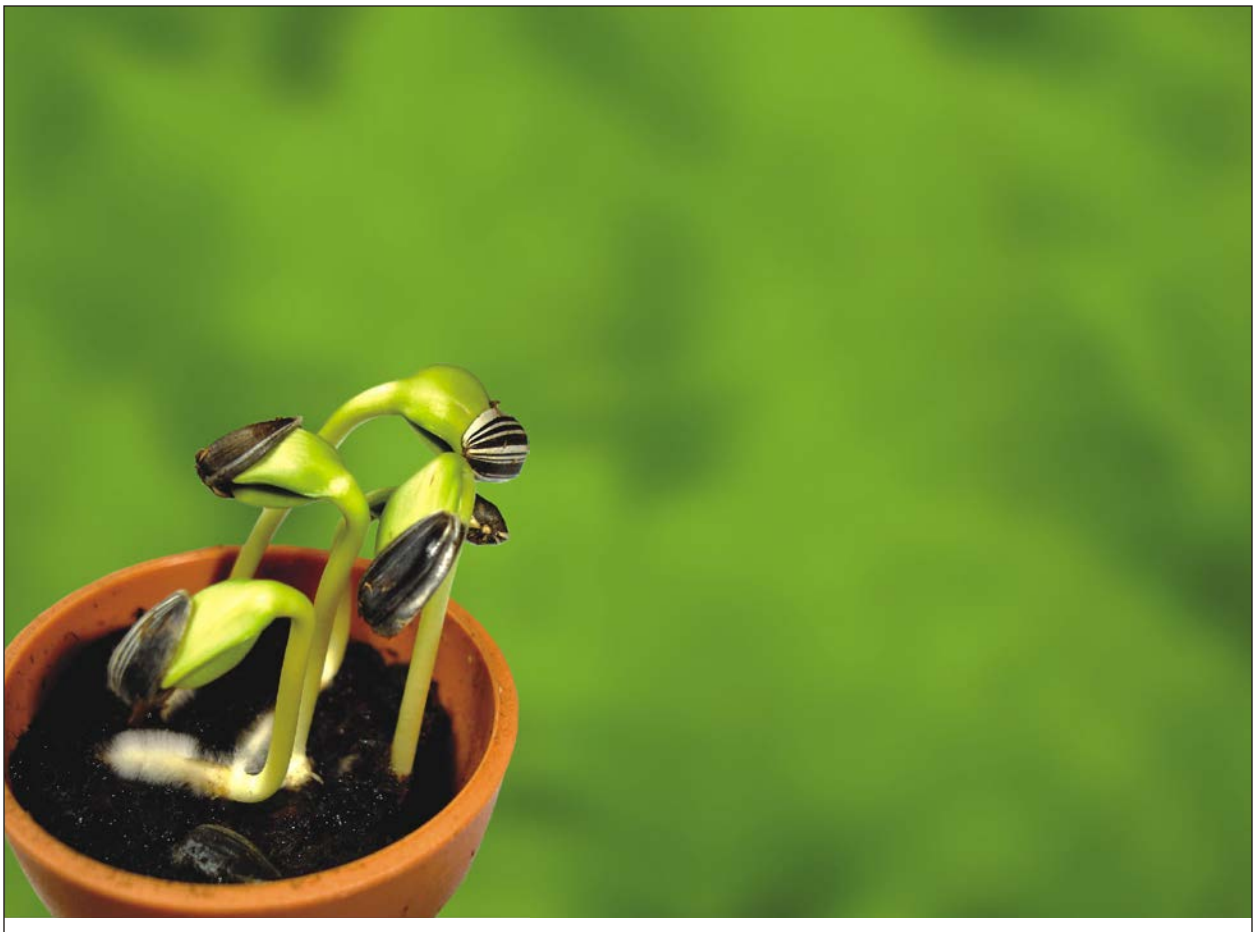

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Identification and Mapping of Landrace Derived QTL Associated with Yield and its Components in Rice under Different Nitrogen Levels and Environments

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Abstract: Wild/weedy species and primitive landraces of rice are valued as unique sources of genetic variability. However they have been hardly used in breeding for improvement of complexly inherited traits. The aim of the present study is to identify yield enhancing novel QTL (quantitative trait loci) from a primitive cultivar INRC10192 from Assam Rice Collection (India). To this end, a mapping population of 140 recombinant inbred lines (RILs) derived from the cross between IR64 and INRC10192 was developed. In all 46 QTL for 12 agronomically important traits under two nitrogen (N) levels at two locations were identified. Of them, 28 (62.22%) had beneficial alleles derived from INRC10192 the donor parent. Interestingly, the regions RM1-RM495 on chromosome 1 and RM481-RM427 on chromosome 7 harbor QTL under high dose to N, while the region RM331-RM404 on chromosome 8 for normal dose of N. The fertilizer responsive regions may be of value in developing higher nitrogen responsive new plant type based varieties. Many QTL have been detected in more than one environment. Thus, there is evidence for the presence of stable and major effect yield-enhancing QTL derived from the landrace. Such QTL are potential value for yield improvement of rice by marker assisted breeding.

Key words: Rice, landrace, nitrogen, yield, QTL (quantitative trait loci), SSR markers

INTRODUCTION

Rice needs to be produced 50% more than what is produced now by 2050 to cope with the growing demand (Ashikari *et al*., 2005). The challenge lies in developing technologies capable of breaching yield levels of the currently available high yielding varieties and hybrids. Of the various strategies being contemplated towards this goal, finding new and still not exploited yield related variability from wild/weedy species and primitive landraces is considered important (Tanksley and McCouch, 1997). The fact that very less amount of variability available in wild/weedy gene-pool has been utilized in the improvement of rice has necessitated going back to such source pools in search of still uncovered genetic variability (Tanksley and McCouch, 1997). The strategy is on the belief that in the long process

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of origin, domestication and continuous improvement of rice, not all the initially available variability had been captured and thus the prospects of identifying and using such variability remaining hidden in the putative ancestor species and primitive cultivars. The proof of the concept has already been demonstrated in rice by identifying yield influencing genomic regions by QTL mapping approach (Brondani *et al*., 2002; Cho *et al*., 2003; Marri *et al*., 2005; McCouch *et al*., 2007).

Studies pertaining to identification of yield and its components under different nitrogen levels in rice are very limited. Recently Cho *et al*. (2007) identified 28 single QTLs and 58 pairs of epistatic loci identified for nitrogen concentration of straw and shoot, harvest index, grain yield and straw yield under ordinary (100 kg ha^{-1}) and low nitrogen doses (50 kg ha^{-1}). In a similar kind of study by Xie *et al*. (2008) also detected QTLs for yield and its associated traits from double haploid lines derived from Azucena/IR64. Hence, the present study was undertaken to identify genomic regions associate with yield and its components under different nitrogen levels and environments from an advanced generation of cross between a primitive landrace INRC10192 and the high yielding variety IR64.

MATERIALS AND METHODS

Choice of Parents and Development of Mapping Population

The popular semidwarf high yielding variety IR64 was used as female parent while INRC10192, a tall, lodging-prone, photosensitive, medium duration landrace from Assam Rice collection (India) as male parent based on differences in their relative response to fertilizer and genetic distance between them (Hariprasad, 2003). Genetic diversity study of 40 landraces employing 14 ISSR primers revealed that the landrace INRC10192 found to be significantly distant from IR64 with similarity coefficient ranging from 0.70 to 0.86 (Supl. Fig. 1). In addition, the landrace INRC10192 showed highest grain yield per plant, number of productive tillers per plant and high biomass compared to the IR64 (Supl. Table 1, 2). Recombinant inbred lines (RILs) comprising 140 lines at F_7 was developed from the cross of IR64/INRC10192 employing single seed decent method which formed the final mapping population.

