Received: 26 Aug 2022 | Revised: 24 Jul 2023 | Accepted: 28 Jul 2023

Electronic Journal of Plant Breeding

Research Article

Diallel analysis in sorghum for forage yield and attributes by Griffing and Hayman's approaches

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Abstract
Five sorghum (*Sorghum bicolor* (L.) genotypes were crossed in a half-diallel mating design. Analysis of variance for combining ability revealed that general combining ability (GCA) was significant for all the traits except days to flowering, while specific combining ability was significant for all the studied traits. The variance ratio (δ^2GCA / δ^2SCA) was less than unity for all characteristics, demonstrating the role of non-additive gene action in controlling yield and component traits. The result of general combining ability (GCA) indicated that the parents SH 1488 and SH 1813 were as good general combiners for both green and dry fodder yield per plant. Result of specific combining ability (SCA) showed that crosses SSG 59 × SH 1488, SH 1488 × SH 1813, SH 1488 × S 652 and SH 1811 × S 652 recorded the highest *sca* effect for the traits green and dry fodder yield per plant. The t^2 test specified the fulfilment of the assumption required under diallel analysis for all studied traits except leaf length (cm) and green fodder yield per plant (g). Non-significant result of t^2 value suggested additive dominance model for all the traits except leaf length (cm) and green fodder yield per plant (g). The higher value of H_1 compared to H_2 for most of the characters suggested that gene sharing frequency in parent genotypes was not equal and that was also supported by the $H_2 / 4H_1$ (<0.25). The greater than one value of KD/KR components for most of the traits except leaf width (cm) and HCN content (ppm) suggested the higher frequency of dominant genes than recessive genes in the parents. The estimation of the F component was positive and non-significant for all the traits except leaf width (cm), whose value was negative. In Hayman's graphical analysis, the regression line interrupted Wr axis below the origin suggested over dominance for days to flowering, leaf: stem ratio, number of leaves per plant, stem girth and Brix content.

Keywords: Sorghum, GCA, SCA, Diallel, Hayman's graphical method

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) is a major cereal grain that belongs to the grass family *Gramineae*. It is a 5th most important crop in respect of area under cultivation and total production after wheat, rice, maize, and barley (FAO, 2018). It is a chief meal for about 500 million people in Sub-Saharan Africa (SSA) and the semi-arid tropics of Asia. Sorghum grains are high in the levels of carbohydrates (73%), protein (11.6%) and fat (3%) (Sebnie and Mengesha, 2018). The nation's economic sorghum area is estimated to be approximately 4.10 million hectares, with an annual yield of 4.74 million tonnes and a productivity of 1156 kg/ha (Anonymous, 2020-21).

The generation of suitable recombinants for high yield and attributes can be aided through hybrid vigor among genetically diverse sorghum genotypes (Mohammed *et al.,* 2015). Due to cross-pollination and high heterosis, one of the most key procedures in the sorghum breeding

program is the selection of parents based on combining ability and the choice of parental sorghum lines and their use in the breeding programme to generate superior hybrids.

For selecting suitable parents and hybrids, general combining ability (GCA) and specific combining ability (SCA) are frequently employed. Different biometrical approaches to estimate GCA and SCA effects through the diallel mating design is commonly used by sorghum breeders. GCA is linked to additive gene effects, whereas SCA is linked to non-additive gene effects. Diallel mating design has been extensively used in crops to understand the nature of gene action involved in the inheritance of quantitative traits. It also provides estimates of components of variance, *gca* and *sca* variances and their effects. Thus, it helps in the selection of parents suitable for hybridization and to frame an efficient breeding plan leading to rapid improvement. Combining ability analysis was carried out according to the procedure given by Griffing (1956[a]).

Graphical analysis method for Wr-Vr assessment that detects the presence of linkage disequilibrium and/or epistasis (Jinks and Hayman, 1953; Hayman, 1954[a]) are most frequently used. With certain assumptions, this approach is based on a simple additive-dominance model of gene function. For example, Hayman's methodology is based on genetic assumptions, while Griffing's study strictly involves statistics in GCA and SCA.

