

# Genetic options for improving fodder yield and quality in forage sorghum

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## Abstract

Improving yield and quality of fodder from forage sorghum is important, especially in the semi-arid tropics, where sorghum is a major source of fodder. The aim of this work was to understand the genetic basis of fodder yield and quality traits, and character associations, and to estimate combining ability of the parents. The experiment was carried out during 2 successive rainy seasons using 10 parents crossed in a half-diallel design. Significant differences among the genotypes for fodder yield, quality and cell wall constituents were observed. Important quality traits, crude protein and digestibility (IVOMD), were not correlated with fodder yield, indicating the potential to improve yield and quality simultaneously in forage sorghum. General combining ability and specific combining ability variances showed that, for almost all characters, both additive and non-additive gene effects were important, with a predominance of non-additive effects. Parental lines SEVS4, HC308 and UPMC503 were good general combiners for yield and quality. The brown midrib lines, EC582508 and EC582510, were good general combiners for low lignin and high IVOMD. Strategies for improving forage sorghum to suit animal and biofuel industries are discussed.

## Resumen

El mejoramiento del rendimiento y la calidad del sorgo forrajero (*Sorghum* spp.) es especialmente importante en zonas tropicales semiáridas, donde esta gramínea es un importante forraje. El objetivo de este trabajo fue entender la base genética de importantes características de rendimiento y calidad y sus relaciones, así como estimar la aptitud combinatoria de los genotipos parentales. El experimento se realizó en Hyderabad, India, durante 2 períodos sucesivos de lluvia utilizando 10 líneas parentales que se cruzaron en un diseño dialélico medio. Se observaron diferencias significativas entre los genotipos en rendimiento de forraje y calidad, especialmente en los constituyentes de la pared celular. No se encontró correlación entre el rendimiento de forraje y factores importantes de calidad (proteína cruda y digestibilidad in vitro de la materia orgánica), resultados que indican que en sorgo forrajero existe potencial para mejorar estas características del forraje en forma simultánea. Las varianzas de las aptitudes combinatorias general y específica mostraron que para la mayoría de las características en estudio, tanto los efectos aditivos de genes como los no-aditivos fueron importantes, con un predominio de estos últimos. Las líneas parentales SEVS4, HC308 y UPMC503 fueron buenos combinantes generales para rendimiento y calidad, mientras que las líneas Brown Midrib EC582508 y EC582510 fueron buenos combinantes generales para baja concentración de lignina y alta digestibilidad. En el trabajo se discuten estrategias de mejoramiento de sorgo forrajero para su adaptación a los requerimientos de producción animal y la industria de biocombustibles.

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## Introduction

Sorghum is a versatile species with potential for high biomass production. It can be used as a source of human food, grain and forage for livestock and fuel in the arid and semi-arid tropics. The demand for fodder has increased because of recent efforts to increase milk and meat production, which necessitates increased quantity and quality of green and dry fodder. In semi-arid situations, sorghum can be the major supplier of fodder, and its role becomes important during winter and summer months. Management practices to improve fodder yield and quality, such as higher application of nitrogen, may not be suitable in semi-arid regions, where the environment is highly unpredictable and drought-prone (Hall et al. 2004). The best option for increasing yield and quality of forage sorghum appears to be genetic improvement of both these characteristics in currently available cultivars through multi-dimensional programs. There is limited information available on feed quality of improved forage sorghums, which is important for commercialization of forage cultivars (Akabari and Parmar 2014).

Besides its utility as a fodder crop, sorghum has the potential to provide lignocellulosic biomass for the production of ethanol as biofuel (Carpita and McCann 2008). The shorter life cycle of bioenergy grasses compared with perennial biomass crops, and their different cell wall composition, specifically lower lignin content, make processing of biomass from grasses much less energy-intensive (Vermerris 2011). To enhance use of sorghum as a fodder and biofuel crop, it is important to improve biomass quality in terms of digestibility and saccharification of the stalk. Lignin content of cell walls determines, among other factors, sugar release and thus the efficiency of the fermentation process (Vermerris et al. 2007; Lorenz et al. 2009). The main goal of forage sorghum breeders is to develop cultivars with high fodder yield as well as high digestibility.

