Molecular mapping of genomic regions harbouring QTLs for root and yield traits in sorghum (*Sorghum bicolor* L. Moench)

Rajkumar · B. Fakrudin · S. P. Kavil · Y. Girma · S. S. Arun · D. Dadakhalandar · B. H. Gurusiddesh · A. M. Patil · M. Thudi · S. B. Bhairappanavar · Y. D. Narayana · P. U. Krishnaraj · B. M. Khadi · M. Y. Kamatar

Abstract Root system is a vital part of plants for absorbing soil moisture and nutrients and it influences the drought tolerance. Identification of the genomic regions harbouring quantitative trait loci (QTLs) for root and yield traits, and the linked markers can facilitate sorghum improvement through marker-assisted selection (MAS) besides the deeper understanding of the plant response to drought stress. A population of 184 recombinant inbred lines (RILs), derived from E36-1 × SPV570, along with parents were phenotyped for component traits of yield in field and root traits in an above ground rhizotron. High estimates of heritability and genetic advance for all the root traits and for most of the yield traits, presents high scope for improvement of these traits by simple selection. A linkage map constructed with 104 marker loci comprising 50 EST-SSRs, 34 non-genic nuclear SSRs and 20 SNPs, and QTL analysis was performed using composite interval mapping (CIM) approach. A total of eight and 20 QTLs were mapped for root and yield related traits respectively. The QTLs for root volume, root fresh weight and root dry weight were found co-localized on SBI-04, supported by a positive correlation among these traits. Hence, these traits can be improved using the same linked markers. The lack of overlap between the QTLs of component traits of root and yield suggested that these two sets of parameters are independent in their influence and the possibility of combining these two traits might enhance productivity of sorghum under receding moisture condition.

Keywords Sorghum · Root traits · Variability and correlation analysis · Linkage map · QTLs mapping

Rajkumar · B. Fakrudin (✉) · S. P. Kavil · D. Dadakhalandar · B. H. Gurusiddesh · A. M. Patil · S. B. Bhairappanavar · P. U. Krishnaraj
Institute of Agri-Biotechnology, University of Agricultural Sciences, Dharwad, Dharwad 580 005 Karnataka, India
e-mail: bfakrudin@gmail.com

Present Address:
Y. Girma
School of Plant Sciences and NRMES, Haramaya University, Alemaya City, Ethiopia

Present Address:
S. S. Arun
Bioinformatics Core, Purdue University, West Lafayette IN 47907, USA

Present Address:
M. Thudi
International Crop Research Institute for Semi-Arid Tropics, Patancheru, Hyderabad, India

Present Address:
Y. D. Narayana · M. Y. Kamatar
All India Coordinated Sorghum Improvement Programme, Main Agricultural Research Station, Dharwad, India

Present Address:
B. M. Khadi
University of Agricultural Sciences, Dharwad, Dharwad, India

Introduction

Sorghum is grown principally in the semi-arid regions of tropics and subtropics of Africa and India, largely under stored soil moisture situations. It is an important staple food crop for millions of people and an excellent cattle feed across the world. Due to its adaptation to arid environments, diverse germplasm, close degree of relatedness to other economically important crops, and availability of whole genome sequence from recent past, sorghum has been considered as an excellent crop model of choice for studying the

genetic and physiological mechanisms of drought tolerance (Andrew et al. 2009). In India, sorghum is grown during both rain (*kharif*) and post-rain (*rabi*) seasons, and the *rabi* sorghum is the major form of sorghum grain preferred for human consumption due to superiority of the grain, largely owing to its maturation under dry and cloud free conditions (Seetharama et al. 1990). The *rabi* sorghum generally experiences terminal drought as the rains recede during this season by and large all over the country. Thus, moisture stress is a major constraint limiting *rabi* sorghum productivity. Therefore, drought tolerance has been a prime breeding objective in *rabi* sorghum improvement efforts.

Drought tolerance is a complex trait affected by several interacting plant and environmental factors. Traits such as stay-green, water use efficiency (WUE), early maturity, long root and increased root density along with wax content on leaves and stem are the target traits considered for improvement of drought tolerance in sorghum (Ludlow and Muchow 1990; Hsiao et al. 1976). However, attempts to improve these traits through conventional breeding approach were considerably slow and difficult (Ludlow and Muchow 1990) under field conditions, because of the large environmental influence and lack of control over intensity and timing of drought stress occurrence (Ceccarelli and Grando 1996). Conventional breeding supplemented by MAS could help in improving drought tolerance. Construction of genetic linkage map and identification of drought tolerance QTLs would not only help in understanding of genetic regulation of drought tolerance but also would pave a way for efficient marker-assisted introgression of these QTLs.

In sorghum, many genetic linkage maps have been developed using different marker types, including Restriction Fragment Length Polymorphism (RFLPs), Randomly Amplified Polymorphism DNA (RAPDs), Amplified Fragment Length Polymorphism (AFLPs), Simple Sequence Repeats (SSRs) and Diversity Arrays Technology (DArTs) markers (Mace and Jordan 2011). QTLs have been identified using these genetic linkage maps predominantly containing anonymous molecular markers for many agronomically important traits including plant height, plant early development (anthesis and maturity), yield and its component traits, (Pereira and Lee 1995; Tuinstra et al. 1998; Rami et al. 1998; Hart et al. 2001; Murray et al. 2008; Srinivas et al. 2009), pre- and post-flowering drought stress (stay-green) tolerance (Tuinstra et al. 1996, 1997; Crasta et al. 1999; Subudhi et al. 2000; Tao et al. 2000; Kebede et al. 2001; Haussmann et al. 2002) and for important biotic stresses. Unlike other genomic marker, EST-SSR (Expressed Sequence Tags) and Single Nucleotide Polymorphism (SNP) show the position of functional part of the genome and provides functional association to the linked markers. Further, the codominant and polymorphic natures of these marker systems have increasingly made them the marker of choice for population genetics analyses and trait dissection (Anderson and Lubbersted 2003).

The stay-green trait, delays leaf senescence during grain filling under moisture stress conditions has been proved to be useful to improve drought tolerance (Rosenow et al. 1983). In sorghum, concerted efforts have been made in the past for identification of stay-green genotypes and mapping of QTLs associated with this trait (Tuinstra et al. 1996, 1998; Crasta et al. 1999; Tao et al. 2000; Xu et al. 2000; Kebede et al. 2001; Sanchez et al. 2002; Haussmann et al. 2002). Despite the critical role of roots in harnessing moisture and nutrients from the soil and its essential role in plant growth and adaptation, the root system in general has been studied far less intensively than the shoot due to difficulty of measuring root features in soil for larger number of plants under field conditions. Hence, most of the research endeavors to study root system are conducted in greenhouses, growth chambers and rarely in rhizotrons. Nonetheless, simulation of field situations in artificial structures can greatly aid in understanding the traits related to root system.

