A major QTL for plant height is linked with bloom locus in sorghum [Sorghum bicolor (L.) Moench]

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Abstract Plant height is one of the most important agronomic traits in sorghum with its relevance for biomass, grain yield, fodder and lodging. To understand its genetic basis, the quantitative trait loci (QTL) were identified using a recombinant inbred line (RIL) population consisting of 168 RILs derived from the cross between the two sorghum inbred lines 296B (dwarf) and IS18551 (tall) over six seasons. Two major QTL were identified one each on chromosomes SBI-06 and SBI-07 corresponding to the Dw2 and Dw3 gene loci together accounting 41 % plant height variation. In addition, a morphological bloom trait locus which remained unlinked in the linkage map was found to be significantly linked with plant height in single marker analysis explaining 22 % of the trait variation. By comparing the map positions of $Dw1$, $Dw2$ and $Dw3$, the new locus for plant height linked with bloom is proposed as $Dw4$ locus. Both SSR and the morphological bloom loci linked with height QTL of the present study can be employed as effective tools in marker-assisted breeding for rapid conversion of selected inbred parent lines either as dwarf seed (male sterile) parents or taller pollinators for hybrid seed industry, or for developing high biomass lines in sweet sorghum for exploitation as high bio-fuel crop.

Keywords Sorghum - Plant height - Dwarfing genes - Bloom trait

Introduction

Sorghum [Sorghum bicolor (L.) Moench] is one of the most important cereal crops grown in the semi-arid tropics of the world. It is traditionally grown as food and fodder crop at subsistence levels by resource poor farmers who cannot afford much input. In recent years, sorghum has emerged as a potential alternative bioenergy crop due to great demand for fuel-grade ethanol (Calvino and Messing [2012](#page-8-0)). In addition, its tolerance to high temperatures and drought makes sorghum a crop of choice for climate change.

Sorghum produces excellent green and dry fodder (stover), demand for which is extremely high during the summer seasons in the arid and semi-arid regions. It is estimated that sorghum fodder constitutes up to 45 % of the total dry weight of feed of dairy animals during normal seasons, and up to 60 % during summer seasons (Vilas et al. [2011](#page-9-0)). While breeding sorghum as a fodder crop, it is important to improve its biomass and quality. Biomass yield is highly determined by agronomic traits such as plant height and stem diameter. In this regard, it is necessary to genetically manipulate plant height trait which has direct relevance for improving total biomass. Genetic control of plant height in sorghum has been characterized in terms of factors with qualitative effects (Quinby and

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Karper [1954](#page-9-0)). Recent QTL studies have also identified several genomic regions associated with plant height in sorghum (Feltus et al. [2006;](#page-8-0) Hart et al. [2001;](#page-9-0) Klein et al. [2001](#page-9-0); Lin et al. [1995](#page-9-0); Pereira and Lee [1995](#page-9-0); Rami et al. [1998;](#page-9-0) Srinivas et al. [2009\)](#page-9-0).

Among cereals, sorghum is known for its adaptation to drought stress with its higher water use efficiency. Of the several key feature of sorghum that is pertinent to drought tolerance is epicuticular wax (bloom) present on culm and leaf sheath. Bloom deposition is highly visible on the abaxial side of the leaf blade, leaf sheath, and peduncle. Single recessive gene controls bloom trait in sorghum (Burow et al. [2008\)](#page-8-0), and is reported to be associated with green bug resistance (Weibel and Starks [1986\)](#page-9-0), improved forage digestibility (Cummins and Sudweeks [1976\)](#page-8-0) and enhanced water use efficiency by regulating nighttime water loss (Burow et al. [2008;](#page-8-0) Premachandra et al. [1994](#page-9-0)).

In our earlier study (Srinivas et al. [2009](#page-9-0)) we reported mapping of two major dwarfing genes (Dw2 and Dw3) using three cropping seasons data. In the present study, we revalidated the consistent expression of Dw2 and Dw3 by additional three phenotypic experimental data sets, and also report the operation of a third major locus for plant height linked with bloom trait in sorghum. The gene locus is different from already reported major three dwarfing gene loci (Dw2 on SBI-06, Dw3 on SBI-07 and Dw1 on SBI-09), and could be the locus Dw4. We also report few epistatic QTL involved in plant height expression in sorghum.