Field Experimentation and Phenotyping

The recombinant inbred lines (RILs) were evaluated along with the parents at two locations viz., Agricultural Research Institute, Hyderabad (L1) and Regional Agricultural Research Station, Maruteru, West Godavari Andhrapradesh (L2) in *kharif*, 2005 at two levels of nitrogen (N1 = 100 kg and N2 = 150 kg ha^{-1}) each with two replications. A split-plot design was followed with N levels as main plot treatment and plant material as sub-plot treatment. Nitrogen fertilizer was applied in three split doses, one as basal and two by top dressing at 44^{th} and 66^{th} day after sowing. Each of the RILs and the parents consisted of 24 plants planted in 2 rows of 12 plants each adopting a uniform spacing of 20×15 cm^2. Six plants in the middle of each of these lines were tagged and leaf samples were collected for DNA isolation. Phenotypic data was recorded from the tagged plants for 12 yield related traits viz., Plant height (PH) - length in cm of the tallest tiller from soil surface to the tip of the panicle, tiller number per plant (NT) - total number of tillers per plant, number of productive tillers per plant (NPT) - panicle bearing tillers per plant, panicle length (PL) length in cm from the neck to the tip of the panicle, number of filled grains per panicle (FG) - number of filled spikelets per panicle averaged over five randomly chosen panicles in each plant, number of chaffy grains per panicle (CG) - number of unfilled or sterile spikelets per panicle averaged over five

randomly chosen panicles in each plant, number of spikelets per panicle (SN) - number of spikelets including empty and filled ones averaged over five randomly chosen panicles in each plant, spikelet fertility (SF) - ratio of filled spikelets to the total number of spikelets per panicle, expressed in percentage, grain weight (GW) - weight in g of 1000 filled spikelets averaged over six samples taken from the bulk-harvested grain from each plant, biomass (BM) - total dry weight in g of plant including straw, filled and chaffy grains, grain yield per plant (GY) - weight in g of total filled grains of the plant and harvest index (HI) - ratio of weight in gram of the filled grains to biomass (filled grains, unfilled grains and straw of the plant) expressed in percentage.

Construction of Linkage Map and QTL Mapping

DNA was isolated from fresh leaf samples of tagged plants using the modified CTAB (Cetyl-Tri Methyl Ammonium Bromide) method (Murray and Thompson, 1980). The PCR was performed with 10 μL final volume containing 25-50 ng of genomic DNA, 10 μ buffer, 0.125 mM final concentration of each dNTPs, 0.2 μM of each forward and reverse primer and 1U of Biogene Taq DNA Polymerase. The PCR was set up with an initial denaturation of 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 45 sec, annealing at 55°C for 45 sec, extension at 72°C for 1 min, followed by the final extension of 72°C for 10 min. Amplified PCR products are run on 3% agarose gel electrophoresis and documented in gel documentation system. The resulting bands were scored and used for construction of linkage map employing MAPMAKER/EXP v.3 (Lincoln *et al*., 1993) with LOD score of 3 and recombination frequency of 0.4. The marker order within a linkage group was determined using the compare, try and ripple commands of MAPMAKER. Map distances were based on Kosambi mapping function. Twelve traits in two locations (L1 and L2) and each with two N levels (N1 and N2) total 48 traits have been subjected to QTL analysis. QTL were identified using Simple Interval Mapping (SIM) and Composite Interval Mapping (CIM) methods of QTL Cartographer version 2.5 (Wang *et al*., 2006). Those QTL which are identified in both the methods (IM and CIM) only considered for final QTL number. A LOD score of 2.5 was used as the threshold for detecting QTL.

RESULTS AND DISCUSSION

Performance of Parents at L1 and L2 Locations

The parents INRC10192 and IR64 differed significantly for all the traits except PL and BM in L1N1 and SN and BM in L1N2 while they showed significant difference in PH, FG, SN, BM, GY and HI in L2N1 and L2N2 levels. NT, NPT and CG significant differences were observed between the parents in N2 level only. IR64 had significant differences for PH, NPT, FG, SN, SF, BM, GY and HI and highly significant differences for PH, FG, SN, SF, GY and HI at both the N levels and locations. In contrast, INRC10192 showed significant differences for PH, FG, SF and HI at L1, while at L2 it had significant differences for PH, NPT, PL, BM, GY and HI at N levels (Suple. Table 3). The decrease of difference between the parents at higher N level (N2) for characters like CG and SN at L1 and for FG, SN, SF, GY and H at L2, as compared to optimum N level (N1), reveals the landrace to show relatively higher response to N fertilization than IR64.

Performance of RILs at L1 and L2 Locations

Study of the RILs reveals the range of phenotypic values for most of the traits which vary with the N level and location. Phenotypic values of RILs for most of the traits had wider

range in N2 level as compared to the N1 level. Grain yields of RILs are lower in L2 than L1 with mean yield reduction of the population being 19.62 and 19.71%, respectively under N1 and N2 levels. Mean phenotypic values of the RILs in N2 were relatively higher for some of the traits than those in N1 at L1. Especially BM, GY and HI were 4.37, 20.57 and 9.84%, respectively higher than in N1 level. In respect of PH and FG the increase under N2 was less than 1.6% over N1. On the other hand at L2 the traits HI, GY, BM, SN, FG and PH showed higher performance in N2 than in N1 level, the increase being 30.06, 8.47, 7.22, 4.46, 4.37 and 2.12%, respectively (Table 1).

Transgressive segregation was observed in the RIL in both the directions for most of the traits ranging from 2.90% for PH to 99.28% for NT at L1 and 17.99% for PH to 100% for CG and SF at L2 indicating that neither of the parents carried all positive or negative alleles. Occurrence of such transgressive segregants is possibly due to accumulation of complementary alleles from the parents at multiple loci in certain RILs (Tanksley, 1993) and G×G interactions (epistasis) (Lanceras *et al*., 2004). Most of the traits showed normal distribution except, NT under both the N levels, NPT and BM under N2 at L1; while CG under N2 and SF under N1 at L2 showed near normal distribution suggesting that they are governed by the polygenic inheritance (Fig. 1, 2). Plant height though a quantitative trait showed bimodal distribution at both the locations, which is in conformity with many earlier reports. The pattern reflecting monogenic Mendelian inheritance could be attributed to a major dwarfing gene (sd1) tightly linked to a set of minor genes in this region behaving like a complex locus.

Trait Correlations

The nature and strength of relationship between yield and its components were studied of material raised under both the N levels at the two locations (Supl. Table 4). The data

Table 1: Mean performance of the parents, IR64 and INRC10192 and 140 RILs for yield and its components under two N-levels across two locations