A few reports have presented evidence of genotypic variation for root traits in sorghum (Bhan et al. 1973; Mayaki et al. 1976; Jordan et al. 1979) and these studies have focused on few breeding lines with a limited genetic base. Mace et al (2012) for the first time reported the mapping of four QTL for nodal root angle (*qRA1_5*, *qRA2_5*, *qRA1_8*, *qRA1_10*) in addition to three QTL for root dry weight (*qRDW1_2*, *qRDW1_5*, *qRDW1_8*). A drought tolerant sorghum line possessed roots at least 40 cm deeper than a drought sensitive one and deeper rooting of stay-green lines under drought conditions was reported (Salih et al. 1999; Vadez et al. 2005). It is therefore essential to characterize sorghum root system features along with the yield related traits. In this study, we aimed at characterization of genetic basis for root and yield related traits, determination of the relationships among contributing traits towards drought tolerance, construction of genetic linkage map and identification of the QTLs for component traits of root and yield.

Materials and methods

Plant material

A population of 184 F_8 RILs derived from the cross E36-1 × SPV70, segregating for root length was used in this study. The E36-1 is a high yielding line from guinea-caudatum hybrid race with Ethiopian origin, well adapted to tropical environment and has thin and short roots. The SPV570 a hybrid variety with good grain and fodder quality, a promising restorer line on *Milo* cytoplasm and has the thick and long roots.

Field experiment and characterization

The RIL population along with their parental lines and a check were evaluated during *rabi* 2010–11 in a simple lattice design with three replications. In an effort to minimize the border effect, three rows of M35-1 were sown on all sides of the field. Three randomly selected plants from each replication for each entry (RIL) was used for recording observation on early seedling vigour, days to 50 % flowering, plant height (cm), number of leaves, panicle length (cm), panicle exertion (cm), number of spikelets per plant, plant girth (cm), 100-seed weight (g) and seed yield per plant (g), as described in descriptor for sorghum (IBPGR/ICRISAT 1993).

Phenotyping of root traits

The parents, a check and RILs were root phenotyped in the rhizotron, an above ground type structure (25 m long, 4 m wide and 1.5 m height, with collapsible walls on all four sides with cement blocks). The RILs were sown under three replications in the month of March 2011 as summer crop with spacing of 45×15 cm. All recommended package of practices were followed throughout the cropping season to raise the good crop. Irrigation was applied to field capacity until flowering (up to 55 days after sowing, (DAS)) and thereafter, daily irrigation was applied only to wet the treatment until harvest. Roots were sampled for observation of root traits on 110 DAS. One side of the rhizotron wall was collapsed and the whole root system of each line was carefully taken out by loosening the soil around the root profile and the soil adhered to root was carefully washed using a very slow water spray, to minimise disturbance of the root system. After all soil was removed, the intact root system was separated from shoot and the root parameters such as root length (cm), root volume (cm^3), number of roots per plant, root to shoot ratio, root fresh weight (g) and root dry weight (g) (after drying fresh roots in hot air oven at 105 °C for 48 h) were recorded.

Statistical analysis

The average data recorded for root and yield related traits were subjected to the analysis of variance according to formula suggested by Burton and Devane (1953). Heritability and genetic advance estimates were calculated following the method of Allard (1960) and Johnson et al (1955), respectively. The phenotypic and genotypic correlations between pairs of characters were calculated using method suggested by Singh and Choudhary (1985).

Preparation of genetic linkage map and QTL mapping

A total of 938 markers, which consisted of 270 non-genic nuclear SSRs, 530 EST-SSRs and 138 SNPs were screened for parental polymorphism. Selection of non-genic nuclear SSR markers was based on the linkage maps of Bhattarmakki et al. (2000), Taramino et al (1997) and Haussmann et al (2002, 2004). The EST-SSRs (Arun 2006) and SNP (Girma 2009) markers were developed at the Institute of Agri-Biotechnology (IABT), India, by mining publicly available sorghum ESTs at NCBI. Genotyping of SSR markers was done with either 2.5 % agarose by ethidium bromide staining or 6 % polyacrylamide gels (PAGE) in a manual DNA sequencing apparatus (Bio–rad, USA) and visualized following silver staining, while the SNP markers were genotyped on 15 % SSCP gel (Single Strand Confirmation Gel) (Orita et al. 1989). The goodness of fit for segregation of marker loci in RILs was checked using chi-square test.

The genetic linkage map was constructed using MAPMAKER/EXP 3.0b (Lander et al. 1987). The criteria used were the minimum LOD of 2.0 and maximum recombination frequency of 49 %. The recombination frequencies were converted into genetic distances using Kosambi mapping function. Based on the genetic distances obtained from MAPMAKER, the map figure (Fig. 1) was drawn using QTL Cartographer 2.5 (Wang et al. 2007). Based on the mean data of root and yield component traits, the genotypic data of 104 markers and the genetic distances, QTL interval mapping was carried out following CIM (Zeng 1993, 1994) using QTL Cartographer 2.5b (Zeng 1993; Basten et al. 1994). Cartographer's Zmap QTL, model 6 with a window size of 10 cM was used for CIM analyses.

Result and discussion

Genetic potential

Development of drought tolerant cultivars is one of the prime breeding objectives in *rabi* sorghum improvement programmes. Genetic variability studies on the characters related to drought tolerance and grain yield is essential to know their inherent potential and for crop improvement. The phenotypic trait means of the parents (E36-1 and SPV570), range, mean phenotypic values of RIL population, estimates of heritability and genetic advance for root and yield related traits are presented in Table 1. Parental genotypes and RILs displayed considerable amount of differences in their mean performance with respect to all the characters studied (Table 1). Genetic variability among these RILs would be obvious; as the population was developed from deliberately selected, phenotypically distinct parents for root traits, especially root length.