Materials and methods

Plant material

The experimental material consisted of a set of 168 RILs derived from the cross between 296B and IS18551. The genotype 296B is a three-gene dwarf, and is the seed parent of several commercial sorghum hybrids in India with abundant bloom on its culm and leaf sheaths (Fig. 1). It is a dwarf statured plant with mean total plant height around 100 cm. The genotype IS18551 is a landrace from Ethiopia having sparse bloom (bloomless) with an average plant height of about 200 cm at anthesis stage.

Field evaluation for plant height and bloom traits

RILs and parents (296B and IS18551) were evaluated at the research farm of the Directorate of Sorghum Research, Hyderabad during six crop seasons; one rainy season of 2008 (K08) and five post-rainy seasons of 2003 (R03), 2004 (R04), 2006 (R06), 2010 (R10) and 2011 (R11). The RILs were planted in a randomized block design (RBD) with three replications. The

Fig. 1 Photographs of 296B (profuse bloom) and IS18551 (bloomless) at anthesis

experimental units were 1-row plot of 4 m length and 0.75 m space between rows. The crop was protected from insect pests, shoot fly and stem borer by the application of 5–6 Carbofuron granules per leaf whorl during the initial crop growth stages followed by a chemical spray of Cypermethrin at the recommended dose of 2 ml 1^{-1} of water.

Phenotypic measurements for plant height (cm) were recorded from the base of culm to the tip of plant (including panicle) at physiological maturity from six tagged plants in the center of each row. The bloom/ bloomless phenotypes were scored at booting stage based on visual observation of the presence/absence of copious amount of bloom on culms and leaf sheath. The RILs with ''bloom'' were scored as ''A'' (Parent 296B type) while RILs which were ''bloomless'' were scored as "B" (parent IS18551 type) on a binary scale. Similarly, the parents and RILs also segregated on a binary scale for other qualitative traits viz., leaf midrib type (Mrco; Juicy vs. Dry), seed glume cover (GlumeT; Covered vs. Open) and plant pigmentation (Plcor; Purple vs. Tan), and the map positions for these loci are reported in our previous report (Srinivas et al. [2009\)](#page-9-0).

Phenotypic data analysis

Phenotypic data on plant height for individual and across seasons was analyzed using the statistical software, Minitab (http:/[/www.minitab.com\)](http://www.minitab.com). The data from individual seasons for all traits was subjected to analysis of variance (ANOVA).

Linkage map

The updated genetic linkage map of cross 296B \times IS18551 reported by our group (Satish et al. [2009](#page-9-0); Srinivas et al. [2009](#page-9-0)) was further updated (Satish et al. [2012\)](#page-9-0) and was used for genetic analysis of plant height. A total of 20 SSR markers remained unlinked. Genotyping of RILs, linkage map construction and naming of chromosomes were also described in our previous reports (Satish et al. [2009,](#page-9-0) [2012\)](#page-9-0).

QTL mapping

The main effect QTLs were identified by composite interval mapping employing MapQTL 5.0 (Van Ooijen [2005\)](#page-9-0). The mean plant height (cm) data of each season and average of six seasons were used to detect the main effect QTLs. The details of QTL mapping are described in our earlier report (Srinivas et al. [2009](#page-9-0)). For the 20 unlinked markers, non-parametric Kruskal– Wallis (KW) test (Lehmann, [1975](#page-9-0)) was performed to associate with plant height. The KW test is equivalent to one-way ANOVA. The test while classifying the individuals into each marker class of binary unit ranks the individuals according to their quantitative trait value. A QTL (with large effect) segregating with the linked marker will result in large difference in the mean rank values of marker classes. The KW test is distributed approximately as a Chi-square distribution with ' $n - 1$ ' degrees of freedom, where 'n' is the number of marker classes (Van Ooijen [2005](#page-9-0)). Regression analysis of bloom data on plant height was also estimated using the software, Minitab.

