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Genetics of Physiological and Yield Traits of Stay Green in Sorghum to Drought Stress in Rabi

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ABSTRACT: Sorghum is a major staple food crop for the people in semi-arid areas of Asia. Post-flowering drought is a global constraint of sorghum production with this the present study is to study the genetics of stay green and yield traits to the drought stress tolerance of the stay green introgressed lines. The significance of scaling test except for traits days to flowering for the traits studied indicates that the simple additive - dominance model or simply additive model is not adequate to explain the gene effects of stay green and grain yield component traits in sorghum. This result shows that traits presence of non-allelic interaction controlling these traits. With respect to stay-green, comparison between generation means revealed non-additive gene action for trait inheritance of stay green traits. The predominance of mean effect, dominance and dominance × dominance gene effects indicating dominant gene action play major role controlling the SPADB, SPADM, total number of green leaves at booting and maturity, green leaf area at booting and maturity in both crosses studied. With respect to gene effects mean followed by dominance and additive × dominance gene effect is significant and predominance in controlling the trait. However, the dominance and additive × dominance gene effect are in negative direction in both the crosses. The non-allelic gene action shows duplicate gene interaction. Duplicate epistasis signifies dispersion of alleles at the interacting loci and will decrease variation in S_2 or F_2 and subsequent generations and will delay the pace of progress through selection.

Keywords: Drought Stress, Stay Green and Yield traits.

INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] (2n=2x=20, family Poaceae) is well- known universal multipurpose crop for food, fodder, and potential biofuel feedstock. It is the fifth important cereal crop in the world in production and fifth in acreage after wheat, rice, maize and barley. Under diminishing moisture regimes of rabi season, sorghum crop severely suffers from drought leading to severe crop lodging, besides loss of stover, grain quality and productivity. In sorghum, stay-green (delayed-senescence) is a post-flowering drought tolerance trait and well characterized by the maintenance of green leaves (upper) and green stems although the plants are under severe moisture deficit conditions. The genotypes carrying the stay green trait maintain more photosynthetically active leaf area as compared to senescent genotypes, and continue to fill their grains normally under drought and heat stress conditions. Stay green is also associated with resistance to stalk lodging and charcoal rot superior fodder quality, increased stem sugars in stem and higher grain yield (Jordan *et al.*, 2012). Further, contribution of the stay-green to stable yield production under post maturity moisture stress has been documented (Rama Reddy *et al*., 2014) B35 is a widely used stay-green donor. Inheritance of stay green in this background is reported to be less complex and QTL`s controlling stay-green have been identified by different groups across the globe. Among these four QTL`s (*stg1*, *stg2*, *stg3* & *stg4*) are reported to be consistent by Subudhi *et al*. (2000).

The choice of best breeding program for developing superior high yielding drought tolerant stay green is depends on gene action and their interaction involved in expression of stay green, grain yield and its component traits. Generation means analysis is used for dissecting gene action controlling quantitative traits by analyzing basic generations based on means and variances using standard statistical models. This model provides information on average effects of the genes (additive effects), dominance deviations, and epistatic effects,

which can assist in quantifying the genotypic value of individuals, and in turn, would contribute to determining the average generation genotypic value. In this regard, it is valuable that the magnitude of gene action and type of epistasis can results in the designing of breeding strategies (Rajan *et al*. 2018).

The sorghum stay green genotypes K260 and K359w which carries *stg3A* and *stg3B* QTL`s are used as donor parent in the present study to generate different basic generations to use these lines as donors in breeding. Therefore, the experiment is planned to understand the genetics of stay green and yield traits, to study the association of stay green with yield traits and to study variability for yield and stress tolerant traits in different generations of crosses involving popular but stress (terminal drought) susceptible varieties GS-23 and stay green genotypes K260 and K359w.

MATERIALS AND METHODS

Study Area

The experiment was conducted at Agricultural Research Station, Kalaburgi and Hagari during *rabi* season of 2017-18. Kalaburagi is situated in Deccan Plateau located at 17.33°N 76.83°E and the general elevation ranges from 300 to 750 meters above mean sea level. Kalaburgi comes under north-eastern dry-zone of Karnataka with average annual rainfall of 717 mm and black soil being predominant soil type and the average ambient temperature remains 26.9°C, varies from 14.9°C to 42°C. The average relative humidity remains around 58.9%, varies from 14.7% to 97.9%. Hagari is situated at N 15° 9' 4"latitude and E 77° 3' 0" longitude and 495 m elevation. Hagari comes under northern dry-zone of Karnataka with average annual rainfall of 515 mm. The soil type and climatic conditions of both locations are well suited for *rabi* sorghum cultivation. Hence, these are ideal places for *rabi* sorghum for generating and evaluation of F_1, F_2, F_3, BC_1 and BC_2 generations for yield and stay green traits.

Experimental material

The experimental material consisted of three inbred lines of which GS-23 (P_1) is a non-stay green lines used as female parent, which are crossed with two stay green donor lines K260 (P_2) and K359w (P_3) received from ICRISAT, Hyderabad. These lines were used to develop experimental material used in present study, which comprised of six basic generations P_1, P_2, F_1, F_2, BC_1 and BC_2. (Fig.1a, 1b, 2, 3a, 3b, 4a, 4b and 5)

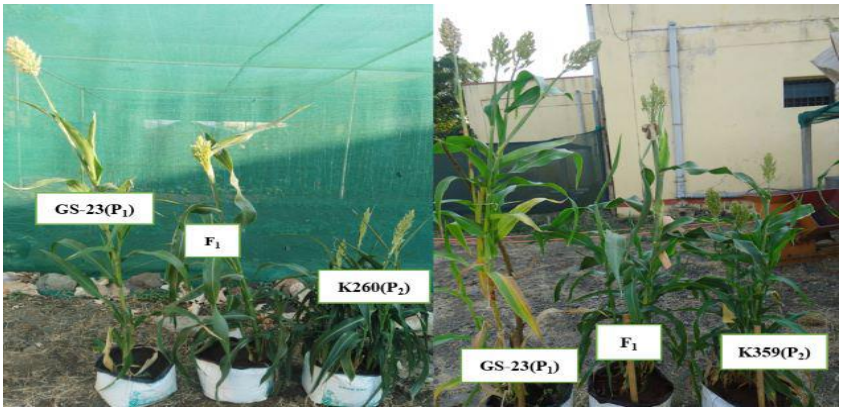
Experimental design and layout

At the research station Hagari, the experimental material consists of 11entries (three parents, two F_1's, two F_2's and four BC's) comprising six generations of two selected crosses *viz*., GS-23× K260 and GS-23× K359w two checks (B 35 and R16) was laid out during *rabi*, 2018 in a Randomized Block Design (RBD) with two replications. The non-segregating generations, *viz.*, parents, F_1's and checks were raised with 2 rows, while segregating generations *viz*., F_2's were raised with 10 rows and BC_1 and BC_2 populations were grown with 4 rows each. The entries were planted in rows of 4m length with spacing of 60×15 cm.

Fig. 1a. Panicle photographs of the parents used in the study.

