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ORIGINAL PAPER

Mapping QTL for grain yield and other agronomic traits in post-rainy sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract Sorghum, a cereal of economic importance ensures food and fodder security for millions of rural families in the semi-arid tropics. The objective of the present study was to identify and validate quantitative trait loci (QTL) for grain yield and other agronomic traits using replicated phenotypic data sets from three post-rainy dry sorghum crop seasons involving a mapping population with 245 F_9 recombinant inbred lines derived from a cross of M35-1 × B35. A genetic linkage map was constructed with 237 markers consisting of 174 genomic, 60 genic and 3 morphological markers. The QTL analysis for 11 traits following composite interval mapping identified 91 QTL with 5–12 QTL for each trait. QTL detected in the population individually explained phenotypic variation between 2.5 and 30.3 % for a given trait and six major genomic regions with QTL effect on multiple traits were identified. Stable QTL across seasons were identified. Of the 60 genic markers mapped, 21 were found at QTL peak or tightly linked with QTL. A gene-based marker XnhsbSFCILP67 (Sb03g028240) on SBI-03, encoding indole-3-acetic acid-amido synthetase GH3.5, was found to be involved in QTL for seven traits. The QTL-linked markers identified for 11 agronomic traits may assist in fine mapping, map-based gene isolation and also for improving post-rainy sorghum through marker-assisted breeding.

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Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important cereal crops grown in the semi-arid tropics of the world. The crop is tolerant to several biotic and abiotic stresses and is widely grown in water-limited environments (Kresovich et al. 2005). Worldwide, sorghum is cultivated in an area of 42 m ha with an annual production of 58.5 m t with Africa and India accounting for 70 % of area under cultivation (FAO 2009). In India, sorghum is cultivated in both rainy and post-rainy seasons for food, fodder and feed purposes. Of the total sorghum area of 7.8 m ha in India, dry sorghum grown under post-rainy season occupies the major share with 4.7 m ha (60 %). Post-rainy sorghum is normally grown in vertisols under stored and receding soil moisture conditions after the rainy season, where it experiences both soil and atmospheric drought (Jirali et al. 2007). It is vital for food and fodder security in the drought-prone dry vertisol belts of Maharashtra, Karnataka and Andhra Pradesh states of India as there is no alternative cereal that can be effectively grown during this dry season when only 8 % of the annual rainfall is received (Gorad et al. 1995). While rainy sorghum grain is mostly used for non-food purposes due to grain mold disease, 98 % post-rainy sorghum is used

primarily for human consumption as the grain is clean, pearly white, lustrous and bold (Rao et al. 2010). Apart from grain, sorghum stover is an important feed for livestock mainly in dry seasons in India, when other feed resources are in short supply (Blummel and Rao 2006). Thus, post-rainy sorghum plays an important role in ensuring food and fodder security for millions of rural families in these states. In contrast to rainy sorghum, where grain productivity is high (1,345 kg/ha), the productivity of post-rainy sorghum is very low (600 kg/ha). Crop improvement efforts have not had much impact on the productivity of post-rainy sorghum due to lack of genetic diversity, non-availability of heterotic hybrids, large-scale cultivation of landraces, susceptibility to terminal drought, shoot fly insect and charcoal rot disease (Biradar et al. 2004; Reddy et al. 2009; Kumar et al. 2011; Sajjanar et al. 2011). Cultivar M35-1 was released more than 60 years ago and is still popular among the farmers due to its excellent grain and fodder quality, and its tolerance to shoot fly and drought (Biradar et al. 2004). Hence, M35-1 is considered as an important sorghum variety with adaptation to post-rainy conditions (Reddy et al. 2009).

Progress in genetic improvement of important traits such as grain yield and component traits is essential to meet the increasing demand for food in view of changing climatic conditions. But, the genetic improvement of post-rainy sorghum at present is hindered by lack of genetic variability among breeding lines as most of the post-rainy sorghum genotypes belong to *durra* race of Indian origin. Hence, improving grain yield in post-rainy sorghum by traditional breeding methods is slow and the phenotypic selection has been less productive due to terminal drought stress that coincides with the flowering and maturity stage of the crop besides high G × E interactions (Prabhakar 2010; DeLacy et al. 2010). Grain yield is a complex trait with several component traits involved, each such being controlled by many genes, epistasis and G × E interactions. This complicates selection and adversely affects genetic gain (Clarke et al. 1992) especially under post-rainy conditions.

Recent progress in sorghum genomics has generated a series of important genomic resources which can be used for the development of molecular markers and to identify favourable genes and alleles for grain yield and its component traits for genetic enhancement. For example, well-established genetic, physical, and cytological maps facilitate the mapping and identification of genes involved in the expression of important agronomic traits. Furthermore, the construction of cDNA microarrays provides a platform for high-throughput gene discovery (Buchanan et al. 2005; Salzman et al. 2005). An important milestone was the completion of the genomic sequence for the sorghum inbred line, BTx623 (Paterson et al. 2009) (http://www.phytozome.net/sorghum). With the above useful information, identification of sorghum genes contributing to the enhanced grain yield will undoubtedly be accelerated.

Quantitative trait loci (QTL) mapping is an important approach that received growing attention in plant breeding for dealing with polygenic traits. Polygenic characters that were difficult to manipulate by traditional breeding methods can be dissected into individual QTL using DNA markers, and these markers allow plant breeders to locate and follow the numerous interacting genes that affect a complex trait (Tanksley 1993). The identification of QTL governing agronomically important traits can create a base for rapid, detailed, and direct genetic manipulation of such traits through marker-assisted selection (MAS) and facilitate combining various component traits into a single genotype (Collard et al. 2005; Gupta et al. 2009).

Various DNA based markers such as RFLPs, AFLPs, SSRs and DArTs have been developed in sorghum and used to construct linkage maps (Bhattramakki et al. 2000; Mace et al. 2008; Ramu et al. 2009; Satish et al. 2009). QTL studies in sorghum identified several genomic regions associated with agronomically important traits viz., plant height (Pereira and Lee 1995; Lin et al. 1995; Rami et al. 1998; Hart et al. 2001; Klein et al. 2001; Feltus et al. 2006; Srinivas et al. 2009b), maturity (Lin et al. 1995; Childs et al. 1997; Crasta et al. 1999; Kebede et al. 2001; Feltus et al. 2006; Srinivas et al. 2009b), grain yield and related traits (Rami et al. 1998; Klein et al. 2001; Feltus et al. 2006; Srinivas et al. 2009b) and post-flowering drought tolerance (Subudhi et al. 2000; Tao et al. 2000; Xu et al. 2000; Haussmann et al. 2002).

With the recent advances in sorghum genomics, emphasis has shifted towards the development of molecular markers from transcribed regions of the genome with a goal to associate trait phenotypic variability with genic-marker polymorphisms. A large number of genic-SSRs have been placed into genetic maps of rice (Temnykh et al. 2000), sorghum (Srinivas et al. 2008, 2009a; Ramu et al. 2009; Satish et al. 2012), wheat (Yu et al. 2004; Nicot et al. 2004; Gao et al. 2004) and maize (Anderson et al. 2006). Construction of genetic maps using genic markers with specific function permits evaluation of co-location of genic markers and QTL (Aubert et al. 2006; Srinivas et al. 2009b) and may also increase our understanding of the biochemical pathway and mechanisms affecting agronomic traits (Matthews et al. 2001; Zhang et al. 2004). However, such applications in associating genic-markers with QTL regulating the agronomically important traits are not many in sorghum, especially in post-rainy sorghum. Thus identification of QTL controlling grain yield and its component traits of post-rainy sorghum would increase our understanding of the genetics of these traits and may elucidate

the relationships of QTL to candidate genes and provide the basis for MAS to improve grain yield in post-rainy sorghums. The objectives of the present study were to identify and validate QTL for grain yield and other important traits using a mapping population developed from a cross between important sorghum inbreds M35-1 and B35. Second, we report the association of gene-derived microsatellite markers with QTL involved in the expression of various agronomic traits in post-rainy sorghum.

Materials and methods

Field experiment

Plant material

The experimental material used in the present investigation comprised a recombinant inbred lines (RIL) population (245 F_9 RILs) developed from the cross of M35-1 × B35. M35-1 is the most popular post-rainy tall, single-dwarf sorghum variety (Hammer et al. 2010) cultivated in India since 1930 for its excellent grain and fodder quality, bold and lustrous grains, resistance to biotic and abiotic stresses (Rana et al. 2000) and yield stability across different sowing dates (Reddy et al. 1987). The other parent B35 is a 3-gene dwarf genotype developed from a germplasm accession from Ethiopian origin IS12555 (Rosenow et al. 2002) and is known for its slower senescence (Rosenow et al. 1983).