Epistatic QTL and $Q \times E$ were identified using the QTL network 2.0 based on the mixed linear model (Yang and Zhu [2005](#page-9-0)). Significant thresholds for QTL detection were calculated for each data set using 1,000 permutations. Significance level was fixed at 0.05 for candidate interval selection, QTL detection and its effects.

Results

Phenotypic data analysis

The parental lines (296B and IS18551) of the RIL population differed significantly $(P<0.1)$ for their plant height in individual seasons as well as across six seasons (Table [1\)](#page-3-0). IS18551 was significantly taller than 296B with plant height differences averaging 142 cm across seasons. A wide range in plant height among the RILs was observed. The recombinant inbred lines recorded population mean of 158 (R03), 184 (R04), 156 (R06), 234 (K08), 172 (R10), 173 (R11) and 180 cm (over seasons). The mean plant height among the RILs and parents was higher during K08 rainy season.

The frequency distributions for plant height in all the seasons showed normal distributions (Fig. [2](#page-3-0)). ANOVA indicated highly significant differences for plant height ($P < 0.001$) among the 168 RILs and also highly significant seasonal effects, and significant genotype \times season interactions (ANOVA table not shown).

Plant height ^a	Parental lines		RIL population				
	296B	IS18551	Min	Max	Mean		
R ₀ 3	102	223	88	233	158		
R ₀₄	93	192	102	267	184		
R ₀₆	113	325	85	233	156		
K ₀₈	100	236	110	337	234		
R10	105	240	105	245	172		
R ₁₁	95	225	95	265	173		
PHAye	102	244	113	252	180		

Table 1 Mean phenotypic values of parental lines, RILs for plant height

Plant height in individual season

QTL analysis

Main effect QTLs were identified by composite interval mapping using MapQTL 5.0 software. Mean plant height data of individual seasons and the average data over seasons was used. A LOD of 2.5 was used as

a threshold to declare the presence of a QTL. The results of the QTL analysis are presented in Table [2](#page-4-0).

Five QTLs distributed on four chromosomes (SBI-04, 06, 07 and 10) were detected for plant height. In R03, four QTLs were detected for plant height, one each on SBI-06 and 10, and two on SBI-07. These four QTLs together accounted for 46.1 % of plant height variation and individually explained 5.8 to 21.9 % of trait variation among the RILs. QTL on SBI-06 between the two morphological markers, GlumeT and mrco contributed for the highest proportion of plant height variation (21.9 %). The QTL on SBI-07 between SSR markers, Xtxp92 and Xtxp295 was detected with a LOD value of 4.86 accounting 12 % variation. A second QTL on SBI-07 was also detected accounting 5.8 % variation between Drenhsbm7 and Xtxp92. On SBI-10, QTL between Xnhsbm1008 and Xgap1 contributed 6 % of the trait variation. During R04, R06, R10 and R11, two QTLs which were common in all the individual seasons were identified on SBI-06 and SBI-07. In R04 and R11, one more QTL

Fig. 2 Frequency distribution of plant height (cm) in RILs showing good fit for normal distribution in different seasons