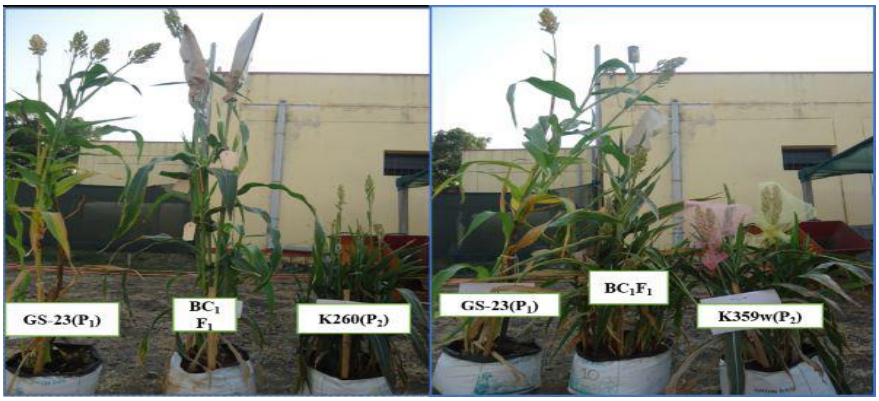
Fig. 1B. Panicles of the checks used for the study.

Fig. 2. Field view of F_2 population of the cross GS-23×K260.



(a) **(b)**

Fig. 3 (a) Phenotype of the plants of parents and F_1 the cross GS 23×K260; (b) Phenotype of the plants of parents and F_1 the cross GS-23×K359w.



(a) **(b)**

Fig. 4. (a) Phenotype of the plants of parents and $BC_1F_1$the cross GS-23×K260; (b) Phenotype of the plants of parents and $BC_1F_1$the cross GS-23×K359w.

Fig. 5. Phenotype of the plants of BC_2F_1 s of K260 and K359w.

Observations recorded. Data was recorded on five randomly selected tagged plants in each of the parents, F_1 and checks, hundred plants in F_2 and fifty plants each in BC_1 and BC_2 generations of both the crosses. The observations on component traits of stay green, grain yield and quality were recorded on each tagged plant.

Yield traits. Days to booting, days to panicle exertion, days to 50 per cent flowering, days to maturity, plant height (cm), panicle length (cm), panicle width (cm), panicle weight (g), stem girth (cm), grain yield per plant (g), test weight (g), fodder yield per plant (g), harvest index per panicle, grain number per panicle.

Physiological traits. Canopy temperature (°C), leaf temperature (°C), photosynthetic rate at booting (PRB) (µmole co_2 m^{-2} s^{-1}), photosynthetic rate at maturity (PRM) (µmole CO_2 m^{-2} s^{-1}), transpiration rate at booting (TRB) (mole H_2O m^{-2} s^{-1}), transpiration rate at maturity (TRM) (mole H_2O m^{-2} s^{-1}), chlorophyll content at booting (SPADB), chlorophyll content at maturity (SPADM), total number of green leaves at booting (GLB), total number of green leaves at maturity (GLM), per cent green leaves retained at maturity (PGLM), green leaf area at booting (GLAB) (cm/m^2) green leaf area at booting (GLAM) (cm/m^2), per cent green leaf area retained at maturity (PGLAM %), rate of leaf senescence.

Statistical analysis

Joint scaling test. The parameters such as m, the mean of all possible genotypes arising out of selfing of a cross, [$\hat{d}$] additive gene effect and [$\hat{h}$] dominance deviation effects were estimated from the observed means of six generations (P_1, P_2, F_1, F_2, B_1, and B_2) using joint scaling test as described by Mather and Jinks (1982).

Estimation of gene effects using perfect fit solutions

The six-parameter model (Mather and Jinks, 1971) were used to estimate gene effects for the traits for which additive-dominance model was inadequate as indicated by joint scaling test of Mather (1949).

RESULTS AND DISCUSSION

Scaling test. Segregating and non-segregating generation of the GS-23×K260 and GS-23 × K359w were studied in respect of grain yield traits, stay green trait and physiological traits for scaling tests. This was done to test the adequacy of simple additive dominance model in the genetic control of the traits. Further, the "t" test was conducted with respect to four parameters A, B, C and D of scaling tests. The results on scaling tests (A, B, C and D) in respect of grain yield traits, stay green trait and physiological traits have been tabulated in Tables 1, 2, 3 and 4.

In the cross GS-23×K260, for days after booting, scaling test A was significant at 1% level indicating the presence of epistasis. With respect to cross GS-23×K359w, A scaling tests were significant for days to booting indicating the epistasis (Table 1 and 2). These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. For days to panicle emergence, B and C scaling tests were non-significant in the cross GS-23×K260 indicating the absence of epistasis and remaining tests, test A and D were significant at 1% level indicating the presence of epistatic. With respect to cross GS-23×K359w, scaling tests of test A were sowing significant at 5 % level and test D were significant at 1% level which also revealed the presence of epistatic gene interaction.

Table 1: Estimates of scaling tests for grain yield component traits in six generations of a cross GS-23 × K260 of sorghum.

Sl. No.	Traits	Scaling tests			
		A	B	C	D
1	DAB	0.18**±1.29	10.84±1.34	6.86±4.29	-2.08±0.92
2	DPE	0.14**±6.20	11.80±5.67	10.10±14.50	-0.92**±1.603
3	DF	-1.94±3.13	14.96±3.16	2.70±6.99	-5.16±1.33
4	DM	-2.88**±1.57	11.58**±1.66	2.94±4.75	-2.88±1.02
5	PH	0.54±0.02	2.05**±0.02	0.68±0.08	-0.95**±0.01
6	PL	-4.418±0.95	7.88**±1.08	±3.64	-6.23**±0.86
7	PW	-1.54±1.33	13.18**±1.59	1.53±3.43	-5.05±0.71
8	PWT	29.17**±26.06	54.47**±22.57	22.27±113.75	-30.69±26.16
9	SG	-0.20±0.04	1.87**±0.08	-1.79±0.16	-1.72**±0.02
10	GYP	25.45**±22.18	45.98**±18.27	25.24±110.09	-23.10±23.83
11	TW	-1.28±0.22	1.29**±0.06	-1.32*±0.30	-0.66±0.04
12	FYP	-30.69*±2987.83	145.72±2132.28	119.89±6609.20	2.43*±643.24
13	HIP	4.49±11.21	7.14*±14.07	12.13±26.80	0.24±3.63
14	GNP	1035.30±30098.07	692.81**±14817.18	1015.91*±67412.72	-356.10±19739.03

* Significant at 5% level, ** Significant at 1% level

DAB: Days after booting, DPE: Days to panicle emergence, DF: Days to flowering, DM: Days to maturity, PH: Plant height, PL: Panicle length, PW: Panicle width, PWT: Panicle weight, SG: Stem girth, TW: Test weight, FYP: Fodder yield per plant, HIP: Harvest index per panicle, GNP: Grain number per plant, GYP: Grain yield per panicle.