	Location-1 Hyderabad							Location-2 Maruteru					
Trait	N-level	IR64 (n=10)	INRC10192 (n=10)	RILs (n=140)	SD	Range	TS (%)	IR64 (n=10)	INRC10192 (n=10)	RILs (n=140)	SD	Range	TS (%)
PH	N1	66.5	136	110.75	22.05	69.88-145.67	13.67	64.5	121.25	103.41	21.69	66.25-144.5	28.15
	N2	71	143	112.47	21.69	75.00-157.75	2.90	82.25	151.75	105.6	20.96	67.25-159.5	17.99
NT	N1	31.5	19.25	12.1	2.55	7.00-28.00	98.56	23	17.75	14.5	3.47	8.25-29.75	88.15
	N2	35	22.5	12.72	3.02	7.25-34.00	99.28	25.5	19.75	14.62	3.96	8.25-33.00	94.96
NPT	N1	21.5	15.25	10.42	1.96	5.00-21.00	98.56	14.75	9	10.97	2.91	5.50-22.25	36.30
	N2	24	16.67	10.93	2.66	6.88-28.50	98.56	18.5	13	11.29	3.32	5.75-29.00	79.86
PL	N1	20.25	23.5	23.67	2.18	19.25-29.67	57.25	23	23.25	23.81	1.91	19.37-28.38	96.40
	N2	21.2	25.5	23.63	1.97	18.13-30.60	26.81	24.85	25.25	23.9	1.67	18.4-30.25	87.41
FG	N1	64	102	111.27	23.76	43.25-188.38	64.75	82.25	136	100.31	22.7	35-167.75	30.37
	N2	72	113	112.38	27.32	63.25-205.08	43.88	102.5	140.25	104.69	23.39	44.5-161.75	56.12
CG	N1	15.5	36.5	22.36	12.31	6.13-74.25	46.76	5.25	5.5	25.42	16.46	5.00-123.50	99.28
	N2	13	33.5	22.36	12.94	3.00-69.80	47.10	4.3	6.25	24.14	13.06	7.25-86.00	100.00
SN	N1	79.5	139	133.65	24.66	78.75-227.00	33.09	88	141.6	124.44	26.08	69.5-229.50	29.63
	N2	85	146.5	134.42	29.5	80.38-215.00	32.37	106.75	146.25	129.99	28.09	80.5-213.75	45.32
SF	N1	80.58	73.4	83.17	8.17	37.48-94.51	81.29	93.65	95.21	80.89	9.25	20.31-95.47	98.56
	N2	84.5	77.06	83.33	8.44	47.43-97.80	70.50	96.64	95.65	80.64	9.23	42.70-94.39	100.00
GW	N1	21.75	22.48	22.7	3.77	9.65-46.52	89.86	22.1	22.29	21.95	2.61	16.09-31.84	91.79
	N2	21.8	22.35	23.26	4.13	14.40-40.93	93.48	22.45	22.36	22.03	2.44	17.57-36.76	98.56
BM	N1	77.5	75.67	54.2	12.51	34.00-136.00	98.55	59	73	50.4	10.58	32.75-95.25	86.03
	N2	79	81.5	56.57	14.22	35.79-110.00	99.27	62.5	78.3	54.04	11.56	36.00-105.00	87.05
GY	N1	21.6	14.2	23.14	6.54	7.28-53.52	58.99	23.3	18.6	15.45	3.79	5.95-26.45	81.29
	N2	27.75	16.37	27.9	7.8	5.46-71.28	46.76	28.2	22.4	16.8	4.37	7.21-32.46	97.04
HI	N1	27.87	18.77	37.64	6.06	7.68-50.04	95.52	39.27	25.47	27.68	5.34	13.50-40.51	34.78
	N2	35.13	20.09	47.48	6.39	19.28-61.29	98.35	45.18	28.61	36	22.54	12.17-66.02	33.83

Columns 3, 4, 5 and 9, 10, 11 are mean values in L1 and L2, respectively; RILs = recombinant inbred lines. SD: Standard deviation. Range: minimum-maximum. TS: Transgressive segregation: For codes of the traits; Refer M andM section of the text

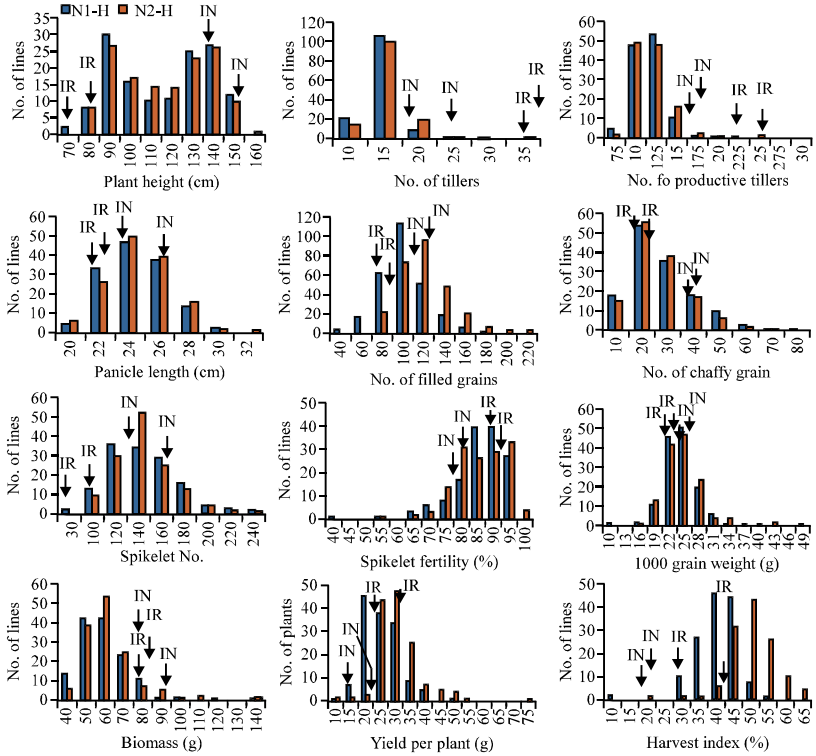

Fig. 1: Phenotypic distributions of yield and its components of 140 RILs evaluated at Location 1 (Hyderabad); IN-INRC10192 and IR-IR64

relating to Hyderabad revealed Grain Yield (GY) to show highly significant positive correlation with PH, NPT, FG, SN, SF, BM and HI at N1 and N2 levels. Equally strong positive correlation was observed between GY and PL at N1 level only. At Maruteru, NT, NPT, PL, FG, SN, SF, BM and HI showed positive significant correlations with GY under both the N levels. SW, however, showed positive significant correlation with GY only at N1 level. The mean of the yield and its components varied significantly with the level of N at Hyderabad, while at Maruteru, except SF, GY and HI; all the traits were significantly different across N-levels. N-levels across locations showed significant effects for PH, PL, CG and SW (N1 with N1), while N2 with N2 had significant effects for PH, PL, CG, SW and SN. In general, associations among yield components were well correlated at both the locations (Supl. Table 4).

Construction of Linkage Map

Of 412 rice microsatellite primers used to screen the parents, 113 (32.28%) were found to be polymorphic and distributed throughout the genome. Linkage map was constructed using MAPMAKER/EXP v.3. The linkage map was found to cover 1978.9cM employing Kosambi mapping function. Higher genetic distance observed between markers on chromosome 5 could be attributed to stretching effect of markers on chromosomes caused by small population size contribute to increased map length (Subudhi and Huang, 1999) and map expansion due to excess heterozygosity in segregating markers. Total map length increase due to stretching effect is known in many crops including rice (Subudhi and Huang, 1999), sorghum (Biovin *et al*., 1998) and barley (Becker *et al*., 1995).

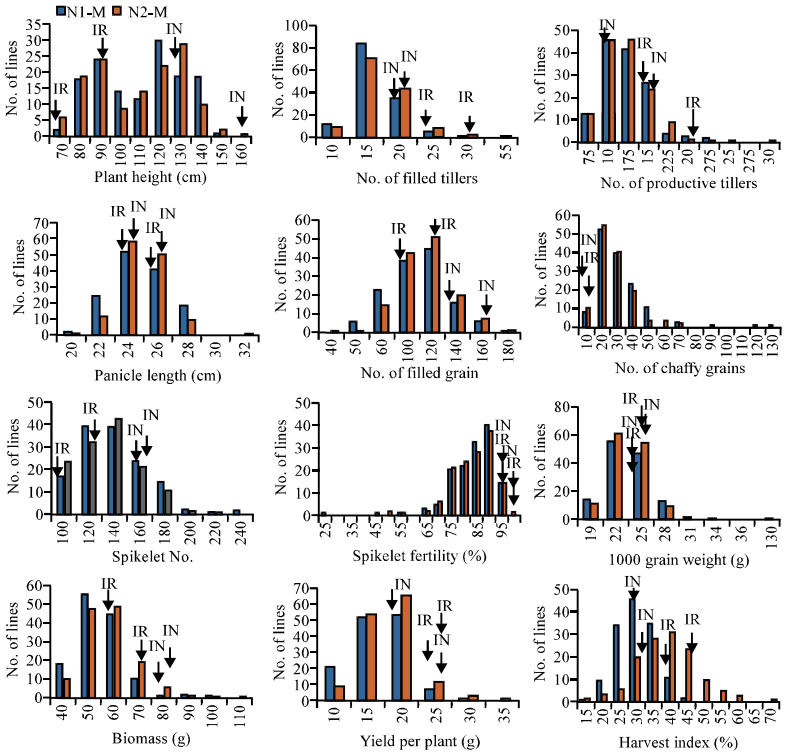

Fig. 2: Phenotypic distributions of yield and its components of 140 RILs evaluated at Location 2 (Maruteru); IN-INRC10192 and IR-IR64