The objective of this study was to evaluate the performances of five sorghum parental lines for breeding potential in specific combinations (SCA) and overall performance in crosses (GCA).

MATERIALS AND METHODS

Five sorghum diverse parents were crossed in all possible combinations using half diallel fashion, excluding the reciprocals and evaluated in a randomized block design with three replications during the *kharif* 2020 at Center for Millets Research, S. D. Agricultural University, Deesa (Gujarat). The resulting ten F_1's hybrids were used for diallel analysis. Simultaneously, the parents were selfed to acquire pure seeds of parents for investigation. Each genotype was planted in rows of 3.0 m length, with 45cm and 15 cm inter and intra-row spacing. The biometrical observations were recorded for the traits namely, days to flowering, plant height (cm), leaf: stem ratio, number of leaves per plant, leaf length (cm), leaf width (cm), stem girth (mm), brix value, green fodder yield per plant (g), dry fodder yield per plant (g), HCN (ppm). The observations were recorded on five randomly selected plants in each genotype in each replication for all characters except days to flowering, which was recorded on plot basis. To ensure a favorable crop, appropriate agronomical practices were implemented. Using Randomized Block Design, the average value from each replication in each genotype for the 11 characters were examined as suggested by Panse and Sukhatme, 1985. The Analysis of Variance (ANOVA) for combining ability was performed as per the method suggested by Griffing (1956[b]) Model-I and Method-2. The correctness of the additive-dominance model hypothesis was confirmed by demonstrating the unit slope of Wr and Vr regressions and a non-significant value of t^2 as suggested by Hayman (1954[b]).

RESULTS AND DISCUSSION

The ANOVA for combining ability for eleven traits (**Table 1**) indicated considerable heterogeneity among crosses for all characters, revealing notable genetic diversity in the parents and their hybrids under study for each character assessed. Variation among the genotypes for such desired attributes is required for effective selection.

The results revealed that mean sum of squares due to general combining ability were found significant for all the traits except days to flowering, whereas the specific combining ability effects were found significant for all the traits. The variance ratio (δ^2GCA / δ^2SCA) was less than unity for all characteristics, demonstrating the role of non-additive gene action in determining yield and its component traits (**Table 1**). This indicates that every character has a massive effect on the genetic diversity among parents and hybrids and that both additive and

Table 1. Analysis of variance for combining ability of different traits in sorghum

Sources of variation	d. f.	Days to flowering	Plant height	Leaf: stem ratio	Number of leaves per plant	Leaf length	Leaf width	Stem Girth
GCA	4	3.06	102.50**	0.002**	1.86**	52.78**	0.84**	2.59*
SCA	9	5.69**	109.30**	0.004**	1.28**	54.65**	0.40**	3.2 **
Error	28	1.63	15.06	0.00	0.17	3.24	0.06	0.75
δ^2GCA		0.20	12.49	0.00	0.24	7.08	0.11	0.26
δ^2SCA		4.06	94.24	0.004	1.11	51.41	0.34	2.50
δ^2GCA / δ^2SCA		0.05	0.13	0.071	0.22	0.14	0.33	0.11

* P ≤ 0.05, ** P ≤ 0.01

Table 1 Conti…

Sources of variation	d.f.	Brix value	Green fodder yield per plant	Dry fodder yield per plant	HCN (ppm)
GCA	4	1.82**	7335.34**	492.24**	145.92**
SCA	9	2.85**	10660.09**	669.60**	328.40**
Error	28	0.36	371.50	16.92	2.23
δ^2GCA		0.21	994.84	67.90	20.53
δ^2SCA		2.49	10288.59	652.69	326.17
δ^2GCA / δ^2SCA		0.08	0.10	0.10	0.06

* P ≤ 0.05, ** P ≤ 0.01

non-additive gene effects were crucial for the appearance of these characteristics. The variance attributable to specific combining ability was larger than that of the variance due to the general combining ability, indicating that non-additive gene action was more important in controlling these characteristics. Kumar and Chand (2015), Dehinwal *et al.* (2017), Jadhav and Deshmukh (2017), Joshi *et al.* (2022) and Chudasama *et al.* (2022) previously documented non-additive gene action for controlling these characteristics.