Table 2: Estimates of scaling tests for stay green component traits in six generations of a cross GS-23 × K260 of sorghum.

Sr. No.	Traits	Scaling tests			
		A	B	C	D
15	**CT**	-0.38*±0.83	0.92±0.96	-0.36*±1.96	-0.45±0.22
16	**LT**	0.17*±0.40	-0.09±0.52	-3.47*±1.09	-1.788*±0.15
17	**PRB**	-0.46*±4.81	-0.81*±6.38	-7.27±12.06	-2.99±1.47
18	**PRM**	6.00±5.02	-1.14*±6.80	-13.8±12.73	-9.36±1.31
19	**TRB**	0.40±0.05	1.04±0.05	1.43±0.13	-1.87*±0.02
20	**TRM**	0.11±0.03	1.33±0.03	-0.04*±0.06	-0.74±0.01
21	**SPADB**	-1.72±2.44	-1.99±1.93	-5.23±8.92	-0.75*±2.42
22	**SPADM**	-8.55*±5.07	-21.98*±6.89	-4.92±19.71	12.80±3.70
23	**GLB**	-0.37±0.34	1.98±0.33	-2.02±1.06	-1.81±0.19
24	**GLM**	-0.84±0.17	0.16*±0.24	-2.05±0.84	-0.68±0.13
25	**PGLM**	-5.59±23.47	-7.31±28.73	-12.36±76.40	0.27*±9.15
26	**GLAB**	-1167.07±44589.31	-237.80±19351.73	-464.33*±88169.63	470.26±15573.96
27	**GLAM**	-105.47±19568.83	-646.18±25028.77	-154.40*±106472.80	298.62*±12452.07
28	**PGLAM**	18.73±15.45	-13.39±12.85	3.71*±62.17	-0.81*±7.62
29	**RLS**	-9.42*±4.57	2.84±2.46	-2.69±13.21	1.94*±1.31

* Significant at 5% level, ** Significant at 1% level

CT: Canopy temperature, LT: Leaf temperature, PRB: Photosynthetic rate at booting, PRM: Photosynthetic rate at maturity, TRB: Transpiration rate @ booting, TRM: Transpiration rate @ maturity, SPADB: SPAD reading at booting stage, SPADM: SPAD reading at maturity stage, GLB: Green leaves at booting, GLM: Green leaves at maturity, PGLM: Percent of green leaves at maturity, GLAB: green leaf area at booting, GLAM: green leaf area at maturity, PGLAM: Percentage GL @ maturity, RLS: Rate of leaf senescence.

Table 3: Estimates of scaling tests for grain yield component traits in six generations of a cross GS-23 × K359w of sorghum.

Sr. No.	Traits	Scaling tests			
		A	B	C	D
1	**DAB**	-0.56**±1.19	5.28±1.35	4.72±4.35	_
2	**DPE**	-0.60*±7.52	4.04±4.54	.80±13.85	0.18**±1.35
3	**DF**	-0.04±3.86	5.46±4.12	-2.78±8.27	-4.10±1.11
4	**DM**	-3.72±1.49	1.92**±2.10	0.04±4.14	0.92*±0.81
5	**PH**	0.41±0.01	1.64**±0.03	0.35±0.07	0.85**±0.01
6	**PL**	-3.93±1.03	8.10±1.67	-5.81*±5.03	-4.98**±0.94
7	**PW**	-0.58**±1.49	8.91±0.73	1.96*±2.14	-5.15±0.72
8	**PWT**	35.35**±29.25	24.64*±33.64	57.53±152.56	-2.23±29.42
9	**SG**	-0.22±0.05	-1.31**±0.06	-2.02±0.17	-1.35**±0.02
10	**GYP**	26.98±21.47	23.99**±25.05	51.16*±123.87	0.08±24.40
11	**TW**	-1.27±0.19	1.26**±0.09	-1.26*±0.36	-0.62±0.05
12	**FYP**	-27.02*±2393.22	56.91±2012.95	7.1±5203.48	-11.34*±672.98
13	**HIP**	1.63±14.21	6.52*±10.03	9.02±25.15	0.43±3.56
14	**GNP**	969.92±24454.79	335.17 **±29119.47	1958.39*±124690.70	326.64±26829.36

* Significant at 5% level, ** Significant at 1% level

DAB: Days after booting, DPE: Days to panicle emergence, DF: Days to flowering, DM: Days to maturity, PH: Plant height, PL: Panicle length, PW: Panicle width, PWT: Panicle weight, SG: Stem girth, TW: Test weight, FYP: Fodder yield per plant, HIP: Harvest index per panicle, GNP: Grain number per plant, GYP: Grain yield per panicle.

Table 4: Estimates of scaling tests for stay green component traits in six generations of a cross GS-23 × K359w of sorghum.

Sr. No.	Traits	Scaling tests			
		A	B	C	D
15	**CT**	-1.22*±0.72	-1.68±0.59	-2.18*±0.99	0.35±0.23
16	**LT**	-0.29*±0.29	2.07±0.46	-3.7**1±0.73	-2.74*±0.14
17	**PRB**	-1.26±4.48	-2.83±4.58	-5.47**±7.46	-0.68*±1.09
18	**PRM**	3.83**±5.67	-8.93±7.50	-22.49±16.82	-8.69±1.28
19	**TRB**	0.02±0.05	1.32±0.07	1.58*±0.17	0.12±0.02
20	**TRM**	-0.32±0.03	1.44±0.04	-0.43*±0.08	-0.77±0.01
21	**SPADB**	-1.84±2.00	-3.84±2.06	5.66*±6.44	5.67±2.01
22	**SPADM**	-6.83±4.56	-26.28±3.66	4.95*±10.86	19.03*±3.09
23	**GLB**	-0.42±0.35	-0.97±0.23	-2.10±0.78	-0.35±0.15
24	**GLM**	-1.04±0.17	-0.14*±0.16	-0.94±0.55	0.12±0.09
25	**PGLM**	-6.64±24.01	3.84±22.24	0.79*±59.34	1.79±8.65
26	**GLAB**	-1096.94±44031.59	-495.81±30924.15	-780.40*±110782.80	406.18±17454.34
27	**GLAM**	-149.43±18059.57	904.11±25321.50	664.92*±104488.10	194.31*±12678.88
28	**PGLAM**	16.24±14.72	-14.97±12.54	-5.23*±50.62	-3.25±*4.82
29	**RLS**	-8.16±4.36	3.68±2.67	-0.68*±11.14	1.89±0.78

* Significant at 5% level, ** Significant at 1% level

CT: Canopy temperature, LT: Leaf temperature, PRB: Photosynthetic rate at booting, PRM: Photosynthetic rate at maturity, TRB: Transpiration rate @ booting, TRM: Transpiration rate @ maturity, SPADB: SPAD reading at booting stage, SPADM: SPAD reading at maturity stage, GLB: Green leaves at booting, GLM: Green leaves at maturity, PGLM: Percent of green leaves at maturity, GLAB: green leaf area at booting, GLAM: green leaf area at maturity, PGLAM: Percentage GL @ maturity, RLS: Rate of leaf senescence.

