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Full Length Research Paper

Genetic and GGE biplot analyses of sorghum germplasm for stem sugar traits in Southern Africa

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Breeding of suitable sweet sorghum (*Sorghum bicolor* L. Moench) cultivars can boost biofuel production and farmer income in southern Africa. To generate the information necessary for breeding, eight female lines were crossed with 10 male lines in a North Carolina design II mating scheme. The 80 hybrids, parents and check varieties were evaluated across four environments during 2008 to 2009. Analyses were performed in GenStat. Genotype stability was assessed using the genotype and genotype by environment interaction (GGE) biplot procedure. Results showed significant ($P \leq 0.05$) differences between genotypes for stem brix, stem biomass and associated traits. Hybrids were predominant in the top 20 ranked genotypes for stem brix and stem biomass, demonstrating their superiority. The entries attained yield advantage over standard check of up to 128% for stem sugar and 245% for stem biomass, indicating the potential for identifying cultivars for immediate use by farmers. The GGE biplot showed that the majority of the genotypes displayed general adaptation although specifically adapted ones were identified. Nine hybrids displayed above 10% positive higher-parent heterosis for stem brix and 16 hybrids for stem biomass. Three hybrids were common for both traits, indicating the gains that can be realised by developing hybrids. General and specific combining ability effects were significant for the major traits, confirming reports that genes with both additive and non-additive action controlled them. Therefore, a breeding programme for general adaptation that exploits both additive and non-additive gene action can result in the delivery of high yielding hybrid sweet sorghum cultivars.

Key words: Combining ability, genotype and genotype by environment (GGE), biplot, heterosis, sorghum hybrids, stem sugar traits.

INTRODUCTION

The potential of sweet sorghum to stimulate rural growth due to its potential industrial use in bioethanol production from stalk sugars has not received enough attention, especially in southern Africa. However, elsewhere, the interest on the use of sweet sorghum for ethanol production is increasing (Rooney et al., 2007) and southern Africa can benefit immensely from the enterprise. Sweet sorghum has a clear comparative advantage over the leading bioethanol crops, sugarcane (*Saccharum officinarum* L) and maize (*Zea mays* L), in bio-fuel production because it can grow under dryland conditions where sugarcane cannot grow (Tsuchihashi and Goto, 2008) and does not compromise, but rather complement food security efforts, unlike maize. This makes it a desirable crop for southern Africa and Sub-Saharan Africa in general. Further, the use of hybrid sorghums can improve productivity because they have been demonstrated to be more productive than pure line varieties in sorghum, with reports of up to 60% advantage being reported (Li and Li 1998; Kenga et al., 2004; Kamau, 2007). Higher parent heterosis levels of up to 45% for stem brix and 150% for stem biomass have been reported (Corn, 2008; Makanda et al., 2009; Pfeiffer et al., 2010). The high potential for exploiting heterosis in hybrid development can therefore not be over emphasised.

The gene action involved in controlling stem sugar, stem biomass and the associated traits have been reported from the current set of germplasm, but only under non-traditional dry off-season conditions under

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irrigation (Makanda et al., 2009). The hybrids have not been evaluated for performance and gene action for the traits during the summer season (November to March) in the tropical low- and mid-altitude environments where sorghum plays a significant role in southern Africa. The germplasm is likely to behave differently hence the need for multi-environment testing covering these environments. Studies on sweet sorghum have concentrated on production (Guiying et al., 2000; Woods, 2000; Claassen et al., 2004; Tsuchihashi and Goto, 2004; Corn, 2008; Tsuchihashi and Goto, 2008), but very little has been done on the genetics and hybrid response to environments. In a few studies conducted elsewhere, stem sugar has been reported to be quantitatively inherited with genes showing both additive and non-additive effects being important, showing low to medium heritabilities and some quantitative trait loci being identified (Schlehuber, 1945; Baocheng et al., 1986; Guiying et al., 2000; Natoli et al., 2002; Ritter et al., 2008). Nevertheless, heritability information is pertinent to the environment and set of germplasm used (Falconer and Mackay, 1996), hence the need to evaluate the current set of germplasm across the target environments and quantify genotype by environment interaction effects (G × E).

Approaches that identify entries showing high performance in both specific and general environments are desirable for G × E quantification. This relationship is easily shown with the assistance of graphical displays (Yan et al., 2000). The GGE biplot method achieves this by graphically showing the G × E in a two dimensional space thereby giving a visual presentation of the relationships between genotypes and environments. It identifies genotypes performing best, poorest and those generally stable across the evaluation environments. The application of the GGE biplot procedure in crops for G × E analysis has been extensively discussed by many authors including Yan et al. (2000), Yan (2001), Yan and Kang (2002), Blanche et al. (2007) and Ding et al. (2007).

Given the foregoing, the current study aimed at generating information on gene action controlling stem sugar traits under the traditional in-season growing conditions across four tropical low and mid-altitude environments. This complements the off-season information presented in Makanda et al. (2009), thereby aiding formulation of a breeding strategy for sweet sorghum cultivar targeting the two potential growing conditions in the region. Further, the study quantified G × E for the stem sugar traits using the GGE biplot method using data from the four environments generated in the current study and the two additional off-season environments data reported in Makanda et al. (2009).

MATERIALS AND METHODS

Experimental materials, sites and management

The study was conducted using 80 experimental hybrids generated from crossing 10 male-fertile lines (males) with eight male-sterile (female) lines in accordance with a North Carolina design II mating scheme (Table 1). The experiments were conducted during 2008 to 2009 as row-column α-lattice designs with two replications at Chokwe research station (CRS-S) (24°31′S; 33°0′E, 40 m.a.s.l) in Mozambique, Makhathini research station (MRS-S) (27º24'S; 32º11'E, 72 m.a.s.l.) in South Africa, Rattray-Arnold research station (RARS-S) (17º40'S; 31º14'E, 1308 m.a.s.l.) in Zimbabwe and at Ukulinga research farm (URF-S) (30º24'E; 29º24'E, 781m.a.s.l.) in South Africa during summer (November 2008 to April 2009). Both CRS-S and MRS-S represent the tropical lowland environments in southern Africa. The two sites have annual long term mean rainfall of about 600 mm and maximum temperatures of about 25 to 30°C (Figure 1). RARS-S and URF-S represent the mid-altitude environments with annual rainfall of about 800mm and maximum temperatures of 20 to 30°C (Figure 1). These four environments were used for the agronomic and gene action analyses in this manuscript, while two additional off-season environments described in Makanda et al. (2009) were used for the GGE biplot analysis.