According to Harer and Bapat (1982), the criteria for selecting the parents for hybridization are based on the general combining ability. Parents with strong GCA effects are preferred for producing productive segregants in early generations. Based on GCA estimations, the parents were classified as good, average and poor general combiners for several features. The parents SH 1488 and SH 1813 were good general combiners for both green and dry fodder yield per plant. SSG-59-3 was a good general combiner for leaf length and width (**Table 2**). The potential of parents to produce better offspring with better genes was evaluated in terms of the general combining ability effect. In the present research, many parental lines have been found to have good combining ability potential for various yields and yield-related attributes.

Table 2. General combining ability (*gca*) effects for different traits in sorghum

Parents	Days to flowering	Plant height	Leaf: stem ratio	Number of leaves per plant	Leaf length	Leaf width	Stem girth
SSG-59-3	-0.07 (A)	-2.81* (P)	-0.004 (A)	0.12 (A)	4.78** (G)	0.42** (G)	-0.43 (A)
SH-1488	0.98* (P)	0.38 (A)	-0.013** (P)	-0.54** (P)	-0.15 (A)	0.32** (G)	0.84** (P)
SH-1813	-0.83 (A)	-4.55** (P)	-0.010*(P)	-0.50** (P)	-1.26* (P)	-0.14 (A)	0.27 (A)
SH-1811	-0.26 (A)	5.15** (G)	0.029** (G)	0.26 (A)	-1.55* (P)	-0.25** (P)	-0.72* (G)
S-652	0.17 (A)	1.83 (A)	0.003 (A)	0.66** (G)	-1.83** (P)	-0.35** (P)	0.05 (A)
S. E. (g_i) (±)	0.43	1.31	0.004	0.14	0.61	0.08	0.29

* P ≤ 0.05, ** P ≤ 0.01

Table 2. Cont...

Parents	Brix value	Green fodder yield per plant	Dry fodder yield per plant (g)	HCN (ppm)
SSG-59-3	-0.38 (A)	-33.56** (P)	-9.73** (P)	-0.25 (A)
SH 1488	0.52* (G)	41.84** (G)	10.88** (G)	-2.47** (G)
SH 1813	-0.68** (P)	16.78* (G)	4.77** (G)	-1.72** (G)
SH 1811	0.20 (A)	-31.49** (P)	-6.71** (P)	-3.46** (G)
S 652	0.35 (A)	6.43 (A)	0.79 (A)	7.90** (P)
S. E. (g_i) (±)	0.20	6.52	1.39	0.50

* P ≤ 0.05, ** P ≤ 0.01

Where letter in parenthesis indicate the status of gca effects**;** G = Good general combiner; A = Average general combiner; P = Poor general combiner

The results of ten crosses for specific combining ability revealed that none of the crosses showed high specific combining ability consequences for all of the characteristics. The crosses namely, SSG 59 × SH 1488, SH 1488 × SH 1813, SH 1488 × S 652 and SH 1811 × S 652 recorded higher specific combining ability effects for green and dry fodder yield per plant (**Table 3**).

The material under current study was tested for the treaty with assumptions basic to Hayman diallel analysis. The maternal effects are presumed to be absent in the present material. For testing other assumptions, two general tests *i.e.* t^2 test and regression of Wr on Vr were used. The outcomes of t^2 test specified the fulfillment of assumptions required under diallel analysis for all the characters except for leaf length and green fodder yield per plant. Which failed to meet the assumptions in these features demonstrated the unjustifiability of the hypothesis with simple additive-dominance gene action and the presence of epistasis and linkage disequilibrium. Ravindrababu (1998) and Patel *et al*. (2022) revealed non-significant t^2 values in sorghum diallel analysis for forage yield and constituent attributes.

