of genotype -environment interaction of an unpredictable type.

The model involves the estimation of three stability parameters: mean (μ_i), regression co-efficient (b_i) and deviation from regression ($S^2_{d_i}$), which are defined by the following mathematical formula.

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

Where,

Y_{ij} : mean of the i^{th} genotype in the j^{th} environment.

μ_i : mean of the i^{th} genotype over environments.

β_i : regression co-efficient that measures the response of i^{th} genotype to varying environment.

δ_{ij} : deviation from regression of the i^{th} genotype in the j^{th} environment and

I_j : environmental index obtained by subtracting the grand mean of the i^{th} genotype from the mean of all genotypes in the j^{th} environment.

Stability parameters

The mean (μ_i), the regression co-efficient (b_i) and mean square deviation from linear regression line ($S^2_{d_i}$) are the three stability parameters proposed by [33] in their stability model. The three parameters are computed using the following formulae:

$$\text{Mean: } \mu_i = \sum_j Y_{ij} / n$$

$$\text{Regression co-efficient } b_i = \frac{\sum_j Y_{ij} I_j}{\sum_j I_j^2}$$

$$\text{Deviation from regression co-efficient } (S^2_{d_i}) = \frac{\sum_j \hat{a}_{ij}^2}{n-2} - \frac{\hat{a}^2_e}{r}$$

Where,

δ^2_e/r : mean square estimate of pooled error

n : number of environments

Y_{ij} : performance of i^{th} genotype in j^{th} environment

$\sum_j \hat{a}_{ij}^2$: sum of squares of deviations from the regression line

I_j : environmental index

$$I_j = \frac{\sum_i Y_{ij}}{v} - \frac{\sum_i Y_{ij}}{nv}$$

Sl. No.	Season	Location	Conditions	Material used	Traits
1	1	MRS, Hebbal	low moisture stress	QTL-NILs	Shoot, root and yield traits
			well watered conditions	pyramids	
2	2	Farmer's field, Pavagada, Tumkur	low moisture stress	QTL-NILs	Shoot and yield traits
			well watered conditions	pyramids	
3	3	MRS, Hebbal	low moisture stress	QTL-NILs	Shoot and root traits
			well watered conditions	pyramids	
4	3	ZARS, GKVK	low moisture stress	QTL-NILs	Shoot, root and yield traits
			well watered conditions	pyramids	
5	3	Farmer's field, Dodjala, Bangalore	submerged	QTL-NILs	Shoot, root and yield traits
				pyramids	
6	3	Farmer's field, Shettigere, Bangalore	aerobic, non-stress	QTL-NILs	Shoot, root and yield traits
				pyramids	

Table 4: List of field experiments conducted in this study.

Where,

n : number of environments

v : number of genotypes with $\sum I_j = 0$

The total variation is partitioned into genotypes, environment, environment (linear), genotype x environment (linear), pooled deviation and pooled error.

F test

a. To test the significance of differences among the genotypic means, the 'F' test followed was:

$$F = MS_1 / MS_3$$

Where, MS_1 : mean sum of squares of varieties

MS_3 : mean sum of squares of pooled deviation

b. To test individual from linear regression, the formula is as follows,

$$F = \left(\sum_j \delta_{ij}^2 / n - 2 \right) / MS_e$$

Where, n : number of environments

$\sum_j \delta_{ij}^2$: sum of squares of deviations from the regression line

MS_e : pooled error

c. To test the hybrids/ varieties which do not differ for their regression on the environmental index, the appropriate test was,

$$t = \frac{b_i - 1}{SE(b)} \text{ or } \frac{b_i}{SE(b)}$$

$$SE(b) = \left[\frac{\left[\sum Y^2 - (\sum Y)^2 / n \right] - \left[\sum X^2 - (\sum X)^2 / n \right]}{n - 2 \left[\sum X^2 - (\sum X)^2 / n \right]} \right]$$

Where,

X : environmental index

n : number of environments

A joint consideration of the three parameters such as

1. The mean performance of the genotype over the environments (x)
2. The regression co-efficient (b)

3. The deviation from linear regression (S^2d) is used to define stability of a genotype.

The estimate of deviations from regression (S^2d) suggests that the degree of reliance that should be put to linear regression in interpretation of the data. If these values are significantly deviating from zero, the expected phenotype cannot be predicted satisfactorily. When, deviations (S^2d) are not significant, the conclusion may be drawn by the joint consideration of mean, yield and regression co-efficient (b) values as given below (Table 1).

