

# ARTICLE

# General and specific combining ability in sweet sorghum

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**Abstract:** In breeding of sweet sorghum hybrids, non-additive genetic effects are important in phenotypic expression of the traits of interest. The aim of this study was to evaluate the general combining ability (GCA) of sweet sorghum lines and the specific combining ability (SCA) of the hybrids for agronomic and technological traits. Five fertility restorer lines, four male-sterile lines, and their hybrids from partial diallel crosses were evaluated in experiments laid out in a 5 x 6 triple rectangular lattice design in the municipalities of Lavras, MG and Sete Lagoas, MG, Brazil. Diallel analysis was performed using the Griffing model adapted to partial diallel crosses. There was a significant effect of GCA and SCA for most of the traits evaluated, indicating the participation of additive or dominant genes in inheritance. The restorer lines CMSX508, BRS 511, CMSXS643, and CMSXS646 show potential for use as parents in sorghum breeding programs. **Keywords:** Sorghum bicolor, parent selection, partial diallel, hybrid breeding.

#### **INTRODUCTION**

Brazil is prominent worldwide for its use of renewable sources for energy production. Biofuel produced in Brazil is largely ethanol, with sugarcane (*Saccharum* spp. L.) as the main feedstock. Nevertheless, the sugarcane crop has some particular features that compromise the feedstock supply for sugarcane mills, such as the renewal rate of crop areas (~20% each year) and the off-season period (Souza et al. 2013). Currently, about 2 mi ha of sugarcane crop area is under renewal, and the period from March to April is the off-season. This is the context for strategic efforts to diversify bioenergy crops.

Sweet sorghum [Sorghum bicolor (L.) MOENCH] is an alternative for ethanol production during the off-season of sugarcane, and it can be sown in sugarcane areas under renewal. Sweet sorghum has high concentrations of fermentable sugars in its stalks, and it is possible to process it using basically the same equipment used for sugarcane. Moreover, sweet sorghum has additional advantages, such as its short cycle, propagation by seeds, easy mechanization, wide adaptation, and fewer requirements for agricultural inputs (Kumaret al. 2011, Regassa and Wortmann 2014). Despite these advantages, sweet sorghum has basically been cultivated in experimental areas or on a small scale on farms, where some genotypes have been tested for validation in agricultural and industrial systems. Development of improved cultivars is another important

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<sup>3</sup> Universidade Federal de Lavras, Departamento de Agricultura, 3037, 37.200-000, Lavras, MG, Brazil factor in establishing this crop in the Brazilian ethanol production chain.

Breeding strategies depend on the type of cultivar intended for commercial use. Although sweet sorghum is an autogamous plant, breeding programs have been conducted to obtain hybrids using the milo-kafir genetic-cytoplasmic male sterility system (Reddy et al. 2005, Bunphan et al. 2013). Adoption of this strategy is more justifiable if there is evidence of non-additive gene action in genetic control of the traits of interest, which can be investigated through the use of suitable genetic cross-breeding, such as diallel crosses.

The method of diallel analysis proposed by Griffing (1956) is widely used in the choice of parents since it allows estimation of general combining ability (GCA) and specific combining ability (SCA), previously defined by Sprague and Tatum (1942). Sweet sorghum has been studied in this manner in several countries, with emphasis on characterizing combining ability to produce ethanol (Makanda et al. 2009, Indhubala et al. 2010, Sandeep et al. 2010, Vinaykumar et al. 2011, Umakanth et al. 2012, Bunphan et al. 2015). These studies have encouraged breeding sorghum to obtain hybrids. However, in Brazil, information on the combining ability of sorghum lines is scarce. Information on GCA and SCA can greatly assist more assertive definition of cross-breeding between parents.

The purpose of the present study was to evaluate the general combining ability of elite lines of sorghum and the specific combining ability of the hybrid combinations for agronomic and technological traits.