Diallel analysis can be used to provide information on general and specific combining abilities (GCA and SCA), determine genetic variances and estimate heritability. Combining ability describes the breeding value of parental lines to produce hybrids. Combining ability analysis helps in the identification of parents with high GCA and parental combinations with high SCA.

The objectives of this study were to: (1) assess the genotypic variation for fodder yield and quality in a set of forage sorghum genotypes; (2) study possible associations between yield and forage quality traits; (3) determine combining ability of these forage sorghum genotypes; and (4) understand the genetic basis of the important fodder yield and quality traits. Parents with ap-

propriate attributes could then be used in forage sorghum breeding programs to improve fodder yield and quality.

## Materials and Methods

The study was conducted on the research farm of the Directorate of Sorghum Research (DSR), Hyderabad, India during the rainy seasons of 2009 and 2010. In both years, all genotypes were sown during the second week of June, while harvesting occurred during the third or fourth week of August, depending on when the particular genotype flowered. Rainfall, temperature and humidity details during the growing periods of the years under study are given in Table 1.

**Table 1.** Meteorological data during the growing periods.

Year and month	Temperature (°C)		Relative humidity (%)		Rainfall (mm)
	Max	Min	Max	Min	
<b>2009</b>					
June	36.3	24.8	72	41	82.0
July	32.0	23.4	80	57	154.0
August	31.2	23.3	81	64	203.7
<b>2010</b>					
June	35.2	24.7	82	60	113.7
July	29.4	22.5	89	77	278.9
August	30.3	22.6	91	75	203.1

### Field material for the study

Ten sorghum cultivars (Table 2) were used, including: 7 forage sorghums; 1 sweet sorghum; and 2 brown midrib genotypes; plus 45 hybrids derived by crossing the 10 parents in a half-diallel fashion. The parents and F<sub>1</sub>s were evaluated in a randomized complete block design with 3 replications. The experimental unit was a single 4 m row with spacings of 45 cm between rows and 10 cm within rows. Parents and F<sub>1</sub>s were randomly assigned to experimental units within blocks.

### Observations recorded

Observations on fodder yield and quality parameters were made each year. Days to flowering was recorded on a plot basis, while other parameters were recorded on 10 random plants/plot, avoiding plants at the ends of rows.

**Field observations.** Days to flower (DTF) was recorded when 50% of the plants in a plot had reached mid-anthesis. Plant height (PH) was the height from

**Table 2.** Description of the parents used in the study.

Parental line	Origin	Characteristics
SSG59-3	HAU, Hisar, India	Popular multi-cut forage sorghum variety released under All India Co-ordinated Sorghum Improvement Program (AICSIP)
UPMC503	GBPUAT, Pantnagar, India	Male parent of the popular forage sorghum hybrid, CSH 20MF
UPMC512	GBPUAT, Pantnagar, India	Improved forage sorghum line from Pantnagar
PC23	IARI, New Delhi, India	Forage sorghum variety from Indian Agricultural Research Institute (IARI), New Delhi, India
HC308	HAU, Hisar, India	Popular forage sorghum variety released under AICSIP
Keller	USA	Sweet sorghum variety
EC582510	N598 from University of Nebraska, USA	Brown midrib line
EC582508	Atlas bmr-12 from University of Nebraska, USA	Brown midrib line
Nizamabad forage	Nizamabad, India	Forage sorghum variety from Nizamabad area of Andhra Pradesh, India
SEVS4	AICSIP, India	Dual-purpose sorghum variety under AICSIP

ground level to the tip of the main stem at flowering. The number of leaves per plant (NLP) was counted at flowering. Plants were harvested at 50% flowering by cutting the stems at the base and weighing the harvested material immediately to estimate fresh fodder yield (FY). Representative whole plant samples were collected and chopped, before drying in a hot air drier at 60–70 °C for 72 h. Dried samples were ground in a mill with a 1 mm sieve.