Table 3. Specific combining ability (*sca*) effects of F_1 hybrids for different traits in sorghum

S. No.	Hybrids (F_1)	Days to flowering	Plant height	Leaf: stem ratio	Number of leaves per plant	Leaf length	Leaf width	Stem girth
1	SSG 59 × SH 1488	1.06	9.22**	-0.08**	1.42**	-1.54	-0.04	2.94**
2	SSG 59 × SH 1813	1.21	-6.29*	0.05**	-0.85**	-9.83**	-0.39*	-1.76**
3	SSG 59 × SH 1811	-3.37**	6.57*	0.02**	-0.50	3.56**	1.15**	1.02
4	SSG 59 × S 652	0.21	-19.00**	0.06**	-1.57**	-3.14*	-0.34*	-0.98
5	SH 1488 × SH 1813	0.16	3.97	0.03**	1.03**	1.49	0.38*	0.45
6	SH 1488 × SH 1811	-0.41	9.83**	0.05**	-1.17**	4.54**	-0.19	-1.18
7	SH 1488 × S 652	-0.84	-6.41*	-0.07**	0.32	-7.21**	-0.40*	0.85
8	SH 1813 × SH1811	-3.60**	-4.35	-0.08**	0.56	-8.99**	-0.74**	-1.71**
9	SH 1813 × S 652	2.97**	6.19*	0.02*	-0.95**	-4.34**	-0.50**	-0.75
10	SH 1811 × S 652	0.40	5.38	-0.04**	0.40	3.90**	0.16	1.79**
	S. E. (S_{ij}) (±)	0.88	2.68	0.01	0.29	1.24	0.16	0.60
	Range	-3.60** to 2.97**	-19.00** to 9.83**	-0.08** to 0.06**	-1.57** to 1.42**	-9.83** to 4.54**	-0.74** to 1.15**	-1.76** to 2.94**

*** P ≤ 0.05, ** P ≤ 0.01**

Table 3 Cont...

S. No.	Hybrids (F_1)	Brix value	Green fodder yield per plant	Dry fodder yield per plant (g)	HCN
1	SSG 59 × SH 1488	1.76**	161.25**	37.01**	27.38**
2	SSG 59 × SH 1813	-0.40	-75.81**	-20.01**	11.94**
3	SSG 59 × SH 1811	1.91**	1.02	4.43	-12.83**
4	SSG 59 × S 652	1.73**	-44.30**	-8.60**	-23.25**
5	SH 1488 × SH 1813	1.43**	94.02**	29.85**	-4.57**
6	SH 1488 × SH 1811	-0.99*	-76.84**	-16.08**	-1.86
7	SH 1488 × S 652	-0.15	121.13**	23.00**	-13.42**
8	SH 1813 × SH1811	0.54	46.59**	5.76	-6.42**
9	SH 1813 × S 652	-2.07**	-71.90**	-21.90**	7.08**
10	SH 1811 × S 652	0.24	43.90**	21.28**	31.64**
	S. E. (S_{ij}) (±)	0.42	13.30	2.84	1.03
	Range	-2.07** to 1.91**	-76.84** to 161.25**	-21.90** to 37.01**	-23.25** to 27.38**

* P ≤ 0.05, ** P ≤ 0.01

Component D assessed the cumulative effects of genes and was found to be non-significant for all characteristics (**Table 4**). It indicated that these characteristics might be simply fixed in the first generation. The presence of a substantial H_1 and H_2 component indicated non-additive (dominance or epistatic) genetic factors that played a significant role in the transmission of the characteristics under study.