While interpreting the results, s^2di is first looked into. A non-significant deviation from $s^2di=0$, then stability is interpreted based on b_i and mean values. If $b_i=1$, a genotype is considered to possess average stability i.e., same performance in all the growth conditions. If b_i is more than unity, then the genotype is said to have less than average stability i.e., good performance under favorable environments. If b_i is less than unity, then the genotype is said to possess above average stability i.e., good performance under poor environments. Thus, genotypes possessing unit regression coefficient and non-significant deviation from regression were considered ideal, widely adapted and stable genotypes.

Results

Environment- wise analysis of variance indicated a significant mean sum of squares for the QTL-NILs and the generated pyramids for most characters studied. Combined Analysis of Variance for the pyramids qRT24-9 x qRT11-7 (data not shown) indicated significant variance for genotype as well as for genotype x environment [33] model for stability analysis was applied as the genotype x environment component of variance was found significant. The performance of genotypes in different environments for five selected characters based on two-way analysis of variance and Bartlett's test are elaborated below (Table 5).

Plant height

The varying environmental indices indicated that there was a significant difference for plant height across environments and across genotypic entries. qRT6-2 x qRT19-1+7 was the shortest (47.74cm), while qRT6-2 x qRT11-7 was the tallest (62.77 cm). The b_i and s^2di were found to be non-significant for all the genotypes studied.

Seed yield per plant

As indicated by the environmental indices and the environmental means, seed yield per plant showed significant differences across

Genotypes	Source	df	PHT	NOT	NOP	PWT	PL	DFL	NS	NC	TWT	SWT/ PLT	TBM	MRL	RTN	RTT
QTL-NILS	Genotype	28	1094.50**	36.30**	10.85**	65.67**	10.19**	23.71**	390.17**	100.23**	2.44**	34.01**	414.09**	319.86**	1123.27**	0.01**
	Env+(Genotype x Env)	261	55123.9	2222.91	2195.92	72521.79	9984.15	1149.08	103713.8	18870.1	163.87	8091.21	347401	47868.35	144351.2	40.06
	Envt (linear)	1	37864.8	1676.49	1811.52	64602.31	9786.47	1148.46	96768.12	17994.6	144.85	4407.73	296222	33922	64009.25	38.98
	Genotype x Env (linear)	28	44	0.99	3.55**	132.42**	2.21**	0.001	102.02**	16.35**	0.13**	21.40**	392.98**	373.76**	263.53**	0.01**
	Pooled Deviation	232	60.04	1.95	1.03	13.95	0.48	0.002	13.94	1.34	0.06	11.36	146.23	7.52	272.38	0.003
	Pooled Error	280	6.93	1.13	0.6	3.34	0.41	0.002	6	2.34	0.03	10.72	49.08	1.4	19.92	0.001
	Genotype	40	876.55**	24.49**	9.77**	87.17**	8.99**	13.75**	383.28**	82.08**	0.97**	31.35**	321.83**	345.57**	1982.65**	0.03**
	Env+(Genotype x Env)	369	226.88	8.65	6.91	75.99	15.72	3.95	350.09	51	1.07	39.64	37	132.48	659.26	0.15
	Envt (linear)	1	52978.2	1937.42	1514.66	13773.78	4628.64	1256.84	88796.11	12487.9	360.68	8906.99	690332	32944.4	112931.1	51.19
	Genotype x Env (linear)	40	113.47**	1.27	3.73**	156.19**	8.02**	0.41	143.71**	25.32**	0.38**	32.88**	721.85**	348.74**	243.31**	0.02**
qRT11-7 x qRT18-1+7	Pooled Deviation	328	79.89	3.67	2.7	24.45	2.6	0.56	105.61	16.21	0.06	13.43	282.64	6.07	367.7	0.01
	Pooled Error	410	8.3	1.65	1.24	2.09	0.34	0.55	5.95	15.8	0.03	9.36	51.35	1.65	9.28	0.002
	Genotype	43	660.47**	25.69**	10.89**	96.77**	19.34**	20.49**	318.33**	30.55**	0.77**	36.40**	271.54**	335.19**	2294.08**	0.01*
	Env+(Genotype x Env)	396	229	7.65	10.85	106.96	20.3	7.85	290.78	45.75	0.16	48.77	2182.51	145.14	1461.25	0.13
	Envt (linear)	1	68261.8	1641.78	3041.87	22075.17	7027.26	1113.94	88336.55	15618.3	323.9	10459.2	738492	37439.92	297064.9	44.87
	Genotype x Env (linear)	43	67.20**	1.22	6.76**	208.98**	10.95**	3.24	138.93**	18.35**	0.35**	50.57**	811.15**	398.62**	2233.28**	0.01
	Pooled Deviation	352	55.5	3.79	2.74	32.09	1.53	5.27	58.63	4.86	0.07	18.98	258.25	8.23	527.16	0.01
	Pooled Error	440	8.18	1.99	1.45	10.73	0.43	5.19	6.02	4.58	0.03	8.35	34.77	1.85	25.58	0.002
	Genotype	37	719.33**	21.83**	11.95**	59.90**	14.00**	21.72**	354.92**	20.27**	0.479.31**	29.87**	459.23**	401.46**	1384.50**	0.02**
	Env+(Genotype x Env)	342	259.64	7.47	8.23	146	26.41	3.11	356.3	42.61	35.49	53.28	2019.43	101.77	1319.16	0.15
qRT6-2 x qRT11-7	Envt (linear)	1	60865.2	1639.85	1961.91	34778.48	8008.35	998.57	94034.25	11526	142.22	11256.2	553892	12425.92	231516.1	49.73
	Genotype x Env (linear)	37	66.16	0.96	3.34**	56.92**	11.62**	0.29**	255.65**	5.62	57.68**	46.77**	939.75**	407.11**	1885.27**	0.02**
	Pooled Deviation	304	83.83	2.9	2.39	42.92	1.95	0.18	60.4	9.33	32.44	17.23	335.47	24.06	493.04	0.005
	Pooled Error	380	7.77	1.51	0.47	2.32	0.52	0.3	5.42	2.19	0.02	9.11	16.93	1.58	21.1	0.001
	Genotype	41	698.54**	27.99**	12.16**	80.37**	10.33**	25.36**	374.19**	47.15**	1.08**	26.33**	327.13**	306.75**	1008.60**	0.01**
	Env+(Genotype x Env)	378	239	9.22	10.4	63.23	24.61	3.14	469.09	47.08	0.92	51.03	1886.74	150.4	1102.17	0.13
	Envt (linear)	1	67363.2	2044.62	2789.46	13111.76	8617.55	1005.53	147209.6	14989.1	307.65	13241.2	632768	39825.3	262040.7	45.68
	Genotype x Env (linear)	41	118.94**	1.18	7.16**	99.92**	2.25**	0.48**	364.72**	11.41**	0.45**	21.49**	351.51**	350.40**	1492.14**	0.01**
	Pooled Deviation	336	53.88	4.14	2.52	19.92	1.77	0.48	45.1	6.96	0.07	15.38	196.45	7.92	277.99	0.005
	Pooled Error	420	21.86	1.91	0.51	8.46	1.25	0.82	10.39	3.12	0.03	8.43	63.55	5.79	23.12	0.003