**Observations on fodder quality.** All forage samples were analyzed by Near Infrared Spectroscopy (NIRS), calibrated for this experiment. The NIRS instrument used was a FOSS Forage Analyzer 5000 with software package Win SI. Crude protein (CP) concentration was estimated by determining total nitrogen (N) in the sample by Auto Analyzer, and acid digestible lignin (ADL) according to Goering and Van Soest (1970). In vitro organic matter digestibility (IVOMD) was determined according to Menke and Steingass (1988) using an in vitro gas production test with manual syringes as modified by Blümmel and Ørskov (1993).

#### Data analysis

Data collected over the 2 years were subjected to analysis of variance, and simple correlations using the software Genstat 12 (GENSTAT 2011). The analysis of variance for GCA and SCA effects was carried out according to Griffing's (1956) method 1, model 2, involving parents with one set of  $F_1$ s but reciprocals were not included. Windostat (Indostat Services 2004) software was used for analysis. GCA and SCA effects for different traits were calculated across years. The model was:

$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$ , where  $Y_{ijk}$  was the observed measurement for the  $ij$ th cross grown in the  $k$ th year;  $\mu$  was the population mean;  $g_i$  and  $g_j$  were the GCA effects;  $s_{ij}$  the SCA effect; and  $e_{ijk}$  the error term associated with the  $ij$ th cross evaluated in the  $k$ th year. The restrictions imposed on the combining ability effects were:  $\sum g_i = 0$ , and  $\sum s_{ij} = 0$  for each  $j$  (Griffing 1956). Estimates of  $\sigma^2$ GCA (general combining ability),  $\sigma^2$ SCA (specific combining ability) and their variances were computed for the random-effects model to estimate  $\sigma^2A$ ,  $\sigma^2D$  and  $h^2$  (Zhang and Kang 2005).

Heterosis (MP: mid-parent) and heterobeltiosis (BP: better parent) values, respectively, were calculated by using the formulae: MP = [(value of  $F_1$  – mean of parents)/mean of parents]  $\times$  100; and BP = [(value of  $F_1$  – value of better parent)/value of better parent]  $\times$  100. The critical differences for testing the significance of heterosis were calculated as follows: critical difference (MP) =  $\sqrt{3Me/2r \times t}$ ; and critical difference (BP) =  $\sqrt{2Me/r \times 4t}$ ; where Me is the error mean square, r is the number of replications, and t is the table value of t at 5 or 1% level of significance.

#### Results

##### Mean values and heritabilities

The means and ranges for all fodder yield and quality traits, plus the level of significance for the 55 sorghum genotypes studied, are reported in Table 3. Highly significant ( $P < 0.001$ ) differences among entries were observed for all yield and nutritional traits assessed. Heritabilities for all fodder quality and yield traits were moderate to high.

**Table 3.** Overall means, ranges in individual cultivar means, and heritabilities for sorghum fodder yield and quality traits. Data are from a 55-entry sorghum trial grown in two years (\*\*P<0.001).

Variable <sup>1</sup>	Mean	Range	LSD	Heritability
DTF (no.)	66	59–76.3**	3.1	0.83
PH (cm)	294	165–355**	21.3	0.82
NLP (no.)	11	9–13**	1.2	0.50
FY (g/plant)	1,860	610–2,743**	513.6	0.54
CP (%)	9.62	7.43–11.7**	1.6	0.36
IVOMD (%)	50.8	45.7–55.4**	2.5	0.39
ADL (%)	4.87	3.59–5.68**	0.47	0.47

<sup>1</sup>DTF - Days to flower; PH - Plant height; NLP - Number of leaves per plant; FY - Fresh fodder yield; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin.

**Table 4.** Correlation co-efficients of fodder yield and IVOMD with other traits.

Trait	Year	DTF <sup>1</sup>	PH	NLP	CP	ADL	IVOMD
FY	2009	0.71**	0.73**	0.77**	-0.14	0.09	0.10
	2010	0.59**	0.69**	0.67**	0.13	-0.19	0.21
IVOMD	2009	0.06	-0.21	0.10	-0.09	-0.84**	-
	2010	0.24	-0.29*	0.02	-0.05	-0.83**	-

<sup>1</sup>DTF - Days to flower; PH - Plant height; NLP - Number of leaves per plant; FY - Fresh fodder yield; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin.