#### MATERIAL AND METHODS

Lines and hybrids evaluated and experimental design

We evaluated four male-sterile lines (A-lines): CMSXS5503A, CMSXS5504A, CMSXS5505A, CMSXS5508A and five fertility restorer lines (R-lines): BRS 511, BRS 508, CMSXS643, CMSXS646, CMSXS647from the sweet sorghum breeding program of the Empresa Brasileira de Pesquisa Agropecuária (Embrapa Milho e Sorgo) [Brazilian Agricultural Research Corporation – Maize and Sorghum] in Sete Lagoas, state of Minas Gerais, Brazil.

R-lines were developed from breeding populations obtained from crosses involving traditional varieties, such as Wray, Brandes, and Theis (Silva et al. 2017). A-lines were obtained from breeding populations of crosses between elite R-lines with high sugar content and B-maintainer lines rich in juice with low sugar content. In the segregating generations, individual plants were selected based on juice volume, sugar content, and plant height less than 1.5 m. After that, the sterilization process was initiated by backcrosses with a source of sterile cytoplasm. During this process, some B progenies that restored the fertility of A progenies were discarded. These discarded B progenies had dominant alleles of the fertility restorer gene inherited from R-lines in the initial cross.

A- and R-lines were crossed following a partial diallel design and 20 hybrids were obtained. A- and R-lines, hybrids, and the cultivar CV198, used as a check, were evaluated in experiments laid out in a 5 x 6 triple rectangular lattice design (i.e., partially balanced incomplete block design). The plots consisted of two 5.0-m length rows spaced at 0.70 m.

#### Sites and conduction of field experiments

Two experiments were conducted in the 2014/2015 growing season. The first was carried out in the experimental area of Embrapa Milho e Sorgo in the municipality of Sete Lagoas, Minas Gerais, in the central region of the state (lat 19° 27' N, long 44° 14' W, and alt 767 m asl). The soil classification is *Latossolo Vermelho* and the climate is Cwa, temperate rainy (mesothermal), according to the Köppen classification. The second experiment was conducted in the experimental area of the Muquém Farm of the Universidade Federal de Lavras, in the municipality of Lavras, Minas Gerais (lat 21° 14' N, long 45° 00' W, and alt 918 m asl). The soil classification is *Latossolo Vermelho Distrófico* and the climate is Cwa, temperate rainy (mesothermal), according to the Köppen classification.

Basal fertilization consisted of 450 kg ha<sup>-1</sup> of the 08:28:16 NPK formulation in the planting furrow. At 30 days after planting, 200 kg ha<sup>-1</sup> urea was applied in top-dressing. The experiments were manually sown in November 2014. At 15 days after emergence, plants were thinned to leave a stand of 140,000 plants per hectare. The experiments were conducted without irrigation. Other crop treatments were carried out as recommended (Borém et al. 2014). The sorghum was harvested in March 2015, 120 days after sowing in Lavras and 110 days after sowing in Sete Lagoas.

# **Traits measured**

Agronomic and technological traits were measured. Time to flowering (FLOW), representing the number of days after sowing when 50% of the plants of the plot were in flower, was assessed only in Lavras. The plots were cut at 5.0 cm from the ground upon reaching physiological maturity of the grain. In each plot, we measured the production of green mass (PGM) of the whole plants using a digital suspension scale, in kg, which was converted to t ha<sup>-1</sup>. Six plants per plot were taken at random to assess plant height (PH, m) from the ground surface to the apex of the panicle using a tape measure. These plants (without panicle) were ground and pressed in a hydraulic press (Sete Lagoas) or a mill (Lavras) to extract the juice and determine its quantity relative to stalk weight (EXT, %). Total soluble solids (TSS,  $^{9}$ Brix) in a juice sample were determined using an automatic digital refractometer. Total recoverable sugars (TRS, kg of sugar/t of stalk) was determined according to CONSECANA (2006). We then estimated ethanol production (ETH, L ha<sup>-1</sup>) by the equation: *ETH* = hydrous ethanol production (L) × *PGM*.