Season	${\rm LG}$	Position (cm)	Locus	\rm{LOD}	$%$ PV	Additive effect
R03	6	$\boldsymbol{0}$	GlumeT*-mrco	9.5	21.9	-15.6
	7	$\boldsymbol{0}$	Drenhsbm7*-Xtxp92	3.1	5.8	-7.4
	7	42	Xtxp92-Xtxp295*	4.9	12.4	-11.2
	10	56	Xnhsbm1008-Xgap1*	2.7	6.0	-7.6
				Total	46.1	
R ₀₄	6	$\mathbf{0}$	GlumeT*-mrco	5.0	13.1	-13.2
	7	$\mathbf{0}$	Drenhsbm7*-Xtxp92	3.2	8.6	-11.1
	7	48	Xtxp92-Xtxp295*	7.0	21.1	-16.7
				Total	42.8	
R06	6	$\mathbf{0}$	GlumeT*-mrco	8.5	22.8	-15.7
	τ	48	Xtxp92-Xtxp295*	3.9	10.5	-10.3
				Total	33.3	
K08	$\overline{4}$	42	Xnhsbm1133*-Xcup48	3.1	6.7	-13.9
	6	4	GlumeT*-mrco	7.2	17.3	-23.4
	7	43	Xtxp92-Xtxp295*	7.2	17.4	-22.8
				Total	41.4	
R10	6	3	GlumeT*-mrco	4.8	14.5	-14.0
	τ	43	Xtxp92-Xtxp295*	4.0	11.7	-12.1
				Total	26.2	
R11	6	3	GlumeT*-mrco	6.0	17.1	-14.9
	7	40	Xtxp92-Xtxp295*	5.2	15.7	-14.0
	10	56	Xnhsbm1008-Xgap1*	2.9	7.3	-9.2
				Total	40.1	
PHAve	6	3	GlumeT*-mrco	9.2	21.9	-16.1
	τ	6	Drenhsbm7*-Xtxp92	3.7	7.6	-9.5
	7	41	Xtxp92-Xtxp295*	7.7	19.2	-14.7
	10	56	Xnhsbm1008-Xgap1*	3.0	6.1	-7.9
				Total	54.8	

Table 2 QTLs for plant height detected in sorghum over seasons

* Nearest marker

was identified which was season specific in its expression. During K08, three QTLs were identified of which two were common (on SBI-06 and SBI-07) while the one detected on SBI-04 between SSRs Xnhsbm1133 and Xcup48 was specific to K08 and controlled 6.7 % of the trait variation. In K08, the influence of two QTLs on SBI-06 and SBI-07 were similar each accounting 17 % of the trait variation. All the three QTLs were found to contribute 41.4 % of trait variation.

In the combined season analysis (over six seasons), four QTLs were detected explaining 54.8 % of phenotypic variation. All the four QTLs mapped to the same linkage groups as detected in individual QTL analysis, and had same map positions as in individual seasons. The QTL on chromosome SBI-06 between two morphological markers, GlumeT and mrco had the highest contribution for phenotypic variation (21.9 %) followed by the QTL on SBI-07 explaining 19.2 %.

At all the five QTL positions detected in the study, the favorable alleles for increased plant height were inherited from the taller parent, IS18551. Individually at each QTL locus, the allele from IS18551 increased plant height by 8–17 cm.

Bloom trait linked with plant height

Of the total 234 SSR markers used for the linkage map, 20 remained unlinked. Out of these 20 unlinked markers tested for their association with plant height in Single Marker Analysis (SMA) using non-parametric

KW test, only the morphological marker, bloom had shown very strong association with plant height in each of the season tested (Table 3). The across seasons mean phenotypic difference between the bloom and bloomless RIL classes was 33 cm, and was highly substantial. This difference was significant in all the six testing seasons though it was of higher magnitude (52 cm) during K08. The bloom trait accounted for 14.4 (R03), 17.3 (R04), 21.1 (R06), 19.7 (K08), 12 $(R10)$, 15 $(R11)$ and 22 % (across seasons) of the phenotypic trait variation of plant height (Fig. [3\)](#page-6-0).

QTLs with epistasis

Five pairs of QTLs showing epistatic interactions were identified for plant height, and were mapped on chromosomes SBI-01, 04, 05, 09 and 10 (Table [4](#page-7-0)). The QTLs contributed significantly with their effect ranging from 0.62 to 2.81 %. Three QTL pairs showed significant and positive additive \times additive (aa) epistasis effects, while two had negative interaction. One epistasis QTL between the loci QphA-1/QphI-1 had the largest effect, which contributed the plant height of 10.10 cm and accounted for 2.81 % of the phenotypic variance. Similarly, QphA-3/QphJ-1 and QphA-2/QphD-1 QTL pairs had positive interaction increasing plant height by 8.98 and 7.85 cm respectively. On the other hand, two QTL pairs, QphE-1/ QphI-1 and QphA-3/QphI-2 contributed negatively and decreased plant height by 7.54 and 4.20 cm. Only one pair of the epistatic QTL QphA-3/QphJ-1 showed significant interaction with season (K08), and increased plant height by 5.90 cm.