The value of H_1 was higher than H_2 for all traits, denoting that the frequency of gene allocation in the parental lines was unequal, as proven by the ratio of $H_2/4H_1$ (<0.25), trying to confirm the unbalanced distribution of positive and negative consequences of genes at the loci in the parents, implying dominance for all traits. This result was analogue with that of Ravindrababu (1998) and Ravindrababu *et al.* (2003).

Calculated F component values were positive and non-significant for all parameters except leaf width, indicating the existence of both dominant and recessive alleles in varying quantities. For all variables except HCN content, the value of KD/KR elements larger than one demonstrated a higher frequency of dominant genes over recessive genes in the parents. The value of h^2/H_2 indicated that approximately a single gene group was active for brix value and component attributes such as leaf width and number of leaves per plant (**Table 4**). Environmental component (E) examined the importance of environmental variables in manifesting characteristics under investigation. The estimated narrow sense heritability for yield and most of the characteristics was low indicating that all of the attributes were influenced by additive and non-additive genes. It also implied that selection might be rewarding at subsequent or delayed generation. The negative association among parental order of dominance (Vr + Wr) and parental mean (Y_i) regarding leaf width, brix value, green fodder yield per plant, and HCN content revealed that dominant genes played important role in increasing mean values.

The Wr on Vr regression was close to unity for days to flowering (**Fig. 1**), leaf: stem ratio (**Fig. 2**), number of leaves per plant (**Fig. 3**), leaf width (**Fig. 4**), stem girth (**Fig. 5**), brix content (**Fig. 6**), dry fodder yield per plant (**Fig. 7**), HCN content (**Fig. 8**). In Hayman graphical analysis, the regression line interrupted Wr axis below the origin, which suggested prevalence of over dominance for days to flowering, leaf:stem ratio, number of leaves per plant, stem girth and brix content. All of these conclusions were comparable to those published by Ravindrababu (1998), Ravindrababu *et al.* (2003) and Patel *et al.* (2022) for forage yield and its attributing traits.

In the present study, the variance ratio (δ^2GCA / δ^2SCA) was less than unity for all characteristics, demonstrating the role of non-additive gene action in determining yield and its component traits , Hence hybrid vigour can be exploited for fodder yield and its attributes. The parents SH 1488 and SH 1813 were found to be good

Table 4. Estimation of genetic components of variance and other parameters for eleven traits in sorghum

Parameters	Days to flowering	Plant height	Leaf: stem ratio	Number of leaves per plant	Leaf length	Leaf width	Stem girth	Brix value	Green fodder yield per plant	Dry fodder yield per plant	HCN
b (Wr, Vr)	0.34	-0.14	1.05	1.27	0.46	0.40	0.56	0.89	-0.04	0.04	0.15
t_{b-0}	0.88	-0.52	4.20	1.82	3.57	1.08	1.02	7.10	-0.14	0.12	0.32
t_{1-b}	1.68	4.21*	-0.22	-0.39	4.18*	1.65	0.82	0.90	4.04*	2.92	1.84
t^2	1.19	7.85	1.43	8.90	35.52**	1.45	0.13	1.73	9.79*	4.13	0.52
D	2.72	46.86	0.0021	2.47	-	0.30	1.76	2.04	-	216.72	110.87
H_1	19.07	398.70	0.0140	4.43	-	1.37	11.07	9.59	-	2416.04	1166.99
H_2	13.42	304.28	0.0128	3.65	-	1.12	8.38	7.41	-	1975.61	1162.27
F	6.36	60.03	0.0022	2.66	-	-0.04	2.79	3.17	-	234.79	43.34
h^2	0.16	-3.25	0.0004	0.29	-	0.16	-0.38	3.44*	-	679.43	55.15
E	1.53	14.45	0.0002	0.17	-	0.05	0.76	0.35	-	16.85	2.32
$(H1/D)^{0.5}$	2.65	2.92	-	1.34	-	2.14	2.51	2.16	-	3.34	3.24
$H_2/4H_1$	0.17	0.19	0.25	0.20	-	0.20	0.19	0.19	-	0.20	0.25
KD/KR	2.58	2.57	2.37	9.22	-	0.88	4.42	6.04	-	1.96	-1.13
h^2/H_2	0.01	-0.01	0.03	0.08	-	0.14	-0.05	0.46	-	0.34	0.05
r(P, Wr +Vr)	0.56	0.85	0.36	0.17	0.52	-0.34	0.76	-0.84	-0.23	0.25	-0.14
Heritability	0.17	0.31	0.13	0.21	0.28	0.47	0.23	0.19	0.29	0.29	0.11