Field evaluation

The RIL population along with their parents was planted in a completely randomized block design (CRBD) with three replications and evaluated during three consecutive post-rainy seasons, 2006 (PR06), 2007 (PR07) and 2008 (PR08) at the experimental farm of DSR, Hyderabad. The experiments were performed during the first fortnight of September of each year. The crop comes to maturity at the end of January or early February. The average day temperature ranges between 22 and 29 °C during this period, and the night temperature ranges from 7 to 18 °C. The experimental units were one-row plots of 4 m length with 15 cm spacing between plants and 75 cm between rows. The crop was protected from insect pests including shoot fly, mites and stem borer following recommended plant protection measures. The RILs were characterized for 11 agronomically important traits. All phenotypic measurements of agronomic traits were recorded from five tagged plants at the centre of the row in each replication. The agronomic traits studied include grain yield and its component traits [grain yield per panicle (GY, grain weight per panicle after seed threshing in g); panicle weight per panicle (PW, mass of panicle in g); test weight (TW, 100 seed mass in g); grain number per panicle (GN, number of grains obtained after panicle threshing); number of primary branches per panicle (NPB, number, counted according to Brown et al. (2006)); panicle harvest index (%) (PHI, the ratio of the grain yield to panicle weight and multiplied by 100)], plant morphology traits [panicle length (PL, length of panicle from base to its tip in cm) and plant height (PH, measured from tip of the panicle to the base of the plant in cm)] and phenological traits [days to 50 % flowering (DF; is the number of days counted from planting to 50 % of plants at flowering stage in a plot); days to maturity (DM; is the number of days counted from planting to physiological maturity (50 % of the plants showing black tip at the seed base on the last seed of the panicle) and total number of leaves (TL, number of leaves counted from the base of the plant to the flag leaf)].

Statistical analysis

The statistical software SAS 9.2 (SAS Institute Inc 2008) was used for statistical analysis of phenotypic data. Trait variances were partitioned using the random effects ANOVA model $y = \mu + G + E + G \times E + \text{error}$, where G represents genotype, E represents environment, and G × E represents the genotype by environment interaction. The error term includes the variance between row means for the three replicates of each genotype at each season. We used *ProcGLM* procedure with replication mean data of each trait in each season for studying the effect of genotype (RILs), environment and genotype to environment interactions for observed variance among the RILs by residual maximum likelihood algorithm (REML) as suggested by Patterson and Thompson (1971). Broad-sense heritabilities (h^2) and the correlations were determined at the level of average performance over the seasons using SAS code for estimating heritability from lines evaluated in RCB designs for multiple environments (Holland et al. 2003).

Linkage mapping

The genetic linkage map of M35-1 × B35 was previously reported (Nagaraja Reddy et al. 2012) and was updated in this study by adding six (XnhsbSFC58, XnhsbSFCILP60, XnhsbSFCILP13, XnhsbSFCILP14, XnhsbSFC95 and XnhsbSFCILP67) gene-based markers (Table 1). The final linkage map consists of 237 markers, of which 174 genomic, 60 genic and three morphological markers spanning a distance of 1,235.5 cM were used for QTL analysis. Genotyping of RILs, linkage map construction and nomenclature of chromosomes were described in our previous study (Nagaraja Reddy et al. 2012).

Table 1 Primer sequence information of gene-based markers added in the present study

Marker name	Gene	Repeat motif	Primer location	Forward primer sequence	Reverse primer sequence	Ann temp (°C)	Expected size (bp)	LG SBI-	Putative function
XnhsbSFC58	Sb05g003060	(AG)10	–	TACGGTGTTGCTGGTGATGT	ATTTCATCAGGGATGGGTCA	60	248	5	Similar to second messenger-dependent protein kinase, putative
XnhsbSFCILP60	Sb05g003880	–	Intron-1	CCTGTTTCCTCTCGTGCATT	AACCTTGACCATGCCAGTTC	60	800	5	Similar to actin-1
XnhsbSFCILP13	Sb10g025910	–	3′ UTR	GGTTGGAAGAAGCAGCATTAG	TCATTCATCACGGAGCAAGA	59	201	10	Weakly similar to fibroin heavy chain-like
XnhsbSFCILP14	Sb10g026110	–	Intron-1	CATGACCAACCCGATTGAC	TTGCTGCTATTGTTGGTTGC	59.7	834	10	Similar to putative (R)-(+)-mandelonitrile lyase isoform MDL3
XnhsbSFC95	Sb01g014130	(AC)7	–	AGGTCTGCACATGCATCATC	GGCCGGTATGCAAAATTAAA	60	232	1	Similar to auxin-responsive protein IAA30
XnhsbSFCILP67	Sb03g028240	–	Intron-1	GCAGAAACAGTTCACAAATTTCA	TTGTCATCGGAACTTGAACG	60	839	3	Similar to probable indole-3-acetic acid-amido synthetase GH3.5

QTL analysis

The QTL analysis was performed with trait mean values from individual season (PR06, PR07 and PR08) data, and with across season mean data (AV) for each trait using the software MapQTL® version 5 (Van Ooijen 2005). First, the non-parametric Kruskal–Wallis test (Lehmann 1975) was performed to associate single markers and traits individually. Then, interval mapping (IM) analyses were performed (Lander and Botstein 1989) to locate preliminary QTL positions on the map. IM was used to select markers significantly associated with the trait to constitute an initial set of cofactors. A backward elimination procedure was applied to the initial set of cofactors. Only significant markers at $P < 0.02$ were used as cofactors in the multiple QTL method [MQM = composite interval mapping (CIM)] (Jansen 1993; Jansen and Stam 1994) analysis for QTL detection. To minimize chances of Type 1 error, genome-wide significance logarithm of odds (LOD) threshold for accepting the presence of QTL was determined following cumulative distribution function table for RILs (Van Ooijen 1999). The values were obtained through extensive simulations based on the principle that genome-wide threshold depends on the number and length of chromosome pairs and the density of map. The LOD threshold for the present study was determined to be 3.20 which ensures a genome-wide significance of $P > 0.05$. Only those QTL with LOD equal to or above 3.2 LOD value were treated as significant. A LOD score threshold of 3 is widely considered as a definite indication of a "significant association" between marker and trait. Lander and Kruglyak (1995) proposed the term 'suggestive linkage' for cases that are not significant (<3) but point to a certain level of association between the markers and the trait, based on other considerations. In the present study, we did consider some of the QTL which were detected with LOD between 2.5 and 3.0 as suggestive QTL. The 1-LOD support interval of a QTL was determined by the LOD drop-of method (Lander and Botstein 1989), defined by the points on the genetic map that corresponds to a decrease in the LOD score of 1 unit from the maximum. When two LOD peaks fell in a common support interval, only one QTL was considered present, and its approximate position was taken as the highest peak (Dufey et al. 2012). For the multi-season (M) QTL analyses, the mixed models framework in the procedure QMQTLSCAN implemented in the Genstat 15 was used (VSN International 2012). The procedure QTHRESHOLD calculates a genome wide significance threshold based on a modified Bonferonni correction. This value is used as a critical value to reject the null hypothesis of no QTL effect. For the present study, the genome wide threshold value was found to be 3.43 which was higher than earlier LOD threshold value.

The phenotypic variance explained by a single QTL was calculated as the square of the partial correlation coefficient (R^2) with the observed variable, adjusted for cofactors. The additive effect of a putative QTL was estimated by half the difference between two homozygous classes. The identified QTL were designated with italicized symbol composed of a *Q*, a trait name, a hyphen, name of institute, the symbol for the chromosome in which the QTL is located. In cases where more than one QTL controlling a trait were detected in the same LG, they were numbered alphabetically. For instance, the QTL name *QPh-dsr06-1* refers to the QTL for plant height identified at DSR on sorghum SBI-06. QTL were classified as major if the phenotypic variance explained was larger than 10 %, and minor when it accounted <10 % of phenotypic variance (Collard et al. 2005). QTL for different traits were declared to be coincident (co-located) when their positions with highest LOD scores (peak) were located in the same markers intervals. The co-location was ''positive'' when the additive effects had the same algebraic sign (+ or −) and ''negative'' when they had opposite algebraic signs. Constitutive QTL refer to the QTL stably detected under different environments (Peng et al. 2011). In the present study, a QTL was said to be consistent when it was detected in more than one season, with average over seasons, in the multi-environment QTL analysis and across genetic backgrounds in earlier reports at the same locus.

QTL co-location

The genetic linkage map of the present study has been published recently (Nagaraja Reddy et al. 2012) and was updated with the addition of six genic markers in the current study. Recently, a comprehensive analysis of sorghum QTL was reported (Mace and Jordan 2011) with the projection of 771 QTL relating to 161 traits from 44 QTL studies onto a sorghum consensus map. All the meta- and unique QTL (Mace and Jordan 2011) positions relevant to the 11 traits of the present study have been projected onto the physical map using the flanking SSR markers of each QTL to determine co-localization of QTL with previous studies (Supplementary Fig 1).

Results

Phenotypic trait analysis

The phenotypic trait means and range of the RIL entries along with 2 parents for 11 traits across three seasons are presented in Table 2. The two parental lines varied significantly for their mean performance for all the traits except panicle harvest index. M35-1 flowered and matured (82 and 130 days, respectively) later than parent B35 (74 and 128 days, respectively) across the three seasons. The two parents differed significantly for their plant height as M35-1 was taller (190 cm) than B35 (100 cm). Besides, M35-1 had high leaf number, panicle weight, grain yield, test weight, grain number and primary branches compared with B35. Trait means of the RIL were intermediate, and transgressive segregation was observed for all the traits in the RILs.