These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. For days to 50 per cent flowering the cross GS-23×K260, scaling tests A, B, C and D were found non- significant. It emphasizes the absence of epistasis. With respect to cross GS-23×K359w, all tests (A, B, C, D) were found non-significant, which indicates the absence of epistasis. These results are in line with the reports made by Abebe, *et al*., 2021. Scaling test, A and B was found significant at 1% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, scaling test B was significant at 1% level and D was significant at 5%, emphasizing the presence of non-allelic interaction. The scaling tests A, B, C and D were found non- significant in both the crosses for days to 50 per cent flowering. It emphasizes the absence of epistasis. This indicates that additive dominance model explains the control of trait inheritance. These results are in accordance with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. In the cross GS-23×K260, B and D scaling tests were found significant at 1% level which indicates the presence of epistasis. With respect to cross GS-23×K359w, scaling tests B and D were significant at 1% level, which revealed the presence of epistasis. These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. In the cross GS-23×K260, B and D scaling tests were found significant at 1% level which indicates the presence of epistasis. With respect to cross GS-23×K359w, scaling tests D were significant at 1% level and C was significant at 5%, which revealed the presence of epistasis. These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. Scaling test B was found significant at 1% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, scaling test A was significant at 1% level and C was significant at 5%, emphasizing the presence of non-allelic interaction. Similar reports were made by Keshava Reddy, 2007 and Sunil Puranik, 2013. For panicle weight, A and B scaling tests were significant at 1% in the cross GS- 23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, A, scaling tests were found significant at 1% and B were significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007 and Sunil Puranik, 2013. In the cross GS-23×K260, B and D scaling tests were found significant at 1% which indicates the presence of epistasis. With respect to cross GS-23×K359w, same scaling tests B and D were found significant at 1% level which revealed the presence of epistasis. These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. Scaling test, A and B were found significant at 1% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, scaling test B was significant at 1% level and C was significant at 5%, emphasizing the presence of non-allelic interaction. Similar reports were made by Golabadi, *et al.*, 2006, Rama Reddy, *et al.*, 2014 and Luche, *et al.*, 2015. For test weight, B scaling tests were significant at 1% and C were at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, B scaling tests were found significant at 1% and C was significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the reports made by Sunil Puranik, 2013 and Rama Reddy, *et al.*, 2014. Based on result scaling test, A and D were found significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, A and D scaling tests were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. Only B scaling test, were found significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, scaling tests B were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. Scaling test B were found significant at 1% and C were found significant at 5% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, scaling test B was significant at 1% level and C was significant at 5%, emphasizing the presence of non-allelic interaction. These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. For canopy temperature, A and C scaling tests were significant at 5% in cross GS- 23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, same scaling tests A and C were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. In the cross GS-23×K260, A, C and D scaling tests were found significant at 5% which indicates the presence of epistasis. With respect to cross GS-23×K359w, scaling tests A and D were found significant at 5% level and C were at 1% also which revealed the presence of epistasis. These results are in line with the reports made by Sunil Puranik, 2013 and Rama Reddy, *et al*., 2014. For photosynthetic rate at booting, A and B scaling tests were significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, C scaling tests were found significant at 1% and D was significant at 5% which also revealed the presence of epistatic gene interaction. These results are in line with the reports made by Sunil Puranik, 2013 and Rama Reddy, *et al*., 2014. Only B scaling test, were found significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23 × K359w, scaling tests A were found significant at 1% which also revealed the presence of epistatic gene interaction. These results are in line with the reports made by Keshava Reddy, 2007 and Sunil Puranik, 2013. In the cross GS-23×K260, only D scaling tests were found significant at 5% which indicates the presence of epistasis. With respect to cross

GS-23×K359w, scaling tests C were found significant at 5% level also which revealed the presence of epistasis. These results are in line with the reports made by Keshava Reddy, 2007, and Sunil Puranik, 2013. Scaling test C were found significant at 5% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, same scaling test C was found significant at 5% level emphasizing the presence of non-allelic interaction. These results are in line with the reports made by Keshava Reddy, 2007, and Sunil Puranik, 2013. Based on result only D scaling test, were found significant at 5% in cross GS- 23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, C scaling tests were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007, and Sunil Puranik, 2013. For SPADM, A and B scaling tests were significant at 5% in cross GS-23×K- 260 indicating the presence of epistasis. With respect to cross GS-23×K359w, C and D scaling tests were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007, and Sunil Puranik, 2013. None of the scaling tests were found significant for this trait in the cross GS-23×K260, depicting the absence of epistasis. And in cross GS-23×K359w, no scaling tests were significant indicating the absence of epistatic gene interactions in this trait. These results are in line with the earlier reports of Keshava Reddy, 2007, and Sunil Puranik, 2013. Only B scaling test, were found significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, scaling tests B were found significant at 5 % which also revealed the presence of epistatic gene interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007, and Sunil Puranik, 2013. Scaling test D were found significant at 5% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, scaling test C was found significant at 5% level emphasizing the presence of non-allelic interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al*., 2014. For the trait green leaves area at booting stage, only C scaling tests were significant at 5% in cross GS-23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, same scaling tests C were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in accordance with the earlier reports of Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al*., 2014. In the cross GS-23×K260, C and D scaling tests were found significant at 5% which indicates the presence of epistasis. And with respect to cross GS-23×K359w, same scaling tests C and D were found significant at 5% level also which revealed the presence of epistasis. These results are in accordance with the earlier reports of Audilakshmi *et al.,* 2005, Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al*., 2014. Based on result scaling test C and D, were found significant at 5% in cross GS- 23×K260 indicating the presence of epistasis. With respect to cross GS-23×K359w, same scaling tests C and D were found significant at 5% which also revealed the presence of epistatic gene interaction. These results are in line with the earlier reports of Audilakshmi *et al.,* 2005, Keshava Reddy, 2007 and Sunil Puranik, 2013. Scaling test A and D were found significant at 5% for the cross GS-23×K260, indicating the presence of non-allelic gene interactions. With respect to cross GS-23×K359w, only scaling test C was found significant at 5% level emphasizing the presence of non-allelic interaction. These results are in accordance with the earlier reports of Audilakshmi *et al.*, 2005, Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy *et al*., 2014. The significance of scaling test except for traits days to flowering for the traits studied indicates that the simple additive - dominance model or simply additive model is not adequate to explain the gene effects of stay green and grain yield component traits in sorghum. This result shows that traits presence of non-allelic interaction controlling these traits. This is in line with earlier reports that indicated the role of non-allelic interaction in governing the expression of stay green and yield component traits in sorghum (Keshava Reddy, 2007 and Sunil Puranik, 2013).