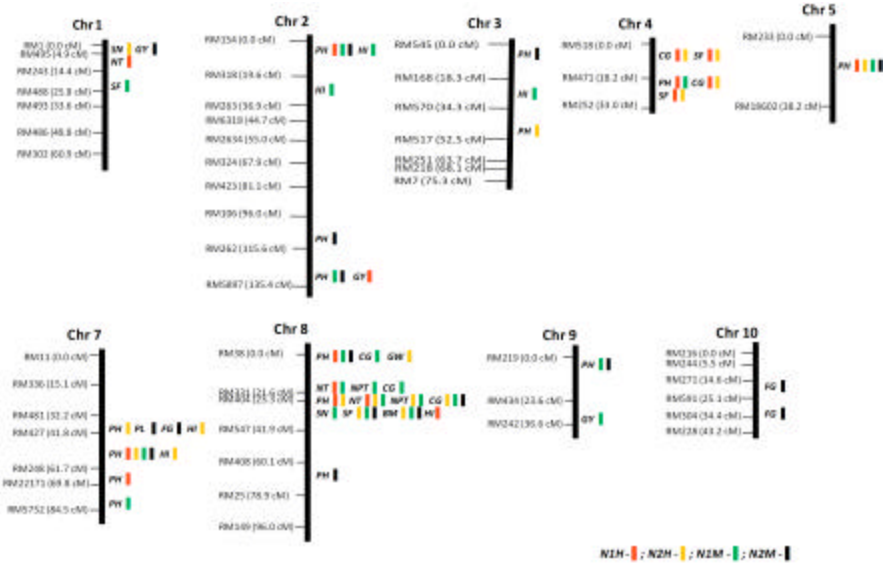

Fig. 3: Distribution of QTLs for yield and its components in the molecular linkage map of IR64/INRC10192. QTLs are indicated right side of the linkage map. Names of the markers represented left side of the linkage map. Numbers in parenthesis are genetic distances between markers in centi morgans (cM)

QTL Mapping

In all 46 QTL for yield and its components have been identified either in L1N1, L1N2 or L2N1, L2N2 and are distributed on 7 chromosomes (Fig. 3). Eighteen of them were identified in one or both the N-levels at one or both the locations, while the remaining 28 QTL were detected in any one N-level and one location. The LOD and phenotypic variation explained by each of the QTL ranging from 2.5 (*qgy2.1*) to 14.74 (*qph7.2*) and from 1.67% (*qsf4.1*) to 24.5% (*qph7.2*), respectively (Table 2).

The QTL *qph7.2* mapped between the markers RM427 and RM248 in the current study has been identified and designated as *qPh7b* in the same region for plant height by Hua *et al*. (2006) with largest additive effect under low nitrogen stress. Possibly this could

Table 2: QTLs for yield and its components identified in 140 RILs of the cross between IR64 and INRC10192 under two N levels at two locations

			Location 1														
			N level		N1			Location 2									
								N2			N1			N2			
Trait	QTL	Chr.	Marker interval (MI)	Distance of MI (cM)	LOD	PVE	a0	LOD	PVE	a0	LOD	PVE	a0	LOD	PVE	a0	Al.ef.
PH	*qph2.1**	2	RM154-RM318	19.6	6.04	12.5	2.34				3.29	11.53	4.64	8.71	12.89	4.56	IR64
	qph2.2	2	RM106-RM262	19.6										4.35	7.99	-1.29	INRC
	*qph2.3**	2[b]	RM262-RM5897	19.8							4.51	15.67	-3.33	3.76	10.01	-2.47	INRC
	qph3.1	3	RM545-RM168	18.3										5.5	8.23	3.33	IR64
	qph3.2	3	RM570-RM517	18.2				2.67	10.34	-3.40							INRC
	*qph4.1**	4	RM471-RM252	14.8	5.17	10.99	1.22				3.08	13.56	4.52				IR64
	*qph5.1**	5	RM233-RM18602	38.2	9.64	19.56	-3.98	7.35	9.13	-4.67	5.85	23.11	-1.31	10.2	22.89	-3.21	INRC
	qph7.1	7[a]	RM481-RM427	9.6				2.58	2.56	1.45							IR64
	*qph7.2**	7	RM427-RM248	19.9	14.74	24.5	4.16	9.48	21.47	3.33	8.94	20.35	3.23	10.87	19.57	3.57	IR64
	qph7.3	7	RM248-RM22171	8.1	3.1	16.78	1.34										IR64
	qph7.4	7[b]	RM22171-RM5752	14.7							4.21	12.13	1.09				IR64
	*qph8.1**	8	RM38-RM331	21.6	6.87	6.53	-0.98				4.5	10.98	-2.45	10.61	15.09	-3.44	INRC
	*qph8.2**	8	RM404-RM547	18.6	4.48	8.32	1.06	4.76	7.67	2.98							IR64
	qph8.3	8	RM408-RM25	18.8										4.05	8.43	2.67	IR64
	*qph9.1**	9[b]	RM219-RM434	23.6							4.76	14.56	-2.67	10.83	9.67	-1.09	INRC
NT	*qnt1.1*	1[a]	RM495-RM243	9.5	2.86	2.56	-0.12										INRC
	*qnt8.1**	8[b]	RM331-RM404	1.7	4.62	15.65	-3.45				4.24	13.45	-2.11				INRC
	*qnt8.2**	8	RM404-RM547	18.6	3.84	16.12	-4.13	3.65	17.14	-1.14	6.13	12.23	-0.17				INRC
NPT	*qnpt8.1**	8	RM331-RM404	1.7							3.61	8.67	-1.09				INRC
	*qnpt8.2**	8	RM404-RM547	18.6				4.9	9.09	-1.67	2.88	6.12	-0.18				INRC
PL	*qpl7.1*	7	RM481-RM427	9.6										2.51	7.89	0.22	IR64
FG	*qfg7.1*	7	RM481-RM427	9.6										2.51	9.93	1.08	IR64
	qfg10.1	10[b]	RM271-RM591	10.5										3	4.36	-1.54	INRC
	qfg10.2	10[b]	RM591-RM304	9.3										2.91	5.42	-2.22	INRC
CG	*qcg4.1**	4	RM518-RM471	18.2	5.32	4.67	-0.47	3.99	4.23	-1.12							INRC
	*qcg4.2**	4	RM471-RM252	14.8	4.42	3.45	-0.11	2.72	2.98	-0.98							INRC
	qcg8.1	8[a]	RM38-RM331	21.6							2.72	5.68	-1.23				INRC
	qcg8.2	8	RM331-RM404	1.7							7.71	6.70	-0.99				INRC
	*qcg8.3**	8	RM404-RM547	18.6				3.99	10.23	-2.21	8.79	8.76	-1.25	5.29	10.09	-1.25	INRC
SN	*qsn1.1*	1	RM1-RM495	4.9				3.13	2.12	-0.14							INRC
	qsn8.1	8[a]	RM404-RM547	18.6							2.57	10.67	-3.56				INRC
SF	*qsf1.1*	1[a]	RM243-RM488	11.4							2.55	2.45	0.78				IR64
	*qsf4.1**	4	RM518-RM471	18.2	3.98	1.67	0.15	3.92	4.56	0.18							IR64
	*qsf4.2**	4	RM471-RM252	14.8	3.68	2.22	0.21	3.45	3.02	0.16							IR64
	*qsf8.1**	8	RM404-RM547	18.6				2.9	3.67	1.09	4.11	4.61	0.18	4.37	5.67	2.11	IR64
GW	*qgw8.1*	8	RM38-RM331	21.6				2.74	5.98	-1.98							INRC
BM	*qbm8.1**	8	RM404-RM547	18.6				4.12	6.78	-2.08	4.65	4.91	-1.45	2.7	5.61	-1.23	INRC
GY	*qgy1.1*	1[a]	RM1-RM495	4.9										2.56	2.35	0.63	IR64
	qgy2.1	2[a]	RM262-RM5897	19.8	2.5	3.45	-0.98										INRC
	qgy9.1	9	RM434-RM242	13							3.2	2.49	-0.53				INRC
HI	*qhi2.1*	2[a]	RM154-RM318	19.6							3.47	6.73	-0.89				INRC
	qhi2.2	2[a]	RM318-RM263	17.3							2.93	5.74	-1.09				INRC
	qhi3.1	3[a]	RM168-RM570	16							2.58	4.99	1.16				IR64
	qhi7.1	7	RM481-RM427	9.6				4.06	2.39	-0.19							INRC
	qhi7.2	7	RM22171-RM5752	14.7				4.11	4.56	-0.22							INRC
	qhi8.1	8	RM38-RM331	21.6	2.68	6.78	1.87										IR64