qRT20-1+7 x qRT18- 1+7	Genotype	42	770.22**	18.57**	6.12**	34.21**	3809.05**	15.24**	426.14**	58.03**	1.29**	22.90**	621.20**	315.25**	1061.88**	0.02**
	Env+(Genotype x Env)	387	440.29	17.78	20.34	76.19	3902.68	3.35	429.79	43.76	0.77	86.12	3459.73	66.46	2177.75	0.1
	Env (linear)	1	128493	4624.31	5874.1	23997.43	65221.28	1229.59	139688.5	16032.7	274.78	26952.5	1141093	7716.41	627347.9	37.93
	Genotype x Env (linear)	42	517.38**	20.07**	25.74**	68.98**	30361.98**	0.20**	235.13**	9.75**	0.18**	46.38**	2647.6	136.89**	3691.99**	0.01**
	Pooled Deviation	344	58.64	4.11	2.67	7.53	493.93	0.17	48.79	1.44	0.05	12.87	251.82**	35.63	175.52	0.003
	Pooled Error	430	11.12	1.81	0.27	2.65	3814.38	0.22	5.84	2.1	0.02	8.21	53.08	1.49	16.34	0.001
	Genotype	43	882.98**	19.55**	2.93**	51.19**	5.28**	42.45**	279.74**	18.38**	1.06**	26.10**	718.26**	344.57**	914.81**	0.01**
	Env+(Genotype x Env)	396	768.12	9.43	8.22	112.61	32.31	12.71	594.65	49.9	0.77	77.82	2717.55	59.79	1374.32	0.12
	Env (linear)	1	249272	3004.72	2765.42	34337.35	12298.66	1370.65	213710.7	18968.7	270.01	22578.5	878866	6046.2	340944.6	48.04
	Genotype x Env (linear)	43	858.08**	2.22**	2.34**	138.73**	4.60**	5.51	335.00**	4.96**	0.14**	74.42**	2447.62**	134.52**	2721.38**	0.01**
qRT11-7 x qRT16-2	Pooled Deviation	352	51.15	1.8	1.1	12.19	0.84	9.73	20.93	1.65	0.08	14.32	261.46	33.65	245.07	0.003
	Pooled Error	440	10.66	1.3	0.27	2.47	0.29	9.57	5.93	1.79	0.01	8.14	33.35	1.28	23.52	0.001
	Genotype	37	1145.51**	20.58**	5.44**	41.71**	6.34**	30.56**	273.61**	42.11**	1.06**	19.34**	382.90**	398.79**	1007.56**	0.01**
	Env+(Genotype x Env)	342	335.54	10.8	12.67	163.99	28.51	4.07	394.86	54.92	0.67	33.31	1205.99	74.74	1035.23	0.13
	Env (linear)	1	95236.6	2721.69	3509.35	42728.02	9294.13	1314.09	104932.5	17797.4	216.81	7209.23	345259	7064.5	233538.7	44.82
	Genotype x Env (linear)	37	164.75**	7.62**	9.02**	215.53**	5.19**	0.35**	321.00**	10.59**	0.11**	7.16	180.05	124.55**	1036.50**	0.004**
	Pooled Deviation	304	44.15	2.27	1.61	17.7	0.87	0.21	59.97	1.95	0.03	12.88	199.1	45.69	270.27	0.003
	Pooled Error	380	15.76	0.91	0.26	2.92	0.36	0.42	5.36	2.07	0.02	8.96	39.66	1.23	15.44	0.001