**Table 5.** Analysis of variance for combining ability for fodder yield and quality traits in forage sorghum involving 10 x 10 half-diallel analysis.

Source of variation	DF	Mean sum of squares						
		DTF <sup>1</sup>	FY	PH	NLP	CP	IVOMD	ADL
Environments	1	683.7**	30087.3**	64279.3**	29.52**	792.0**	3183.6**	5338.6**
Genotypes	54	146.4**	14707.2**	9189.1**	6.62**	4.12**	17.32**	75.7**
Gen * Env	54	52.9 **	3789.6**	724.0**	2.01**	2.84**	8.02**	32.8**
Error	216	7.17	2037.3	350.5	1.17	1.57	4.22	16.66
GCA	9	175.4**	16702.6**	8322.0**	6.39**	2.53**	20.04**	66.9**
SCA	45	23.5**	2542.4**	2011.2**	1.37**	1.14**	2.92**	16.9**
GCA*Env	9	51.2**	1905.4**	196.2	0.7	2.16**	3.35*	23.4**
SCA*Env	45	10.9**	1134.7**	250.4**	0.66**	0.70	2.54**	8.44*
Error	216	2.39	679.1	116.8	0.39	0.52	1.4	5.55
σ <sup>2</sup> GCA		7.21	667.65	341.9	0.25	0.08	0.78	2.56
σ <sup>2</sup> SCA		10.55	931.6	947.2	0.49	0.31	0.76	5.67
σ <sup>2</sup> A		14.42	1335.3	683.7	0.5	0.17	1.55	5.11
σ <sup>2</sup> D		10.55	931.6	947.2	0.49	0.31	0.76	5.67
GCA:SCA Ratio		0.684	0.717	0.361	0.51	0.27	1.026	0.451

<sup>1</sup>DTF - Days to flower; FY - Fresh fodder yield; PH - Plant height; NLP - Number of leaves per plant; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin

#### *Relationships among fodder yield and quality traits*

Highly significant correlation ( $r = 0.84$ ,  $P \leq 0.001$ ) was observed between fresh fodder yield and dry fodder yield in this study. Hence only fresh fodder yield was used further for the association studies and combining

ability studies. No significant relationships were observed between fodder yield and fodder quality traits such as CP, ADL and IVOMD (Table 4). IVOMD was negatively correlated with ADL ( $r = -0.86$ ,  $P \leq 0.001$ ). The yield traits (DTF, PH and NLP) were correlated with one another and also with fodder yield.

*ANOVA, GCA and SCA variances*

The mean square values for inter-genotype differences and combining ability for all traits are presented in Table 5. There were significant genotype differences for all characters studied ( $P < 0.001$ ). Significant differences ( $P < 0.001$ ) due to years (environment) were also observed for all traits. The partitioning of genotype mean squares into GCA and SCA showed GCA and SCA mean squares to be significant ( $P < 0.001$ ) for all traits, viz. DTF, PH, FY, NLP, CP, IVOMD and ADL. Estimates of highly significant GCA and SCA variances for these characters indicated the importance of both additive and non-additive genes in the expression of the characters. Both additive and non-additive gene actions were equally important for the trait, IVOMD, while the non-additive gene actions were predominant for the traits, CP, PH, NLP, ADL, DTF and FY.

Genotype  $\times$  year (environment) interactions were highly significant ( $P < 0.001$ ) for all traits. Partitioning of genotype  $\times$  environment interactions into GCA  $\times$  environment (GCA  $\times$  E) and SCA  $\times$  environment (SCA  $\times$  E) showed that: (a) GCA  $\times$  E was significant ( $P < 0.05$ ) for all the traits except PH and NLP; and (b) SCA  $\times$  E was significant ( $P < 0.05$ ) for all traits except CP. Significant GCA  $\times$  E interactions for the above traits are an indication of variation of general combining ability of lines under different environments. Significant SCA  $\times$  E interactions for the traits mean that specific hybrids differed in the way they expressed these traits in different years.