The estimated broad-sense heritability (h^2) values were high and ranged from 0.17 to 0.96 (Table 2). Panicle harvest index showed lowest heritability (0.17). The pooled

Table 2 Statistical summary for 11 agronomic traits studied

Trait	M35-1[a]	B35[a]	RILs[a]				h^2
	Mean		Min.	Max.	Mean	SEM±	
GY (g)	54.8	31.4	12.5	89.2	42.7	0.914	0.53
PW (g)	71.8	40.7	19.0	116.7	57.1	1.117	0.59
TW (g)	3.4	2.8	1.6	5.0	3.3	0.030	0.89
GN	1,587.2	1,124.0	340.1	3,042.0	1,311	28.301	0.63
NPB	62.7	54.5	36.8	103.2	62.8	0.736	0.68
PHI	76.3	77.1	26.1	90.8	74.5	0.590	0.17
PL (cm)	15.7	20.2	10.7	32.0	19.0	0.215	0.93
PH (cm)	190.5	99.4	75.0	255.0	156.6	2.330	0.96
DF (days)	82.4	74.5	65.0	92.0	77.2	0.330	0.88
DM (days)	129.8	127.8	120.0	140.0	128.5	0.240	0.72
TL	11.1	9.4	6.8	14.2	10.3	0.076	0.88

SEM± standard error of mean, h^2 heritability based on average performance over three seasons, *GY* grain yield per panicle, *PW* panicle weight, *TW* test weight, *GN* grain number, *NPB* number of primary branches per panicle, *PHI* panicle harvest index, *PL* panicle length, *PH* plant height, *DF* days to 50 % flowering, *DM* days to maturity, *TL* total number of leaves

[a] Average over three seasons

ANOVA revealed significant differences ($P < 0.001$) among the RILs for all traits. Significant seasonal and genotype × seasonal interaction effects (Supplementary Table 1) were also observed. The histograms of trait distribution showed normality suggesting quantitative inheritance (Supplementary Fig 2) for all the traits.

Correlations of the traits

Correlations among the 11 measured traits were estimated based on mean trait values over 3 seasons (Table 3). Grain yield was positively correlated with all the traits with varied magnitude. Its correlation was highest with panicle weight (0.90), followed by plant height (0.84) and total leaves (0.80). Panicle weight had a positive correlation with all traits except with panicle harvest index (−0.50). Test weight, an important grain yield component, was negatively correlated with most traits but had positive correlations with panicle harvest index and plant height. On the other hand, grain number per panicle was negatively correlated with panicle harvest index. The number of primary branches per panicle had strong and positive correlations with days to flowering, total number of leaves per plant and its relation with panicle length was negative. Panicle harvest index was positively correlated with grain yield, test weight, and plant height and had no correlation with number of primary branches per panicle, days to maturity and total number of leaves. Panicle length was positively correlated with plant height and panicle weight. Plant height had positive correlations with all traits, the strongest being observed for grain yield, followed by panicle weight. Days to flowering and maturity showed similar correlation with other traits except for panicle harvest index and panicle length. Total number of leaves was also positively correlated with grain yield and days to flowering, followed by panicle weight.

QTL mapping

The results of the QTL analysis for the 11 agronomic traits in the RIL population are shown in Fig. 1 and the QTL statistics are summarized in Table 4. QTL for each trait were identified initially by IM, followed by CIM with cofactors. A total of 91 QTL were detected, 59 QTL having LOD thresholds ≥3.2, and the remaining 32 QTL (suggestive QTL) LOD thresholds of 2.5–3.0. R^2 values for each QTL are from the average performance over three seasons. If a QTL is identified only in one season (season specific), then the given R^2 value is specific to that season.

QTL for yield and its component traits

Grain yield

Six QTL were found for grain yield: three on SBI-09 and one on SBI-03, SBI-04 and SBI-06. Out of the six QTL, five QTL were identified for average performance over the three seasons and three of them were detected in multi-environment QTL analysis. These QTL individually explained 4.0–11.4 % of phenotypic variance based on average performance over three seasons and together accounted for 39 % of the grain yield variation in the population. At majority of the QTL positions, the positive alleles were derived from high-yielding parent M35-1. But, a QTL on SBI-03 for grain yield, the positive allele for increased grain yield was contributed by low-yielding parent B35. A major QTL, *QGy-dsr06-1,* was detected on SBI-06, which explains 11.4 % of phenotypic variance with a LOD of 6.0. Of six QTL detected for grain yield, map position of five QTL coincided with map position of QTL for PW. At these co-locating QTL for grain yield and panicle weight, alleles from M35-1 contributed to increased trait value.

Table 3 Correlation among the 11 agronomic traits studied

	PW	TW	GN	PB	PHI	PL	PH	DF	DM	TL
GY	0.90	0.11	0.59	0.35	0.34	0.14	0.84	0.66	0.44	0.80
PW	1	0.30	0.71	0.35	−0.50	0.24	0.76	0.63	0.38	0.74
TW		1	−0.70	−0.32	0.68	−0.01	0.48	−0.24	−0.20	0.03
GN			1	0.49	−0.76	0.12	0.27	0.69	0.33	0.56
NPB				1	−0.02	−0.22	0.18	0.49	0.13	0.46
PHI					1	−0.75	0.38	−0.22	0.03	−0.02
PL						1	0.76	−0.15	0.03	−0.12
PH							1	0.08	0.16	0.27
DF								1	0.70	0.80
DM									1	0.51

GY grain yield per panicle, *PW* panicle weight, *TW* test weight, *GN* grain number, *NPB* number of primary branches per panicle, *PHI* panicle harvest index, *PL* panicle length, *PH* plant height, *DF* days to 50 % flowering, *DM* days to maturity, *TL* total number of leaves

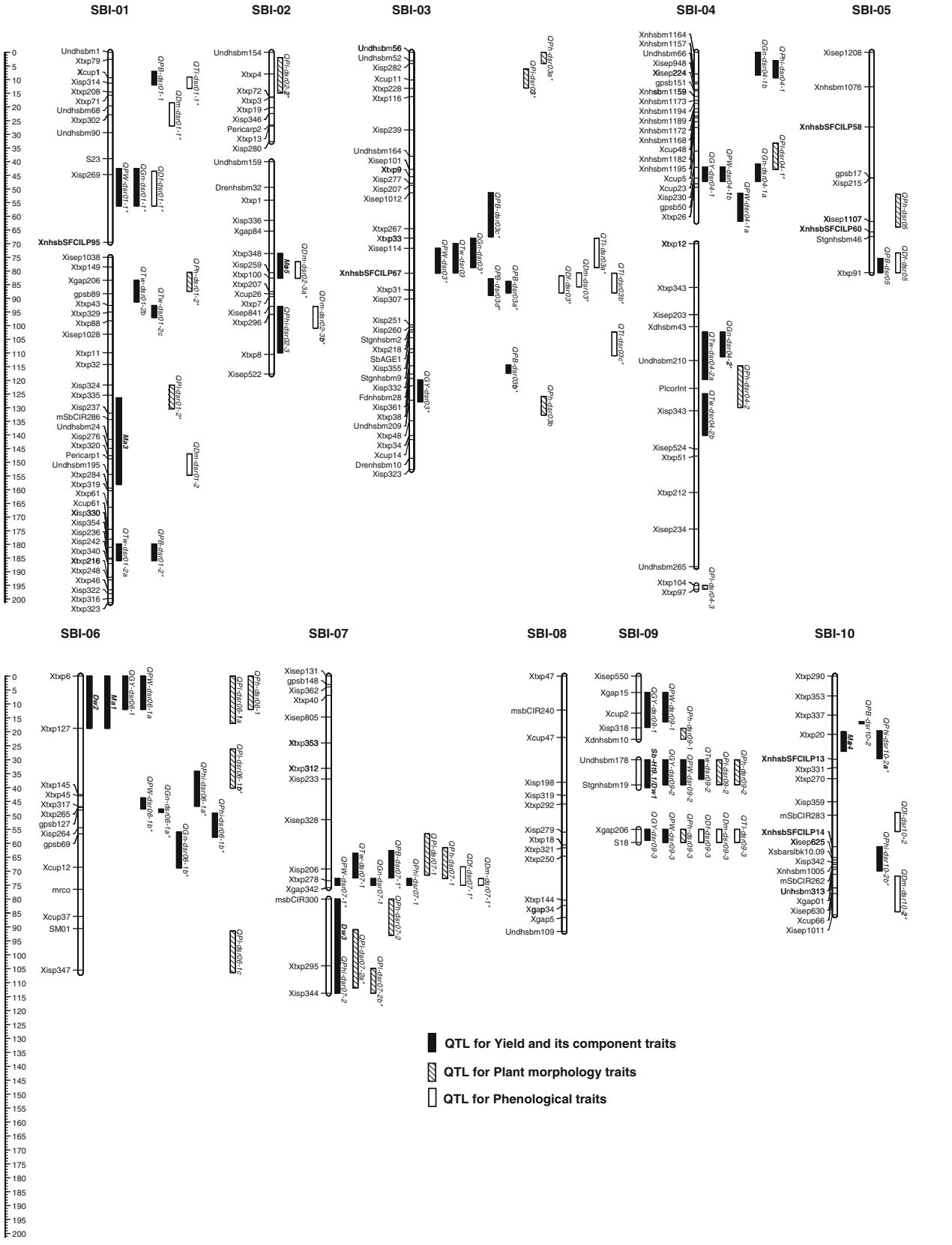

Fig. 1 Genetic linkage map of sorghum showing 91 QTL identified for the 11 traits in M35-1 × B35 RIL mapping population. The useful alleles contributed for the traits by B35 parent are represented by "asterisk" in the QTL name. The length of the *vertical bars* indicates 1-LOD support intervals for each QTL. New markers are depicted in *bold*. Scale in centimorgan (cM)