# Analysis of variance

First, individual analysis of variance was performed with recovery of inter-block information (per site). The Shapiro-Wilk and Q-Q plot tests were applied to check the normality of errors (Ferreira 2005). The relative efficiency of the lattice design was evaluated as described in Ramalho et al. (2012). Experimental precision was determined by the estimate of selective accuracy ( $r_{gg}$ ) (Resende and Duarte 2007). For multi-site analysis, the homogeneity of the residual variances was previously verified by Hartley's test. Statistical analyses were performed using the Im4 R package (Bates et al. 2015, R Development Core Team 2016).

# **Diallel analysis**

The effect of genotypes (lines and hybrids) and the genotype x site interaction was decomposed according to a partial diallel cross design from the adjusted phenotypic means using the Ismeans R package (Russell 2016). In this, we adopted the model proposed by Geraldi and Miranda Filho (1988), which is an adaptation of the Griffing (1956) model for the study of GCA and SCA in a partial diallel design involving parents and F, generations (Cruz et al. 2012).

$$y_{kk'} = \mu + \frac{1}{2} (d1 + d2) + g_k + g_{k'} + s_{kk'} + \overline{e}_{kk'}$$

where  $\overline{y}_{kk'}$  is the mean of the hybrid between the k-th A-line and k'-th R-line;  $\mu$  is the overall mean; d1 and d2 are the contrasts involving the means of the R- and A-lines and the overall mean;  $g_k$  is the GCA effect of the k-th A-line;  $g_{k'}$  is the GCA effect of the k'-th R-line;  $s_{kk'}$  is the SCA effect of the hybrid between the k-th A-line and k'-th R-line; and  $\overline{e}_{kk'}$  is the experimental error.

The significance of the effects present in the diallel model was tested by Student's t-test at 5% probability. Diallel analyses were performed using the Genes software (Cruz 2013).

Radar charts were constructed from the studentized GCA effects of the lines for each trait m  $(t_{k(m)})$  using the following expression:

$$(t_{k(m)}) = \hat{g}_{k(m)} / \hat{s}_{\hat{g}k(m)}),$$

where  $(\hat{g}_{k(m)})$  is the GCA effect of line k for trait m and its respective standard error  $(\hat{s}_{\hat{k}k(m)})$ .

# **RESULTS AND DISCUSSION**

According to the Shapiro-Wilk and Q-Q plot tests, the assumption of normal distribution of errors was not rejected for all traits. The rectangular lattice design did not show a relative efficiency superior to the randomized complete block design (<105%). The experimental precision measured by selective accuracy ( $r_{gg}$ ) was classified as moderate to very high, according to Resende and Duarte (2007).

The multi-site analysis that was performed assumed homoscedasticity because the residual variances did not differ by Hartley's test. The effect of sites was significant (P < 0.05) for all traits evaluated (Table 1), with superior performance of the genotypes in Lavras. These differences can be attributed to variations in macro-environmental conditions, especially rainfall.

# MJ Rocha et al.

There were significant differences (P < 0.05) among genotypes for all traits (Table 1). Several studies have shown genetic variability in sweet sorghum (Umakanth et al. 2012, Elangovan et al. 2014). Genotype × site interaction (P < 0.05) was also observed for most of the traits, except for juice extraction (EXT). Some studies on sweet sorghum have indicated the presence of the genotype × environment interaction for traits related to ethanol yield (ETH) (Umakanth et al. 2012, Souza et al. 2013, Elangovan et al. 2014, Figueiredo et al. 2015).

In general, there were differences (P < 0.05) among the means of the A-lines and the R-lines. This is because the male-sterile lines in this study were initially selected for use in a breeding program for forage and grain sorghum, and thus the A-lines had lower sugar contents in the stalk. The lower height of the A-lines, which is advantageous for mechanical harvest, should also be noted.