L1: Hyderabad; Location 2: Maruteru. N1-N2 refer Nitrogen level 1 (100 kg ha^{-1}) and Nitrogen level 2 (150 kg ha^{-1}) respectively. Chr, refers to Chromosome. LOD, refers to Maximum likely hood ratio of odds i.e LOD score for the QTL. PVE, Phenotypic variance explained by each QTL; a0, Additive effect. Al.ef., Allele effect caused by parents towards QTL (+ = IR64; - = . INRC=INRC10192); [a]Significant only in composite interval mapping.; [b]Significant only in simple interval mapping. *Stable QTLs expressed across N treatment/environment. Individual QTL are designated with italicized abbreviation of the trait and the chromosome number. When more than one QTL affecting a trait is identified on the same chromosome, they are distinguished by decimal numbers. For codes of the traits refer M andM section of the text

be the genomic region having genes governing fertilizer responsiveness. Recently, Onishi *et al.* (2007) have identified a cluster of six QTL responsible for plant architecture. They include QTL relating to culm length (*qCL7*) and panicle length (*qPL7*) on the short arm of chromosome 7 in the mapping population of the inter-specific cross involving *O. sativa* sub. sp. *Japonica* and *O. rufipogon*, the wild relative. Interestingly, the QTL for plant height (*qph7.2*) detected in the present study has also been found to occupy the same genomic region as reported by Onishi *et al.* (2007). Very recently, Tan *et al.* (2008) and Jin *et al.* (2008) have independently identified a semi-dominant gene, PROG 1 (PROSTRATE GROWTH 1) on chromosome 7 at the marker interval RM427-RM481. This gene encoding a single Cys_2-His_2 zinc-finger protein and has been reported to be defective in *O. sativa*, leading to erect growth, high grain number and grain yield. In the present study, *qph7.1* and *qph7.2* found to be associated with these markers tend to support the general conclusion of Tanksley (1993) that a substantial proportion of QTL affecting a trait particularly those having major effect can be identified in different genetic populations and under different environments.

Tian *et al.* (2006) have fine mapped a QTL for grain number per panicle (*gpa7*) to 35 kb region that contains five predicted genes. While fine mapping, they have found five panicle related traits (length of panicle, primary branches per panicle, secondary branches per panicle and ratio of grains on primary and secondary branches) to be associated with the same marker interval RM481-RM427 on chromosome 7 where a QTL has been identified in the present study. Interestingly, Onishi *et al.* (2007) have also detected a cluster of six QTL in this region for plant height, panicle length, primary and secondary branches, grain number on primary and secondary branches. In the present study too, one QTL each for panicle length (*qpl7.1*), filled grains (*qfg7.1*) and harvest index (*qhi7.1*) have been detected exactly in the same region. Possibly, the QTL for harvest index might have resulted from higher ratio of secondary branches and ratio of grains on secondary branches per panicle. Recently, Ashikari *et al.* (2005) have identified a gene underlying the major QTL Gn1a controlling grain number/panicle on chromosome 1. According to them the gene encoding cytokinin oxidase/dehydrogenase (OsCKX2), an enzyme that degrades phytohormone cytokinin reduces the expression of OsCKX2 causing cytokinin accumulation in the inflorescence meristems thereby increasing number of reproductive organs resulting in enhanced grain yield. The QTL detected in the present study, i.e., qsn1.1 and Gn1a are not the same suggesting that *qsn1.1* seemed to harbor other candidate gene(s) that control grain number through mechanism(s) that remain to be elucidated.

A grain weight QTL (*qgw8.1*) has been identified on chromosome 8 at the marker interval RM38-RM331 in the present study. It is nearer to the grain weight QTL *gw8.1* which was fine mapped to about 306.4 kb (_1.2cM) by Xie *et al.* (2006). It may be concluded that the QTL identified in the current study is same as the one identified by Xie *et al.* (2006). Further, they report that this QTL is contributed to an increase of 9% over NIL (in *japonica* background) and 19.3% more grains than the *japonica* parent (Hwaseongbyeo).

The QTL, *qgy9.1* identified on chromosome 9 in the present study for grain yield appears to be the same as the one reported by earlier workers (Brondani *et al.*, 2002; Hittalmani *et al.*, 2003; Thomson *et al.*, 2003) have reported a grain weight QTL (*qgw9.1*) in the same region. Recently, this region has been fine mapped by Xie *et al.* (2008) and dissected into 370.4 kb region containing seven predicted genes. In addition, they have identified seven QTL relating to test-grain weight, spikelets per panicle, grain number per panicle, panicle length, spikelet density, heading date and plant height as a cluster in this region, suggesting the possibility of a single pleiotropic gene acting as a major regulator of this QTL cluster. Yield trials of near isogenic lines (BC_3F_4; Hwaseongbyeo

(*japonica*)/*O. rufipogon*) revealed that the lines containing a homozygous *O. rufipogon* introgression in this region to outyield NILs containing Hwaseongbyeo DNA fragment by 14.2-17.7% and Hwaseongbyeo parent by 16.2-23.7%.

Recently, He *et al.* (2006) have fine mapped a yield improving QTL GY2-1 on chromosome 2, which is 102.9 kb away from the *qgy2.1* identified in the present study and concluded that it had a haplotype of leucine rich repeat (LRR) receptor kinase gene cluster, which showed an extensive allelic variation between parents, Dongxiong, the wild species of *Oryza rufipogon* Griff. and Guichao2 (*Oryza sativa* sp. *indica*). Seven QTL for GY have been reported by Hariprasad (2003) using the same mapping population in F_2. Of them, only two viz., *qgy1.1* and *qgy2.1* correspond to what have been detected in the present study. The striking difference in the identification of yield QTL indicates the complex nature of the trait and environmental influence on its expression.

Those QTL, which are consistently detected over a range of environments are considered to be stable and they are the preferred target loci in crop improvement. According to Wan *et al.* (2005), QTL with major effects are more likely to behave as stable ones over environments. They also facilitate development of near-isogenic lines for dissection and narrowing to candidate genes for use in precision breeding for improvement of the trait concerned. Developed near-isogenic lines each carrying environment specific QTL for the trait can be introgressed into a single genotype so as to develop genotypes performing consistently over a wide range of environments. As against the cumbersome and time consuming conventional breeding, wherein, selections are made in target environment and testing is done in multiple diverse environments, stable marker associated QTL based selection can help accelerate the pace of breeding-selection process for polygenic traits like yield.