Heritability coupled with genetic advance serves as a good index for transmission of characters from one generation to next. Hence, it should be considered in terms of
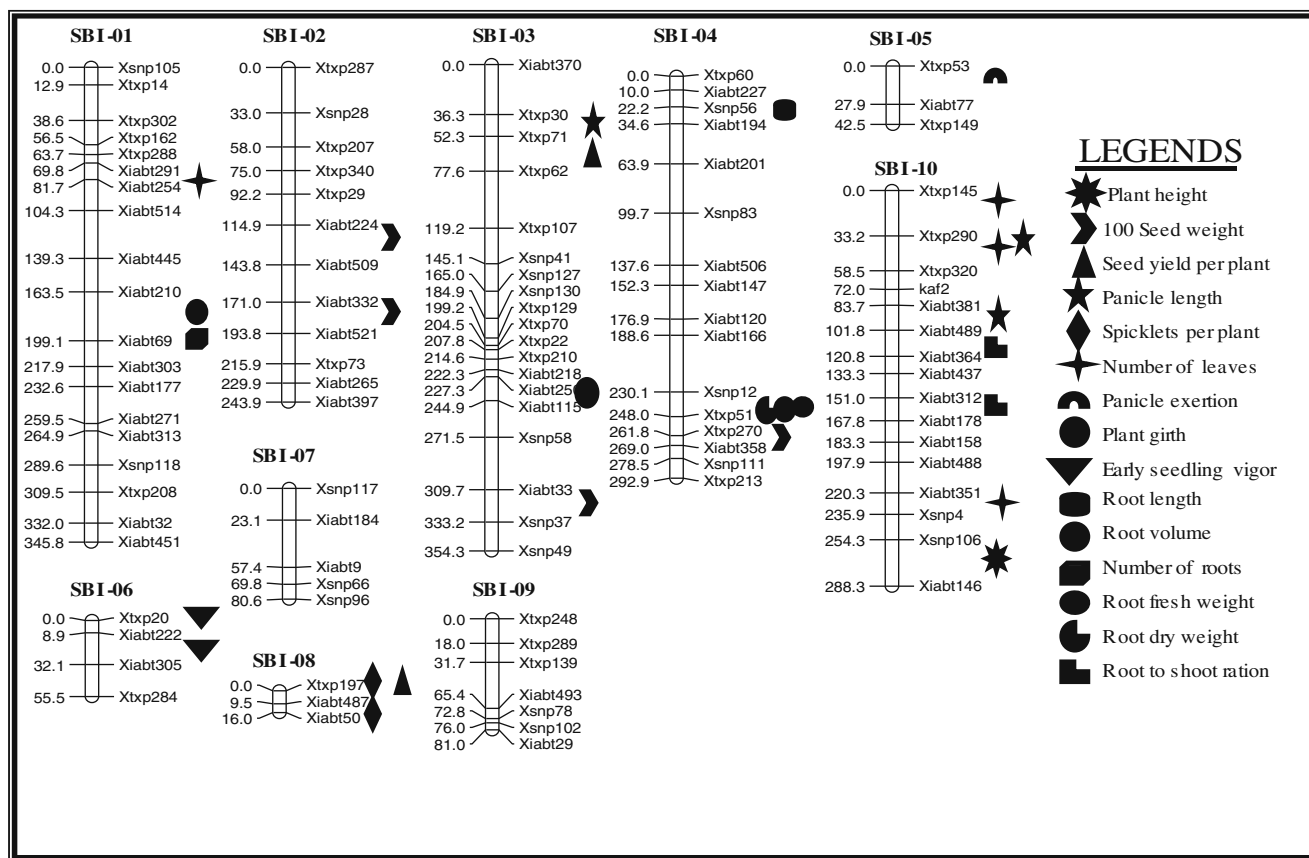
Fig. 1 Linkage map of sorghum showing the putative QTLs influencing root and yield related traits in *rabi* season. The map was developed using the F_8 RIL population of E36-1 × SPV570. The map distances are given in centiMorgans (Kosambi function)

selection (Hanson 1959). Heritability in broad sense ranged from 51.92 % to 98.62 %; and genetic advance as per cent of mean ranged from 12.22 to 78.42 depending on traits. High estimates of heritability coupled with genetic advance as per cent of mean were exhibited for early seedling vigor, plant height, panicle exertion, 100 seed weight, number of spikelets per plant, seed yield per plant, root length, root volume, number of roots per plant, root fresh weight, root dry weight and root to shoot ratio. The observations of yield traits in this study were consistent with results of previous study on RILs derived from contrasting parents for charcoal rot disease in sorghum by Punnuri (2004), Rajkumar et al. (2007) and Patil (2011). Similar high estimates of heritability coupled with genetic advance for root related traits in sorghum accessions was reported by Thudi (2004) and Muhammad et al (2009). Such high estimates for these traits indicate that the selection made through these characters would be effective by simple selection as they are more likely to be controlled by additive gene effects and also gives us a hope for simultaneous improvement of drought and yield together in this population. Similarly high estimates for all root traits studied reflect the proper choice of parents to develop recombinant inbred population (RIP).

Drought tolerance being a quantitative character, it's expression depends on interplay of several component characters. Thus, information regarding relationship of drought tolerant traits (root) with yield would be of immense use for simultaneous selection for both drought and yield characters. Phenotypic and genotypic correlations between the component traits were estimated based on RIL means (Table 2). A total of 72 significant correlation coefficients were observed among the traits. It revealed that genotypic correlation coefficients were higher than phenotypic correlations, which indicates that there was inherent relationship between characters and these contributed to the relative stability of the RILs under study (Davis et al. 1961). Significant positive correlation among the root related traits and the highest correlation ($r=0.998$) between root length and root volume; and root fresh weight and root dry weight recorded in this population is obvious, as the population has reached the homozygous status for root related traits.

All the root related traits were positively related to early seedling vigour (except root length and number of roots per plant), while negatively related with number of spikelets per plant and number of leaves (except root shoot ratio). Root length and number of roots per plant positively associated

Table 1 Means of parents E36-1 and SPV570 and 184 RILs, with their range and broad-sense heritability and genetic advance estimates in *rabi* season for root and yield related traits

Traits	Parental line		RIL population		Mean sum of squares			CD @ 5 %	Heritability (%)	Genetic advance (%)
	E36-1	SPV570	Range	Mean	Genotypes	Replication	Error			
Early seeding vigor	3.33	1.67	1.00–5.00	2.66	3.48**	0.12	0.21	0.95	94.10	78.42
Days to 50 % flowering	54.67	67.67	50.00–91.00	70.00	140.60**	107.05	33.44	12.16	76.21	15.37
Plant height (cm)	153.89	207.78	97.67–350.00	223.65	4770.78***	4728.38	577.16	50.53	87.90	32.29
Number of leaves	10.00	7.22	6.00–13.00	9.00	2.87**	185.52	1.23	2.33	57.20	12.22
Panicle exertion (cm)	6.11	17.44	2.00–25.00	13.91	75.55**	7.71	3.17	3.74	95.80	71.20
Panicle length (cm)	23.67	14.22	1.64–27.00	19.53	20.90**	32.46	6.06	5.18	70.99	19.77
Number of spikelets per plant	53.11	24.78	16.67–76.33	42.00	160.22**	1667.53	49.58	14.81	69.06	24.57
Plant girth (cm)	5.78	3.78	2.33–8.00	4.76	1.38**	26.81	0.66	1.71	51.92	15.23
100 seed weight (g)	3.50	2.23	1.00–5.00	2.93	1.39**	10.04	0.15	0.81	89.45	42.88
Root length (cm)	141.67	175.00	90.00–210.00	153.91	722.45**	11372.14	156.19	26.29	78.38	21.28
Root volume (cm3)	56.00	89.00	22.25–142.65	83.10	1855.33**	784.49	159.80	26.59	91.39	56.34
Number of roots per plant	36.00	50.00	10.00–96.00	51.67	799.72**	225.66	36.40	12.69	95.45	62.13
Root fresh weight (g)	54.00	78.67	39.00–135.00		1541.01**	2513.84	60.03	16.30	96.10	55.22
Root dry weight (g)	21.33	54.00	9.00–97.00	54.03	1239.15**	54.49	17.05	8.68	98.62	76.42
Root to shoot ratio	0.85	0.81	0.41–1.64	0.82	0.07**	0.21	0.02	0.29	73.27	28.03
Seed yield per plant	65.00	34.33	14.00–136.00	68.84	1813.81**	2690.52	115.41	22.60	93.64	68.90