*GCA and SCA effects*

**Fodder yield traits.** Estimates of GCA effects of the 10 genotypes for fodder yield traits showed that SEVS4, HC308 and UPMC503 had the best GCA for fodder yield (FY) (Table 6). SEVS4 and HC308 recorded high per se performance for FY (Supplementary Table 1). Apart from FY, SEVS4 and HC308 had good GCA for other plant characteristics, including plant height (PH) and number of leaves per plant (NLP). For days to flowering (DTF), EC582508, Nizamabad forage, Keller, EC582510 and SSG59-3 were good general combiners with significantly negative GCA effects for flowering. The parents, PC23, Nizamabad forage, EC582508 and Keller, flowered early with DTF less than 65 days.

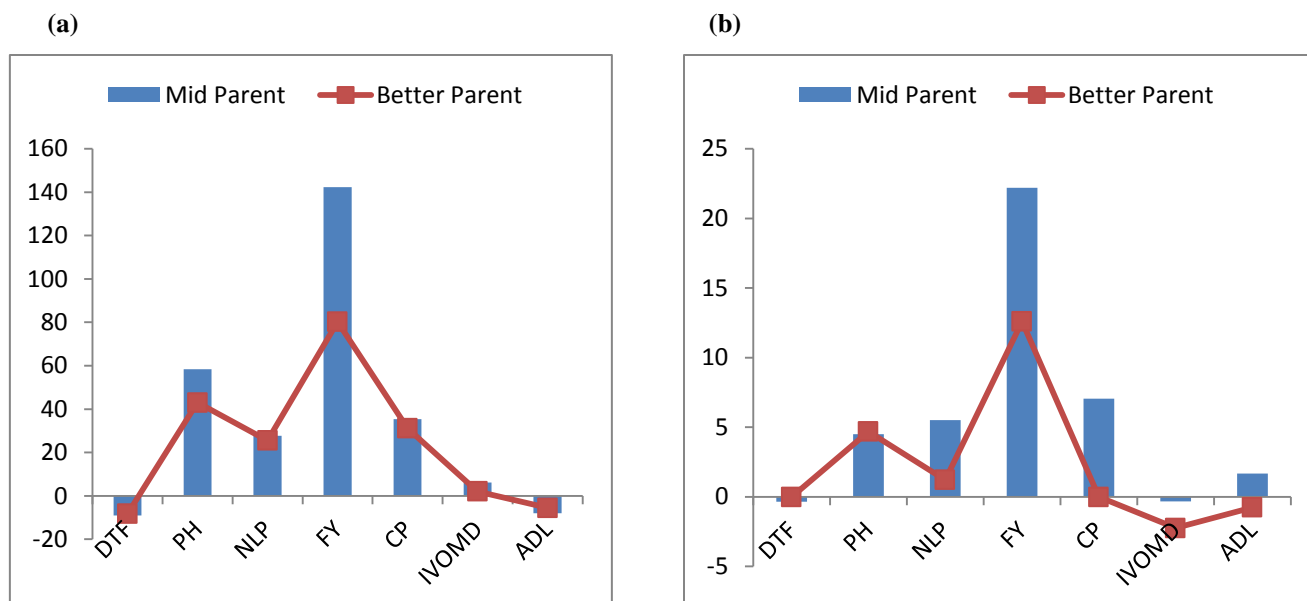
**Fodder quality traits.** Estimates of GCA effects for fodder quality traits indicate that Nizamabad forage had good GCA for increased CP. For IVOMD, the brown midrib genotypes (EC582508 and EC582510) and the sweet sorghum genotype, Keller, had good GCA, as could be expected from parents with reduced lignin due to the bmr trait or with higher sucrose content in the sweet sorghum parent. All 3 parents had high per se performance for IVOMD. For ADL, the brown midrib genotypes (EC582508 and EC582510) had significantly negative GCA effects besides HC308. Both brown midrib lines (EC582508 and EC582510) had low lignin compared with other genotypes.

**Table 6.** General combining ability effects for fodder yield and quality traits in forage sorghum parents from 10  $\times$  10 half-diallel analysis.