* P ≤ 0.05, ** P ≤ 0.01

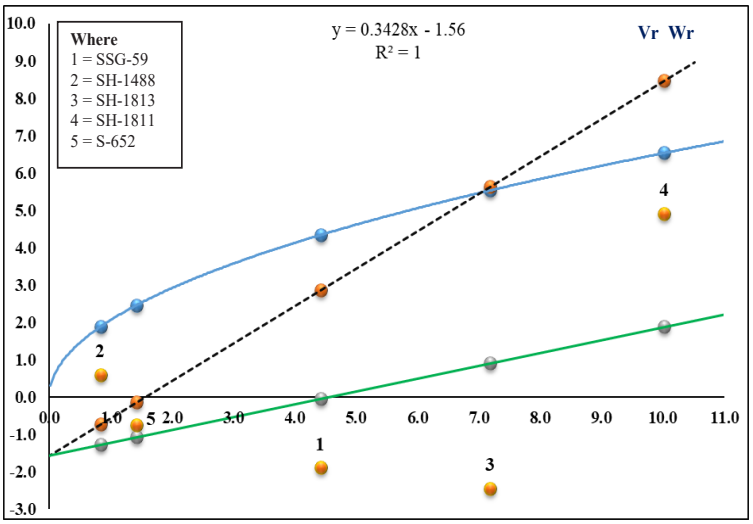

Fig. 1. Vr Wr Graph for days to flowering

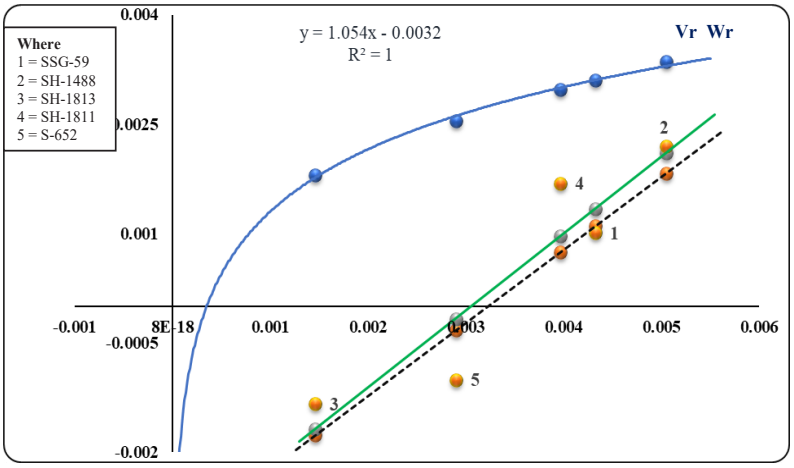

Fig. 2. Vr Wr Graph for Leaf: Stem ratio

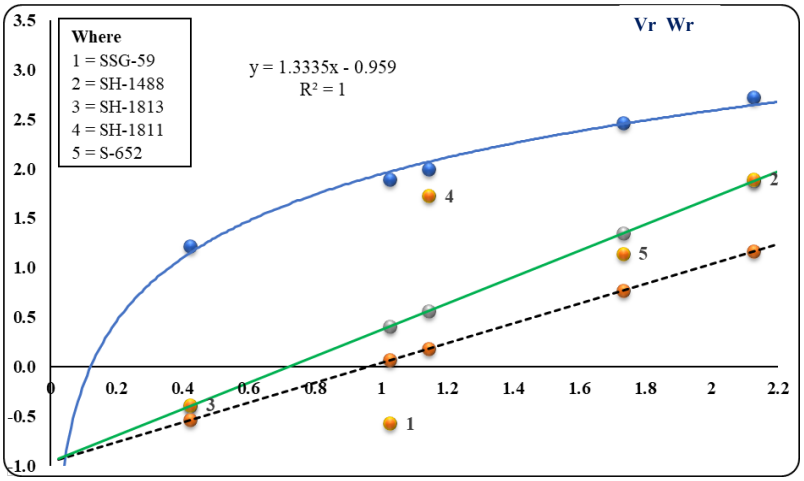

Fig. 3. Vr Wr Graph for Number of leaves per plant

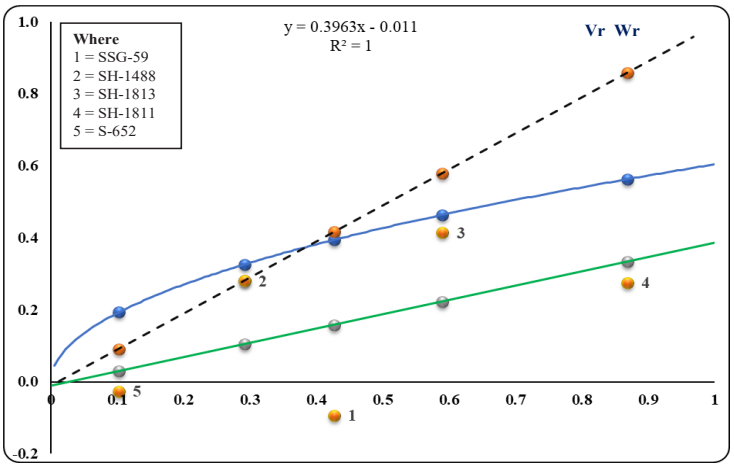

Fig. 4. Vr Wr Graph for Leaf width

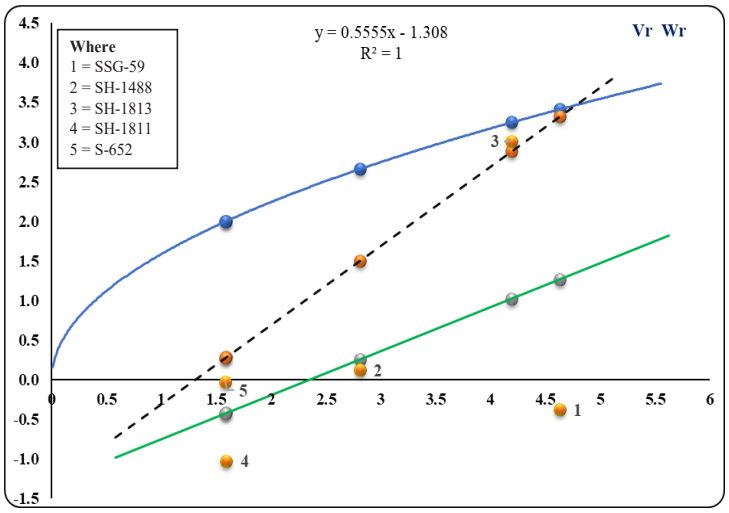