Data collection and analysis

Stem sugar concentration was measured in brix, using an Atago PAL-1 digital hand-held pocket refractometer at the hard dough stage of each entry. The stems were divided into three equal sections and three brix measurements were taken from the middle internode of each section by squeezing the juice into the sample stage of the refractometer using a pair of pliers. Both the pliers and the refractometer sample stage were rinsed with clean water and dried before the next sample was measured to avoid cross sample contamination. Stem diameter and stem juiciness score were also measured from the three mid internode sections using a veneer calliper and a rating scale of 1, 3, 5, 7, and 9; where 1 (juicy) to 9 (dry) depending on the ease of pressing and resultant juice pressed, respectively. The final values for stem brix, diameter and juice score were an average of the three measurements. Stem biomass was measured at the hard dough stage by stripping five plants of all leaves and heads, then cutting at ground level and weighing the stems. Plant height was measured using a graduated 3.0 m measuring stick. Number of days to 50% flowering (time in days taken for half of the plants in a plot to reach anthesis) were also measured by visual inspection.

Data were analysed using restricted maximum likelihood (REML) procedure in GenStat (Payne et al., 2007). Yield advantage over standard check variety (YASC) was computed according to Makanda (2009). General analyses of all entries and combining ability analyses were performed using fixed effects models (Table 2). In the combining ability analysis, the hybrid variation was partitioned into male and female parent main effects giving two independent estimates of GCA effects, while the male × female interaction estimates the SCA effects (Hallauer and Miranda, 1988). The higher parent (HP) heterosis, GCA and SCA effects for the parents and their standard errors (SE) and standard errors of a difference (SED) were calculated according to Makanda (2009). The GGE biplots were computed for stem sugar and stem biomass in GenStat (Payne et al., 2007). The mean stem brix and stem biomass yield of the 18 parents were correlated to their GCA effects and the GCA effects for plant height, stem diameter, stem juiciness, and days to 50% using the Pearson's correlation coefficient (r).

RESULTS AND DISCUSSION

Mean performance and yield advantage over the standard check

Environments, entries, and environments × entry

Table 1. Name, origin and pedigree of parental sorghum lines and introduced check varieties used in the study.

Line number	Name	Fertility status	Origin	Pedigree	Role in crosses
1	ZLR1 †	CMF	Zimbabwe	Landrace	Male
2	MRL15	CMF	-	-	Male
3	ICSV700	CMF	ICRISAT India	(IS 1082 × SC 108-3) -1-1-1-1-1	Male
4	ICSV93046	CMF	ICRISAT India	(ICSV 700 × ICSV 708) -9-1-3-1-1-1	Male
5	S35	CMF	ICRISAT India	-	Male
6	Macia	CMF	Mozambique	SDS 3220	Male
7	ZLR2	CMF	Zimbabwe	Landrace	Male
8	ICSR165	CMF	ICRISAT India	SPV 422	Male
9	ICSR57	CMF	ICRISAT India	(SC 108-3 ×148) -12-5-3	Male
10	IMDP97	CMF	-	-	Male
11	ICSA731	CMS	ICRISAT India	ICSV 1171BF	Female
12	ICSA479	CMS	ICRISAT India	[9ICSB 70 × ICSV 700) × PS 19349B] -5-4-1-2-2	Female
13	ICSA4	CMS	ICRISAT India	[(BT× 622 × UChV2)B lines bulk] -10-1-1	Female
14	ICSA724	CMS	ICRISAT India	ICSP 1B/R MFR-S 7-303-2-1	Female
15	ICSA307	CMS	ICRISAT India	[(ICSB 26 × PM 1861)×(ICSB 22 × ICSB 45) × (ICSB 52 × ICSB 51)]1-3-12-3-1	Female
16	ICSA474	CMS	ICRISAT India	(IS 18432 × ICSB 6)11-1-1-2-2	Female
17	ICSA26	CMS	ICRISAT India	[(296B × BT× 624)B lines bulk] -2-1-1-3	Female
18	ICSA623	CMS	ICRISAT India	(ICSB 11 × PM 17467B) 5-1-2-1	Female
Introduced checks					
Saccaline		CMF	USDA	-	
Grassl		CMF	USDA	-	

† = regional check; CMF = cytoplasmic male fertile; CMS = cytoplasmic male sterile; - = unknown.

interaction effects were significant (P≤0.01) for all traits (Table 2). Site means for stem brix ranged from 7.9° brix at MRS-S to 12.6° brix at URF-S (Table 3). Stem biomass showed similar trends with CRS-S recording the lowest (29,911kg ha-1) and RARS-S the highest (37,708 kg ha-1) (Table 4). High overall means observed at RARS-S and URF-S for stem brix and stem biomass can be attributed to optimum mean temperatures of between 25 and 30°C recorded at these environments compared to MRS-S and CRS-S (Figure 1). Higher tropical-lowland (CRS-S and MRS-S) maximum temperatures of 30 to 45°C recorded during the experiment could largely explain the generally low stem brix values and stem biomass yields observed in those environments. However, an improvement in stem brix and stem biomass yields during the in-season compared to off-season values (Makanda et al., 2009) was noted and could be explained by the fact that growth temperatures were considerably low during the off-season hence reduced growth. This is consistent with the reports that growth is enhanced as temperatures rise from the minimum to about 30°C in sorghum but after which growth is reduced due to too high temperatures (du Plessis, 2008). Generally, the stem brix and stem biomass values observed in this study were comparable to the 13.4 - 18.5° brix and 39.5 t ha^{-1} and 140 t ha^{-1} reported by Guiying et al. (2000),

Table 2. Mean squares for stem brix and associated traits of sorghum hybrids across four summer (in-season) environments.