Table 4 Quantitative trait loci (QTL) detected for 11 agronomic traits studied in M35-1 × B35 RIL population

Traits	QTL name[a]	Environment	QTL × E	Chromosome	Position	Left marker	Right marker	LOD	Increased effect	R^2 (%)[b]	Additive effect[c]
Grain yield and its component traits											
Grain yield per panicle (GY)	***QGY-dsr06-1***	M, AV, I, II	Yes	SBI-06-1	6.0	Xtxp6*	Xtxp127	6.0	M35-1	11.4	2.68
	QGY-dsr09-2	M, AV, II	No	SBI-09-2	3.0	Undhsbm178*	Stgnhsbm19	4.2	M35-1	7.3	2.08
	QGY-dsr04-1	AV, I		SBI-04-1	46.2	Xcup23	Xisp230*	3.5	M35-1	6.4	3.37
	QGY-dsr09-1	M, AV, II	Yes	SBI-09-1	11.9	Xgap15	Xcup2*	3.8	M35-1	5.9	**2.29**
	QGY-dsr03	AV, II		SBI-03	124.9	Xisp332	Undhsbm314*	2.5[d]	B35	4.0	−1.92
	QGY-dsr09-3	II		SBI-09-3	0.0	S18*	Xgap206	2.8[d]	M35-1	4.0	1.95
Panicle weight (PW)	***QPW-dsr06-1a***	M, AV, I, II	Yes	SBI-06-1	5.0	Xtxp6*	Xtxp127	5.0	M35-1	10.2	2.96
	QPW-dsr09-2	M, AV, II	No	SBI-09-2	2.0	Undhsbm178*	Stgnhsbm19	4.6	M35-1	7.9	2.65
	QPW-dsr04-1a	AV, II		SBI-04-1	57.6	Xtxp26	Xcup05*	3.7	M35-1	6.9	2.67
	QPW-dsr04-1b	AV, I		SBI-04-1	44.9	Xcup23	Xisp230*	3.2	M35-1	5.8	3.87
	QPW-dsr09-1	M, AV, II	Yes	SBI-09-1	10.9	Xgap15	Xcup2*	3.8	M35-1	5.2	**2.92**
	QPW-dsr07-1	M, AV, II	Yes	SBI-07-1	74.6	Xtxp278	Xgap342*	3.7	B35	4.9	−2.75
	QPW-dsr01-1	AV, II		SBI-01-1	49.5	Xisp269	XnhsbSFC95*	3.0[d]	B35	4.3	−2.74
	QPW-dsr03	AV, II		SBI-03	75.7	Xisep0114*	XnhsbSFCILP67	2.5[d]	B35	3.7	−2.54
	QPW-dsr09-3	II		SBI-09-3	1.0	S18*	Xgap206	2.8[d]	M35-1	3.4	2.41
	QPW-dsr06-1b	II		SBI-06-1	47.7	Xtxp45	Xtxp317*	2.7[d]	M35-1	3.1	2.24
Test weight (TW)	***QTw-dsr09-2***	M, AV, I, II, III	No	SBI-09-2	2.0	Undhsbm178*	Stgnhsbm19	10.6	M35-1	15.0	0.16
	QTw-dsr04-2a	M, AV, II, III	Yes	SBI-04-2	38.3	Xdhsbm43*	Undhsbm210	2.9[d]	M35-1	8.1	0.13
	QTw-dsr07-1	M, AV, I, II	No	SBI-07-1	69.4	Xisp206	Xtxp278*	4.9	M35-1	8.1	0.11
	QTw-dsr04-2b	AV, II		SBI-04-2	65.1	Xisp343	Xisep0524*	3.0	M35-1	5.2	0.10
	QTw-dsr03	AV, II		SBI-03	75.7	Xisep0114*	XnhsbSFCILP67	3.2	M35-1	4.8	0.10
	QTw-dsr01-2a	II		SBI-01-2	107.8	Xisp330	Xisp354*	3.5	M35-1	4.4	0.09
	QTw-dsr01-2b	II		SBI-01-2	13.3	Xgap206	gpsb089*	2.7[d]	M35-1	3.3	0.07
	QTw-dsr01-2c	II		SBI-01-2	20.0	Xtxp43	Xtxp329*	2.6[d]	M35-1	3.0	0.07
Grain number (GN)	*QGn-dsr04-2*	AV, I, II, III		SBI-04-2	37.3	Xdhsbm43*	Undhsbm210	5.0	B35	10.0	−78.57
	QGn-dsr03	M, AV, II	Yes	SBI-03	74.7	Xisep0114	XnhsbSFCILP67*	4.6	B35	8.7	−91.71
	QGn-dsr01-1	AV, II		SBI-01-1	50.5	Xisp269	XnhsbSFC95*	4.3	B35	8.2	−87.61
	QGn-dsr04-1a	AV, I		SBI-04-1	45.2	Xcup23	Xisp230*	3.9	M35-1	6.9	99.98
	QGn-dsr06-1a	AV, I		SBI-06-1	47.9	Xtxp317	Xtxp265*	4.2	M35-1	5.9	57.71
	QGn-dsr06-1b	II		SBI-06-1	62.8	gpsb069*	Xcup12	2.7[d]	M35-1	5.0	69.57
	QGn-dsr04-1b	AV		SBI-04-1	4.0	Xdhsbm1164*	Xdhsbm1159	2.7[d]	M35-1	4.4	65.73
	QGn-dsr07-1	AV		SBI-07-1	74.6	Xtxp278	Xgap342*	2.8[d]	B35	4.2	−49.87

Table 4 continued

Traits	QTL name[a]	Environment	QTL × E	Chromosome	Position	Left marker	Right marker	LOD	Increased effect	R^2 (%)[b]	Additive effect[c]
Number of primary branches (PB)	***QPB-dsr03a***	M, AV, I, II, III	Yes	SBI-03	85.8	XnhsbSFCILP67	Xtxp31*	10.0	B35	13.0	−3.04
	QPB-dsr03b	M, AV, I, II, III	Yes	SBI-03	116.4	Xtxp38*	Xisp361	9.0	B35	12.1	−2.86
	QPB-dsr03c	AV, I, II, III		SBI-03	58.4	Xisep1012*	Xtxp267	3.9	B35	7.4	−3.36
	QPB-dsr05	M, AV, I, II	Yes	SBI-05	80.6	Stgnhsbm46	Xtxp091*	4.9	M35-1	6.1	1.95
	QPB-dsr07-1	M, AV, II	Yes	SBI-07-1	69.4	Xisp206*	Xtxp278	3.7	B35	4.3	**−2.50**
	QPB-dsr01-1	AV, II		SBI-01-1	9.0	Xisp314*	Xtxp208	3.1	M35-1	3.9	1.59
	QPB-dsr03d	II		SBI-03	87.0	Xtxp31*	Xisp307	3.2	B35	3.9	−2.46
	QPB-dsr01-2	AV, II		SBI-01-2	107.8	Xisp330	Xisp354*	2.9[d]	B35	3.5	−1.50
	QPB-dsr10-2	AV		SBI-10-2	16.3	Xtxp331*	Xtxp270	2.7[d]	M35-1	3.2	1.53
Panicle harvest index (PHI)	***QPhi-dsr07-1***	M, AV, I, II	Yes	SBI-07-1	73.6	Xtxp278	Xgap342*	5.0	M35-1	10.2	**1.16**
	QPhi-dsr04-1	AV, I		SBI-04-1	7.0	Xdhsbm1164	Xdhsbm1159*	4.8	M35-1	7.9	1.49
	QPhi-dsr10-2a	AV, II		SBI-10-2	24.6	Xsbarslbk10.09	XnhsbSFCILP13	3.3	B35	7.4	−1.28
	QPhi-dsr02-3	AV, II		SBI-02-3	60.9	Xtxp296*	Xtxp8	3.2	M35-1	6.5	1.16
	QPhi-dsr07-2	I		SBI-07-2	33.8	Xtxp295	Xisp344*	2.6[d]	M35-1	5.5	1.74
	QPhi-dsr10-2b	AV		SBI-10-2	64.9	XnhsbSFCILP14	Xgap01*	2.9[d]	B35	5.4	−0.99
	QPhi-dsr06-1a	II		SBI-06-1	43.0	Xtxp145*	Xtxp317	2.8[d]	B35	4.5	−0.88
	QPhi-dsr06-1b	II		SBI-06-1	54.2	gpsb127	Xisp264*	2.5[d]	B35	4.1	−0.86
Plant morphology traits											
Panicle length (PL)	*QPl-dsr07-2a*	AV, I, II		SBI-07-2	15.0	msbCIR300*	Xtxp295	11.8	B35	18.2	−1.42
	QPl-dsr06-1a	M, AV, I, II, III	No	SBI-06-1	10.0	Xtxp6*	Xtxp127	8.9	M35-1	12.8	1.14
	QPl-dsr01-2	M, AV, I, II, III	No	SBI-01-2	49.7	Xisp324	Xtxp335*	6.9	B35	11.3	−1.23
	QPl-dsr06-1b	AV, II		SBI-06-1	33.2	Xtxp127*	Xtxp145	6.3	M35-1	9.1	1.04
	QPl-dsr07-2b	M, I	Yes	SBI-07-2	33.8	Xtxp295	Xisp344*	2.8[d]	B35	5.0	−0.92
	QPl-dsr07-1	AV, II		SBI-07-1	64.6	Xisep0328	Xisp206*	3.8	M35-1	4.8	0.67
	QPl-dsr04-1	AV, II		SBI-04-1	37.2	Xcup23*	Xisp230	3.4	B35	4.6	−0.63
	QPl-dsr09-2	M, AV, II	Yes	SBI-09-2	0.0	Undhsbm178*	Stgnhsbm19	4.3	M35-1	4.5	0.67
	QPl-dsr03	AV, II		SBI-03	10.1	Xisp282	Xcup11*	3.2	B35	4.1	−0.54
	QPl-dsr06-1c	AV, II		SBI-06-1	98.5	SM01	Xisp347*	2.7[d]	B35	3.8	−0.57
	QPl-dsr02-2	AV, II		SBI-02-2	7.0	Undhsbm154	Xtxp4*	2.8[d]	B35	3.7	−0.54
	QPl-dsr04-3	II		SBI-04-3	1.0	Xtxp097*	Xtxp104	2.6[d]	M35-1	2.6	0.52