Table 3 Kruskal–Wallis test for plant height between two classes of bloom locus, AA and BB in RIL population

Season	Class AA	Class ВB	Difference $(BB-AA)$	P value ^a	
R ₀₃	147	168	21	0.0	
R ₀₄	168	200	32	0.0	
R ₀₆	139	173	34	0.0	
K ₀₈	211	263	52	0.0	
R ₁₀	165	187	22	0.0	
R11	165	195	30	0.0	
Ave	164	197	33	0.0	

Mean difference of plant height (cm) between class AA (bloom) and BB (bloomless) is highly significant

Discussion

The modification of plant architecture has the potential to enhance biomass production, and plant height is an important component of plant architecture that is highly correlated with biomass yield (Yuan et al. [2008\)](#page-9-0). Sorghum produces excellent green and dry fodder (stover), demand for which is extremely high in the arid and semi-arid regions. Quick and profuse tillering, high dry matter content, leafiness, high palatability, hardiness and suitability for silage making makes it an ideal fodder crop (Iyanar et al. [2010](#page-9-0)).

While breeding sorghum as a fodder crop, genetic enhancement of its biomass is a major target. In sorghum biomass yield is highly correlated and determined by plant height and stem girth. Genetic control of plant height in sorghum has been characterized in terms of four independent loci (Dwl, Dw2, $Dw3$, and $Dw4$) with qualitative effects (Quinby and Karper [1954\)](#page-9-0). Of these genes, $Dw2$ and $Dw3$ show pleiotropic effects (Pereira and Lee [1995\)](#page-9-0). The Dw2 is pleiotropic to grain yield, seed weight, leaf area and panicle length (Graham and Lessman [1966](#page-9-0)), and Dw3 has pleiotropic effect on the number of kernels per panicle and kernel weight, tiller number and panicle size (Casady [1965\)](#page-8-0). In the recent studies with isogenic sets, Dw3 gene was found to consistently reduce grain yield mainly through reduced stem mass and reduced grain size but not the grain number (George-Jaeggli et al. [2011](#page-9-0)). So far, pleiotropic effects for Dw1 and Dw4 genes have not been reported.

Various studies in sorghum have identified QTLs for plant height (Feltus et al. [2006;](#page-8-0) Hart et al. [2001](#page-9-0); Klein et al. [2001;](#page-9-0) Lin et al. [1995](#page-9-0); Pereira and Lee [1995;](#page-9-0) Rami et al. [1998](#page-9-0); Ritter et al. [2008;](#page-9-0) Srinivas et al. [2009](#page-9-0)). QTL with major effects for plant height have been consistently identified in different genetic backgrounds and were related to two qualitative plant height loci, Dw^2 on SBI-06 and Dw^3 on SBI-07 (Brown et al. [2006;](#page-8-0) Feltus et al. [2006;](#page-8-0) Klein et al. [2008;](#page-9-0) Mace and Jordan [2011\)](#page-9-0). In the present study, three genomic regions with major effect on plant height have been detected consistently over seasons. Except for one new locus (proposed as $Dw4$), the other two loci, Dw2 and Dw3 with significant effect on plant height are found to be in agreement with earlier reports for their map locations and phenotypic effects on plant height. Mace and Jordan ([2010](#page-9-0)) report the map position of Dw2 on SBI-06 on the consensus map

Fig. 3 Regression of plant height (y-axis) on bloom locus (x-axis) with single-marker analysis, Class AA (bloom) and Class BB (bloomless)

closely linked with DArT markers, sPb-7169 and sPB-1395, and Dw3 between a SSR marker, mcbCIR300 and a DArT marker, SSCIR57 on SBI-07. For Dw1, the map position was proposed to be on SBI-09 where a major height gene Sb.Ht9.1 has been reported (Brown et al. [2008;](#page-8-0) Pereira and Lee [1995](#page-9-0)). So far, the map position of $Dw4$ is not reported. Of these major loci, Dw3 has been fine mapped and the gene was identified (Sb07g023730) to code for P-glycoprotein that regulates polar auxin transport, and it is orthologous to br2 in maize (Multani et al. [2003\)](#page-9-0).