From the diallel analysis, we observed a significant effect for GCA and SCA (P < 0.05) for time to flowering (FLOW), production of green mass (PGM), total soluble solids (TSS), total recoverable sugars (TRS), and ETH (Table 1). These results suggest that additive and non-additive genetic effects contribute to phenotypic expression of these traits. Similar results were found by Makanda et al. (2009) and Bunphan et al. (2015). These authors detected additive and dominance effects for the traits TSS and PGM. However, divergent results were reported by Bahadure et al. (2015), in which non-additive effects were not important in expression of TSS. Nevertheless, additive and non-additive effects were important for other traits, such as juice and stalk yield. In a study carried out by Kumar et al. (2016), traits related to sugar yield (e.g., TSS, sucrose content) exhibited moderate inbreeding depression, indicating the existence of genes with dominance action on expression of this trait.

For the PH trait, only SCA was significant, suggesting that non-additive effects were more important in phenotypic expression of this trait (Table 1). However, some studies have suggested additive and dominance effects for PH (Makanda et al. 2009, Bunphan et al. 2015). Significant SCA was not detected for the EXT trait (Table 1). However, other studies

Sources of variation	F-Statistics										
	df	<b>FLOW</b> <sup>1</sup>	df	РН	PGM	EXT	TSS	TRS	ETH		
Site (S)	-	-	1	9.62**	9.42*	18.94*	263.43**	247.25**	174.7**		
Genotypes (G)	(29)	14.36**	29	27.57*	15.94**	1.83*	7.15**	4.11**	9.78**		
GCA A	3	2.56	3	2.51	7.05*	0.46	5.69*	3.63*	6.70*		
GCA R	4	17.84*	4	0.40	7.97*	6.84*	19.52*	11.35*	1.57		
SCA	(20)	4.84*	20	17.78*	11.03*	1.56	6.04*	3.93*	9.75*		
G x S			29	1.80*	2.23**	1.52	3.45**	2.34**	3.43**		
GCA A x S			3	2.44	1.31	1.31	11.40*	8.13*	8.26*		
GCA R x S			4	2.09	4.21*	2.20	3.72*	3.26*	3.72*		
SCA x S			20	10.31*	2.57*	1.72*	2.47*	2.06*	2.90*		
Mean/LA		85.61		2.92a	61.87a	67.92b	14.23a	81.31a	3758.13a		
Mean/SL				2.78b	54.68b	70.02a	10.11b	54.82b	2133.03b		
Mean/A		81.70b		1.70b	31.60b	68.92a	10.35b	59.64b	1383.53b		
Mean/R		92.85a		3.05a	62.29a	69.23a	12.07a	65.7a	3013.87a		
Mean/Hybrids		84.51		2.82	57.57	69.00	12.62	70.93	3242.19		
Mean/Check		87.09		3.27	66.81	67.33	10.78	56.67	2936.23		
r <sub>ĝg</sub> LA (%)		96.46		98.73	96.52	60.41	93.18	86.3	94.19		
r <sub>ĝg</sub> SL (%)				94.06	92.27	63.33	84.62	75.84	86.55		

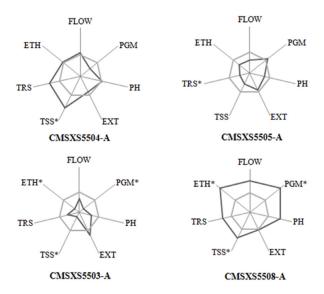
**Table 1.** Summary of analysis of variance and diallel analysis for flowering time (FLOW, days), plant height (PH, m), production of green mass (PGM, t ha<sup>-1</sup>), juice extraction (EXT, %), total soluble solids content (TSS, % juice), total recoverable sugars (TRS, kg sugar/t of stalks), and ethanol production (ETH, L ha<sup>-1</sup>) evaluated in lines and hybrids of sweet sorghum at two sites

<sup>1</sup>measured only in Lavras, MG. \*, \*\*Significant at 5% and 1% probability by the F-test, respectively; Means followed by different letters in the same column are different by the F-test.

have found a non-additive effect for this trait (Umakanth et al. 2012, Bunphan et al. 2015, Kumar et al. 2016). It should be emphasized that SCA depends on genetic divergence between the parental A- and R-lines in the loci related to the target trait with dominance action. Thus, complementarity between the A- and R-lines might not have been observed in the present study.