Table 4 continued

Traits	QTL name[a]	Environment	QTL × E	Chromosome	Position	Left marker	Right marker	LOD	Increased effect	R^2 (%)[b]	Additive effect[c]
Plant height (PH)	***QPh-dsr09-2***	M, AV, I, II, III	No	SBI-09-2	4.0	Undhsbm178*	Stgnhsbm19	21.5	M35-1	30.3	18.47
	QPh-dsr06-1	M, AV, I, II, III	No	SBI-06-1	7.0	Xtxp6*	Xtxp127	10.2	M35-1	14.2	13.04
	QPh-dsr01-2	AV, I		SBI-01-2	9.4	Xgap206*	gpsb089	5.0	B35	6.5	−10.15
	QPh-dsr03a	AV, I, II, III		SBI-03	129.9	Undhsbm314*	Xtxp48	4.1	B35	5.3	−8.03
	QPh-dsr07-1	M, AV, II	Yes	SBI-07-1	70.4	Xisp206*	Xtxp278	4.2	M35-1	5.3	7.57
	QPh-dsr09-1	AV, I		SBI-09-1	22.7	Xisp318	Fdnhsbm10*	4.9	M35-1	5.2	7.37
	QPh-dsr07-2	I		SBI-07-2	0.0	msbCIR300*	Xtxp295	2.9[d]	M35-1	4.2	8.11
	QPh-dsr04-2	AV, II		SBI-04-2	50.7	Undhsbm210	PlcorInt*	2.5[d]	M35-1	3.7	7.01
	QPh-dsr03b	AV, II		SBI-03	0.0	Undhsbm56*	Undhsbm52	3.0[d]	M35-1	3.6	5.83
	QPh-dsr05	AV		SBI-05	60.0	Xisp215	Xisep1107*	2.8[d]	M35-1	3.3	6.06
	QPh-dsr09-3	I		SBI-09-3	0.0	S18*	Xgap206	2.5[d]	M35-1	2.5	6.86
Plant phenological traits											
Days to 50 % flowering (DF)	***QDf-dsr01-1***	M, AV, I, II, III	No	SBI-01-1	49.5	Xisp269	XnhsbSFC95*	6.8	B35	12.4	−1.30
	QDf-dsr03	M, AV, I, II, III	Yes	SBI-03	85.8	XnhsbSFCILP67	Xtxp31*	6.8	B35	11.6	−1.54
	QDf-dsr09-3	M, AV, II, III	No	SBI-09-3	0.0	S18*	Xgap206	3.7	M35-1	5.7	0.85
	QDf-dsr05	I		SBI-05	80.6	Stgnhsbm46	Xtxp091*	2.7[d]	M35-1	4.1	0.87
	QDf-dsr07-1	AV, II		SBI-07-1	72.6	Xisp206	Xtxp278*	2.9[d]	B35	4.0	−0.87
	QDf-dsr10-2	I		SBI-10-2	52.8	mSbCIR262	Xdhsbm1025	2.5[d]	M35-1	3.8	0.84
Days to maturity (DM)	***QDm-dsr02-3a***	M, AV, I, II	Yes	SBI-02-3	56.9	Xisep0841	Xtxp296*	9.7	B35	13.4	−0.88
	QDm-dsr02-3b	AV		SBI-02-3	41.6	Xisp259*	Xtxp100	5.5	B35	10.0	−0.61
	QDm-dsr03	M, AV, II	Yes	SBI-03	82.8	XnhsbSFCILP67	Xtxp31*	4.5	B35	7.0	−0.57
	QDm-dsr10-2	M, AV, II	No	SBI-10-2	76.7	Xisep0630	Xcup66*	5.3	B35	6.9	−0.63
	QDm-dsr09-3	M, AV, II	No	SBI-09-3	1.0	S18*	Xgap206	4.3	M35-1	5.7	0.55
	QDm-dsr01-2	M, AV, II	No	SBI-01-2	74.9	Xisp276	Pericarp*	4.1	M35-1	5.4	0.55
	QDm-dsr07-1	AV, II		SBI-07-1	75.1	Xtxp278	Xgap342*	3.2	B35	4.1	−0.48
	QDm-dsr01-1	II		SBI-01-1	23.0	Xtxp302*	Undhsbm90	2.8[d]	B35	3.8	−0.47

Table 4 continued

Traits	QTL name[a]	Environment	QTL × E	Chromosome	Position	Left marker	Right marker	LOD	Increased effect	R^2 (%)[b]	Additive effect[c]
Total number of leaves (TL)	***QTl-dsr09-3***	M, AV, I, II, III	No	SBI-09-3	3.0	S18*	Xgap206	8.3	M35-1	18.4	0.39
	QTl-dsr03a	AV, II		SBI-03	75.7	Xisep0114*	XnhsbSFCILP67	6.9	B35	12.0	−0.39
	QTl-dsr01-1	M, AV, I, II, III	No	SBI-01-1	11.0	Xisp314*	Xtxp208	6.2	B35	10.0	−0.29
	QTl-dsr03b	M, AV, II	Yes	SBI-03	83.8	XnhsbSFCILP67*	Xtxp31	2.5[d]	B35	4.3	−0.27
	QTl-dsr03c	AV, II		SBI-03	106.4	SbAGE01*	Stgnhsbm9	2.8[d]	B35	4.0	−0.22

The flanking marker indicated by an *asterisk* is the nearest marker to QTL. Seasons I, II, III, AV (average) and M (multi-season) indicate QTL detected in the seasons Post-rainy 2006, Post-rainy 2007, Post-rainy 2008, across all seasons and in multi-season analysis, respectively

[a] QTL in bold are identified in multi-environment QTL analysis also

[b] R^2 (%) is percentage of phenotypic variation explained by individual QTL using average values over seasons. If QTL is identified only in one season, R^2 value specific to that season is given

[c] Additive effect of M35-1. A positive value implies that the M35-1 allele increased phenotypic value, whereas a negative value implies that the M35-1 allele decreased phenotypic value. A QTL effect with bold and underlined indicates inversion of effect in multi-season QTL analysis

[d] Suggestive QTL (LOD <3.0)

Panicle weight

Ten QTL controlling panicle weight were identified in the population with four QTL detected in multi-environment QTL analysis. Three QTL were located on SBI-09, two QTL on SBI-04 and SBI-06 and one QTL each located on SBI-01, SBI-03 and SBI-07. Out of ten QTL, eight QTL were detected in average performance over three seasons and remaining two QTL were identified using data from individual seasons. A majority of QTL alleles responsible for increasing the panicle weight were from the parent M35-1 with high panicle weight. But on SBI-01, SBI-03 and SBI-07 the alleles responsible for increasing the panicle weight were contributed by B35 which had the lowest panicle weight. Individually the phenotypic variance explained by each QTL ranged from 3.1 to 10.2 % and the LOD scores ranged from 2.7 to 5.0. QTL *QPw-dsr06-1a* on SBI-06, explaining 10.2 % of phenotypic variance, was co-located with major grain yield QTL, *QGy-dsr06-1*.