New plant height locus

Single marker analysis is a simple procedure where no linkage map is required, and it allows for the analysis of unlinked markers for their association with the phenotypic traits. SMA for plant height with the 20 unlinked markers of the study was performed by a KW test in the MapQTL5 program. The analysis revealed significant association of plant height only with the bloom locus in each of the phenotyping season. The differences between the phenotypic mean values between the bloom and bloomless classes were highly significant in each of the six seasons and across seasons. On an average, bloom trait explained 22 % of the plant height variation. Amongst the two parents, the bloomless parent, IS18551 was taller with an average height of 244 cm height across seasons while the bloom parent, 296B was significantly shorter (102 cm) establishing the linkage between bloom locus and a major plant height locus. This locus for

OTL i	Flanking markers	Position (cm)	QTL_i	Flanking markers	Position (cm)	\boldsymbol{P}	aa ^a	H^2 (AA, $\%$ ^b	aae4	H^2 (aae4, $\%$ ^b
OphA-	$Unnhsbm1-$ X txp 325	10.4	OphI-	$Xcup02-$ Fdnhsbm10	42.3	< 0.0	$10.10^{\circ\circ}$	2.81		
OphA- 2	Ungnhsbm90- Xtxp302	19.8	$OphD-$	$Xtxp41-Xtxp177$	78.5	< 0.0	7.85°	1.62		
QphA- 3	$Xcup24-$ XnhsbmSFC95	45.9	OphI-	$Xtxp355-$ Unnhsbm30	29.2	< 0.0	-4.20 [#]	0.62		
OphA- 3	$Xcup24-$ XnhsbmSFC95	55.9	OphJ-	$Xnhsbm1044-$ Xnhsbm1048	92.1	< 0.0	8.98°	2.61	5.90^{5}	0.69
$QphE-$	X txp15- X txp23	25	OphI-	$Xcup02-$ Fdnhsbm10	42.3		$< 0.0 -7.54^{\circ}$	1.86		

Table 4 Estimated epistasis and epistasis \times season interaction effects of QTLs for plant height (cm) in four seasons

 $P = 0.000000$, $p \neq P = 0.00$, $p \neq P = 0.03$

^a Epistatic effects, a positive value indicates that the parental two-locus genotypes have a positive effect and that the recombinants have a negative effect

^b Contribution explained by epistatic QTL

plant height linked with bloom trait seems to be different from the other three loci $Dw1$ (SBI-09), $Dw2$ $(SBI-06)$ and $Dw3$ (SBI-07) reported in earlier studies. The bloom marker remained unlinked in the present linkage map though there were sufficient SSR markers near to the Dw1, Dw2 and Dw3 loci to show any linkage if it were to be present there. If the bloom locus were to exist near to any of the above plant height major loci, it could have showed the linkage with the SSR markers available close-by as the density of the SSRs near to these major plant height loci is reasonably sufficient. So far, the map position of $Dw4$ is not reported in sorghum. Since the bloom locus remained unlinked despite the availability of near-by SSR markers to show linkage, it is postulated that the bloom locus linked major plant height locus explaining 22 % of the trait variation in the present study is new and could be the Dw4 locus. Of the two parents, the seed parent 296B is a three-gene dwarf plant with an average height around 100 cm. In our earlier report (Srinivas et al. [2009\)](#page-9-0) and in the present study with additional testing season's data, we could detect only the two major dwarfing genes $(Dw2 \text{ and } Dw3)$. We did not identify any QTL near to the Dw1 locus on SBI-09 possibly indicating presence of same Dw1 allele in both the parents. It is therefore possible that the third locus with its major effect on plant height identified with its association with bloom locus could be $Dw4$ dwarfing gene. However, it needs to be further ascertained the chromosomal location of bloom locus and the linked plant height gene by saturating the uncovered genomic regions with more markers to represent that segment of sorghum genome which is uncovered at present.