Significant effects were detected for GCA of the A-lines for PGM, TSS, TRS, and ETH and also for GCA of the R-lines for FLOW, PGM, EXT, TSS, and TRS (Table 1). These results suggest dissimilarity within the groups of the A- and R-lines for these traits. Thus, these lines are expected to promote variation in the average performance measures of the hybrids produced.

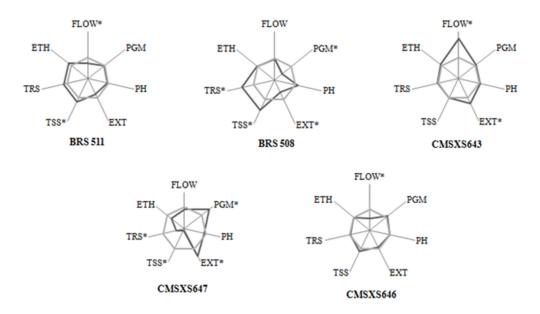
According to Cruz and Vencovsky (1989), the estimate of GCA is considered an efficient and informative criterion for parent selection. However, significant GCA × site interaction was observed for the traits PH, EXT, TSS, TRS, and ETH (Table 1). Moreover, there was also significant SCA × site interaction for all the traits studied. Although these results suggest that GCA and SCA were influenced by the



**Figure 1.** Graphical representation of the studentized effects of the general combining ability of the A-lines of sweet sorghum for the traits evaluated in Lavras and Sete Lagoas, MG, Brazil. \* Significant at 5% probability by t-test.

environment, the average effects across sites can be considered for purposes of the breeding program.

The significance of GCA indicates the existence of different allele frequencies among the A- and R-lines, and the most promising lines can be identified for use in breeding programs to extract lines that exhibit a higher frequency of favorable alleles. Thus, CMSXS5508A and CMSXS5504A can be highlighted as promising male-sterile lines (Figure 1). For the R-lines, BRS 511, CMSXS643, and CMSXS646 showed better GCA regarding ethanol production and traits related to feedstock quality (Figures 2).



*Figure 2.* Graphical representation of the studentized effects of the general combining ability of the lines R of sweet sorghum for the traits evaluated in Lavras and Sete Lagoas, MG, Brazil. \* Significant at 5% probability by t-test.

# MJ Rocha et al.

The BRS 508 line exhibited positive and significant effects for TSS and TRS; however, it led to a decline in the mean PGM of the hybrids (Figure 2). The CMSXS647 line showed positive and significant effects for PGM and EXT, but resulted in lower TSS and TRS. One possibility for the breeding program is crossing these two lines to combine their advantages.