Test weight

Test weight was influenced by eight QTL, of which three QTL were identified on SBI-01, two QTL on SBI-04 and one QTL, each on SBI-03, SBI-07 and SBI-09. Out of these eight QTL, five QTL were identified in average performance over three seasons, and three of them were also identified in multi-environment QTL analysis. All positive alleles were derived from M35-1. The phenotypic variation explained by each QTL ranged from 3.0 to 15.0 % and the LOD scores ranged from 2.6 to 10.6. A major QTL (*QTw-dsr09-2*) explaining 15 % of phenotypic variation was identified on SBI-09.

Grain number

Eight QTL were found to control grain number in the population. The QTL are spread over five chromosomes with three on SBI-04, two on SBI-06 and one each on SBI-01, SBI-03 and SBI-07. At four QTL regions, the parent M35-1 contributed positive alleles. Five genomic regions were identified in average performance over three seasons across the seasons and other genomic regions specifically identified with individual seasons. Only one QTL, *QGn-dsr03,* on SBI-03 was identified in multi-environment QTL analysis. The phenotypic variance explained by each QTL ranged from 4.2 to 10.0 %. A major QTL, *QGn-dsr04-2*, identified on chromosome SBI-04 flanked by SSR markers, Xdhsbm43 and Undhsbm210 explained 10 % of total phenotypic variance.

Number of primary branches

Nine QTL were identified to control primary branch number in the population and were distributed on five

different chromosomes, with four on SBI-03, two on SBI-01 and one each on SBI-05, SBI-07 and SBI-10. Seven QTL were detected in average performance over three seasons while the remaining two QTL were specifically detected using phenotypic data of individual seasons. Four QTL were identified in multi-environment analysis also. At three QTL regions, the parent M35-1 contributed positive alleles. The phenotypic variance explained by individual QTL ranged from 3.2 to 13 % and LOD scores ranges from 2.7 to 10.0. Two major QTL, *QPb-dsr03a* and *QPb-dsr03b,* were detected for this trait on SBI-03 and explained, respectively, 13 and 12.1 % of phenotypic variance.

Panicle harvest index

Eight QTL were significantly affecting panicle harvest index were detected in the population, with two QTL each on SBI-06, SBI-07 and SBI-10 and one each on SBI-02 and SBI-04. Four out of eight QTL were identified in average performance over three seasons. The positive alleles were derived from M35-1 at four QTL and from B35 in other regions. The phenotypic variance explained by each QTL ranged from 4.1 to 10.2 % and the LOD scores ranged from 2.5 to 5.0. A major QTL, *QPhi-dsr07-1*, also identified in multi-environment analysis on SBI-07 explained about 10.2 % of phenotypic variance, with positive allele contributed by M35-1 parent.

QTL for plant morphology traits

Panicle length

Twelve QTL were detected significantly affecting panicle length, with three QTL each on SBI-06 and SBI-07, two on SBI-04 and one each on SBI-01, SBI-02, SBI-03 and SBI-09. Ten out of twelve QTL were identified in average performance over three seasons with four being detected in multi-environment analysis also. At five QTL, the positive alleles were contributed from parent M35-1 while at remaining QTL B35 contributed positively. The phenotypic variance explained by each QTL ranged from 2.6 to 18.2 % and the LOD scores ranged from 2.6 to 11.8. Three major QTL, *QPl-dsr07-2a*, *QPl-dsr06-1a* and *QPl-dsr01-2* explained 18.2, 12.8 and 11.3 % of phenotypic variance, respectively.

QTL for plant height

Eleven QTL were found to control plant height in the population. The QTL were spread over seven different chromosomes with three on SBI-09, two each on SBI-03 and SBI-07 and one each on SBI-01, SBI-04, SBI-05 and SBI-06. The tall parent M35-1 contributed alleles for increased plant height at all QTL, except for QTL on SBI-01(Xgap206) and SBI-03 (near Undhsbm314). Of the eleven QTL detected, eight QTL were identified in combined analysis across the seasons and other QTL specifically identified with individual seasons. Three QTL were also detected in multi-environment QTL analysis. The phenotypic variance explained by each QTL ranged from 2.5 to 30.3 %. Two major QTL, *QPh-dsr09-2*, identified on chromosome SBI-09 flanked by Undhsbm178 and Stgnhsbm19 had LOD score of 21.1 explaining 30.3 % of phenotypic variance, and QTL *QPh-dsr06-1* identified on SBI-06 explained 14.2 % of phenotypic variance.

QTL for phenological traits

Days to 50 % flowering

Six QTL were detected for days to flowering. They were detected on six different linkage groups with one QTL each on SBI-01, SBI-03, SBI-05, SBI-07, SBI-09 and SBI-10. Of the six QTL, four QTL were identified using average performance over three seasons, and three of them were also detected in multi-environment QTL analysis. M35-1 contributed for delayed flowering while at three of the QTL and for earliness at three other QTL. The phenotypic variance explained by each QTL ranged from 3.8 to 12.4 %. A major QTL for this trait, *QDf-dsr01-1,* was detected on SBI-01 between the markers Xisp269 and XnhsbSFC95, explaining 12.4 % of phenotypic variance. The other major QTL (*QDf-dsr03*) was identified on SBI-03 between XnhsbSFCILP67 and Xtxp31 markers and explained 11.6 % phenotypic variation.

Days to maturity

Eight QTL were identified for days to maturity on six chromosomes with two QTL each on SBI-01 and SBI-02 and one QTL on SBI-03, SBI-07, SBI-09 and SBI-10. Five of the QTL were also detected in multi-environment analysis. M35-1 contributed for delayed maturity at six QTL and early maturity at other two QTL. The phenotypic variance explained by individual QTL ranged from 3.8 to 13.4 % with LOD scores of 2.8–9.7. Two major QTL were identified for this trait, *QDm-dsr02-3a* explaining 13.4 % of phenotypic variance on SBI-02 and QDm-*dsr02-3b* explaining 10 % of phenotypic variance. Two QTL (*QDm-dsr03* and *QDm0dsr9-3*) identified for days to maturity were co-located with QTL for days to flowering.

Total number leaves

Five QTL were detected wherein three were on SBI-03, one each on SBI-01 and SBI-09. Three were also detected in multi-environment analysis. The LOD scores ranged

from 2.8 to 8.3 and phenotypic variance explained by individual QTL ranged from 4.0 to 18.4 %. M35-1 contributed positive alleles only at the QTL on SBI-09 and negative alleles at all other QTL. Three major QTL identified for this trait, *QTl-dsr09-3*, *QTl-dsr03a* and *QTl-dsr01-1* explained 13.4, 12.0 and 10.0 % of phenotypic variance, respectively.

Consistency of QTL detection

Of the 91 QTL identified for 11 traits (Table 4), 67 QTL (73.6 %) were identified in more than one season and on the basis of average over three seasons. Significantly, 34 of them (37 %) were also found by multi-environment QTL analysis. Of these 34 QTL, 18 exhibited QTL × E while 16 did not show QTL × E effect. Of the 18 QTL with QTL × E, nine had inversion of effects. As expected, none of the 16 QTL with absence of QTL × E interaction showed an inversion of effects. Besides these stable QTL, there were 24 (26.4 %) season-specific QTL.

Discussion

Genetic improvement of grain yield is a challenging task for breeders. Grain yield in sorghum is a quantitative trait (Beil and Atkins 1967) and is the outcome from several reproductive, morphological and phenological traits. It is, therefore, essential to understand the genetic architecture of grain yield and its component traits for genetic manipulation of grain yield through MAS.

In sorghum, significant positive correlations between grain yield and its component traits have been reported and QTL for correlated traits are known to map together (Rami et al. 1998; Brown et al. 2006; Jordan et al. 2003; Srinivas et al. 2009b; George-Jaeggli et al. 2011; Takai et al. 2012; Zou et al. 2012). Co-mapping of QTL for correlated traits may result from either tight linkage of several genes (Sandhu et al. 2001) or the pleiotropic effect of major genes (Veldboom et al. 1994; Xiao et al. 1996). Co-mapping of QTL is, therefore, important as it provides clue on the interpretation of the relationships among such traits (Lebreton et al. 1995; Tuberosa et al. 2002, 2003; Hochholdinger and Tuberosa 2009) and can assist breeders in identifying the best QTL alleles for manipulating multiple traits simultaneously in MAS.

In the present study, major QTL coincidence was observed at two genomic regions on SBI-09 (between S18-Xgap206 and Undhsbm178–Stgnhsbm19). A cluster of six QTL was observed within a 0.2-cM region located between S18-Xgap206, while QTL co-location for five traits was observed between markers Undhsbm178–Stghsbm19. M35-1 contributed positive alleles for all the traits in both regions. Similar QTL co-location for four different traits was observed at other six different genomic regions on SBI-03 (Xisep0114–XnhsbSFCILP67 and XnhsbSFCILP67–Xtxp31), SBI-07 (Xisp206–Xtxp278 and Xtxp278–Xgap342), SBI-04 (Xcup23–Xisp230) and SBI-06 (Xtxp6–Xtxp127). Besides this, there was one region on SBI-01 (Xisp269–XnhsbSFC95) with co-location for three QTL, and nine genomic regions with co-location for two QTL. In addition, there were 35 individual QTL detected without any co-location.