Estimation of gene effects

Hayman's six parameter model (1958) was followed to estimate gene interaction effects based on mean values of the six generations *viz*., P_1, P_2, F_1, F_2, BC_1 and BC_2. The gene effects estimated were mean effect (m), additive effect (d), dominance effect (h), and additive × additive effect (i), additive × dominance effect (j) and dominance × dominance effect (l). The results obtained are tabulated in Tables 5, 6, 7, and 8 and are presented for each character as below. In cross 1, significant mean (m) effect (32.25) was recorded for the trait. The estimates of additive (d), dominance effects (h) and additive × additive (i) were significant with positive signs. Among the epistatic effects, dominance × dominance effects (l) and additive dominance effect (j) were significant but negative signs. In cross 2, significant mean (m) plays a major role effect (35.34) with positive sign. Additive × dominance effect (j) and dominance × dominance effect (l) significant but negative signs. And additive effect(d), dominance effect(h) and additive × additive (i) no gene effect were noticed this depicted duplicate nature of gene action for the trait. The mean effect (m) for the trait was found significant. Among the various gene effects, all the gene effects were significant in cross 1 (GS-23×K260). Whereas in cross 2 (GS-23×K359w) dominance, additive × dominance and dominance × dominance gene effects were significant. Presence of opposite sign values for both the dominance (h) and dominance × dominance gene effects (l) imply the duplicate epistasis for the expression of this trait. Similar studies were reported by of Audilakshmi *et al.*, 2005, Keshava Reddy, 2007 and Sunil Puranik, 2013.

With respect to days to panicle emergence, all the gene effects except and additive × additive (i) showed significance at the 5 per cent levels. Both additive (d) and

dominance (h) gene effects were significant and the values are positive for d and h, respectively. With respect to the interaction effects, additive × dominance effects (j) and dominance × dominance effect (l) was found with significant negative values -9.30 and -9.06, respectively. This depicted duplicate nature of gene action for the trait. And with respect of cross 2, all the gene effect were significant at 5% level with positive sign except additive × dominance effects (j) and dominance × dominance effect (l) significant with negative sign. The mean effect (m=45.50) was recorded for this trait. The parameter (h) and (l) significant but opposite sign positive and negative shows the presence of duplicate gene action for this trait.

Table 5: Estimates of gene effects for yield component traits in six generations of a cross GS-23 × K260 of sorghum.

Sr. No.	Traits	Cross	Gene effects						Type of Epistasis
			[m]	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{j}$]	[$\hat{l}$]	
1	**DAB**	**GS-23 × K-260**	32.25*	2.75*	14.71*	3.00*	-9.50*	-12.86*	Duplicate
2	**DPE**		46.87*	3.65*	6.29*	-0.52	-9.30*	-9.06*	Duplicate
3	**DF**		66.33*	4.75*	20.71*	6.92*	-13.50*	-16.54*	Duplicate
4	**DM**		103.45*	4.75*	7.09*	2.80*	-11.50*	-8.54*	Duplicate
5	**PH**		-0.30	0.31	7.15*	1.84	-1.43	-4.36*	Duplicate
6	**PL**		11.99*	4.26*	31.65*	11.85*	-11.69*	-14.71*	Duplicate
7	**PW**		2.53*	4.44*	27.17*	7.43*	-12.05*	-16.39*	Duplicate
8	**PWT**		2.14*	3.12*	205.82*	45.49*	-9.41*	-113.26*	Duplicate
9	**SG**		-0.21	0.58	8.79*	3.34*	-1.96*	-4.88*	Duplicate
10	**GYP**		-0.94	3.17	180.02*	36.01*	-10.34*	-97.27*	Duplicate
11	**TW**		3.62*	0.67	1.26	0.91	-2.15*	-0.50	Duplicate
12	**FYP**		212.60*	69.58*	215.76*	-31.02*	-150.25*	-57.85*	Duplicate
13	**HIP**		71.83*	1.87	30.93*	2.15*	-5.30*	-16.43*	Duplicate
14	**GNP**		98.230*	-34.52*	4210.20*	710.96*	343.74*	-2437.83*	Duplicate

* Significant at 5% level of significance, ** Significant at 1% level of significance.
DAB: Days after booting, DPE: Days to panicle emergence, DF: Days to flowering, DM: Days to maturity, PH: Plant height, PL: Panicle length, PW: Panicle width, PWT: Panicle weight, SG: Stem girth, TW: Test weight, FYP: Fodder yield per plant, HIP: Harvest index per panicle, GNP: Grain number per plant, GYP: Grain yield per panicle.

Table 6: Estimates of gene effects for physiological component traits in six generations of a cross GS-23 × K260 of sorghum.

Sr. No.	Traits	Cross	Gene effects						Type of Epistasis
			[m]	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{j}$]	[$\hat{l}$]	
15	**CT**	**GS-23 × K-260**	34.84*	-1.28	-3.12*	-0.96	0.28	2.28*	Duplicate
16	**LT**		27.28*	-1.00	15.35*	5.82*	-2.00*	-8.17*	Duplicate
17	**PRB**		38.83*	-1.32	7.80*	4.52*	0.92	-1.76	Duplicate
18	**PRM**		13.88*	-5.80*	34.12*	15.10*	10.78*	-16.32*	Duplicate
19	**TRB**		2.67*	0.11	2.51*	0.39	-1.02	-2.22*	Duplicate
20	**TRM**		-0.21	0.36	5.14*	1.80	-1.53	-3.56*	Duplicate
21	**SPADB**		48.00*	-1.88	2.82*	1.02	0.38	3.18*	Complementary
22	**SPADM**		65.77*	-9.21*	-83.03*	-29.05*	16.86*	63.01*	Duplicate
23	**GLB**		8.88*	-0.95	2.53*	1.37	-0.05	-0.72	Duplicate
24	**GLM**		3.94*	-0.50	2.74*	1.36	-1.00	-0.68	Duplicate
25	**PGLM**		42.23*	-0.15	21.64*	9.84*	-4.34*	-7.33*	Duplicate
26	**GLAB**		4559.71*	396.13*	-2718.05*	-1066.44*	-803.36*	2597.21*	Duplicate
27	**GLAM**		2834.71*	-308.57*	-1075.33*	-663.72*	607.18*	1481.84*	Duplicate
28	**PGLAM**		61.78*	-15.67*	20.03*	2.48*	31.27*	-8.67*	Duplicate
29	**RLS**		16.32*	6.09*	-15.54*	-4.15*	-12.00*	10.99*	Duplicate

* Significant at 5% level of significance, ** Significant at 1% level of significance.
CT: Canopy temperature, LT: Leaf temperature, PRB: Photosynthetic rate at booting, PRM: Photosynthetic rate at maturity, TRB: Transpiration rate @ booting, TRM: Transpiration rate @ maturity, SPADB: SPAD reading at booting stage, SPADM: SPAD reading at maturity stage, GLB: Green leaves at booting, GLM: Green leaves at maturity, PGLM: Percent of green leaves at maturity, GLAB: green leaf area at booting, GLAM: green leaf area at maturity, PGLAM: Percentage GL @ maturity, RLS: Rate of leaf senescence.

Table 7: Estimates of gene effects for yield component traits in six generations of a cross GS-23 × K359w of sorghum.