1 <b>/</b> 11						
Line/Hybrid	FLOW	РН	PGM	TSS	TRS	ETH
CMSXS5504A	3.07*	-0.37*	-10.04*	-1.46*	-10.16*	-907.82*
CMSXS5505A	3.09*	-0.48*	-11.48*	-0.51	0.93	-422.9
CMSXS5503A	1.25	-0.45*	-10.94*	-1.41*	-9.34*	-793.32*
CMSXS5508A	1.08	-0.65*	-14.42*	-0.95*	-6.79*	-1086.71
3RS 511	-1.22	-0.41*	-8.80*	-0.71*	-3.94	-515.7*
3RS 508	1.49*	-0.52*	-7.73*	-1.19*	-7.23*	-696.66*
CMSXS643	3.88*	-0.41*	-12.83*	-0.64*	-3.48	-669.40*
MSXS646	3.23*	-0.31*	-10.70*	-0.94*	-6.82*	-791.54*
CMSXS647	1.12	-0.29*	-6.82*	-0.85*	-3.96	-537.45*
MSXS5504A x BRS 511	-0.48	0.17*	3.8	1.55*	11.23*	609.46*
MSXS5504A x BRS 508	-2.04*	020*	7.78*	1.01*	7.06*	674.21*
MSXS5504A x CMSXS643	-1.48	0.20*	3.82	-0.29	-2.67	-23.92
CMSXS5504A x CMSXS646	-1.67	0.11	4.25	0.19	5.55	498.61*
MSXS5504A x CMSXS647	-0.45	0.07	0.44	0.46	-0.85	57.26
MSXS5505A x BRS 511	0.84	0.22*	1.86	-0.09	-1.86	-57.06
MSXS5505A x BRS 508	0.22	0.20*	3.54	0.38	-0.48	200.11
MSXS5505A x CMSXS643	-2.84*	0.23*	4.23	0.27	0.58	135.12
MSXS5505A x CMSXS646	-1.77	0.1	3.5	0.19	-0.38	128.07
CMSXS5505A x CMSXS647	-2.65*	0.20*	9.81*	0.27	0.28	439.56*
MSXS5503A x BRS 511	1.41	0.14	3.22	0.26	0.79	139.66
MSXS5503A x BRS 508	-1.96*	0.23*	8.25*	-0.1	1.76	531.37*
MSXS5503A x CMSXS643	-1.31	0.29*	4.95	0.61	4.37	306.61
MSXS5503A x CMSXS646	-1.81*	0.15*	1.8	1.67*	9.59*	394.08*
MSXS5503A x CMSXS647	1.17	0.1	3.68	0.38	2.26	214.94
MSXS5508A x BRS 511	0.68	0.29*	8.72*	-0.31	-2.28	339.34
MSXS5508A x BRS 508	0.79	0.43*	-4.13	1.09*	6.10*	-12.37
MSXS5508A x CMSXS643	-2.13*	0.11	12.67*	0.70*	4.66	920.99*
MSXS5508A x CMSXS646	-1.2	0.26*	11.87*	-0.17	-1.12	562.33*
MSXS5508A x CMSXS647	-0.31	0.22*	-0.29	0.58	6.23*	363.13
tandard deviation ( $s_{kk}$ )	0.73	0.06	2.03	0.28	2.32	147.56
tandard deviation ( $s_{k'k'}$ )	0.69	0.06	1.93	0.27	2.2	139.99
tandard deviation $(S_{kk'})$	0.9	0.08	2.52	0.35	2.86	182.23

**Table 2.** Estimates of the mean effects of the specific combining ability of A-lines  $(s_{kk})$ , R-lines  $(s_{kk})$  and hybrids  $(s_{kk})$  of sweet sorghum for the traits of flowering time (FLOW, days), plant height (PH, m), production of green mass (PGM, t ha<sup>-1</sup>), total soluble solids content (TSS, % juice), total recoverable sugars (TRS, kg sugar/t of stalks), ethanol production (ETH, L ha<sup>-1</sup>)

\*Significant at 5% probability by the t-test.

The SCA of parental lines is used as an indicator of the existence of unidirectional dominance (Cruz and Vencovsky 1989). For FLOW, most of the lines had positive SCA, indicating that the dominance effect contributed to reducing the number of days to flowering (Table 2). In contrast, negative SCA estimates were observed for other traits, indicating that the dominance effect acted to increase phenotypic expression. Kumar et al. (2016) observed a negative heterotic effect for FLOW, whereas this effect was positive for PH, stalk yield, juice volume, EXT, and sugar yield.

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SCA is closely related to heterosis ( $h = dy^2$ , where d is dominance and y is genetic divergence); thus, hybrids with high SCA show greater heterosis. The main goal in breeding of sweet sorghum is ethanol production. Eight hybrids exhibited positive and significant effects of SCA on traits that result in greater ethanol production (Table 2). The importance of non-additive effects on phenotypic expression of several traits related to ethanol production was also found by Makanda et al. (2009), Audilakshmi et al. (2010), Pfeiffer et al. (2010), and Umakanth et al. (2012). This result encourages the use of heterosis in obtaining hybrids to increase ethanol yield from sweet sorghum.

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# MJ Rocha et al.

372

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