Of the six QTL identified for grain yield, three were reported earlier in different genetic backgrounds. The major QTL (*QGy-dsr06-1*) flanked by Xtxp6–Xtxp127 explaining 11.4 % trait variance was also reported (*Gyl-sbi06*) by Srinivas et al. (2009b). Similarly, Brown et al. (2006) and Ritter et al. (2008) also documented QTL *QGY-dsr09-2* (Undhsbm178–Stgnhsbm19) and *QGY-dsr03* (Xisp332–Undhsbm314), respectively. The other three grain yield QTL (*QGY-dsr09-1* and *QGY-dsr09-3* on SBI-09 and the *QGy-dsr04-1* on SBI-04) are new QTL as they were not reported earlier. Both *QGy-dsr06-1* and *QGY-dsr09-2* QTL were reported to be meta-QTL (*QGrnYLD1_6* and *QKWT3_9*) by (Mace and Jordan 2011) and were co-located with QTL for grain yield component traits. *QGy-dsr06-1* was co-located with QTL for panicle weight (*QPW-dsr06-1a* = meta-QTL *QINFLWT1_6*), panicle length (*QPl-dsr06-1*) and plant height (*QPh-dsr06-1*), whereas *QGY-dsr09-2* was clustered with QTL panicle weight (*QPW-dsr09-2*), test weight (*QTW-dsr09-2*), panicle length (*QPl-dsr09-2*) and plant height (*QPh-dsr09-2*). At the corresponding interval for *QGy-dsr06-1*, 12 QTL were co-located for heading date, plant height, number of nodes, stem diameter, flag leaf width and panicle length (Zou et al. 2012), and six QTL for heading date, culm length and width, panicle length and number (Takai et al. 2012). Srinivas et al. (2009b) also reported the QTL cluster for plant height (*QPhe-sbi06*), days to anthesis (*QDan-sbi06*), green leaf area at maturity (*QGlam-sbi06*), panicle length (*QPle-sbi06*), grain yield (*QGly-sbi06*), panicle weight (*QPwe-sbi06*) and seed weight (*QSwe-sbi06*) at this QTL region, whereas co-location of QTL for maturity (*FlrAvgD1*) and height (*HtAvgD1*) has been reported by Lin et al. (1995) and Klein et al. (2008). Co-location of QTL for grain yield and kernel weight was also reported at the *QGY-dsr09-2* by Brown et al. (2006). These QTL are, therefore, stable as they were identified in different genetic backgrounds and also as meta-QTL. These consistent QTL, which can be regarded as hotspots with agronomical importance, need to be fine-mapped to identify the causative genes involved in the genetic control of grain yield and its component traits for candidate gene analysis and marker-assisted breeding. Earlier studies in cereal crops such as rice, maize and wheat have also shown clustering of

QTL for agronomic traits (Börner et al. 2002; Guo et al. 2010; Marri et al. 2005; Xie et al. 2008) supporting the present observations in sorghum.

Plant height is one of the most important agronomic traits in sorghum with its relevance for total biomass, grain yield, harvest index, fodder yield and lodging resistance. A very strong correlation ($r = 0.84$) was observed between plant height and grain yield, supported by co-location of three major plant height QTL with grain yield QTL. Among the four major genes (*Dw1*, *Dw2*, *Dw3* and *Dw4*) influencing sorghum plant height (Quinby and Karper 1954), three have been mapped, *Dw2* on SBI-06, *Dw3* on SBI-07 and *Dw1/Sb.Ht9.1* on SBI-09 (Brown et al. 2006; Feltus et al. 2006; Klein et al. 2008; Mace and Jordan 2011; Morris et al. 2013), and only the gene *Dw3/SbPGP1* was cloned by Multani et al. (2003).

Three meta-QTL for plant height (*QHGT_meta1.6*), maturity (*QDFTL_meta1.6*) and kernel weight (*QKWT_meta1.6*) have been projected (Mace and Jordan 2011) to co-locate with the major grain yield QTL *QGy-dsr06-1*. This QTL region corresponds to the major dwarfing gene *Dw2* conditioning plant height and the major photoperiod-sensitivity maturity locus *Ma1* in sorghum (Pereira and Lee 1995; Lin et al. 1995; Klein et al. 2008). Dwarfing gene *Dw2* is known to be pleiotropic to grain yield, seed weight, leaf area and panicle length in sorghum (Graham and Lessmann 1966). The pleiotropic effect of *Dw2* was also noticed in the present study where QTL corresponding to *Dw2* gene (*QPh-dsr06-1*) was positively associated with grain yield (*QGY-dsr06-1*), panicle length (*QPl-dsr06-1a* = *QHGT_meta1.6/QPANLG1-6*) and panicle weight (*QPW-dsr06-1a* = meta-QTL *QINFLWT1_6*). This region is significant since it accounts for more than 10 % of phenotypic variation for each of these four correlated traits. It is important to note that the parent M35-1 contributed favourable allele to all these traits. This pleiotropic plant height QTL *QPh-dsr06-1* has been identified as a meta-QTL (Mace and Jordan 2011) and was reported in several earlier studies (Feltus et al. 2006; Brown et al. 2006; Ritter et al. 2008; Zou et al. 2012).

A second major QTL for plant height (*QPh-dsr09-2*) identified on SBI-09 was co-located with QTL for grain yield (*QGY-dsr09-2*), panicle weight (*QPW-dsr09-2*), test weight (*QTw-dsr09-2*) and panicle length (*QPl-dsr09-2*). This QTL had its highest contribution to plant height (30 % of variation) and was also a major contributor to test weight (15 %), one of the major grain yield component. This major QTL corresponds to the major QTL (*Sb-HT9.1*) previously identified on SBI-09 for plant height in most of the crosses between tall and dwarf sorghum (Pereira and Lee 1995; Lin et al. 1995; Feltus et al. 2006; Brown et al. 2008) and the height meta QTL (*QHGT-meta3.9*) of Mace and Jordan (2011). Recently, this locus has been proposed to be the major dwarfing gene *Dw1* (Brown et al. 2008). A recent study has indicated distinct allelic distributions across Africa and Asia for *Dw2*, *Dw3* and *Dw1* (Morris et al. 2013). Most Indian and East African durras (>90 %) were found to carry high frequency of tall allele for *Dw1* supporting the greatest contribution of this locus (*Dw1*) for plant height variation in the present study where the parent M35-1 belongs to Indian durra race.

The dwarfing gene, *Dw3,* is known to result in reduced grain yield in sorghum (Hadley et al. 1965; Casady 1967; Campbell and Casady 1969; Campbell et al. 1975), with pleiotropic effects on the number of kernels per panicle and kernel weight, tiller number and panicle size (Casady 1965; Hadley et al. 1965). A recent study has indicated that *Dw3* reduces grain yield mainly through reduced stem mass and grain size but not grain number (George-Jaeggli et al. 2011). In the present study too, there was a negative association between plant height QTL at (*Dw3* harbouring *QPh-dsr07-2*) with panicle length (*QPl-dsr07-2b* = *QHGT_meta1.7*), consistent with earlier observations.

Six qualitative effect genes control plant maturity (*Ma1–Ma6*) in sorghum (Quinby 1967). Of these, *Ma1* was mapped on SBI-06 (Lin et al. 1995, Klein et al. 2008), *Ma3* [Sb01g037340 coding for Phytochrome B (PHYB)] to SBI-01 (Childs et al. 1997), *Ma4* to SBI-10 (Hart et al. 2001) and *Ma5* to SBI-02 (Kim 2003). *Ma3* has been reported as an important regulator of flowering time in plants (Endo et al. 2005). Of these four major maturity genes, QTL harbouring *Ma3* and *Ma5* have been detected for maturity in the present study. The map positions of these two genes, *Ma3* and *Ma5,* matched with the QTL positions of *QDm-dsr01-2* on SBI-01 and *QDm-dsr02-3b* on SBI-02, respectively. Of these, *Ma5* was found to influence maturity with the greatest magnitude, accounting 10 % of trait variation. The favourable allele was contributed by the early parent, B35. However, these two QTL for maturity did not co-locate with QTL for other traits.

The major QTL *QDf-dsr01-1* for days to flowering near the marker Xisp269 explained 12.4 % of the trait variation. It was identified as a meta-QTL (*QTLQDTFL_meta1.1*) by Mace and Jordan (2011) and co-located with the QTL for two important grain yield components, panicle weight (*QPW-dsr01-1*) and grain number (*QGn-dsr01-1*). The other major maturity QTL *QDf-dsr03* on SBI-03 reported as a meta-QTL *QDTFL4_3* (Mace and Jordan 2011) was co-located with QTL *QPB-dsr03a* (for primary branches), *QDm-dsr03* (for maturity) and *QTl-dsr03b* (=metal-QTL *QSTG_meta1.3* for total number of leaves). At these two loci, the favourable alleles were contributed by B35 parent. It is, therefore, possible that the two major QTL for maturity *QDf-dsr01-1* and *QDf-dsr03* could possibly represent either of two qualitative genes *Ma2* and *Ma6* which have been not yet genetically mapped in sorghum.