PHT: Plant height (cm)	TWT: Test weight (g)
NOT: Number of tillers per plant	SWT/PLT: Seed yield (g) per plant
NOP: Number of panicles per plant	TBM: Total biomass (g)
PWT: Panicle weight (g)	MRL: Maximum root length (cm)
PL: Panicle length (cm)	RTN: Total root number
DFL: Days to 50% flowering	RTT: Mean root thickness (mm)
NS: Number of filled seeds per plant	* / **: Significance at P=0.05 and 0.01 respectively
NC: Number of chaffy seeds per plant	

Table 5: ANOVA for stability in QTL introgressed NILs and the generated pyramids as per Eberhart and Russel (1966).

environments. qRT11-7 x qRT6-2 recorded the highest seed yield (9.95 g), while qRT11-7 x qRT18-1+7 recorded the least seed yields (6.92 g). The bi and s²di were found to be non-significant for all the genotypes studied.

Total Biomass per plant

The varying environmental indices indicated that there were significant differences for total biomass across environments. qRT6-2 x qRT19-1+7 was the lightest (35.82 g), while qRT20-1+7 x qRT18-1+7 was the heaviest (50.92 g). The bi and s²di were found to be non-significant for all the genotypes studied.

Maximum root length

As indicated by the environmental indices and the environmental means (11.86 to 18.63), maximum root length showed significant differences across genotypes. The QTL-NILs recorded the highest mean maximum root length (18.63 cm), while qRT11-7 x qRT6-2 recorded the least root length (11.86 cm). The bi and s²di were found to be non-significant for all the genotypes studied (Table 6).

Total number of roots per plant

The varying environmental indices indicated that there were significant differences for total number of roots across environments. qRT6-2 x qRT11-7 had the highest mean number of roots (59.13), while qRT11-7 x qRT18-1+7 had the least mean number of roots (52.65). The bi and s²di were found to be non-significant for all the genotypes studied.

Discussion

Phenotype of an individual is determined by the interaction of the genotype and environment surrounding it, the effects of genotype and environment on phenotype may not always be independent. The phenotypic response to change in environment is not the same for all the genotypes. The interplay in the genetic and non-genetic effects on development is termed as “genotype environment” interaction (Comstock and Moll, 1963) and is of major consequence to the breeder in the process of evolution of improved genotypes.