Sr. No.	Traits	Cross	Gene effects						Type of Epistasis
			[m]	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{j}$]	[$\hat{l}$]	
1	**DAB**	**GS-23 × K-359**	35.34*	1.50	7.70*	1.16	-7.00*	-7.04*	Duplicate
2	**DPE**		45.50*	2.50*	9.50*	2.00*	-7.00*	-7.80*	Duplicate
3	**DF**		62.95*	3.45*	31.47*	11.60*	-8.90*	-20.42*	Duplicate
4	**DM**		107.58*	2.30*	-1.50	1.12	-8.60*	-2.28*	Complementary
5	**PH**		-0.18	0.25	6.80*	1.78	-1.31	-3.91*	Duplicate
6	**PL**		13.19*	4.33*	30.41*	10.59*	-12.65*	-15.36*	Duplicate
7	**PW**		-3.07*	4.50*	42.09*	12.97*	-12.17*	-23.98*	Duplicate
8	**PWT**		28.80*	1.59	173.04*	20.36*	-7.18*	-98.26*	Duplicate
9	**SG**		0.05	0.43	8.22*	3.23*	-1.66	-4.43*	Duplicate
10	**GYP**		26.63*	1.60	135.02*	10.01*	-7.20*	-71.18*	Duplicate
11	**TW**		2.44*	1.08	4.46*	1.68	-2.97*	-2.10*	Duplicate
12	**FYP**		149.60*	53.05*	355.74*	48.85*	-55.05*	-104.89*	Duplicate
13	**HIP**		78.61*	0.76	10.75*	-3.52*	-1.12	-1.99*	Duplicate
14	**GNP**		1625.40*	-198.32*	928.65*	-652.05*	633.51*	-654.29*	Duplicate

* Significant at 5% level of significance, ** Significant at 1% level of significance
DAB: Days after booting, DPE: Days to panicle emergence, DF: Days to flowering, DM: Days to maturity, PH: Plant height, PL: Panicle length, PW: Panicle width, PWT: Panicle weight, SG: Stem girth, TW: Test weight, FYP: Fodder yield per plant, HIP: Harvest index per panicle, GNP: Grain number per plant, GYP: Grain yield per panicle.

Table 8: Estimates of gene effects for physiological component traits in six generations of a cross GS-23 × K359w of sorghum.

Sr. No.	Traits	Cross	Gene effects						Type of Epistasis
			[m]	[$\hat{d}$]	[$\hat{h}$]	[$\hat{i}$]	[$\hat{j}$]	[$\hat{l}$]	
15	**CT**	**GS-23 × K359w**	32.75*	-1.30	2.06*	1.15	-0.70	-0.11	Duplicate
16	**LT**		29.82*	-0.95	7.58*	3.23*	-0.10	-2.75*	Duplicate
17	**PRB**		40.73*	-1.55	4.46*	2.84*	0.05	-0.22	Duplicate
18	**PRM**		8.32*	-6.16*	46.34*	21.02*	9.14*	-19.55*	Duplicate
19	**TRB**		3.74*	0.05	-0.44	-0.62	-0.92	-0.34	Complementary
20	**TRM**		0.38	0.32	3.17*	1.25	-1.46	-2.06*	Duplicate
21	**SPADB**		60.35*	-2.34*	-21.98*	-10.87*	1.51	16.07*	Duplicate
22	**SPADM**		71.96*	-9.81*	-90.86*	-34.64*	16.02*	64.32*	Duplicate
23	**GLB**		7.49*	-1.15	7.33*	2.96*	-1.70	-3.82*	Duplicate
24	**GLM**		5.59*	-0.55	-0.81*	-0.24	-0.45	1.42	Duplicate
25	**PGLM**		65.54*	0.37	-35.91*	-13.98*	-0.05	27.17*	Duplicate
26	**GLAB**		4214.60*	361.26*	-1866.67*	-686.46*	-727.04*	2153.32*	Duplicate
27	**GLAM**		2530.94*	-346.37*	-483.07*	-322.15*	688.21*	1309.23*	Duplicate
28	**PGLAM**		58.99*	-16.05*	21.89*	5.65*	32.07*	-6.07*	Duplicate
29	**RLS**		15.54*	6.25	-12.30*	-3.53*	-12.11*	7.74*	Duplicate

* Significant at 5% level of significance, ** Significant at 1% level of significance
CT: Canopy temperature, LT: Leaf temperature, PRB: Photosynthetic rate at booting, PRM: Photosynthetic rate at maturity, TRB: Transpiration rate @ booting, TRM: Transpiration rate @ maturity, SPADB: SPAD reading at booting stage, SPADM: SPAD reading at maturity stage, GLB: Green leaves at booting, GLM: Green leaves at maturity, PGLM: Percent of green leaves at maturity, GLAB: green leaf area at booting, GLAM: green leaf area at maturity, PGLAM: Percentage GL @ maturity, RLS: Rate of leaf senescence

Days to panicle exertion indicates relative duration of the genotypes. Early genotypes are usually physiologically more efficient and escape from terminal moisture stress. Based on generation means, it was noticed that F_1, BC_1 and BC_2 were on par with mid-parental value in both the crosses indicating involvement of additive action in controlling the trait. With respect to gene effects additive, dominance, additive×dominance and dominance×dominance effects were significant indicate their predominant role in controlling the trait. Dominance and dominance×dominance interactions having signs in opposite directions, indicating the presence of duplicate type of epistasis. The mean effect (m) for the trait was positive and significant played a major role in trait expression. The additive effect (d) was low and positively significant while dominance gene action was observed significant and positive. The estimate of additive×additive (i) interaction effects was significant and positive, and both the additive × dominance (j) and dominance × dominance (l) effects were significant and with negative values. In second cross all gene effect were significant and positive except to additive × dominance (j) and dominance × dominance (l) shows negative sign. Significant opposite signs in 'h' and 'l' components indicated the presence of duplicate nature of epistasis. Such cross specific gene actions for days to 50% flowering were previously reported by Kassahun, *et al.,* 2010 and Rama Reddy *et al.,* 2014. Significant mean (m) effect 103.45 was recorded highest for the trait in cross1. The estimates of additive (d), and dominance effects (h) were significant and had positive signs. Among the epistatic effects, dominance × dominance effects (l) and additive × dominance (j) was also observed with significant negative signs. With