Parental line	DTF <sup>1</sup>	FY	PH	NLP	CP	IVOMD	ADL
SSG 59-3	-1.12**	-16.97**	5.47**	-0.46**	0.24	-0.44	1.42**
UPMC 503	2.04**	10.29*	16.20**	0.051	-0.58**	-0.3	0.1
UPMC 512	-0.57	-19.96**	-15.76**	-0.45**	0.06	-0.99**	1.28**
PC 23	1.25**	-36.46**	18.76**	0.11	-0.11	-1.74**	3.00**
HC 308	5.42**	30.66**	15.48**	0.99**	-0.35	0.43	-1.17*
Keller	-2.56**	-4.26	-20.26**	-0.30*	-0.04	1.07**	-0.83
EC582510	-1.82**	-8.55	-19.31**	-0.21	-0.14	0.51*	-1.29**
Nizamabad forage	-2.19**	-0.93	-0.6	-0.30*	0.59**	-0.13	0.83
EC582508	-2.90**	-8.89	-24.52**	-0.26*	0.17	1.21**	-2.76**
SEVS 4	2.46**	55.06**	24.55**	0.82**	0.15	0.37	-0.59
SE (g <sub>i</sub> )	0.30	5.05	2.09	0.12	0.48	0.23	0.46
SE (g <sub>i</sub> -g <sub>j</sub> )	0.45	7.52	3.12	0.18	0.71	0.34	0.68

<sup>1</sup>DTF - Days to flower; FY - Fresh fodder yield; PH - Plant height; NLP - Number of leaves per plant; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin.





**Figure 1.** Heterosis for fodder yield and quality traits: (a) maximum heterosis observed among the crosses; (b) mean heterosis across all crosses. (Note different scales on the two graphs.) DTF - Days to flower; PH - Plant height; NLP - Number of leaves per plant; FY - Fresh fodder yield; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin.

#### *Heterosis for fodder yield and quality traits*

High heterosis was observed for FY, followed by CP (Figure 1). Mean heterosis for FY was observed to be 22.2 and 12.6% over the mid-parent and better parent, respectively. The best hybrid was PC23 x EC582508 with 142 and 80% heterosis over the mid-parent and better parent, respectively, followed by UPMC503 x EC582508. Both hybrids showed significant heterosis over the better parent, while 13 more hybrids expressed significant heterosis over mid-parent values (data not shown). For CP, the best hybrid was UPMC503 x EC582510, with heterosis of 34.7 and 31.1% over mid-parent and better parent, respectively, followed by SSG59-3 x EC582510 (32.7 and 24.2%) and SSG59-3 x UPMC503 (25.9 and 15.2%). For IVOMD, only one hybrid, PC23 x Nizamabad forage, recorded positive significant heterosis. Heterosis for reduced ADL was observed in PC23 x Nizamabad forage (-7.53 and -2.38% over mid-parent and better parent), HC308 x Nizamabad forage (-5.19 and -1.78%) and UPMC503 x HC308 (-6.96 and -5.5%).

#### **Discussion**

This study has provided interesting results about the potential for breeding more productive genotypes of sorghum. However, our study had some shortcomings:

- Since only a single row of plants was grown in each replicate, competition effects could have affected the results. Only single rows of plants were sown as limited availability of seed restricted how much of each genotype could be sown.
- Fresh forage yields were used in this study rather than dry matter yields. Farmers normally feed the forage fresh and there is a strong positive correlation between fresh and dry matter yields (Tariq et al. 2012; this study).

Despite these factors, we consider that the data obtained reliably indicate the true performance of these genotypes in this area of the semi-arid tropics.

A forage sorghum breeding program should aim for improvement of important fodder quality traits, such as digestibility and protein content, in addition to forage yield. Forage sorghum has good potential as a biofuel and biogas crop (Mahmood and Honermeier 2012). For efficient production of ethanol from plant biomass, reduced lignin percentage is desirable, because during saccharification, lignin acts as a physical barrier and retards the action of cellulases, impeding swelling of cellulose fibers (Vermerris et al. 2007). Reducing lignin has a highly beneficial effect on conversion of cellulose to glucose, resulting in high ethanol yield (Dien et al. 2009).