Source of variation	Adjusted d.f.	Stem brix	Stem juice score	Stem biomass (t ha^{-1})	Plant height (cm)	Stem diameter (mm)	Days to 50% flowering
Evt	3	203.39**	170.70**	64.58**	592.81**	1009.19**	201.14**
Rep (Evt)	4	6.66	0.96	28.77	20.72	29.91	1.40
Block (Rep) (Evt)	132	170.93	54.59	131.30	154.00	212.42	118.47
General analysis of all entries including checks and parents							
Genotypes	99	498.90**	135.58*	732.13**	2511.25**	248.77**	1168.76**
Evt*Genotype	297	547.31**	123.93	387.52**	559.68**	315.59**	417.18**
Error	265	4.96	3.69	164997106.00	556.00	6.02	19.35
Combining ability analysis							
Hybrids	79	386.22**	75.76	361.94**	1511.08**	216.56**	738.12**
GCA_m	9	104.28**	18.46	144.97**	858.29**	105.36**	506.10**
GCA_f	7	79.35**	10.24	43.61**	288.29**	10.40	24.19**
SCA	63	202.59**	47.06	173.36**	364.50**	100.79**	207.83**
Evt*Hybrids	237	612.09**	98.09	295.71**	634.23**	305.26**	487.12**
Evt*GCA_m	27	108.76**	13.29	106.44**	287.34**	90.75**	310.05**
Evt*GCA_f	21	130.12**	17.02	30.53	60.62**	39.06*	24.72**
Evt*SCA	189	373.21**	67.78	158.75	286.26**	175.45	152.35**
Error	185	4.65	4.33	187954118.00	511.30	5.16	17.40

Evt = environments; **, * significant at P≤0.01 and P≤0.05, respectively.

Woods (2000), Tsuchihashi and Goto (2004) and Claassen et al. (2004) in Zimbabwe, Indonesia, Europe, and the USA.

The correlation coefficients between the reported traits and the associated traits were significant, that is plant height and stem biomass ($r = 0.603$; $P<0.001$), stem diameter and stem biomass ($r = 0.423$; $P<0.001$) and stem juice score and stem brix ($r = -0.665$; $P<0.001$). Therefore, only stem brix and stem biomass are reported in detail in this section. Hybrids dominated the top 20 performers, 14 for stem brix (Table 3) and 17 for stem biomass (Table 4) across the four environments. The top 20 performers displayed between 108 and 128% YASC for stem brix and 24 to 245% for stem biomass across the four environments. The dominance of hybrids can be attributed to heterosis and suggested that hybrid cultivars are superior to pure line varieties for both traits. This is consistent with Corn (2008) and Pfeiffer et al. (2010) who found hybrid cultivars to be better performing for the traits and concluded that they are more desirable for increasing sugar content and biomass yields in sweet sorghum. Some entries recording very high or very low values in individual environments were also identified. For example high values of 16.1° brix to 17.9° brix of entries ISCV93046 and ICSV700 × ICSA307 at URF-S and ICSR165 at CRS-S and low values of between 5.7 and 9.2°brix for ICSV93046 and Saccaline at MRS-S and Macia × ICSA307 at URF-S (Table 3). Stem biomass yields showed similar trends with high yields being recorded at RARS-S and entries Grassl, ICSR165×ICSA26 and ICSR165×ICSA474 attaining above 80,000 kg ha^{-1}. Most entries showed consistency of performance across the environments for both stem brix and stem biomass. A few inconsistencies

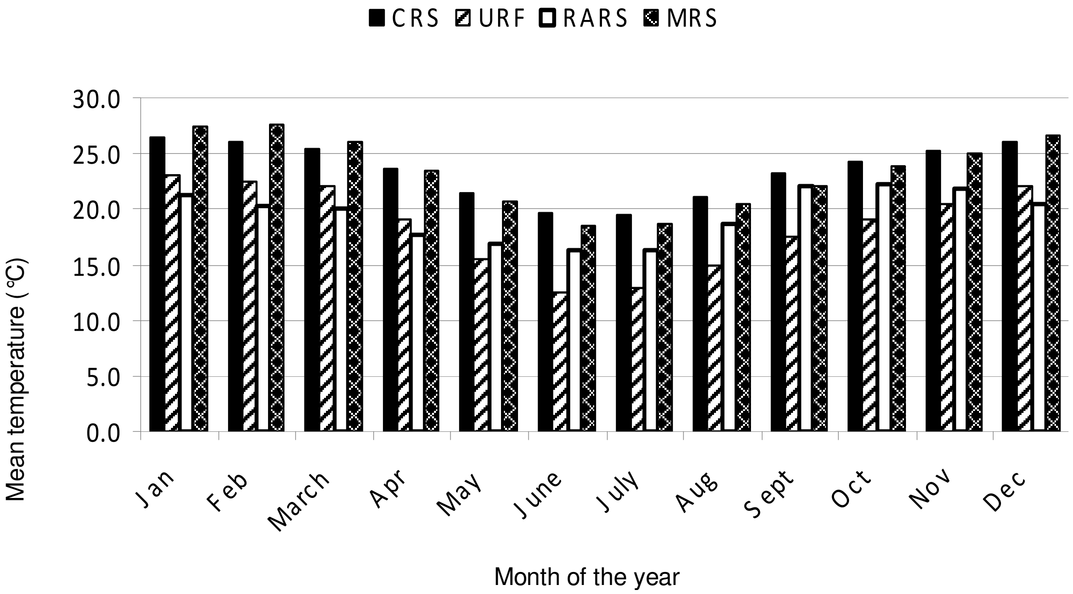


Figure 1. Mean temperatures for Chokwe Research Station, Ukulinga Research Farm, Rattray Arnold Research Station and Makhathini Research Station (Source: Makanda, 2009).