Out of the 46 QTL, 18 have been identified as stable of which, 11 viz., *qph2.1*, *qph4.1*, *qph5.1*, *qph7.2*, *qph8.1*, *qnt8.1*, *qnt8.2*, *qnpt8.2*, *qcg8.3*, *qsf8.1* and *qbm8.1* have been consistent across the locations and N-levels (Table 2). Such QTL would be of value in breeding for wide adaptation of the trait concerned over locations and crop conditions for regions akin to Deccan plateau (Hyderabad) and coastal Andhra (Maruteru). The remaining seven QTL viz., *qph2.2*, *qph8.2*, *qph9.1*, *qcg4.1*, *qcg4.2*, *qsf4.1* and *qsf4.2* identified across N-levels in one and the same location have been equally stable but with relatively narrow adaption confined to one location. These QTL might be useful for specific areas. For instance, the QTL *qph8.2* and *qsf4.2* can be of value in Telangana (Hyderabad) region, while *qph2.2* and *qph9.1* in Coastal Andhra (Maruteru) region. The remaining 28 QTL are regarded as of minor effect as they have been identified in either of the environments only.

It will not be out of context to discuss the utility of QTL of minor effect. Those QTL explaining low phenotypic variance, but consistently detected could as well be of value, considering the fact that major genes with small effect characteristic to quantitative traits govern yield and major components of it. In harmonious combinations such QTL would help step up genetic yield level, though not in large measure. In the course of the present investigation few QTL such as *qfg7.1*, *qpl7.1*, *qgy2.1* etc could with minor effect were identified for yield and its related traits.

QTL Clusters

In the present study, most of the QTL detected have been found to cluster in different genomic regions across the rice genome. In all, 10 marker intervals on chromosomes 1, 2, 4, 5, 7 and 8 have been found to harbor multiple QTL affecting the same or different traits related to yield (Table 3). The number of QTL in each such cluster is ranging from 2 to 8. It

Table 3: QTL clusters identified for yield and its components

S.No.	Marker interval	Chr	Traits	Total No. of traits
1	RM1-RM495	1	SN, GY	2
2	RM154-RM318	2	PH (3), HI	2
3	RM262-RM5897	2	PH (2), GY	2
4	RM518-RM471	4	CG (2), SF(2)	2
5	RM471-RM252	4	PH (2), CG (2), SF (2)	3
6	RM481-RM427	7	PH, PL, FG, HI	4
7	RM427-RM248	7	PH (4), HI	2
8	RM38-RM331	8	PH (3), CG, GW	3
9	RM331-RM404	8	NT (2), NPT, CG	3
10	RM404-RM547	8	PH (2), NT (3), NPT (2), CG (3), SN, SF (3), BM (3), HI	8

Values in parenthesis indicates no. of QTLs for the respective traits under different N levels and environments:Chr: Chromosome: For codes of the traits refer M and M section of the text

is interesting to note that some of the QTL for important yield related traits are clustered together. For instance, on chromosome 1 two QTL for SN and GY have been found to co-locate in the marker interval of RM1-RM495 suggesting that these two traits can be exploited simultaneously in breeding for yield enhancement employing marker-assisted selection. The interval RM481-RM248 on chromosome 7 has been found to contain five QTL for PH, one QTL each for PL, FG and two for HI. Considering the reports by Tian *et al*. (2006) and Onishi *et al.* (2007) on panicle traits and grain number and Tan *et al.* (2008) and Jin *et al.* (2008) on plant height (PROG 1 gene in this region) in *O. rufipogon* genome, it is presumed that this region might have played a strong role in the domestication related traits of rice plant architecture.

It is of interest that at the marker interval of RM404-RM547 on chromosome 8, a cluster of 8 QTL for yield components viz., PH, NT, NPT, CG, SN, SF, BM and HI had been found to repeatedly occur across N-levels and locations. Further characterization of this region by fine mapping and identification of genes underlying would throw light on whether the same set of genes regulated differentially or an entirely different set of genes governing these phenotypes. Similarly, the region between the markers RM331 and RM404 associated with QTL for chaffy grains, number of tillers and number of productive tillers might be involved in tillering efficiency as number of productive tillers is determined by number of tillers.

One more region at the map interval RM38-RM331 on chromosome 8 harbors QTL for PH, CG and GW. For all these QTL INRC10192 has contributed favorable alleles. Recently, Zhang *et al.* (2006) have reported a QTL cluster in this region for four traits viz., spikelets per panicle, grains per panicle, heading date and plant height. In addition, in this region, positive and negative QTL have been found (GW and PH) indicating two tightly linked genes but not of pleiotropic effect. Association of positive and negative QTL at the same chromosomal regions has earlier been reported in studies involving wild/weedy parents, where positive QTL for grain weight and panicle length as a cluster has been reported to be linked with negative QTL for plant height (Brondani *et al*., 2002; Septiningsih *et al*., 2003). In view of the instances of association of positive and negative QTL at one and the same chromosomal regions, a careful selection strategy is warranted so as to avoid negative characteristics interfering with the targeted crop improvement programmes.

In the course of the present investigation, three regions have been identified as N-specific regions. They include the region on chromosome 1 (RM1-RM495) containing one QTL each for SN and GY under N2-level. The region (RM481-RM427) on chromosome 7 harboring QTL for PH, PL, FG and HI under N2-level and the region on chromosome 8 (RM331-RM404) containing QTLs for NT, NPT and CG under N1-level. These fertilizer responsive regions may be of great value in developing new plant type based higher N responsive varieties.

Table 4: Potential QTL with nearest marker identified for marker assisted selection (MAS) relating to yield and yield components

Trait	N-level and Location	Chr	Marker	Marker-QTL distance	Allele effect
NT	N1 L I	1	RM495	2.04	INRC10192
	N1 L I, L II	8	RM331	2.01	INRC10192
	N1 L I, L II and N2 L I	8	RM404	2.06-2.49	INRC10192
NPT	N1, L II	8	RM331	2.01	INRC10192
	N2 L I and N1 LII	8	RM404	2.06-2.49	INRC10192
CG	N2 L I,LII and N1 LII	8	RM404	0.49	INRC10192
SN	N2, L I	1	RM1	2.01	INRC10192
SF	N1 andN2, L I	4	RM471	0.0	IR64
BM	N2 L I and N1 LII	8	RM404	2.06	INRC10192
GY	N2, L II	1	RM1	2.01	IR64
	N1 L I	2	RM262	0.04	INRC10192
HI	N2, L I	7	RM427	0.0	INRC10192
	N1 L I	8	RM404	2.06	IR64

Location I: Hyderabad; Location II: Maruteru. N1-N2 refer nitrogen level 1 (100 kg ha^{-1}) and nitrogen level 2 (150 kg ha^{-1}), respectively. Chr, refers to Chromosome. For codes of the traits refer M and M section of the text

Potential Markers for Marker-Assisted Selection (MAS)

It is difficult and time consuming for breeders to improve quantitative traits through conventional breeding relying excessively on phenotype based selection. Molecular markers, tightly linked to these target traits, could be of help in exercising precision in the selection relatively in a shorter period of time. Prerequisite for MAS is the tight association of the markers with the target QTL. According to Wan *et al.* (2006) distance between the marker and the QTL should be as low as possible (<2.6 cM) to avoid linkage drag during introgression of the QTL of interest. Xie *et al.* (2006) have identified eight functional markers, which spans around 0.4cM in the region of grain weight QTL (*qgw-9.1*) and used the same for marker assisted introgression of the trait. Further, the same group introgressed another grain weight QTL, *qgw8.1* on chromosome 8 using 9 SSR markers (1.2 cM). In the present study, 7 tightly linked markers for eight different traits have been identified for yield and its components (Table 4). Of these markers, RM331 and RM404 seem to be of value. Apart from being reasonably tightly linked, they contribute higher phenotypic variance for the traits, with which they are linked. The markers which are so tightly linked could be employed effectively in marker assisted breeding for improvement of yield.