Another QTL, *QDf-dsr09-3* on SBI-09, co-located with QTL *FlrF* (Lin et al. 1995), *Qma.txs-F*$_1$ (Hart et al. 2001)and *QMa50.txs-F*$_1$ (Feltus et al. 2006) and was reported to be a maturity meta QTL (*QDTFL_meta2.9*) by Mace and Jordan (2011). This QTL region could be important as co-location of QTL for grain yield (*QGY-dsr09-3*) and its component traits, panicle weight (*QPW-dsr09-3*), plant height (*QPh-dsr09-3*), total number of leaves (*QTl-dsr09-3*) and for maturity (*QDm-dsr09-3*) was observed. This is significant since as many as six QTL for yield and its component traits are clustered with positive allele contributed from parent M35-1 for all the traits, possibly indicating the role of pleiotropic gene in the expression of all these traits. Fine mapping of this locus is also necessary to identify the causative gene involved. Gene *Ma1* (Sb06g014570) encoding pseudoresponse regulator protein 37 (PRR37) is a major regulator of maturity in sorghum (Murphy et al. 2011). However, there was no QTL detected corresponding to this major locus on SBI-06 in this population. This could be due to presence of same allele at this locus in both the parents.

There were four other genomic regions: (Xisep0114–XnhsbSFCILP67 on SBI-03, Xcup23–Xisp230 on SBI-04, Xtxp278–Xgap342 and Xisp206–Xtxp278 on SBI-07) at which QTL co-location for four traits was observed. At Xcup23–Xisp230, co-location for grain yield (*QGY-dsr04-1*), panicle weight (*QPW-dsr04-1b*), grain number (*QGn-dsr04-1a*) and panicle length (*QPl-dsr04-1*); at Xisep0114–XnhsbSFCILP67, co-location for panicle weight (*QPW-dsr03*), test weight (*QTw-dsr03*), grain number (*QGn-dsr03*) and total number of leaves (*QTl-dsr03a*); at Xtxp278–Xgap342, co-location for panicle weight (*QPW-dsr07-1*), grain number (*QGn-dsr07-1*), panicle harvest Index (*QPhi-dsr07-1*) and days to maturity (*QDm-dsr07-1*) was observed. It is important to note that favourable allele for increased trait values at these QTL clusters were contributed mainly by B35 parent. Again, three of these co-located QTL were reported to be meta-QTL, *QTw-dsr03* (*QKWT_meta1.3*), *QTl-dsr03a* (*QSTG_meta1.3*), *QTw-dsr07-1* (*QKWT_meta1.7*), by Mace and Jordan (2011) indicating their consistent expression across genetic backgrounds. There were other eight regions with co-locations for two traits. Of these, four QTL [number of primary branches per panicle (*QPBRNB1_5*), days to 50 % flowering (*QDTFL_meta1.5*), test weight (*QKWT2_4*) and panicle length (*QHGT_meta1.7*)] have been reported by earlier studies and were also identified as meta-QTL by Mace and Jordan (2011).

Of the 35 individual QTL involved in the expression of various traits, 13 were reported earlier and were also confirmed to be meta-QTL (Mace and Jordan 2011). Of these, four QTL were for plant height (*QPh-dsr03a* as *QHGT_Meta2.3*, *QPh-dsr03b* as *QHGT_meta1.3*, *QPh-dsr05* as *QHGT1_5*, *QPh-dsr09-1* as *QHGT3_9*), two each for number of primary branches per panicle (*QPB-dsr03c* as *QPBRNB1_3*, *QPB-dsr05* as *QPBRNB1_5*), panicle length (*QPl-dsr06-1b* as *QHGT_meta1.6/QPANLG1-6*, *QPl-dsr07-2a* as *QHGT_meta1.7*), test weight (*QTw-dsr04-2a* as *QKWT2_4* and *QTw-dsr01-2c* as *QKWT_meta2.1*), and one each for grain yield (*QGY-dsr03* as *QGRNYLD1_3*), days to maturity (*QDm-dsr01-1* as *QDTFL_meta1.1*) and total number of leaves (*QTl-dsr03c* as *QSTG_meta2.3*). These QTL could be considered as reliable as they have been identified as meta-QTL, and form valuable genetic loci for marker-assisted breeding to improve sorghum for grain yield via its component traits.

Consistency of QTL detection

One of the primary goals of QTL studies is to provide marker-QTL associations for MAS programmes. It is, therefore. essential to have detailed knowledge about the location and effects of genetic factors influencing the target trait (Bohn et al. 2001). The large variation in the effects of the QTL across different environments (QTL × E) and genetic backgrounds is a significant hindrance to MAS. QTL × E interactions could result in change of magnitude of significant QTL effect or direction across seasons. For this reason, QTL that are stable across environments are of greater interest in MAS (Dudley 1993). In the present study, 34 QTL were found to be consistent in their effect over seasons in multi-environment QTL analysis. Around 50 % of these had no QTL × E interaction indicating environment independent and consistent effects of these QTL on trait expression. There were 18 stable QTL with QTL × E interaction, and 9 of them showed inversion of effects. Four QTL of test weight trait, two QTL each of panicle weight and its harvest index and one QTL for grain yield had shown inversion of effects. It was observed that inversion of effect was specific to the season PR08 for eight of the QTL. These results indicate globally that several QTL detected for yield and its component traits of the present study are consistent and are reliable for marker-assisted breeding of sorghum for enhanced grain yield. The consistent QTL indicates the broad-based environment independent expression of the gene(s) involved in trait expression. Several season-specific QTL were also detected which may be exploited through marker-assisted QTL pyramiding to accumulate alleles conferring wider adaptation to post-rainy environments.

Linkage of genic-SSRs with QTL

In the present study, 21 genic markers were found as flanking markers with the QTL of 11 traits studied. (Table 4; Fig. 1). Interestingly, a genic marker,

XnhsbSFCILP67 (Sb03g028240), which is known to encode indole-3-acetic acid-amido synthetase GH3.5, was co-located with QTL of grain number, total number of leaves, panicle weight, test weight, days to flowering, days to maturity and number of primary branches on SBI-03. The expression of this gene is inducible by presence of auxin (Woodward and Bartel 2005). In rice, LOC_Os01g12160 encoding indole-3-acetic acid-amido synthetase GH3.3 has been identified as important candidate gene controlling a QTL SPP1, controlling the number of spikelets per panicle, grains per panicle and yield per plant (Liu et al. 2009). Similarly, an EST marker, *Stgnhsbm19* on SBI-09, which is derived from a chlorophyll *a–b* binding protein gene (CAB gene), was co-located with the majority of the traits of the present study. CAB proteins are essential pigment-binding proteins of light-harvesting complex (LHC), which is involved in photosynthesis (Green et al. 1991; Liu and Shen 2004). CAB proteins also play an important role in plant development (Armstrong et al. 2000) and leaf senescence (Hörtensteiner 2009; Barry 2009). Therefore, the CAB gene could be the candidate gene for traits which are influenced by photosynthesis.

Utility for post-rainy sorghum improvement

In India, the cultivar M35-1 is a mega sorghum variety cultivated commercially on the largest post-rainy area, due to its wider adaptability, attractive pearly white bold grain (fetches higher market price), nutritious fodder, and for its superior tolerance to post-flowering drought, shoot fly and charcoal rot. The present study revealed opportunities that exist to further improve the cultivar M35-1 for its agronomic performance by introgressing genes from the male parent, B35. In sorghum, grain yield is the final trait contributed by important component traits like panicle weight, panicle length, grain number, grain mass and number of primary branches per panicle. In the present study, QTL regions at which B35 alleles increase the trait value were identified for each of these component traits. For instance, in the case of panicle length, alleles from B35 improved panicle length at seven QTL regions. Similarly, alleles from B35 increased the trait value for one QTL for grain yield, three QTL for panicle weight, four QTL for grain number and at six QTL for primary branches. Thus, introgression of important alleles from B35 into M35-1 through marker-assisted gene pyramiding may effectively further improve the agronomic value of M35-1. It is important to note that there are several transgressive segregants in the study for each of the 11 agronomic traits, indicating allelic dispersion of favourable alleles in both parents and the contribution of favourable alleles from B35. Therefore, if the positive alleles from the parent B35 are stacked up in the genetic background of cultivar M35-1 through MAS, the agronomic performance of M35-1 could be improved further. Thus, the present QTL study should contribute to the genetic improvement of post-rainy sorghum cultivars through MAS, where progress in breeding for high-yielding cultivars has so far been met with less success employing conventional breeding approaches.

Conclusion

Mapping QTL underlying agronomically important traits is a key step in understanding their genetic control and for using the tightly linked markers for marker-assisted breeding to improve crop performance. In the present study, many of the QTL influencing the agronomic traits were identified consistently across seasons. Most of the QTL were validated and are in agreement with previous QTL reports in different genetic backgrounds and seasons. New (67) QTL tagged with SSR markers were identified revealing new chromosomal regions with additional loci controlling various agronomic traits in sorghum. Consistent QTL were identified and the new genic markers along with genomic-SSRs linked to the QTL would help sorghum breeders to construct desirable allelic combinations and accelerate breeding programmes for the development of sorghum cultivars with improved agronomic performance through MAS for post-rainy sorghum.

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