Table 3. Stem brix of selected sorghum hybrids, parents and check varieties over four environments in southern Africa (genotype by environment mean matrix SED = 1.11).

Entry	CRS-S	MRS-S	RARS	URF	Mean	YASC (%)
Top 20 stem brix performers						
ICSV93046 × ICSA4	14.50	11.55	15.15	14.53	13.93	128.17
ICSV700 × ICSA731	13.77	12.35	15.45	13.40	13.74	126.43
ICSR165 × ICSA4	15.88	12.90	10.35	15.20	13.58	124.95
ZLR1 × ICSA307	14.75	9.50	15.18	14.82	13.56	124.77
ZLR1 × ICSA26	13.78	12.57	14.03	13.82	13.55	124.66
ICSR165 × ICSA479	11.00	-	16.00	-	13.50	124.20
ICSV700 × ICSA307	15.80	11.75	10.15	16.10	13.45	123.74
MRL15 × ICSA4	11.38	12.38	13.90	15.38	13.26	121.99
ICSR165 × ICSA307	14.32	10.95	14.70	13.07	13.26	121.99
ICSB479*	12.57	10.25	13.90	15.72	13.11	120.61
ICSR165*	16.27	10.53	12.68	12.72	13.05	120.06
ICSR165 × ICSA26	13.25	10.75	14.70	13.20	12.98	119.37
MRL15 × ICSA26	15.38	12.43	13.68	10.10	12.90	118.65
ICSR165 × ICSA724	12.65	9.75	15.47	13.57	12.86	118.31
ICSV700 × ICSA4	14.57	9.90	13.40	13.15	12.76	117.34
ICSB4*	-	-	12.23	-	12.23	112.51
ICSB307*	13.05	7.55	11.22	16.82	12.16	111.87
Saccaline ‡	-	9.22	12.02	14.88	12.04	110.76
Macia×ICSA307	15.52	10.60	13.15	8.28	11.89	109.36
ICSV93046*	12.75	5.72	11.06	17.85	11.85	108.97
Bottom 5 stem brix performers						
MRL15 × ICSA724	3.73	4.97	11.22	9.48	7.35	67.62
Robbocane 11/59	9.10	4.65	5.10	9.62	7.12	65.48
ZLR2 × ICSA724	1.88	6.58	6.75	12.35	6.89	63.39
Msinga	-	6.03	4.90	9.30	6.74	62.04

Table 3. Contd.

ICSV700 × ICSA474	8.55	4.08	8.22	6.42	6.82	62.72
Parents						
ZLR1 †	13.05	8.57	9.82	12.02	10.87	100.00
ICSV700*	13.12	7.85	10.55	15.77	11.82	108.76
IMDP97	10.28	7.58	-	13.05	10.30	94.79
ICSB724	13.85	4.70	8.32	16.23	10.78	99.13
ICSB731	15.05	4.82	11.40	12.38	10.91	100.39
ICSB623	10.10	12.10	4.90	14.22	10.33	95.03
Macia	13.65	7.62	8.16	15.40	11.21	103.10
MRL15	12.57	7.55	8.25	12.52	10.22	94.04
S35	11.28	5.75	5.58	16.65	9.82	90.29
ICSB26	9.93	4.33	9.90	13.50	9.42	86.61
ICSR57	11.00	8.10	8.93	10.68	9.68	89.03
ZLR2	10.78	5.75	3.33	11.15	7.75	71.32
ICSB474	8.85	5.47	9.25	9.70	8.32	76.52
Site means	10.88	7.90	10.70	12.56		
Trial (overall) mean					10.51	

†, ‡ = regional and introduced stem brix checks, respectively; * = parents in the top 20 and bottom 5; – = data not available; YASC (%) = percent yield advantage over standard check variety.

Table 4. Stem biomass (kg ha^{-1}) performance of selected sorghum hybrids, parents and check varieties over four environments in southern Africa (genotype by environment mean matrix SED = 6422.56).

Entry	CRS-S	MRS-S	RARS	URF	Mean	YASC (%)
Top 20 biomass performers						
Grassl ‡	63114	69904	82381	95089	77622	245
ICSR165×ICSA26	48643	49291	94143	68549	65157	206
ICSR165*	55971	72827	50571	64732	61025	193
ICSR165×ICSA474	46429	53764	85714	55022	60232	190
MRL15×ICSA474	33200	107557	38857	47768	56846	179
ICSV93046*	33243	53296	48190	92232	56740	179
MRL15×ICSA4	34857	71196	60000	42411	52116	164
ICSR165×ICSA4	47164	58664	51762	47121	51178	161
ICSR165×ICSA307	57557	42125	49667	53616	50741	160
ICSV93046×ICSA26	39657	48211	65190	36607	47416	150
ZLR1×ICSA479	27343	60018	52571	44643	46144	146
S35×ICSA4	45643	68854	33429	35525	45863	145
ICSV93046×ICSA307	54929	43380	51667	32701	45669	144
S35×ICSA307	46693	56798	53000	25558	45512	144
ICSV700×ICSA731	43021	32112	57905	45089	44532	140
ICSV93046×ICSA731	50914	35564	51000	39576	44264	140
ICSV700×ICSA307	28414	51143	54048	42411	44004	139
IMDP97×ICSA4	41029	46836	33190	37054	39527	125
ZLR1×ICSA474	28136	26450	70286	30089	38740	122
ICSV700×ICSA474	30357	29150	55714	33973	37299	118
Bottom 5 biomass performers						
Macia*	17505	22012	15238	17031	17947	57
ICSB724*	14836	15284	15000	27991	18278	58
ICSB731*	17550	6736	6667	30513	15367	48

Table 4. Contd.