The brown midrib mutants (bmr) in forage maize and sorghum with reduced lignin and greater digestibility

(Barriere et al. 2004; Sattler et al. 2010; Rao et al. 2012) could lead to the development of forage and sweet sorghums as novel biomass crops (Sarath et al. 2008). Bio-refineries present a system comparable with the rumen digestive system, where improved cellulose breakdown to sugars is achieved with enzyme mixtures rather than rumen bacteria. Programs to improve forage and biomass feedstock share the following goals: high biomass yield and low lignin content.

In the present study, these traits showed significant variation among genotypes, indicating that there is sufficient genetic variability in the parents and hybrids to obtain genetic gains in hybrid combinations. The estimates of heritability of pertinent fodder quality traits were around 0.5, suggesting opportunities for further improvement of fodder quality by genetic enhancement. The magnitudes of genotypic differences should prove meaningful for animal performance, as small changes in IVDMD of 3–4 percentage units have been observed to result in improvements of 17–24% in daily gains and production per hectare (Vogel and Sleper 1994). However, the very large genotype  $\times$  year interactions observed in this study could seriously reduce the rate of genetic gain for biomass quality. Although few studies have been specifically designed to examine genotype  $\times$  year interactions for stover quality, there are reports of highly significant genotype  $\times$  year interactions for *in vitro* digestibility (Aruna et al. 2012), while other studies failed to find major genotype  $\times$  environment interactions for stover digestibility (Badve et al. 1994). The presence of significant genotype  $\times$  environment interactions for yield and quality traits suggests that evaluation in more than one environment may be required for accurate selection for biomass yield and quality, as was reported for maize (Lorenz et al. 2009).

Associations amongst the fodder yield and quality traits, and their interaction with the environment, will help in guiding future plant breeding strategies. In general, associations between fodder yield and important fodder quality traits, such as IVOMD, CP and ADL, were not found, indicating that these traits have independent inheritance. This paves the way for simultaneous genetic improvement of both fodder yield and quality. Significant positive association of fodder yield with PH, NLP and DTF was observed, showing that these traits contributed to the variation in fodder yield. Strong positive genotypic and phenotypic correlations between fodder yield and stem diameter, leaf length, plant height and number of leaves have already been reported (Iyanar et al. 2010; Tariq et al. 2012). Our findings indicate that, to improve fodder yield, the important traits to be addressed are PH and NLP. The leaf component is im-

portant for both yield and quality, not only because of the generally high nutritive value in leaves compared with stems, but also because leaves are more acceptable to animals, as they are easier to chew and more digestible (Reddy et al. 2003).

Since genotypic variance was significant, varietal improvement could help raise the nutritional quality of sorghum forage above current levels. Presence of highly significant GCA and SCA effects for most characters indicated the importance of both additive and non-additive genes in the expression of the traits. In the present study, the ratio of GCA:SCA variance was  $<1$  unit for all characters, except IVOMD where it was slightly higher than 1 unit, which indicated the pre-ponderance of non-additive genetic variance, as reported earlier (Prakash et al. 2010; Aruna et al. 2012). For traits where both additive and non-additive gene effects were important, dominance variance ( $\sigma^2D$ ) was found to be larger than the additive variance ( $\sigma^2A$ ), showing the importance of non-additive gene effects in the control of these traits, indicating good prospects for the exploitation of non-additive genetic variation for fodder yield and quality traits in forage sorghum through hybrid breeding. As well as hybrid breeding, population breeding, which gives a chance to accumulate genes from different genotypes, can be one of the approaches for yield and quality improvement. Epistatic interactions have been found to play a major role in the genetic basis of fiber-related traits (Shiringani and Friedt 2011).

The GCA effect is considered as the intrinsic genetic value of the parent for a trait, which is due to additive gene effects and is fixable (Simmonds 1979). To get outstanding recombinants in segregating generations, the parents of the hybrids must be good general combiners for the characters to be improved (Gravois and McNew 1993; Manonmani and Fazlullah Khan 2003).