Where, * and ** = significant at $P>0.05$ and $P>0.01$, respectively

RIL Recombinant Inbred Population; *CD* Critical difference

Table 2 Coefficients of Genotypic (G) and Phenotypic (P) correlation among root and yield related traits in the E36-1 × SPV570 RIL population

Traits		X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	X16
X1	G	1	0.07	-0.142**	-0.089*	-0.157**	-0.193**	-0.085*	0.031	0.038	0.057	0.103*	0.077	0.148**	0.143**	0.181**	0.029
	P	1	0.062	-0.112**	-0.076	-0.149**	-0.159**	-0.049	0.032	0.033	0.041	0.095*	0.071	0.139**	0.133**	0.135**	0.027
X2	G		1	0.130**	-0.005	0.106*	-0.110**	0.247**	0.131**	0.067	-0.007	0.062	0.005	0.009	0.04	-0.076	-0.038
	P		1	0.090*	-0.002	0.091*	-0.081	0.114**	0.076	0.05	-0.002	0.063	0.002	0.005	0.031	-0.054	-0.037
X3	G			1	0.560**	-0.133**	0.176**	0.359**	0.403**	0.140**	-0.106*	-0.084*	-0.101*	-0.095*	-0.098*	-0.013	0.102**
	P			1	0.426**	-0.097*	0.153**	0.247**	0.288**	0.089*	-0.063	-0.054	-0.069	-0.066	-0.071	-0.024	0.071
X4	G				1	0.063	0.321**	0.186**	0.352**	0.042	-0.085*	-0.100*	-0.086*	-0.072	-0.08	0.024	0.135**
	P				1	0.057	0.254**	0.140**	0.279**	0.028	-0.07	-0.090*	-0.082	-0.063	-0.072	0.009	0.118**
X5	G					1	0.215**	-0.037	-0.153**	-0.094*	0.076	0.031	0.03	0.029	0.044	-0.086*	-0.175**
	P					1	0.192**	-0.032	-0.119**	-0.084*	0.076	0.025	0.029	0.025	0.041	-0.07	-0.169**
X6	G						1	0.389**	0.093*	-0.123**	-0.074	-0.155**	-0.109**	-0.136**	-0.120**	-0.198**	0.079
	P						1	0.256**	0.075	-0.091*	-0.061	-0.114**	-0.098*	-0.108*	-0.105*	-0.149**	0.049
X7	G							1	0.439**	0.052	-0.064	-0.113**	-0.082	-0.150**	-0.108*	-0.177**	0.195**
	P							1	0.307**	0.031	-0.034	-0.073	-0.055	-0.091*	-0.076	-0.078	0.134**
X8	G								1	0.276**	-0.098*	-0.137**	-0.110**	-0.152**	-0.136**	0.038	0.243**
	P								1	0.212**	-0.106*	-0.114**	-0.095*	-0.118**	-0.108*	0.038	0.199**
X9	G									1	0.093*	0.046	0.098*	0.064	0.069	0.027	0.579**
	P									1	0.08	0.046	0.088*	0.065	0.063	0.038	0.522**
X10	G										1	0.998*	0.978**	0.988**	0.985**	0.284**	-0.072
	P										1	0.874**	0.943**	0.891**	0.882**	0.270**	-0.064
X11	G											1	0.994**	0.990**	0.976**	0.356**	-0.014
	P											1	0.916**	0.949**	0.928**	0.284**	-0.012
X12	G												1	0.978**	0.937**	0.400**	-0.017
	P												1	0.931**	0.918**	0.328**	-0.023
X13	G													1	0.998**	0.372**	0.008
	P													1	0.980**	0.310**	0.003
X14	G														1	0.332**	-0.022
	P														1	0.282**	-0.023
X15	G															1	-0.01
	P															1	-0.005
X16	G																1
	P																1

Where, * and ** = significant at $P>0.05$ and $P>0.01$ respectively, X_1: Early seeding vigor; X_2: Days to 50 % flowering; X_3: Number of leaves; X_4: Plant height (cm); X_5: Panicle exertion (cm); X_6: Panicle length (cm); X_7: Plant girth (cm); X_8: Number of spikelets per plant; X_9: 100 seed weight (g); X_{10}: Root length (cm); X_{11}: Root volume (cm^3); X_{12}: Number of roots per plant; X_{13}: Root fresh weight (g); X_{14}: Root dry weight (g); X_{15}: Root to shoot ratio; X_{16}: Seed yield per plant (g)

with 100 seed weight. Likewise, root length, root volume, number of roots per plant negatively associated with plant height, in a similar way root volume, root fresh weight, root dry weight and root to shoot ratio negatively associated with plant girth. Except for root length, other root related traits showed significant and negative correlation with panicle length.

Based on the above association among the root and yield traits it can be concluded that the root parameters viz., root volume, root fresh weight, root dry weight and root to shoot ratio with early seedling vigour; and root length and number of roots per plant with 100 seed weight, could be selected simultaneously due to significant positive relationship among these traits and this also signifies that these parameters could be utilized as selection criteria for drought tolerance. However, the lack of significant negative correlation among the root related traits and seed yield per plant in this population gives us the scope for simultaneous selection for both root and yield related traits in this population. Turner (1986) found positive correlations between seed yield and root development in cereals, especially in barley, wheat and sorghum. Matsuura et al. (1996) also reported a positive relation between drought tolerance and root length in four gramineous crops (barnyard millet, maize, pearl millet and sorghum). Further, the positive correlation of seed yield per plant with number of leaves, plant height, plant girth, number of spikelets per plant and 100 seed weight indicates that the yield in this population can be improved by selecting these traits simultaneously. The significant correlations recorded among these different component traits enabled the CIM for identification of pleiotropic QTLs.

Genetic linkage map

Of the 938 markers surveyed among parental lines E36-1 and SPV570, 104 markers were polymorphic consisting of 50 EST-SSRs (9.43 %), 34 non-genic nuclear SSRs (12.59 %) and 20 SNPs (14.49 %) and these were used for genotyping RILs. All markers showed expected parental allelic composition in a 1:1 ratio, which suggests that these RILs are a random set of genotypes drawn from the cross and suitability of these markers for mapping purpose. EST-SSR markers showed less polymorphism compared to non-genic nuclear SSRs. This could be because of greater DNA sequence conservation in transcribed region (Russell et al. 2004). The higher polymorphism of SNP would be because of high frequency of SNP in sorghum (Girma 2009; Singhal et al. 2011).

The marker data from all the 104 markers was used to construct the genetic linkage map. The details on linkage group (LG) to which markers were assigned and genetic distances among the marker loci are given in Fig. 1. All the 104 markers were assigned to sorghum chromosomes SBI-01 to SBI-10, based on the positioning of the commonly

mapped SSRs like the Xtxp markers (Bhattarmakki et al. 2000; Haussmann et al. 2002, 2004; Menz et al. 2002), Xiabt (Reddy et al. 2008; Patil et al. 2010; Patil 2011) and Xsnp markers for the first time. The marker order was in good colinearity with previously published linkage maps of sorghum (Bhattarmakki et al. 2000; Haussmann et al. 2004; Murray et al. 2008; Reddy et al 2008; Burrow et al. 2008; Mace et al. 2009; Srinivas et al. 2009; Patil et al. 2010). The linkage map constructed had a total length of 1800.1 cM spanned across all the 10 LGs with an average distance of 14.45 cM. The number of markers mapped per LG ranged from 3 on SBI-05 and SBI-08 to 19 on SBI-01. The map length reported in the present study (1800.1 cM) is comparable with the previously reported maps—for example, Mace et al (2009) reported a map length of 1603.5 cM using SSRs, DArT and RFLPs; and Murray et al (2008) reported a map length of 1836 cM.