ICSB26*	14807	8807	16143	15558	13829	44
Robbocane 11/59	6600	12693	20667	12768	13182	42
ICSB623*	9543	3196	12000	6161	7725	24
Parents						
ZLR1 †	23143	27941	57500	31696	35070	111
ICSV700	16821	36968	25714	55737	33810	107
IMDP97	31629	38395	-	12768	27597	87
ICSB474	17493	22468	49286	24554	28450	90
MRL15	39957	29168	27333	22857	29829	94
S35	32271	35773	10429	12455	22732	72
ICSB479	2910	457	24952	35714	16008	51
ICSR57	29729	16971	15571	27232	22376	71
ICSB307	26914	5814	11429	26741	17725	56
ZLR2	20764	8014	17286	15000	15266	48
ICSB4	-	-	3333	-	3333	11
Site means	29911	33235	37708	30200		
Trial (overall) mean					32763	

†, ‡ = regional and introduced stem brix checks, respectively; * = parents in the top 20 and bottom 5; – = data not available; YASC (%) = percent yield advantage over standard check variety.

were also noted. For example, for stem biomass entries such as ZLR1 × ICSA474 and MRL15 × ICSAS474 showed high levels of inconsistencies (Table 4).

Overall, genotype behaviour during the in-season tropical low- and mid-altitude environment conforms to the off-season tropical lowland results reported in Makanda et al. (2009). This implies that any of the three environments can be used for selection of genotypes with adaptation to all the environments. The result is a shortened breeding cycles because the off-season will also be used for selection, rather than for merely advancing of breeding generations as is usually the case. Further, the observation that at least 18 entries for stem brix and 20 for stem biomass had above 110% YASC suggested that it was possible to identify cultivars with higher performance than the currently used variety for immediate use by farmers while breeding efforts continue. However, although hybrids were largely superior, the high performance demonstrated by pure line entries such as ICSB479, Saccaline, ICSR57, ICSR165, ICSB4, ICSB307, and ICSV93046 for stem brix and Grassl, ICSR165 and ICSV93046 for stem biomass (Tables 3 and 4) shows that pure line varieties still have a role to play. Further, the variable times to 50% flowering, indicated the possibility for selection for stem sugar traits for different season lengths found in the tropical lowland and dry mid-altitude environments in the region. Long season, high biomass cultivars can be developed for the mid-altitude environments, such as RARS-S and URF-S, to take advantage of moisture available thereby maximise sugar yields. Alternatively, short season cultivars can be bred for the tropical lowland environments such as MRS-S and CRS-S.

GGE biplot stability analysis

The stem brix GGE polygon biplot (Figure 2a) showed that the environments MRS-W, MRS -S and CRS-S were positively correlated having an angle of the less than 90° between them from the origin as explained by Ding et al. (2007). These occupied the same sector in the biplot, demonstrating their similarity, implying that they discriminated the genotypes in a similar way for stem brix (Ding et al., 2007). The similarities among these environments could have been brought about by having experienced similar temperatures during the evaluation periods (Figure 1). Genotypes ICSB623 (IMDP16) and ribbocane 11/59, which occupied the vertexes in the sector occupied by these environments in the stem brix biplot, showed high performance in them (Figure 2a). The same applies to URF-S and RARS-S which are both mid-altitude environments (Figure 2a). CRS-W, though showing high positive correlation with MRS-S, occupied its own sector and the genotype ICSB307 (IMDP13) showed high performance in it. URF-S and RARS-S were also positively correlated with each other and hybrid ICSV700 × ICSA479 (IMDP34) showed high performance in both environments (Figure 2a). However, genotypes such as ICSR165 × ICSA26 (IMDP71) and ICSV93046×ICSA731 (IMDP41), which occupied the vertexes opposite those sectors occupied by the