The landrace (INRC10192) alleles have beneficial effect on 62.22% (Table 2) of the QTL obtained for yield and its components as against the previous reports of alleles from wild species showing beneficial effect in 35-58% of the QTL (Thomson *et al.*, 2003; Septiningsih *et al.*, 2003; Xiao *et al.*, 1998; Moncada *et al.*, 2001). It is interesting to report here that high percentage of transgressive segregants observed for nearly all the traits, especially for NPT, SF and SN, in the mapping population involving the landrace INRC10192 which is not known for superior traits. Recovery, however of useful transgressive segregants in such a population indicates that alleles of the primitive cultivars like INRC10192 might be interacting with those of high yield background like IR64.

Keeping the objective of the present investigation in view, it is important to identify QTL with enhancing favorable alleles from the landrace for exploitation in the crop improvement programme. The present study has yielded many QTL of promise for improvement of yield and its components *viz.*, number of productive tillers per plant, percent spikelet fertility, biomass, grain yield and harvest index, for which the trait enhancing favorable alleles have been drawn from the donor parent INRC10192 (Table 2). These results are in agreement with those of Brondani *et al.* (2002), Li *et al.* (2006) and McCouch *et al.* (2007) who have detected QTL with trait enhancing alleles drawn from phenotypically inferior parental sources in rice.

Table 5: Comparison of quantitative trait locus (QTL) reported across the *Oryza* genus

S.No.	QTL	Chr	Marker/Interval	QTLs in Previous studies shared common regions
1	*qsn1.1*	1	RM1-RM495	*sp1*(Xiong *et al.*, 1999); *SPKNB* (Brondani *et al.*, 2002; Zhuang *et al.*, 2002), gn1.1 Septiningsih *et al.* (2003a); spp1.2 (Cho *et al.*, 2007)
2	*qspy1.1*	1	RM1-RM495	*yld1.1* (Xiao *et al.*, 1998; Marri *et al.*, 2005); GRYLD (Li *et al.*, 1997) Xiong *et al.* (1999); *yldp1.1* (Brondani *et al.*, 2002), *yldp1.2* (Septiningsih *et al.*, 2003), (Zhuang *et al.*, 2002); yld1.1 (Cho *et al.*, 2007)
3	*qnt1.1*	1	RM495-243	tp1, *NT* (Li *et al.*, 2000, 2006); ppp1.1 (Cho *et al.*, 2007); *NP-1* (Zhuang *et al.*, 2002)
4	*qspy2.1*	2	RM262-RM5897	*yldp2.1* (Brondani *et al.*, 2002); *yldp2.1* (Marri *et al.*, 2005); *yd2* (Yoon *et al.*, 2006)
5	*qhi2.1*	2	RM318-RM263	*hi2.1* (Marri *et al.*, 2005)
6	*qph3.1*	3	RM545-RM168	*qPH-3-2* (Li *et al.*, 2006)
7	*qph3.2*	3	RM570-RM517	*qPH-3-3* (Li *et al.*, 2006)
8	*qph4.1*	4	RM471-RM252	*PTHT* (Li *et al.*, 2006)
9	*qsf4.1*	4	RM471-RM252	sf4 (Zhao *et al.*, 2008)
10	*qph7.1*	7	RM336-RM481	*qPh7b* (Hua *et al.*, 2006)
11	*qph7.2*	7	RM481- RM427	*qPh7b* (Hua *et al.*, 2006); qCL7 (Onishi *et al.*, 2007)
12	*qpl7.1*	7	RM427-RM248	qpl7 (Onishi *et al.*, 2007),pl7 (Tian *et al.*, 2006)
13	*qfg7.1*	7	RM427-RM248	qfg7 (Onishi *et al.*, 2007), gpa7 (Tian *et al.*, 2006)
14	*qhi7.1*	7	RM427-RM248	hi7b (Cho *et al.*, 2007)
15	*qbm7.1*	7	RM427-RM248	sy7b (Cho *et al.*, 2007)
16	*qph8.3*	8	RM408-RM25	Qph8 (Mei *et al.*, 2005); ht8 (Aluko *et al.*, 2004); qPH-8 (Li *et al.*, 2006)
17	*qph8.2*	8	RM404-RM547	QPh8a (Zhang *et al.*, 2006); ph (Zhuang *et al.*, 1997; Xiong *et al.*, 1999)
18	*qsn8.1*	8	RM404-RM547	QSpp8, QGpp8 (Zhang *et al.*, 2006); spp (Lin *et al.*, 1996; Xiao *et al.*, 1996; Zhuang *et al.*, 1997; Xiong *et al.*, 1999)
19	*qgw8.1*	8	RM38 - RM331	*gw8.1* (Xie *et al.*, 2006)
20	*qspy9.1*	9	RM242-RM205	yld9.1 (Thomson *et al.*, 2003; Marri *et al.*, 2005); qYLD9-1 (Hittalmani *et al.*, 2003); gy9 (Cho *et al.*, 2007); gy9.1 (Zhao *et al.*, 2008); yld9.1 (Cho *et al.*, 2007)

For codes of the QTLs refer Table 2

Comparison of QTLs Across the Genus Oryza

In rice (*Oryza sativa* L.) 8646 QTLs have so far been identified (V.28, www.gramene.org; September 2008). Comparison of QTL positions detected in the present study with earlier reports across populations and environments allows researchers to develop testable hypotheses about the behaviour of genetic factors underlying the putative QTL. When comparing previously published QTL results across the genus *Oryza* 20 of the 46 QTL identified in the current study have been mapped to similar locations on the chromosomes (Table 5) indicating that genes underlying such QTL have wide adaptability to different genetic backgrounds (populations) and environments. The remaining 26 QTL appear to be novel and have been identified for the first time. These findings encourage us to identify more and more novel QTL for yield and its components in new cross combinations especially involving wild/primitive cultivars. The novel QTL could be good candidates for fine mapping and positional cloning studies, while the QTL that are mapped to the region consistent with other studies can be right away applied in marker assisted transfer of them into widely adopted high yielding varieties.

Based on the results of the present study as well as from the previous reports, two important chromosomes could be identified to carry yield enhancing QTL/genes. Chromosome 7 regarded as plant architecture chromosome since it harbors QTL/genes for plant height (PROG 1) and panicle characters, while chromosome 8, termed as productivity chromosome as it harbors QTL for as many as 8 important yield components, most of which are from landrace parent. The promising QTL detected on these chromosomes can be used for pyramiding to develop high yielding rice varieties.

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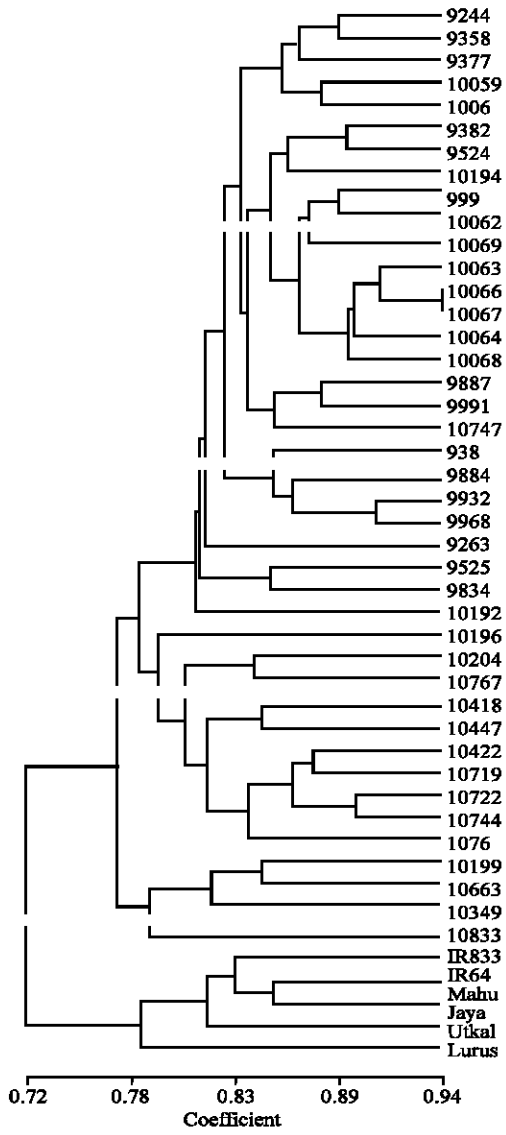
APPENDIX