In the present study, twenty nine near isogenic lines of IR64 introgressed with QTL regions on four chromosomes: 1,2,7 and 9 from Azucena, 7 pyramids generated from these lines and the checks: IR64, Azucena, Budda and Moroberekan were grown in three seasons. 2011, Season I. 2012 wet and dry seasons. (Season II and Season III). During season 1, they were grown under reproductive stage low moisture stress and well watered conditions for growth, yield and root traits at MRS, Hebbal. During season 2, they were grown under reproductive stage low moisture stress and well watered conditions at Farmer's field, Pavagada for growth and yield traits. During season 3, the genotypes were grown under reproductive stage low moisture stress and well watered conditions at ZARS, GKVK, under submerged conditions at Farmer's field, Dodjala and under aerobic non-stress conditions at Farmer's field, Shettigere for growth, yield and root traits. The genotypes were also grown under vegetative stage low moisture stress and well watered conditions for growth and root traits at MRS, Hebbal.

Mean performance of the QTL-NILs and generated pyramids

The aerobic, non stress growth condition of Farmer's field, Shettigere (data not shown) during season 3 was the most conducive

environment for plant height in the QTL-NILs, with a mean height of 71.85 cm. Low moisture stress condition of season 2, Farmer's field, Pavagada was the least conducive for the QTL-NILs. qRT21-1+7 was the tallest genotype across locations. All the generated pyramids recorded maximum plant height under aerobic, non-stress condition at Farmer's field, Shettigere. The tallest pyramids generated were qRT11-7 x qRT18-1+7-7, qRT24-9 x qRT11-7-12, qRT6-2 x qRT11-7-15, qRT11-7 x qRT19-1+7-21, qRT20-1+7 x qRT18-1+7-4, qRT11-7 x qRT6-2-1 and qRT6-2 x qRT19-1+7-3. Among the pyramids, qRT11-7 x qRT18-1+7 was significantly taller, while qRT6-2 x qRT19-1+7 was significantly shorter.

For grain yield in QTL-NILs, the submerged conditions provided by Farmer's Field, Dodjala during season 3 was the most conducive, while the least mean yield were recorded under low moisture stress, MRS, Hebbal during season 1. A highest mean yield across environments was recorded in qRT11-7. For the pyramids, qRT11-7 x qRT18-1+7, qRT24-9 x qRT11-7, qRT11-7 x qRT19-1+7, qRT11-7 x qRT6-7 and qRT6-2 x qRT19-1+7, the most conducive environment was the aerobic non-stress condition during season 3 at Farmer's field Shettigere while qRT6-2 x qRT11-7 and qRT20-1+7 x qRT18-1+7 recorded highest mean yields under submerged conditions, season 3, Farmer's field, Dodjala. The highest yielding pyramids were qRT11-7 x qRT18-1+7-15, qRT24-9 x qRT11-7-1, qRT6-2 x qRT11-7-15, qRT11-7 x qRT19-1+7-16, qRT20-1+7 x qRT18-1+7-17, qRT11-7 x qRT6-2-1 and qRT6-2 x qRT19-9.

The highest mean total biomass was recorded by the QTL-NILs under well watered condition, season 2, Farmer's field, Pavagada, while the least biomass was recorded under season 1, low moisture stress at MRS, Hebbal. Highest biomass across location was recorded by qRT18-1+7. For the pyramids qRT11-7 x qRT18-1+7, qRT6-2 x qRT11-7, qRT11-7 x qRT19-1+7 and qRT6-2 x qRT19, the most conducive environment for total biomass production was season 2, Farmer's field, Pavagada, while for qRT24-9 x qRT11-7, qRT20-1+7 x qRT18-1+7 and qRT11-7 x qRT6-2 yielded highest biomass under aerobic, non-stress conditions during season 3 at Farmers field, Shettigere. Highest biomass were produced by qRT11-7 x qRT18-1+7-4, qRT24-9 x qRT11-7-13, qRT6-2 x qRT11-7-25, qRT11-7 x qRT19-1+7-20, qRT20-1+7 x qRT18-1+7-8, qRT11-7 x qRT6-2-38 and qRT6-2 x qRT19-30.

Mean maximum root length was recorded by the QTL-NILs under low moisture stress, season 1, MRS, Hebbal, with the maximum root length being recorded in qRT26-9. For the pyramids qRT11-7 x qRT18-1+7, qRT24-9 x qRT11-7, qRT6-2 x qRT11-7, qRT11-7 x qRT19-1+7, and qRT6-2 x qRT19, the most conducive environment for longer root production was low moisture stress condition, season 1, MRS, Hebbal, while qRT20-1+7 x qRT18-1+7 and qRT11-7 x qRT6-2 recorded longest roots under well watered conditions, ZARS, GKVK during season 3. Longest roots were produced by qRT11-7 x qRT18-1+7-27, qRT24-9 x qRT11-7-32, qRT6-2 x qRT11-7-28, qRT11-7 x qRT19-1+7-10, qRT20-1+7 x qRT18-1+7-33, qRT11-7 x qRT6-2-12 and qRT6-2 x qRT19-24.