respect to second cross (cross 2) dominance effect (h) and additive × additive (i) was non-significant with opposite sign. The parameters'd' (2.30) and 'l' (-2.28) obtained significant but opposite signs. This depicted complementary nature of gene action for the trait. In cross 1 (GS-23 × K260) all the gene effects were significant with predominance of mean, followed by additive×dominance and dominance×dominance gene effects. The duplicate epistasis involved in the controlling of the trait. Whereas in cross 2 (GS-23 × K359w), except dominance and addsitive×additive other gene effects are significant with predominance of mean effect followed by additive × dominance and additive gene action. The complementary epistasis involved in the controlling of the trait. There by, this confirms that these interaction effects are cross specific. and these results are in accordance with the earlier reports of Keshava Reddy, 2007 and Sunil Puranik, 2013. Also such cross specific gene actions for grain iron and zinc in pearl millet were previously reported by Pujar *et al*. 2022. Plant height mean (m) effect (-0.30) was found non-significant with negative sign. With respect to interaction effects significant dominance × dominance effects (l) were noticed for this trait and the estimates are in negative direction. The estimates of dominance and dominance × dominance effects showed opposite signs. This indicated the duplicate epistatic gene interaction involved in controlling the trait. In cross 2 only dominance effect (h) and dominance × dominance effects (l) estimation was found significant with opposite signs. This indicated the duplicate epistatic gene interaction involved in controlling the trait. In the present study, the two parents differed significantly in the cross in both cross (GS-23 × K260 and GS-23 × K359w). F_1 and BC_1 and BC_2 mean values are superior than high value parents indicating dominance nature of increased plant height in this cross. With respect to gene effects, only dominance and dominance×dominance gene actions were significant and opposite signs direction indicating the operation of duplicate type of epistasis. For panicle length cross 1 mean effect (m) for the trait was found to be significant (11.99). Among the epistatic effects, additive × dominance (j) and dominance × dominance (l) components were found significant but they are in negative direction. The estimates of (h) and (l) gene effects observed in opposite direction indicating role of duplicate epistasis. With the respect of cross 2, all the effect were found significant but estimation of dominance effect (h) and dominance × dominance (l) observed in opposite direction indicating role of duplicate gene effects. Similar studies were reported by Keshava Reddy, 2007, Kassahun, *et al*., 2010 and Sunil Puranik 2013. In the first cross mean effect (m) for the trait was found to be highly significant (2.53). Among the epistatic effects, additive × dominance (j) and dominance × dominance (l) components were found significant but they are in negative direction. The estimates of (h) and (l) gene effects observed in opposite direction indicating role of duplicate epistasis. With respect of second cross among mean effect (m) -3.07, additive × dominance (j) and dominance × dominance (l) components were found significant but they are in negative direction. The estimates of (h) and (l) gene effects observed in opposite direction indicating role of duplicate epistasis. In the both the crosses (GS-23 × K260 and GS-23 × K359w), the two parents differed significantly for panicle length and panicle width. The mean of F_1, BC_1 and BC_2 generation is more inclined toward the better parents indicating the trait is under control of dominance gene action. However, the panicle length controlled by additive gene action. All the gene effects are significant in both the crosses. The dominance and dominance×dominance gene actions are predominant in trait expression and they are under duplicate epistasis. Selection may not be effective in improving genetic gain for these traits as dominance and dominance × dominance gene effects are non-fixable (Shalaby, 2013). Therefore, the selection of desirable lines should be followed in advanced segregating generations or selfing generation by evaluating a large number of families. Inter mating among the selected segregates followed by one or two generations of selfing will leads to the break of undesirable linkage, decrease additive variance and allow for the accumulation of favorable alleles. Significant mean effect (m) was observed for the trait (2.14) in cross 1. All the epistatic effects were found significant in which additive × additive (i) effect was in positive direction, and additive × dominance and dominance × dominance interaction effects in negative direction. The contrasting signs observed for 'h' and 'l' effects indicated duplicate epistasis in controlling the trait. And in the second cross additive effect (d) was found non-significant. Additive × dominance and dominance × dominance interaction effects in negative direction and dominance effect (h) and additive × additive (i) effect was in positive signs. The estimates of (h) and (l) gene effects observed in opposite direction indicating role of duplicate epistasis. Significance for all the six genetic parameters m, d, h, i, j and l were noticed for panicle weight in both the crosses (GS-23 × K260 and GS-23 × K359w) studied. The dominance effect was significant and played a prominent role in the control of this trait. Among the interaction effects only dominance × dominance type (l) of epistasis was predominant followed by additive × additive gene interaction. The opposite signs observed for dominance and dominance × dominance gene effects indicated the duplicate gene interaction in inheritance of the trait. Previously similar studies were done by Shalaby, 2013. Mean effect expressed for the trait was non-significant (-0.21) found in cross 1. The estimates of dominance and additive × additive gene effects were found significant and with positive values. Among the epistatic gene effects dominance × dominance interaction effects (l) played a prominent role as evidenced by significant negative values. The estimates of 'h' and 'l' observed in opposite direction indicate duplicate epistasis in controlling the trait. For cross 2, mean effect (m), additive effect (d), additive × dominance (j) was expressed non-significant effect for this trait. The estimates of 'h' and 'l' observed in opposite direction indicate duplicate epistasis in controlling the trait.

Similar studies were reported by Keshava Reddy, 2007 and Sunil Puranik, 2013. Non-significant mean effect (m) for the trait (-0.94) with negative direction was observed in cross 1. The estimates of additive effects (d) were found non-significant. Among the epistatic gene interactions, additive × dominance effects were found significant. The observation on presence of opposite signs for the components 'h' and 'l' indicates duplicate epistasis for the trait. For second cross additive effect (d) sowing non-significant component. The epistatic gene interactions, dominance × dominance effects were found significant with negative sign. The estimates of (h) and (l) gene effects observed in opposite direction indicating role of duplicate epistasis. Grain yield per plant is the primary trait of any breeding programme. High grain yield forms the major objective in any crop breeding programme. The mean of F_1, BC_1 and BC_2 is higher than better parents in both the cross. This indicates the involvement of dominance as well as non-allelic gene interaction for this trait. With respect to gene effects, except additive gene effect, all other gene effects are significant in first cross (GS-23 × K260) and mean effect followed by dominance and dominance × dominance gene effects are predominant in controlling the trait. Whereas in second cross additive and additive × dominance gene interaction is non-significant (GS-23 × K359w) and mean effect followed by dominance and additive × additive gene effects are predominant in controlling the trait. Dominance and dominance × dominance interactions having signs in opposite directions, indicating the operation of duplicate type of epistasis. Regarding first cross mean effect (m) was found to be significant for the trait (3.62). Among the gene effects only additive × dominance effects were found significant. Further, the opposite signs observed for dominance and dominance × dominance gene effects indicated the duplicate gene interaction. Further, in cross 2, mean effect (m) is significant with positive sign (2.44) dominance and dominance × dominance gene effects are significant with opposite signs indicating duplicate allelic interaction. With respect to cross GS-23 × K260, significant dominance (h), additive × additive (i), additive × dominance (j) and dominance × dominance (l) was noticed with predominance of dominance (180.2) and dominance × dominance (-97.27) the opposite sign value for h and l indicated duplicate epistasis in controlling the trait expression. In the cross GS-23 × K359w, except additive gene effects, other gene effects are significant predominance of dominance (135.02) and dominance × dominance (71.18) with non- additive gene action showing duplicate epistasis in inheritance of trait. These results are in line with the previous studies done by Keshava Reddy, 2007. For this trait expression, mean effect (m) was found highly significant (212.60) in first cross. Among the gene effects only additive × dominance (j) effects were found significant. The observation on presence of opposite signs for the components 'h' and 'l' indicated the duplicate epistasis for the trait. And into second cross all components of these traits were found significant. The opposite signs for the components 'h' and 'l' indicated the duplicate epistasis for the trait. This trait is of equally important as that of grain yield per plant, because sorghum is most popular fodder crops in world. Fodder yield of F_1, BC_1 and BC_2 are more inclined towards mid parent in both the crosses studied indicates involvement of additive gene action. With respect to gene effects only mean and additive × dominance gene interaction is significant in the first cross. For the cross GS-23 × K359w, except additive and additive × dominance gene interaction all other gene effects are significant. Comparing both the crosses the gene effect of additive × dominance is significant and the value is near to the mean indicating the major involvement of additive × dominance gene effect in trait expression. This indicate selection for the trait is effective after one or more generation of selfing which exposes additive variance for selection and then crossing between lines can exploit dominance gene action involved in the trait expression. Similar reports were reported for fodder yield per plant in Kumar *et al*., 2011. Into first cross the mean effect (m) was found to be significant for the trait (71.83). With respect to genetic control, all the gene effects were found significant for this trait excluding additive effect (d). The additive × additive effect (i) was manifested in positive direction. The observation on presence of contrasting signs for the components 'h' and 'l' indicates the duplicate epistasis for the trait and with respect of second cross except to additive effect (d) and additive × dominance, the entire gene effects were found significant. The contrasting signs observed in dominance and dominance × dominance gene effects indicated the duplicate gene interaction. With respect to cross GS-23×K260, mean and all gene effects are significant dominance (30.93), mean (71.83) and additive × additive (2.15) are predominant in trait expression. Whereas in the second cross (GS-23 × K359w), dominance (10.75) and mean (78.61) are predominant in trait expression. The opposite sign value for h and l indicated duplicate epistasis in controlling the trait expression in the both the crosses Similar reports were reported by Kumar *et al*., 2011 and Sunil Puranik, 2013. Regarding first cross, mean effect (m) was found to be significant for the trait (98.230). Among the different gene effects, additive effects (d) significant with negative sign, dominance effects (h) and additive × dominance effects were found to be significant. The opposite signs observed for dominance and dominance × dominance gene effects indicated the duplicate gene interaction. For second cross all the gene effects were found significant and the opposite sign observed in h and l components indicating duplicate gene interaction. The mean of F_1, BC_1 and BC_2 is higher than better parents in both the cross (GS- 23 × K260 and GS-23 × K359w. This indicates the involvement of dominance as well as non-allelic gene interaction for this trait. All the gene effects are significant in the first cross dominance and dominance × dominance gene effect is predominant with opposite sign values indicating duplicate epistasis involved in trait expression. With respect to second cross GS-23 × K359w, mean value is predominant followed by dominance (h), dominance × dominance (l) and additive