QTL mapping

Phenotypic and genotypic data for 184 RILs were subjected to QTL analysis using QTL Cartographer V 2.5b. The putative QTLs for each trait identified by CIM in the population are listed in Table 3, and chromosomal location of QTLs is depicted in Fig. 1. A total of 28 putative QTLs significantly associated with root and yield related traits were identified with distribution all over the segments of 8 chromosomes except on SBI-07 and SBI-09.

QTLs for yield related traits

A total of 20 QTLs were mapped for yield and its component traits. Single QTL was identified for plant height, panicle exertion and plant girth in this population. The QTL for plant height (qPH10) was mapped near to QTL for number of leaves (qNL10), this is supported by the significant positive correlation between plant height and number of leaves (r=0.560), which supports the general trend in sorghum; the taller plants with more number of leaves can contribute to increased biomass yield. This also provides scope for selecting transgressive seggregants from this population for fodder purpose. An independent QTL for panicle exertion (qPE5) and a major QTL for plant girth (qPG3) were detected on SBI-05 and SBI-03 respectively, at these QTL regions (qPE5 and qPG3) SPV570 was associated with 6.04 % and 23.27 % of phenotypic variation, this implicates that a wide plant girth may contribute to biomass production. The QTL identified for plant height, panicle exertion and plant girth does not correspond to any of the QTLs reported earlier. Therefore, they may be considered as new loci regulating plant development.

For early seedling vigor and number of spikelets per plant, two QTL were mapped at different positions on SBI-06 and SBI-08 respectively. QTLs for early seedling

Table 3 Features of putative QTLs detected for root and yield traits in the E36-1 × SPV570 RIL population

Trait	QTL name	LG	Marker interval	Position	Length (cM)	LOD scored	a_ib^2	R^2(%)
Early seeding vigor	qSV6	SBI-06	Xtxp20-Xiabt222	8.01	8.9 cM	2.91	0.32	6.83
	qSV6.1	SBI-06	Xiabt222-Xiabt305	14.91	23.2 cM	3.38	0.41	13.44
Plant height (cm)	qPH10	SBI-10	Xsnp106-Xiabt146	254.31	34.0 cM	2.62	0.34	6.04
Number of leaves	qNL1	SBI-01	Xiabt291-Xiabt254	77.81	11.9 cM	2.27	−15.53	8.42
	qNL10.2	SBI-10	Xtxp145-Xtxp290	26.01	33.2 cM	3.13	−16.3	13.76
	qNL10.1	SBI-10	Xtxp290-Xtxp320	43.21	25.3 cM	3.95	−19.8	19.7
	qNL10	SBI-10	Xiabt351-Xsnp4	224.31	15.6 cM	2.02	−14.82	8.01
Panicle exertion (cm)	qPE5	SBI-05	Xtxp53-Xiabt77	14.01	27.9 cM	2.77	1.7	11.45
Panicle length (cm)	qPL3	SBI-03	Xtxp30-Xtxp71	42.31	16.0 cM	2.61	0.75	7.96
	qPL10	SBI-10	Xtxp290-Xtxp320	49.21	25.3 cM	2.45	1.14	14.5
	qPL10.1	SBI-10	Xiabt381-Xiabt489	97.71	18.1 cM	2.38	0.83	6.98
Number of spikelets/plant	qNS8.1	SBI-08	Xtxp197-Xiabt487	8.01	9.5 cM	4.69	−0.24	11.2
	qNS8	SBI-08	Xiabt487-Xiabt50	11.51	6.5 cM	5.04	−0.25	11.9
Plant girth (cm)	qPG3	SBI-03	Xiabt250-Xiabt115	235.31	17.6 cM	4.61	4.51	23.27
100 seed weight (g)	qSW2	SBI-02	Xiabt224-Xiabt509	142.91	28.9 cM	2.56	−0.2	5.82
	qSW2.1	SBI-02	Xiabt332-Xiabt521	171.01	22.8 cM	3.60	−0.25	7.58
	qSW3	SBI-03	Xiabt33-Xsnp37	327.71	23.5 cM	2.38	−0.21	7.82
	qSW4	SBI-04	Xtxp270-Xiabt358	263.81	7.2 cM	2.32	−0.18	5.39
Seed yield per plant (g)	qSY3	SBI-03	Xtxp71-Xtxp62	60.31	25.3 cM	2.39	−5.25	8.35
	qSY8	SBI-08	Xtxp197-Xiabt487	8.01	9.5 cM	2.57	−5.85	6.5
Root length (cm)	qRL4	SBI-04	Xsnp56-Xiabt194	32.21	12.4 cM	2.84	5.38	8.33
Root volume	qRV1	SBI-01	Xiabt210-Xiabt69	183.51	35.6 cM	2.01	10.93	13.96
	qRV4	SBI-04	Xtxp51-Xtxp270	258.01	13.8 cM	3.62	13.3	13.09
Number of roots/plant	qRN1	SBI-01	Xiabt210-Xiabt69	181.51	35.6 cM	2.62	7.37	17.87
Root fresh weight (g)	qRF4	SBI-04	Xtxp51-Xtxp270	258.01	13.8 cM	2.60	18.69	9.21
Root dry weight (g)	qRD4	SBI-04	Xtxp51-Xtxp270	258.01	13.8 cM	2.60	8.42	9.21
Root to shoot ratio	qRS10	SBI-10	Xiabt489-Xiabt364	101.81	19.0 cM	3.63	0.06	8.07
	qRS10.1	SBI-10	Xiabt312-Xiabt178	155.01	16.8 cM	2.42	0.05	7.96

Where, LG: linkage group; a_ib^2: additive effect (positive: allelic effect of SPV570; negative: allelic effect of E36-1); cM: centiMorgans; R^2 (%): Percentage of phenotypic variation explained by individual QTL, QTL name indicates q for QTL followed by trait name to which the QTL was detected and by the chromosome number on which it was detected. If more than one QTL were detected on the same chromosome for a trait, QTLs identified were serially numbered

vigour (qSV6 and qSV6.1) explaining 20.31 % phenotypic variance were from male parent, SPV570. This could be partly true, as this trait showed positive correlation with other root traits (r=0.103 to 0.181). Similar observation of two QTLs for early seedling vigour in RIP developed from the cross IS22380 × E36-1 were reported by Rajkumar (2004), Reddy et al (2008) and Patil (2009). The QTLs for number of spikelets per plant were mapped at position corresponding to 8.01 cM (qNS8) and 11.51 cM (qNS8.1) on SBI-08. The qNS8 was co-localized with qSY8 and this was supported by significant positive correlation between number of spikelets and seed yield per plant (r=0.243), which indicates that qNS8 is same as qSY8. This result allows the possibility of plant type with more number of spikelets per plant can increase yield.