Epistasis

Epistasis is the interaction between different genes involved in the expression of a quantitative trait. The presence of epistasis is a cause of concern, since, if the effect of one locus is altered or masked by effects at another locus, power to detect the first locus is likely to be reduced and elucidation of the joint effects at the two loci will be hindered by their interaction (Cordell [2002\)](#page-8-0). Involvement of more than two loci leads to complex multi-way interactions among the contributing loci. Increased plant height has direct effect on the biomass of the plant. In sorghum, high correlation between the plant height and plant biomass is reported (Murray et al. [2008\)](#page-9-0). Sorghum being an important and potential biofuel crop, it is highly beneficial to exploit the plant height genes $(Dw1$ to $Dw4$) besides the epistatic QTL regions for increased plant height.

In the present study, five pairs of epistatic QTL for plant height were identified besides the two major QTL on SBI-06 $(Dw2)$ and SBI-07 $(Dw3)$. It is important to note that three pairs of epistatic QTL, QphA-1/QphI-1, QphA-2/QphD-1 and QphA-3/QphJ-1 had positive additive/additive interaction which is fixable. The epistatic QTL QphA-3/QphJ-1 also had positive interaction with season, K08. The sorghum grown during rainy season is usually taller by 1 m as compared to post-rainy season crop. Effect of seasonal differences on plant height is well documented in sorghum. Thus, besides exploiting the main effect QTL on SBI-06 ($Dw2$), SBI-07 ($Dw3$), SBI-09 ($Dw1$) and new Dw4 in marker-assisted improvement of plant height (biomass), these three pair of epistatic QTL can also be fixed and exploited through linked markers for increased plant height. On the other hand, other two pairs of epistatic QTL between QphA-3/QphI-2 and QphE-1/QphI-1, showed negative epistatic additive/ additive effects. These negative epistatic QTL also become useful in developing dwarf hybrid seed parents for ease in pollination from a restorer parent. Thus, both positive and negative epistatic interactions were involved in the expression of plant height in sorghum.

It is important to note that 296B, the female parent of the study is the topmost seed parent exploited for its excellent combining ability in sorghum hybrid seed industry in India. Several public and private hybrids based on this seed parent are cultivated extensively throughout India. From the F_1 hybrid seed production point, the hybrid seed industry prefers to use dwarf seed parents as it aids in effective pollination from a taller pollinator parent, and also amenable for mechanical harvesting. The three major QTL with linked markers identified for plant height in this study may accelerate marker-assisted conversion programme to develop dwarf seed parents (male sterile lines) or taller pollinator lines by manipulating the three dwarfing genes.

In the recent times, sorghum has been considered as a model crop to understand the genetics, genomics and gene expression among high biomass and high bioenergy crops (Calvino and Messing 2012). The demand for biomass as source of renewable energy is increasing, and this is leading to a paradigm shift in the manipulation of plant architecture in various crops including sorghum (Salas Fernandez et al. [2009\)](#page-9-0). Plant height is the most relevant trait of plant architecture that is highly correlated with biomass yield. Sweet sorghum (sorghum with high stalk sugar content) is a promising high energy crop that can be cultivated worldwide under diverse agro-climatic conditions with less input compared to sugarcane and maize (Reddy et al. [2005](#page-9-0)). Plant height was highly correlated with various sugar related traits (Ritter et al. [2008](#page-9-0)),

and therefore manipulating plant height through marker-assisted breeding for developing taller sweet sorghum cultivars may have significant contribution in increasing the biomass and sugar traits useful for bioenergy.

The present study identified genomic regions linked with three major QTL contributing to significant variation for plant height in sorghum. Of the four dwarfing genes with qualitative effects, we detected consistent expression of Dw2, Dw3 and the proposed new Dw4 loci over seasons. The proposed Dw4 locus had major effect on plant height and is linked with the bloom locus. The map position however needs to be established using more polymerase chain reaction based markers covering more genomic region. Both SSR markers and the morphological bloom locus linked with height QTL of the present study can be employed as effective tools for marker-assisted breeding for rapid conversion of selected inbred parent lines either as dwarf seed (male sterile) parents or taller pollinators for hybrid seed industry or for developing high biomass lines in sweet sorghum for exploitation as high bio-fuel crop.

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