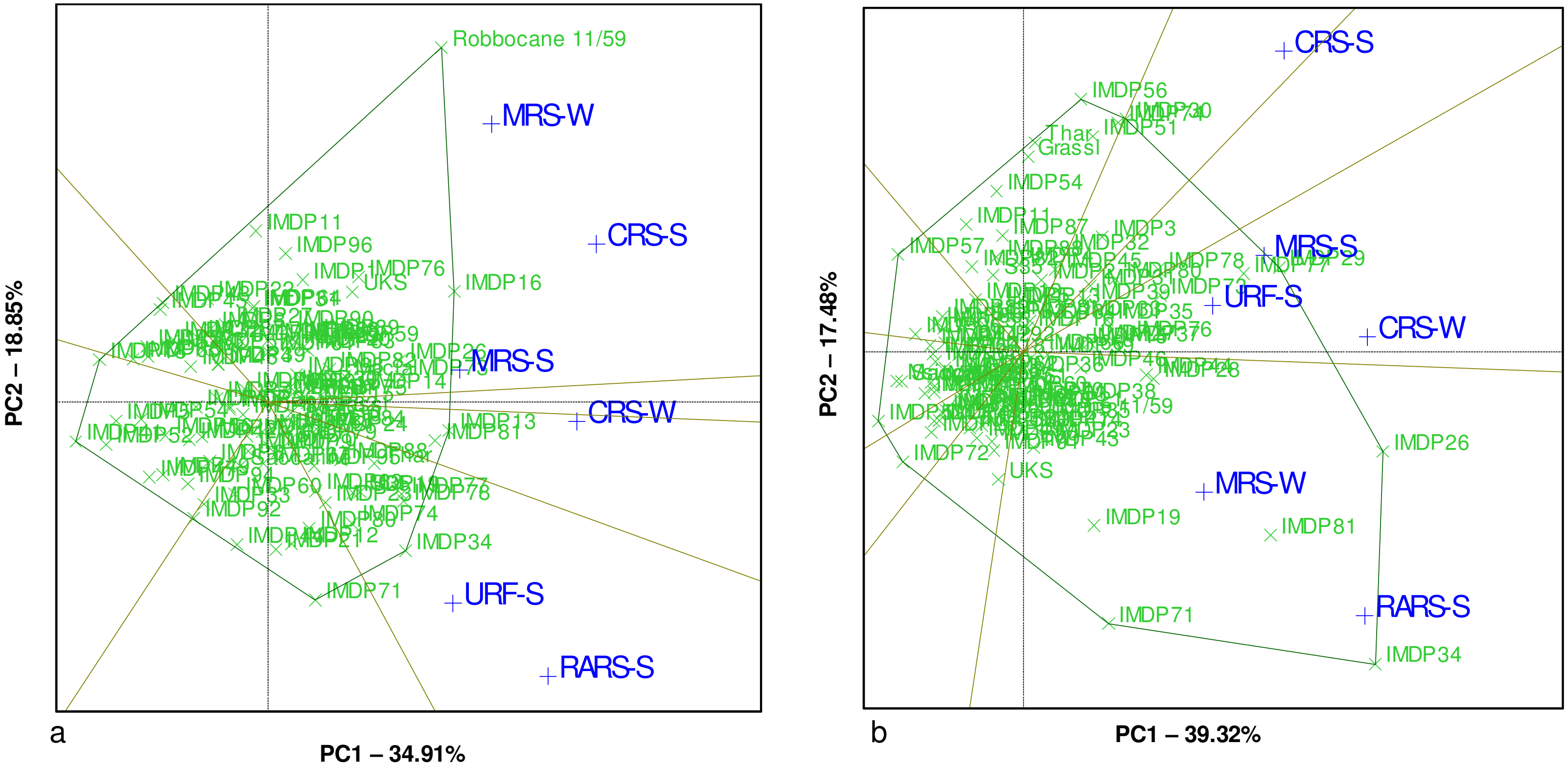


Figure 2. GGE biplot for (a) stem sugar concentration (°brix) and (b) stem biomass (kg ha^{-1}) of genotypes with the environments.

environments (Figure 2a), showed poor performances in all the environments. The rest of the genotypes did not show any specific adaptation and hence showed general adaptation across environments. Stem biomass showed similar trends. CRS-S was in its own sector and was associated with the hybrid MRL15 × ICSA474 (IMDP30) (Figure 2b). However, warmer environments MRS-S, URF-S and CRS-W were highly correlated with each other and genotype MRL15 × ICSA307 (IMDP29) showed high performance in them (Figure 2b). Cooler environments MRS-W and RARS-S were also correlated and had hybrids MRL15 × ICSA479 (IMDP26), ICSV700 × ICSA479 (IMDP34) and ICSR165 × ICSA26 (IMDP71) showing high performance in them (Figure 2b). As was the case with stem brix, the rest of the genotypes were generally stable across the environments, except for ICSR165 × ICSA623 (IMDP72), Macia × ICSA623 (IMDP57) and ZLR2 × ICSA731 (IMDP56), which occupied vertexes opposite the environments, demonstrating poor performance in all of them.

It seemed, therefore, that temperature was the major determining factor on how the environments discriminated the entries and hence how they were grouped. This implied that testing could be done once in one of the environments showing similar discriminating power for the genotypes (Kroonenberg, 1997). This could see the reduction of testing environments to three out of the six used in this study (two additional environments

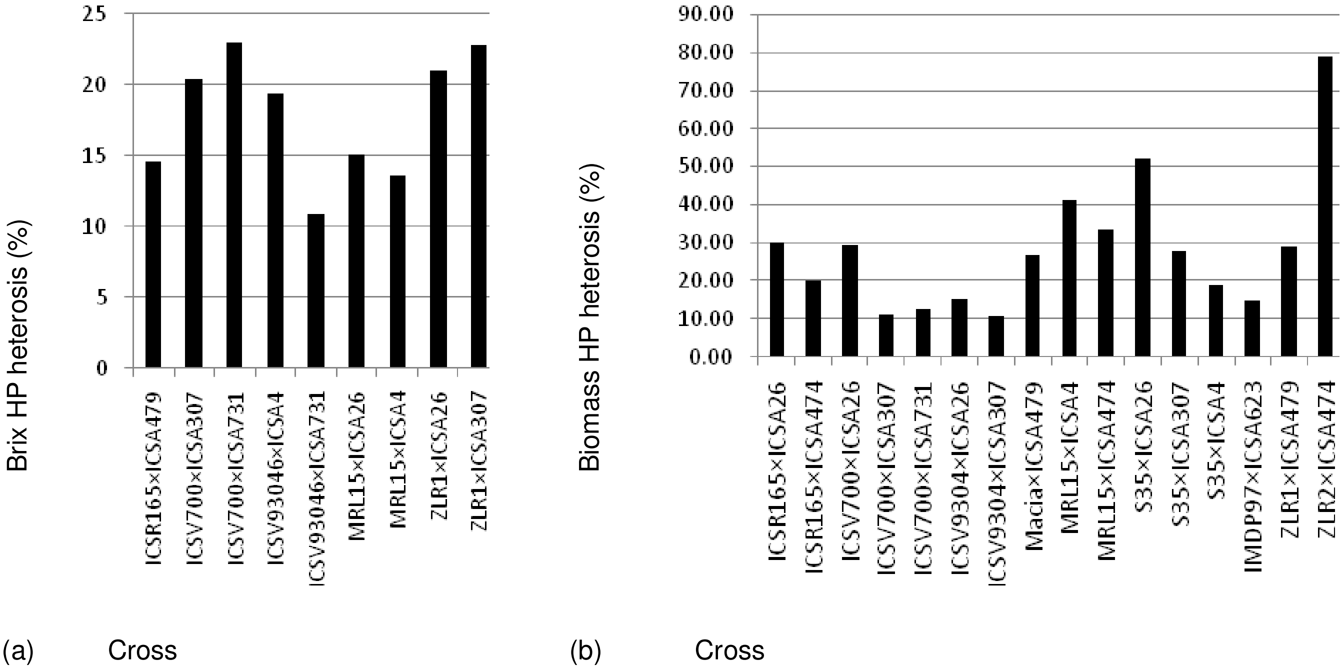


Figure 3. Sorghum hybrids displaying above 10% higher-parent heterosis across the four environments for (a) stem sugar and (b) stem biomass.

from Makanda et al. (2009) used in the GGE Biplot analysis). This, coupled with the possibility of both off-season and in-season selection in the tropical lowland environments like Makhathini and Chokwe and in-season selection in the mid-altitude environments like RARS and Ukulinga, may result in the saving of resources and an improvement on the speed of cultivar delivery to the farmers. The study also showed that most of the genotypes demonstrated general adaptation which is an advantage because in a young breeding programme, such as the current one, breeding for general adaptation might result in a higher impact because the cultivars are still scarce in the region. Cultivars can therefore be deployed in a large area. Therefore, this can be pursued as a breeding strategy. However, the identification of specifically adapted genotype that showed high performance in specific environments, for both stem sugar (Figure 2a) and biomass yields (Figure 2b), indicated that there was also potential, from the current germplasm set, to breed for specific adaptation.