Panicle length is an important component of seed weight per panicle (Rami et al. 1998). A total of three QTLs were detected for panicle length, of which two QTLs were located on SBI-10 and another on SBI-03. The qPL3 was mapped near to qSY3. The non significant correlation between panicle length and seed yield per plant (r=0.079), implies that plant type with longer panicles does not affect seed yield per plant in this population. This result is consistent with previous study of Srinivas et al (2009), who also reported significant negative correlations of panicle length with seed yield per plant (r=−0.250).

Number of leaves produced per plant is an important component of forage yield. Four QTLs were dissected out for number of leaves, of which three QTLs located on SBI-10 (qNL10, qNL10.1, qNL10.2) and another one on SBI-01

(*qNL1*), together account for 49.25 % of phenotypic variance. The *qNL10*.1 was co-localized with *qPL10*.1 and the co-localisation of QTLs is favourable, as the number of leaves and panicle length have significant positive association ($r=0.176$), suggesting that plant with more number of leaves can increase the panicle length, by means of transport of increased photosynthate from leaf to panicle. Srinivas et al (2009) also identified four QTLs for number of leaves located on SBI-01, SBI-03 and SBI-07 in RILs derived from cross 296B × IS18551. Similarly, four QTLs were detected for 100 seed weight, of which two QTLs were mapped on SBI-02 (*qSW2* and *qSW2*.1), and one each on SBI-03 (*qSW3*) and SBI-04 (*qSW4*). The *qSW4* mapped near *qRF4*, *qRD4* and *qRV4* on SBI-04. The non significant correlation of 100 seed weight with root related traits viz., root fresh weight ($r=0.065$), root dry weight ($r=0.063$), and root volume ($r=0.046$), clearly indicated that the improvement in 100 seed weight at least in part cannot be achieved by improving root related traits. QTL identified for 100 seed weight in the present study were also reported by other studies on SBI-02 by Srinivas et al (2009) and Patil (2009); and on SBI-03 by Tuinstra et al (1996).

Two QTLs for seed yield per plant were mapped on SBI-03 and SBI-08. The QTL detected for this trait in the present study on SBI-03 was also reported by Tuinstra et al (1996) and Patil (2009); on SBI-08 by Patil (2009) and Patil (2011). QTL for seed yield per plant on SBI-08 *(qSY8)* was co-localized with *qNS8*, and on SBI-03 (*qSY3*) was mapped near to *qPL3*. The positive significant correlation of seed yield with number of spikelets per plant ($r=0.243$) and non significant association with panicle length ($r=0.079$) indicates that plant with more number of spkelets per plant can increase the yield rather than plant with longer panicle length. The negative additive effect shown by the QTLs viz., number of leaves, 100 seed weight and seed yield per plant indicates that the alleles were derived from E36-1 parent.

QTLs for root related traits

Root traits are the best indicator for studying the drought. A total 8 QTLs for root traits were mapped in this study. Single QTL for root length and number of roots per plant was mapped on SBI-04 (*qRL4*) and SBI-01(*qRN1*), respectively. The QTL for number of roots per plant (*qRN1*) was mapped near to *qRV1* ($r=0.994$). Two major QTLs for the root volume were mapped on the SBI-01 (*qRV1*) and SBI-04 (*qRV4*) explaining phenotypic variance of 13.96 and 13.03 %, respectively. QTL for root volume (*qRV4*) found co-localized with root fresh weight (*qRF4*) and root dry weight (*qRD4*) on SBI-04 and located near to number of roots per plant (*qRN1*) on SBI-01, and was further supported by significant positive correlation of root volume with root fresh weight ($r=0.990$), root dry weight ($r=0.976$) and

number of roots per plant ($r=0.974$). Thus, it proves the fact correlated traits often have QTLs mapping to the same chromosomal locations (Veldboom et al. 1994; Xiao et al. 1996). These correlations may result from either tight linkage of several genes controlling the traits or the pleiotropic effect of a single gene (Aastveit and Aastveit 1993; Ritter et al. 2008). Venuprasad et al (2002) also reported that root volume in rice also found co-localized with root dry weight on LG 03 (RM231- RZ329), root thickness on LG 02 (RG157-RZ318) and root length on LG 09 (RZ12-RM201). Likewise, in maize co-localization of root density and root dry weight on LG 01 was reported by Rahman et al (2011).

The co-localization of QTL identified for root related traits (root volume, root fresh weight and root dry weight) can help in improvement of these traits at a time using the same linked markers. Also indicate plant type with increased rooting density with extended root length enable plants to penetrate deeply and extract moisture from the deeper zone and meets the transpirational demands of the shoot. Further, the common QTL mapped for root fresh weight (*qRF4*) and root dry weight (*qRD4*) at position 258.01 cM on SBI-04, suggests they are controlled by same genetic loci. Two QTLs (*qRS10* and *RS10*.1) were mapped for root to shoot ratio on SBI-10, the *qRS10* was mapped near to *qPL10*. The significant but negative correlation of root to shoot ratio with panicle length ($r=-0.198$) implicates that improvement in the root to shoot ratio would costs onto the yield related parameters.

The QTLs identified in the present study explained relatively less phenotypic variation could be due to the low genome coverage and it suggests there are additional QTLs controlling these traits. This also warrants further saturation of the present map with the additional functional markers like SNPs. Further, identification of stable QTLs for these traits will help to introgress them effectively into the elite sorghum genotype via marker-assisted backcrossing. From the present study, it can be concluded that the root related QTLs in this population were distinct from rest of the QTLs for component traits of yield supported with non-significant but positve association of root traits with seed yield per plant in this population, indicating that the selection for both root (drought) and yield related traits will not have unforeseen consequences. It is thus possible to combine higher grain yield and desirable root morphological traits, favourably, to enhance productivity of sorghum under receding moisture condition.