Supl. Fig. 1: Dendrogram comparing 40 accessions (INRC) of landraces with five improved varieties based on the banding profiles generated using 14 ISSR primers

Supl. Table 1: Relative performance of three prospective landraces under optimum and high nitrogen levels

Trait	Landrace	N100 (kg ha^{-1})		N 150 (kg ha^{-1})		Mean		Increase due to propping (%)
		P	UP	P	UP	P	UP	
Grain number per panicle	INRC 10062	173.5	158.4	201.4	173.0	187.5	165.7	11.6
	INRC 10066	119.5	115.0	108.4	114.2	114.0	114.6	-0.5
	INRC 10192	123.7	106.2	140.6	119.0	132.2	112.6	14.8
	IR64 (check)	139.2	107.2	112.4	119.5	125.8	113.4	9.9
Percent spikelet fertility	INRC 10062	75.4	67.4	81.5	71.7	78.5	69.6	11.3
	INRC 10066	65.7	62.4	67.1	62.0	66.4	62.2	6.3
	INRC 10192	82.5	82.4	83.4	78.7	83.0	80.6	2.9
	IR64 (check)	87.0	97.6	91.2	86.3	89.1	92.0	-3.3
Grain yield per plant	INRC10062	17.1	12.9	14.5	12.4	15.8	12.7	19.6
	INRC 10066	10.0	7.7	10.3	9.5	10.2	8.6	15.7
	INRC 10192	22.1	14.3	11.5	10.5	16.8	12.4	26.2
	IR64 (check)	25.7	20.1	16.4	15.8	21.1	18.0	14.7
Biomass per plant	INRC 10062	63.1	60.9	62.6	49.4	62.9	55.2	12.2
	INRC10066	54.2	50.3	68.7	50.2	61.5	50.3	18.2
	INRC 10192	77.9	64.2	77.0	73.1	77.5	68.7	11.4
	IR64 (check)	49.8	40.5	40.6	39.9	45.2	40.2	11.1

P: Propped; UP: Unpropped; N: Nitrogen

Supl. Table 2: Best performed two landraces for each of the nine different traits at two levels of N under propped and unpropped conditions

Trait	Well responding landraces to N levels of			
	-------(100 (kg ha^{-1})-------		----------150 (kg ha^{-1})---------	
No. of productive tillers/plant				
P	37	1	25	35
UP	32	1	17	35
Panicle length				
P	15	18	40	32
UP	40	18	6	10
Grain number per panicle				
P	3	4	45	16
UP	16	6	24	18
Test grain weight				
P	2	19	2	19
UP	19	2	2	19
Grain yield per plant				
P	32	30	25	35
UP	43	6	14	39
Percent spikelet fertility				
P	22	10	32	43
UP	43	10	24	39
Harvest index				
P	34	33	43	40
UP	35	19	39	43
Biomass per plant				
P	42	16	2	25
UP	16	14	15	16
Plant height				
P	13	18	21	18
UP	18	14	21	18

P: Propped; UP: Unpropped; N-Nitrogen; 1. INRC9244 2. INRC9358 3. INRC9377 4. INRC9380 5. INRC9382 6. INRC9524 7. INRC9525 8. INRC9623 9. INRC9834 10. INRC9884 11. INRC9887 12. INRC993213. INRC9968 14. INRC9991 15. INRC9999 16. INRC10059 17. INRC10060 18. INRC10062 19. INRC10063 20. INRC10064 21. INRC10066 22. INRC10067 23. INRC10068 24. INRC10069 25. INRC10192 26. INRC10194 27. INRC10196 28.INRC10199 29. INRC10204 30. INRC10349 31. INRC10418 32. INRC10422 33. INRC10447 34. INRC10663 35. INRC10719 36. INRC10722 37. INRC10747 38. INRC10760 39. INRC10767 40. INRC10833 41. Lunisree 42. Utkal Prabha 43. Jaya 44. IR64 45. Mahsuri

Supl. Table 3: Test of significance of the parents for yield and its components measured under two levels of N at two locations

	Hyderabad (L1)				Maruteru (L2)			
	IR64	INRC10192	IR64/INRC10192		IR64	INRC10192	IR64/INRC10192	
Trait	N1/N2	N1/N2	N1/N1	N2/N2	N1/N2	N1/N2	N1/N1	N2/N2
PH	**0.02**	**0.05**	**S**	**S**	**0.003**	**0.00016**	**S**	**S**
NT	0.07	0.57	**0.03**	**0.02**	0.48	0.47	0.3	**0.004**
NPT	**0.03**	0.48	**0.05**	**0.001**	0.33	0.08	0.2	**0.003**
PL	0.4	0.34	0.08	**0.02**	0.09	**0.04**	0.74	0.7
FG	**0.0005**	**0.00023**	**S**	**S**	0.06	0.61	**0.0005**	**0.007**
CG	0.32	0.67	**0.001**	**0.008**	0.3	0.69	0.88	**0.01**
SN	**0.03**	0.81	**0.01**	0.09	0.08	0.66	**0.0004**	**0.01**
SF	**0.03**	0.085	**0.006**	0.002	**0.007**	0.68	0.1	0.6
GW	0.6	0.68	**0.01**	0.01	0.71	0.89	0.86	0.9
BM	**0.014**	0.32	0.8	0.38	0.13	**0.01**	**0.0014**	**0.0001**
SPY	**0.017**	0.06	**0.038**	**0.013**	**0.0002**	**0.04**	**0.00048**	**0.006**
HI	**0.00086**	**0.05**	**S**	**S**	**0.004**	0.26	**S**	**0.001**

S: p>0.00001; Note: Values in bold are significant at corresponding probability levels; For codes of the traits refer M andM section of the text. N1-N2 refer Nitrogen level 1 (100 kg ha^{-1}) and Nitrogen level 2 (150kg ha^{-1}), respectively L1: Hyderabad; Location 2: Maruteru

Supl. Table 4: Correlation between yield and its components and among component traits under two N-levels at two locations

	Component traits with yield in L1		Component traits with yield in L2		L1	L2	L1 with L2	
Trait	N1	N2	N1	N2	N1 with N2	N1 with N2	N1 vs. N1	N2 vs. N2
PH	0.373**	0.292**	0.191	0.142	0.876**	0.574**	0.739**	0.641**
NT	0.121	0.128	0.235*	0.445**	0.568**	0.327**	0.232*	0.163
NPT	0.461**	0.351**	0.289**	0.515**	0.376**	0.330**	0.158	0.058
PL	0.350**	0.148						
0.242*	0.263**	0.606**	0.451**	0.475**	0.246*			
FG	0.554**	0.444**	0.372**	0.355**	0.434**	0.200*	0.197*	0.120
CG	-0.158	-0.188	-0.086	-0.072	0.530**	0.242*	0.207*	0.062
SN	0.446**	0.299**	0.255**	0.282**	0.446**	0.343**	0.313**	0.113
SF	0.316**	0.385**	0.217*	0.236*	0.536**	0.114	0.177	0.076
GW	0.138	0.007	0.237*	0.127	0.428**	0.280**	0.445**	0.263**
BM	0.638**	0.617**	0.457**	0.509**	0.633**	0.202*	0.135	-0.182
GY	1.000	1.000	1.000	1.000	0.442**	0.110	0.037	-0.178
HI	0.588**	0.348**	0.626**	0.379**	0.229*	0.022	0.018	-0.051

*p<0.05; **p<0.01. Location I: Hyderabad; Location II: Maruteru; For codes of the traits refer M andM section of the text. N1-N2 refer Nitrogen level 1 (100 kg ha^{-1}) and Nitrogen level 2 (150 kg ha^{-1}), respectively

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