Higher parent heterosis

Higher-parent (HP) heterosis values are presented for stem brix and stem biomass because of the relationships (correlations) between these and the associated traits described earlier. Twenty-seven hybrids displayed positive HP heterosis of up to 23% for stem brix. Nine of the hybrids had above 10% HP heterosis of which four were from crosses involving local, adapted parents ZLR1 and MRL15 (Figure 3a). Twenty-five hybrids displayed positive HP heterosis for stem biomass of up to 79%, of which 16 were above 10% (Figure 3b), of which six were constituted from crosses involving local parents ZLR1, ZLR2, IMDP97 and Macia (Figure 3b). Three hybrids ICSV700×ICSA307, ICSV700 × ICSA731 and MRL1 5× ICSA4 displayed above 10% HP heterosis for both stem brix and stem biomass. These heterosis values surpass those reported in the literature (Corn, 2008) but were lower than the 45% stem brix and 150% stem biomass HP heterosis levels reported under off-season tropical lowland conditions from the current set of germplasm (Makanda et al., 2009). The high heterosis levels for both traits could be attributed to higher diversity in the germplasm because both local and introduced parents were used for hybrid production. This is confirmed by the observation that four of the nine crosses for stem brix and six of the 16 crosses for stem biomass with above 10% HP heterosis were constituted from crosses involving local unimproved parents. Heterosis for stem biomass could in part be explained by gene additivity and epistatic effects as reported by Sleper and Poehlman (2006). However, the observation that the majority of the hybrids (53) did not perform better than the higher parent should not be surprising because sorghum, being a self pollinated crop, is vigorous in the homozygosity state and its breeding was for high performance in the homozygous state (Sleper and Poehlman, 2006).

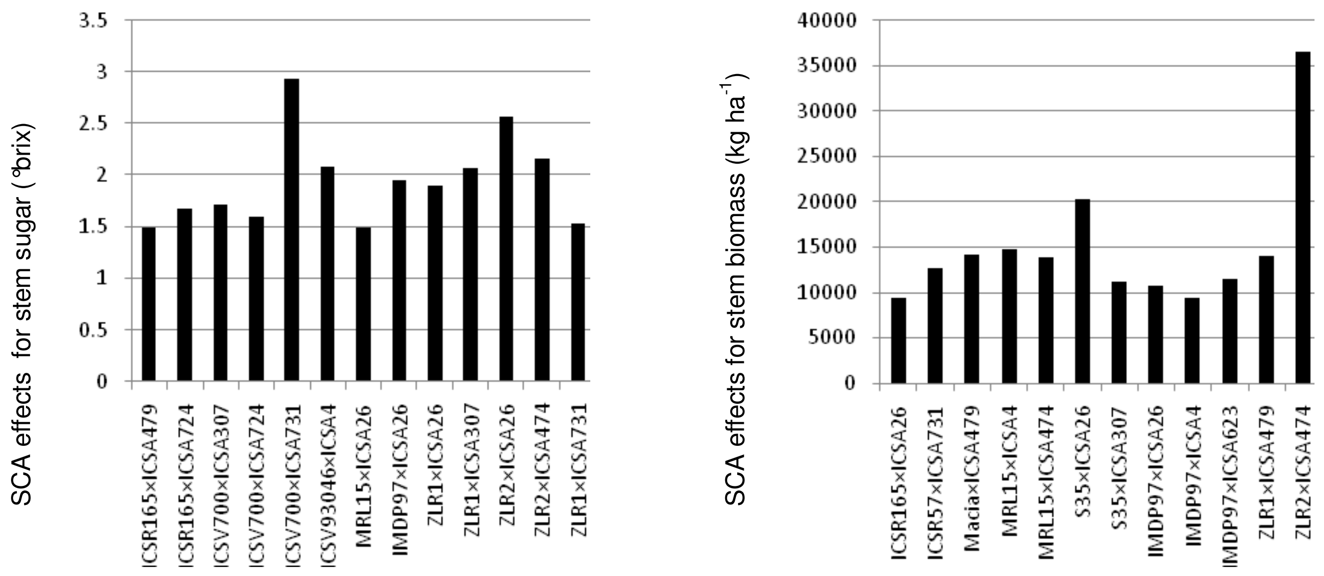
Table 5. GCA effects for the male and female sorghum parents for stem brix, stem biomass and associated traits across four environments in southern Africa.

Parents	Stem °brix	Stem juice score	Plant height (cm)	Stem diameter (mm)	Stem biomass (kg ha^{-1})	Days to 50% flowering
Male parents						
ZLR1	0.45*	-0.51*	12.3**	-1.7**	933.1	-7.8**
MRL15	0.19	-0.31	-2.2	0.5	452.3	3.7**
ICSV700	0.69**	-0.63*	33.2**	-0.7*	4653.8*	-0.8
ICSV93046	0.18	-0.30	27.1**	0.0	6335.0**	1.3*
Macia	-0.04	-0.31	-30.3**	-1.0**	-5808.0**	-7.6**
ZLR2	-1.52**	1.37	-34.9**	-1.0**	-2948.2	-0.1
ICSR165	2.03**	0.86	31.2**	0.8*	15224.7**	10.2**
ICSR57	-0.29	-0.45	-51.1**	-0.9**	-11530.8**	-5.0**
S35	-0.51**	0.31	17.5**	1.8**	748.8	6.0**
IMDP97	-1.20**	-0.20	5.9*	0.9**	-7284.7**	0.9
SE	0.28	0.26	2.95	0.28	1713.7	0.55
SED	0.39	0.37	4.17	0.40	2423.5	0.78
Female parents						
ICSA731	-0.37	0.26	-1.3	-0.4	567.8	1.5*
ICSA479	0.32	0.14	19.4*	-0.3	-3697.2*	-2.1**
ICSA4	1.19**	0.14	-4.6*	-0.7*	1998.6	-1.3*
ICSA724	-1.33**	-0.24	-20.9**	0.1	-4458.8*	1.0
ICSA307	0.56*	-0.74*	-8.6**	-0.6*	-1247.2	0.5
ICSA474	-0.69**	-0.12	38.8**	0.5*	7693.5**	-2.2**
ICSA26	0.72*	0.16	10.2**	0.3	5727.4**	0.5
ICSA623	-0.43	0.43*	-39.4**	0.5*	-7204.7**	1.3*
SE	0.25	0.23	2.64	0.25	1532.8	0.49
SED	0.35	0.32	3.73	0.36	2167.7	0.70