References

Aastveit AH, Aastveit K (1993) Effect of genotype environment interactions on genetic correlations. Theor Appl Genet 86:1007–1013

Allard RW (1960) Principles of plant breeding. Wiley, New York, p 85

Anderson JR, Lubbersted T (2003) Functional markers in plants. Trends Plant Sci 8:554–560

Andrew HP, John EB, Rémy B, Inna D, Jane G, Heidrun G, Georg H, Uffe H, Therese M, Alexander P, Jeremy S, Manuel S, Haibao T, Xiyin W, Thomas W, Arvind KB, Jarrod C, Alex F, Udo G, Igor VG, Eric L, Christopher AM, Mihaela M, Apurva N, Robert PO, Bryan WP, Asaf AS, Yu W, Lifang Z, Nicholas CC, Michael F, Alan RG, Thomas H, Beat K, Patricia K, Stephen K, Maureen CM, Ray M, Daniel GP, Mehboob-ur-Rahman, Doreen W, Peter W, Klaus FX, Mayer JM, Daniel SR (2009) The *Sorghum bicolor* genome and the diversification of grasses. Nature 457:551–556

Arun SS (2006) *In silico* EST data mining for elucidation of repeats biology and functional annotation in sorghum (*Sorghum bicolor* (L.) Moench). M. Sc. (Agri.) Thesis, Univ. Agric. Sci, Dharwad, Karnataka (India)

Basten CJ, Weir BS, Zeng ZB (1994) Zmap -a QTL cartographer. In: Smith C, Gavora JS, Benkel, B, Chesnais J, Fairfull W, Gibson JP, Kennedy BW, Burnside EB (eds) World congress on genetics applied to livestock production, 5th, 7th-12th August, 1994, Guelph, ON, Canada. Proceedings Computing strategies and software. Guelph, Organizing Committee, 1994, pp. 65–66

Bhan S, Singh HG, Singh A (1973) Note on root development as an index of drought resistance in sorghum (*Sorghum bicolor* L. Moench). Indian J Agric Sci 43:828–830

Bhattarmakki D, Jianmin D, Ashok K, Chhabr B, Hart GE (2000) An integrated SSR and RFLP linkage map of *Sorghum bicolor* (L.) Moench. Genome 43:988–1002

Burrow GB, Franks CD, Acosta-Martinez V, Xin Z (2008) Molecular mapping and characterization of BLMC, a locus for profuse wax (bloom) and enhanced cuticular features of sorghum (*Sorghum bicolor* (L.) Moench). Theor Appl Genet 118:423–431

Burton GW, Devane EM (1953) Estimating heritability in tall fescae (*Festuca arumdincea*) from replicated clonal material. Agron J 45:478–481

Ceccarelli S, Grando S (1996) Drought as a challenge for the plant breeder. Plant Growth Regul 20:149–155

Crasta OR, Xu WW, Rosenow DT, Mullet J, Nguyen HT (1999) Mapping of post-flowering drought resistance traits in grain sorghum: association between QTLs influencing premature senescence and maturity. Mol Gen Genet 262:579–588

Davis WW, Middleton GK, Herbert TT (1961) Inheritance of protein, texture and yield in wheat. Crop Sci 12:235–238

Girma Y (2009) Mining of genomic resources for SNP and SNP-CAPs Markers and divergence for drought tolerance in sorghum (*Sorghum bicolor* L. Moench), M. Sc. Thesis. Univ. Agri. Sci, Dharwad, Karnataka (India)

Hanson WD (1959) Early generation analysis of lengths of heterozygous chromosome segments around a locus held heterozygous with backcrossing or selfing. Genet 44:833–837

Hart GE, Schertz KF, Peng Y, Syed NH (2001) Genetic mapping of *Sorghum bicolor* (L.) Moench QTLs that control variation in tillering and other morphological characters. Theor Appl Genet 103:1232–1242

Haussmann BIG, Mahalakshmi V, Reddy BVS, Seetharama N, Hash CT, Geiger HH (2002) QTL mapping of stay-green in two sorghum recombinant inbred populations. Theor Appl Genet 106:133–142

Haussmann BIG, Hess DE, Omanya GO, Folkertsma RT, Reddy BVS, Kayentao M, Welz HG, Geiger HH (2004) Genomic regions influencing resistance to parasitic weed *Striga hermonthica* in two recombinant inbred populations of sorghum. Theor Appl Genet 109:1005–1016

Hsiao TC, Fereres E, Acevedo E, Henderson DW (1976) Water stress dynamics of growth and yield of crop plants. In: Lange OL, Kappen L, Schulze ED (eds) Water and plant life-problems and modern approaches. Springer, Heidelberg, pp 281–305

IBPGR/ICRISAT (1993) Descriptors for Sorghum [*Sorghum bicolor* (L) Moench]. International Board of Plant Genetic Resources. Rome, Italy/International Crop Research Institute for Semi-Arid Tropics, Patancheru, India

Johnson HW, Robinson HF, Comstock RE (1955) Estimates of genetic and environmental variability in soybean. Agron J 47:314–318

Jordan WR, Miller FR, Morris DE (1979) Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci 19–23

Kebede H, Subudhi PK, Rosenow DT (2001) Quantitative trait loci influencing drought tolerance in grain sorghum (*Sorghum bicolor* L. Moench). Theor Appl Genet 103:266–276

Lander ES, Green PL, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genome 1:174–181

Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improving crop yields in water-limited environments. Adv Agron J 43:107–153

Mace ES, Jordan DR (2011) Integrating sorghum whole genome sequence information with a compendium of sorghum QTL studies reveals uneven distribution of QTL and of gene-rich regions with significant implications for crop improvement. Theor Appl Genet 123:169–191

Mace ES, Rami JF, Bouchet S, Patricia EK, Robert R, Kilian A, Wenzl P, Xia L, Halloran K, David RJ (2009) A consensus genetic map of sorghum that integrates multiple component maps and high-throughput Diversity Array Technology (DArT) markers. BMC Plant Biol 9:13

Mace ES, Singh V, Van Oosterom EJ, Hammer GL, Hunt CH, Jordan DR (2012) QTL for nodal root angle in sorghum (Sorghum bicolor L. Moench) co-locate with QTL for traits associated with drought adaptation. Theor Appl Genet 124:97–109

Matsuura A, Inanaga S, Sugimoto Y (1996) Mechanism of interspecific differences among four graminaceous crops in growth response to soil drying. Jpn J Crop Sci 65:352–360

Mayaki WC, Stone LR, Teare ID (1976) Irrigated and nonirrigated soybean, corn, and grain sorghum root systems. Agron J 68:532–534

Menz MA, Klein RR, Mullet JE, Obert JA, Unruh NC (2002) A high-density genetic map of *Sorghum bicolor* (L.) Moench based on 2926 AFLP, RFLP and SSR markers. Plant Mol Biol 48:483–499

Muhammad AA, Amjad A, Shahid N, Zulkiffal M, Shiraz A (2009) Morpho-physiological criteria for drought tolerance in sorghum (*Sorghum bicolor*) at seedling and post-anthesis Stages. Int J Agric Biol 11:1814–9596

Murray SC, Sharma A, Rooney WL, Klein PE, Mullet JE, Mitchell SE, Kresovich S (2008) Genetic improvement of sorghum as a biofuel feedstock: I. QTL for stem sugar and grain non-structural carbohydrates. Crop Sci 48:2165–2179

Orita M, Suzuki Y, Sekiya T, Hayashi K (1989) Rapid and sensitive detection of point mutations and SNP polymorphisms using the polymerase chain reaction. Genome 5:874–879

Patil AM (2009) Genome-wide molecular mapping, introgression of stable QTLs and expressional quantitation of transcription factor

genes in charcoal rot manifestation in *Sorghum bicolor* (L.) Moench, Ph. D. Thesis. Univ. Agric. Sci, Dharwad, Karnataka (India)

Patil S (2011) Genome-wide QTL mapping for post-flowering drought tolerance and validation of charcoal rot resistance QTLs NILs of sorghum. Ph. D. Thesis. Univ. Agri. Sci, Dharwad, Karnataka (India)