Fig. 5. Vr Wr Graph for stem girth

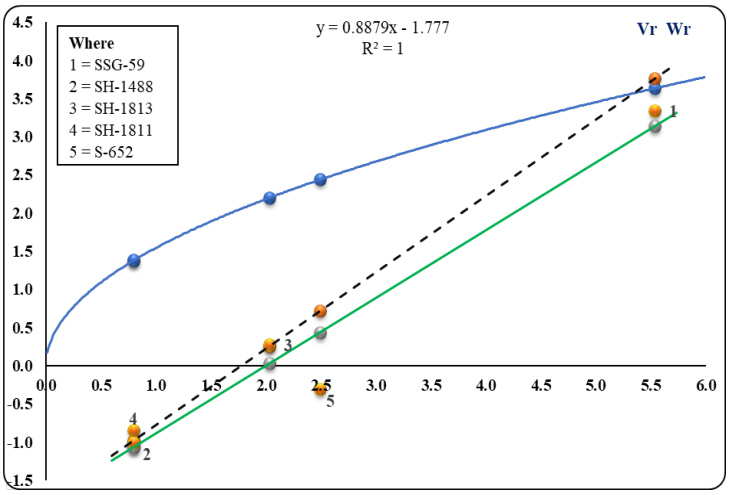

Fig. 6. Vr Wr Graph for Brix content

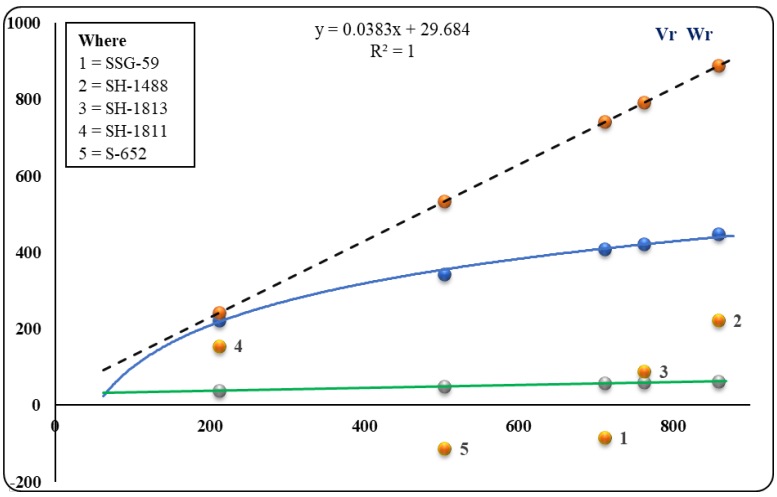

Fig. 7. Vr Wr Graph for dry fodder yield per plant

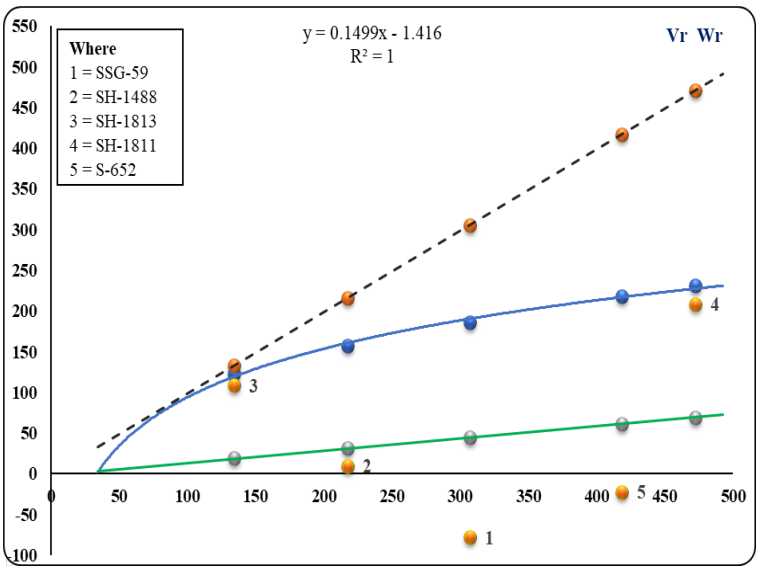

Fig. 8. Vr Wr Graph for HCN content

general combiners for green and dry fodder yield and its attributes.These parents can be utilized in future breeding programmes for improvement of forage yield in sorghum. The crosses SSG 59 × SH 1488, SH 1488 × SH 1813, SH 1488 × S 652 and SH 1811 × S 652 recorded higher specific combining ability effects for green and dry fodder yield per plant. These were observed to be governed by non-additive gene action and hence heterosis breeding could be adopted to improve the traits

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