Highest number of roots were produced by the QTL-NILs under well watered conditions, season 3, ZARS, GKVK, with the highest number of roots being produced by qRT17-1+7. For the pyramid qRT11-7 x qRT18-1+7 the most conducive environment for number of root production was well watered conditions, season 3, ZARS, GKVK, while for qRT24-9 x qRT11-7, qRT11-7 x qRT19-1+7, qRT11-7 x qRT6-2 and qRT6-2 x qRT19, the most conducive environment for number of root production was season 3, aerobic, non-stress condition, Shettigere and for qRT6-2 x qRT11-7 and qRT20-1+7 x qRT18-1+7

the most conducive environment was submerged condition, season 3, Farmer's field, Dodjala. Highest number of roots were produced by qRT11-7 x qRT18-1+7-14, qRT24-9 x qRT11-7-1, qRT6-2 x qRT11-7-31, qRT11-7 x qRT19-1+7-6, qRT20-1+7 x qRT18-1+7-8, qRT11-7 x qRT6-2-13 and qRT6-2 x qRT19-4.

The aerobic non-stress condition therefore is the most conducive environment to grow the present genotypes. Similar results were obtained by [3,34]. This was opined to be due to aeration of roots leading to efficient utilization of resources [35-38].

Genotype x environment interaction

Prior to stability analysis, Bartlett test was done. Based on this test, five characters were selected. Homogeneity in the error variances allowed pooled analysis.

The mean sum of squares due to genotypes as well as environments was found to be significant in the two way analysis. Significant GXE interaction was obtained both by two-way analysis and the [32] model. The analysis of variance for stability indicated significant differences among the QTL-NILs as well as between and within the generated pyramids for all the characters. The significant environment (linear) variance indicated considerable additive environmental variance. Variance due to GXE interaction was found to be significant for all the characters indicating differential response of the genotypes in different environments. G X E (linear) was significant for all the characters indicating a contribution of linear portion of GE interaction. The more pronounced linearity of characters indicated that variation among the genotypes could be largely explained by the differences [3,39-41].

Stability parameters

Five characters were selected on the basis of homogeneity of error variances and after significance of G X E interactions. Identification of genotypes that perform stably over a range of growth environments would therefore be necessary. Of the many models proposed to this effect, the Eberhart and Russel model was used in the present study. Taller plants were preferred as these could lend to fodder yield in a mixed cropping system. Increase in height coupled with increase in total biomass content could result with increase in number of tillers per plant and flowering mattered for the escapes [42]. Maximum root length as a mechanism of drought tolerance ensures higher crop yields under stress situations. Based on the five characters taken together, among the QTL-NILs, qRT24-9 was found to be best in performance across locations, moisture regimes and seasons. While qRT26-9 performed better with respect to the root traits, qRT16-1+7 and qRT17-1+7 performed better for shoot morphology over the various growth regimes. Among the pyramids, qRT11-7 x qRT18-1+7-17 recorded increased performance for plant height and seed yield while qRT11-7 x qRT18-1+7-32 recorded increased performance for total biomass and maximum root length. qRT24-9 x qRT11-7-32 recorded increase in performance for root traits only across environments. qRT6-2 x qRT11-7-15 recorded increase in performance for plant height and seed yield across environments qRT20-1+7 x qRT18-1+7-15 was the best in performance considering seed yield, total biomass and number of roots per plant. qRT6-2 x qRT19-1+7-30 recorded best performance for seed yield per plant and total biomass. Since all these genotypes recorded non-significant deviation of the regression coefficient (bi) from 1 and s²di approaching zero, we can conclude that these genotypes have average stability across locations [3,38].

Conclusion

The pyramids of root QTL are very relevant as root morphological parameters are controlled by quantitative genes and these do not act independently. When they are moved into new background the effect and the stability of the QTL in environment play a major role. Both environment specific and pyramids suitable for wider range of environments are useful. Hence root QTL pyramiding is useful for developing genotypes for using in water saving technologies like aerobic cultivation or in case where dry spells prevail and roots help to tide over and minimize the economic loss to the rice growing farmers.

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