Patil AM, Fakrudin B, Narayana YD, Bhat R, Koti RV, Salimath PM (2010) Molecular mapping of gene based markers in sorghum. Karnataka J Agric Sci 23(5):681–686

Pereira MG, Lee M (1995) Identification of genomic regions affecting plant height in sorghum and maize. Theor Appl Genet 90:380–388

Punnuri SM (2004) QTL mapping of charcoal rot resistance in sorghum (*Sorghum bicolor* (L.) Moench) using SSR markers. M. Sc. Thesis, Univ. Agri. Sci, Dharwad, Karnataka (India)

Rahman H, Pekic S, Lazic-Jancic V, Quarrie SA, Shah SMA, Pervez A, Shah MM (2011) Molecular mapping of quantitative trait loci for drought tolerance in maize plants. Genet Mol Res 10(2):889–901

Rajkumar (2004) Genetic and molecular analysis of charcoal rot resistance in sorghum. M. Sc. Thesis. Univ. Agri. Sci, Dharwad, Karnataka, (India)

Rajkumar, Fakrudin B, Kuruvinashetti MS (2007) Genetic variability and correlation studies in sorghum. Indian J Genet Plant Breed 67(2):198–199

Rami JF, Dufour P, Trouche G, Fliedel G, Mestres C, Davrieux F, Blanchard P, Hamon P (1998) Quantitative trait loci for grain quality, productivity, morphological and agronomical traits in sorghum (*Sorghum bicolor* L. Moench). Theor Appl Genet 97:605–616

Reddy PS, Fakrudin B, Rajkumar, Punnuri SM, Arun SS, Kuruvinashetti MS, Das IK, Seetharama N (2008) Molecular mapping of genomic regions harboring QTLs for stalk rot resistance in sorghum. Euphytica 159:191–198

Ritter KB, Jordan DR, Chapman SC, Godwin ID, Mace ES, McIntyre CL (2008) Identification of QTL for sugar related traits in a sweet × grain sorghum (*Sorghum bicolor* L. Moench) recombinant inbred population. Mol Breed 22:367–384

Rosenow DT, Quisenberry JE, Wendt CW, Clark LE (1983) Drought tolerant sorghum and cotton germplasm. Agric Water Manag 7:207–222

Russell J, Booth A, Fuller J, Harrower B, Hardly P, Machray G, Powell W (2004) A comparison of sequence based polymorphism and haplotype content in transcribed and anonymous regions of the barley genome. Genome 47:389–398

Salih AA, Ali IA, Lux A, Luxova M, Cohen Y, Sugimoto Y, Inanga S (1999) Rooting, water uptake and xylem structure adaptation to drought of two sorghum cultivars. Crop Sci 39:168–173

Sanchez AC, Subudhi PK, Rosenow DT, Nguyen HT (2002) Mapping QTLs associated with drought resistance in sorghum (*Sorghum bicolor* (L) Moench). Plant Mol Biol 48:713–726

Seetharama N, Singh S, Reddy BVS (1990) Strategies for improving postrainy sorghum productivity. Proc Indian Natl Sci Acad 1990(56):455–467

Singh RK, Choudhary BD (1985) Biometrical methods in quantitative genetic analysis. Kalyani, New Delhi, India

Singhal D, Gupta P, Sharma P, Kashyap N, Anand S, Sharma H (2011) *In silico* single nucleotide polymorphisms (SNP) mining of Sorghum bicolor genome. African J Biotechnol 10(4):580–583

Srinivas G, Satish K, Madhusudhana R, Reddy RN, Mohan SM, Seetharama N (2009) Identification of quantitative trait loci for agronomically important traits and their association with genic-microsatellites markers in sorghum. Theor Appl Genet 118:1439–1454

Subudhi PK, Rosenowm DT, Nguyen HT (2000) Quantitative trait loci for the stay-green trait in sorghum (*Sorghum bicolor* L. Moench). Theor Appl Genet 101:733–741

Tao YZ, Henzell RG, Jordan DR, Butler DG, Kelly AM, McIntyre CL (2000) Identification of genomic regions associated with stay-green in sorghum by testing RILs in multiple environments. Theor Appl Genet 100:1225–1232

Taramino G, Tarchini R, Ferrario S, Lee M, Pe ME (1997) Characterization and mapping of simple sequence repeats in *Sorghum bicolor* (L.) Moench. Theor Appl Genet 95:66–72

Thudi M (2004) Molecular profiling and phenotyping of root and shoot traits in selected Rabi Sorghum [*Sorghum bicolour* (L.) Moench] genotypes. M.Sc. Thesis, Univ. Agric. Sci, Dharwad, Karnataka (India)

Tuinstra MR, Grote EM, Goldsborough PB, Ejeta G (1996) Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. Crop Sci 36:1337–1344

Tuinstra MR, Grote EM, Goldbrough PB, Ejeta G (1997) Genetic analysis of post-flowering drought tolerance and components of grain development in *Sorghum bicolor* (L.) Moench. Mol Breed 3:439–448

Tuinstra MR, Ejeta G, Goldsbrough PB (1998) Evaluation of near isogenic sorghum lines contrasting for QTL markers associated with drought tolerance. Crop Sci 38:835–842

Turner NC (1986) Crop water deficits: a decade of progress. Adv Agron 39:1–51

Vadez V, Kashiwagi J, Krishnamurthy L, Serraj R, Sharma KK, Devi J, Bhatnagar-Mathur P, Hoisington D, Chandra S, Gaur PM, Nigam SN, Rupakula A, Upadhyaya HD, Hash CT, Rizvi SMH (2005) Recent advances in drought research at ICRISAT: using root traits and rd29a:DREB1A to increase water use and water use efficiency in drought-prone areas. Poster presented at the Interdrought II conference, Rome, 24-28 September

Veldboom LR, Lee M, Woodman WL (1994) Molecular facilitated studies of morphological traits in an elite maize population II: Determination of QTLs for grain yield and yield components. Theor Appl Genet 89:451–458

Venuprasad R, Shashidhar HE, Hittalmani S, Hemamalini GS (2002) Tagging quantitative trait loci associated with grain yield and root morphological traits in rice (*Oryza sativa* L.) under contrasting moisture regimes. Euphytica 128:293–300

Wang S, Basten CJ, Zeng ZB (2007) Windows QTL cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh, USA (http://statger.ncsu.edu/qtlcart/WQTLCart.htm)

Xiao J, Li J, Tanksley SD (1996) Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific rice cross. Theor Appl Genet 92:230–244

Xu W, Subudhi PK, Crasta OR, Rosenow DT, Mullet JE, Nguyen HT (2000) Molecular mapping of QTLs conferring stay-green in grain sorghum (*Sorghum bicolor* L. Moench). Genome 43:461–469

Zeng ZB (1993) Theoretical basis of precision mapping of quantitative trait loci. Proc Natl Acad Sci USA 90:10972–10976

Zeng ZB (1994) Precision mapping of quantitative trait loci. Genet 136:1457–1468