**,* significantly different from 0 at P≤0.01 and P≤0.05, respectively.

Combining ability effects

The male and female GCA effects and SCA effects were significant (P≤0.05) for all the traits, except male GCA effects for juice score and female GCA effects for stem diameter (Table 2). The interaction of both the GCA and SCA effects by the environmental effects were also significant (P≤0.05) for most traits (Table 2). The significance of the GCA effects implied that genes with additive effects were important for most of the traits. This finding supports the reports of a quantitative nature of the genes controlling the traits (Schlehuber, 1945; Baocheng et al., 1986; Guiying et al., 2000; Natoli et al., 2002; Ritter et al., 2008) and contrast to the reports of a single gene controlling stem sugar reported by Ayyangar et al. (1936). Therefore, breeding progress can be achieved through selection. The significance of the SCA effects for the traits suggested the importance of non-additive gene action, results that further support the quantitative nature of the traits and implied that further gains could be achieved through hybridisation of the good general combiners capitalising on non-additive gene effects. However, for stem juiciness, the non-significance of gene additivity contrasts reports by Schlehuber (1945) and off-season reports from the same set of germplasm (Makanda et al., 2009). This could be attributed to different set of germplasm and environments as put across by Falconer and Mackey (1996) thereby emphasising the need to evaluate germplasm in the recommendation domain. For a sweet sorghum hybrid oriented breeding programme, parental lines ICSV700, ICSV93046, ICSA4 and ICSA26 are attractive based on their GCA effects for both stem brix and stem biomass (Table 5). Further, Parents ZLR1, ICSA26 and ICSA307 were involved in crosses that displayed significant SCA effects (Figure 4a and b) and high HP heterosis for stem brix and stem biomass (Figure 3a and b) and also exhibited high GCA effects for stem brix and positive GCA effects for stem biomass (Table 5). These parents showed high potential for sweet sorghum hybrid cultivar development. Therefore, further gains in sugar and biomass performance could be realised through hybridisation after selecting parents with desirable GCA effects and identifying those showing high SCA, in



(a) Cross (b)

Figure 4. Sorghum crosses showing positive and significant SCA effects for (a) stem brix (SE = 0.78; SED = 1.11) and (b) biomass weight (SE = 4847.09; SED = 6854.82) across the four environments. Genetic and GGE biplot analyses of sugar traits in sorghum germplasm.

addition to hybrid means, because they are the ultimate measure of yield performance in the farmers' fields.

Mean performances versus GCA effects

The *per se* mean performance of the parents for stem sugar and stem biomass yield were highly significantly (P≤0.01) correlated to their GCA effects (Table 6), implying that a parent's *per se* performance is a reasonable estimator of its performance *inter se*. In addition, the observed positive and highly significant (P≤0.01) correlation between the stem brix GCA effects and stem biomass GCA effects implied that parental selection can be based on either of the traits and it can be inferred that the parent is a good combiner for the other. This might be useful in situations where data is available for one trait alone but not the other. However, whether this is applicable to all sweet sorghum germplasm is subject to further evaluation, but this was the case in the current germplasm set. The GCA effects for stem biomass were also positively and highly significantly (P≤0.01) correlated with the GCA effects of the parents for plant height (Table 6). This supports the significant correlation reported earlier and provide an avenue for indirect selection of parental germplasm should the stem brix or stem biomass data be lacking.

Conclusions

From the study, it can be concluded that sweet sorghum production could be enhanced by exploiting heterosis in hybrids. The study also confirmed earlier reports that genes with both additive and non-additive effects were important in controlling stem brix, stem biomass and the associated traits in sorghum and lines for use as base germplasm source were identified. Breeding was shown to be possible for either general or specific adaptation. Results also indicated that the mean *per se* performance of a parent for stem brix and stem biomass was a reasonable indicator of its GCA performance. Therefore, selecting of parents based on their GCA effects and mean performance followed by hybridisation is recommended for cultivar development.

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Table 6. Correlation coefficients between parental performances *per se* for stem brix and stem biomass and the combining ability effects.

Parameter	Days to 50% flowering GCA	Plant height (cm) GCA	Stem biomass ($t\ ha^{-1}$) GCA	Mean stem biomass ($t\ ha^{-1}$)	Stem °brix GCA	Mean stem °brix	Stem diameter (mm)	Stem juice score
Days to 50% flowering GCA	1.000							
Plant height (cm) GCA	0.321*	1.000						
Stem biomass ($t\ ha^{-1}$) GCA	0.490	0.790**	1.000					
Mean stem biomass ($t\ ha^{-1}$)	0.348	0.571*	0.602**	1.000				
Stem °brix GCA	0.194	0.417	0.609**	0.351	1.000			
Mean stem °brix	0.143	0.300	0.229	0.276	0.686**	1.000		
Stem diameter (mm)	0.760**	0.337	0.246	0.181	-0.099	-0.111	1.000	
Stem juice score	0.462	-0.107	0.190	-0.084	-0.105	-0.259	0.247	1.000

**, * significant at P≤0.01 and P≤0.05, respectively.

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