The presence of heritable variation for both fodder yield and quality traits and their independence suggest that simultaneous improvement of fodder yield and quality is possible. Genotypes HC308 and SEVS4 were the best combiners for most fodder yield parameters such as plant height, leaf number etc. and for some of the fodder quality traits, such as low lignin (HC308). The brown midrib genotypes, EC582508 and EC582510, were good combiners for early flowering, IVOMD and low lignin concentration, and can be used as a source of genes to improve fodder quality in terms of digestibility. Keller was a good combiner for early flowering and fodder quality traits such as high IVOMD and low lignin. Nizamabad forage was a good combiner for CP and early flowering. These have potential for crossing with HC308 and SEVS4 for improvement of forage sorghum for

animal feed. Breeding programs can be designed to utilize these lines for improving biomass/fodder yield and quality, and multiple crosses involving these parents would result in identification of superior segregants with favorable genes for most traits associated with fodder yield and quality.

Biparental mating in early segregating generations of the crosses, involving these parents for simultaneous exploitation of both additive and non-additive gene action, can be recommended to develop sorghum genotypes with improved fodder yield and quality. It is suggested that inter-mating of the randomly selected progeny in early segregating generations (especially in  $F_2$  and  $F_3$ ) obtained by crossing these parents will release the hidden genetic variability through breakage of undesirable linkages involved in different characters. It may produce an elite population for selection of lines with high fodder yield and quality in advanced generations.

## Conclusion

The main conclusion from this study is that both additive and non-additive gene effects are important, with a predominance of non-additive gene effects governing fodder yield and quality in sorghum. Multiple crosses involving the best combiners for different traits would result in the identification of superior  $F_1$  hybrids with favorable genes for most of the traits associated with fodder yield and quality. The study also indicates the brown midrib genotypes can be used to develop cultivars with low lignin and high digestibility, which would be suitable for both animal and biofuel industries. This confirms that there is a great opportunity to improve both fodder yield and quality in breeding programs aiming at genetic enhancement of forage sorghums.

Hybrids low in lignin appear to be attainable without sacrificing high yield levels. We conclude that exploiting heterosis in forage sorghum to improve quality traits might be promising. Since many traits contribute to fodder yield and quality, population breeding or marker-assisted selection would be fruitful in forage sorghum improvement. Identifying markers for the component traits associated with yield and quality and pyramiding them into elite cultivars would help in developing forage sorghum cultivars with improved quality. The improvement in the quantity and nutritional quality of the fodder of forage sorghum cultivars could have a significant impact on livestock productivity in the sorghum-growing areas. The extent to which these results could be extrapolated to other regions is unclear, because of large genotype x environment interactions noted.

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**Supplementary Table 1.** Mean performance of the 10 sorghum parents for fodder yield and quality traits over two years.

Parental line	DTF <sup>1</sup>	PH (cm)	FY (g/pl)	NLP	CP (%)	IVOMD (%)	ADL (%)
SSG 59-3	67.2	278.0	261.7	10.1	10.8	49.7	4.96
UPMC 503	68.2	289.4	326.3	11.0	7.9	50.5	4.92
UPMC 512	65.3	165.0	240.0	10.0	11.6	50.0	4.94
PC 23	60.0	258.8	122.0	9.5	11.4	45.7	5.68
HC 308	76.3	303.0	443.3	13.2	10.1	50.7	4.77
KELLER	63.0	224.4	270.3	9.8	10.1	53.7	4.47
EC582510	65.2	204.9	207.3	9.9	9.1	54.2	3.69
Niz forage	61.7	280.6	335.3	9.7	12.4	49.5	5.11
EC 582508	62.5	211.6	250.0	10.3	11.9	55.4	3.59
SEVS 4	72.8	305.7	450.7	12.5	10.3	52.1	4.35
Mean	66.2	252.1	290.7	10.6	10.6	51.2	4.65
C.V.	3.90	4.59	23.09	7.34	9.66	4.25	5.85
C.D. (5%)	4.33	19.34	125.3	1.38	1.75	3.50	0.50
C.D. (1%)	5.93	26.50	171.6	1.89	2.40	4.80	0.69

<sup>1</sup>DTF - Days to flower; PH - Plant height; FY - Fresh fodder yield; NLP - Number of leaves per plant; CP - Crude protein; IVOMD - In vitro organic matter digestibility; ADL - Acid digestible lignin.

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