× additive gene effects. This indicates trait is under the control of dominance and equally on non-allelic gene interaction. The duplicate epistasis shows the dispersion of alleles and selection in early generation is difficult. Similar reports were reported by Kumar *et al*., 2011 and Sunil Puranik, 2013. The mean effect (m) for this trait was found to be significant (34.84) in first cross. With respect to gene effects, additive (d), additive × additive (i) and additive × dominance gene effects were found non-significant. The opposite signs noticed for dominance and dominance × dominance gene effects indicated duplicate epistasis for this trait. For second cross dominance and dominance × dominance gene effects were found significant with opposite direction showing duplicate epispastics for this trait. Canopy temperature and leaf temperature are important high throughput field phenotyping physiological traits utilized for selection of drought and heat tolerance in different crops (Puttamadanayaka *et al*., 2020). The plants which are having low canopy temperature and leaf temperature will have better root system to maintain evapotranspiration which keeps canopy cool under stress condition and such genotypes will be photosynthetically more efficient. The dominant gene action is significant and predominant for canopy temperature and leaf temperature in both crosses and also the F_1 mean of both the crosses on par with the better parents (K260 and K359w) indicate dominant genes play role in trait expression. This shows that canopy temperature and leaf temperature can be exploited through heterosis. Significant mean effect (m) was observed for leaf temperature in first cross. Dominance effect (h) was significant and played a major role in this trait. Among the epistatic interactions, additive × dominance effect was found significant but it was in negative direction. Further, duplicate epistasis was evident based on opposite signs of 'h' and 'l' effects. With respect of second cross mean effect was also significant. Additive effect (d) and additive × dominance effect was found non-significant. The opposite sign was observed in 'h' and 'l' gene effect indicating duplicate gene interaction for this trait. Similar reports were reported by Sunil Puranik, 2013 and Rama Reddy, *et al.,* 2014. The mean effect (m) for the photosynthetic rate at booting was found significant (38.83) first cross. Both the dominance (h) and additive × additive type of gene interaction effects was found to be significant. Further, the observation on opposite signs of 'h' and 'l' gene effects indicated the expression of the trait under the control of duplicate epistasis. In the second cross contrasting gene effect was observed in 'h' and 'l' with opposite sign indicates the expression of these traits under control of duplicate epistasis. Similar reports were made by Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al.,* 2014. Regarding first cross significant mean effect (m) was noticed for this trait (13.88). All gene effects were found significant. The opposite signs noticed for dominance (h) and dominance × dominance gene effects (l) indicated evidence of duplicate epistasis for this trait. With respect of second cross, mean effect (m) was significant with observed value of 8.32 and all the components for this cross found significant. The observation on opposite signs of 'h' and 'l' gene effects indicated the expression of the trait under the control of duplicate epistasis. The photosynthetic rate was estimated during booting (PRB) and maturity (PRM) stage. The mean of F_1 generation for the trait on par with the better parental means of K260 and K359w indicating presence of dominant gene action in the both the crosses GS-23 × K260 and GS-23 × K359w. For PRB, apart from mean effect, dominance and additive × dominance gene effects are significantly predominant among all the gene effects. Hence early generation selfing and then selection for the trait will be effective for PRB. Similarly, for PRM dominance, dominance × dominance and additive × dominance was significantly predominance with duplicate epistasis. Similar reports were made by Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al.,* 2014. Regarding first cross mean effect was found to be significant with respect to transpiration rate at booting (2.67). With respect to gene effects, dominance effect (h) and dominance × dominance gene effects (l) were found to be significant which played a prominent role. No other gene effects were found to be significant for this trait. Further, the observation on opposite signs of 'h' and 'l' gene effects indicated the expression of the trait under the control of duplicate epistasis. For second cross only the mean effect was found to be significant for this trait (3.74). Presence of similar but negative signs observed for both the dominance (h) and dominance × dominance gene effects (l) imply the complementary epistasis for the expression of this trait. For the trait TRB, in cross 1 (GS-23 × K260) the mean, dominance, and dominance × dominance gene effects were significant and predominant with gene interaction is controlled by duplicate epistasis. Whereas, in second cross (GS-23 × K359w) only mean effect is significant and all other gene effects are non-significant. Thereby, this confirms that these interaction effects are cross specific. Such cross specific gene actions for grain iron and zinc in pearl millet were previously reported by Rama Reddy, *et al*., 2014 and Pujar *et al*., 2022. For first cross the mean effect was found to be non-significant for this trait (-0.21). None of the gene effects were found to be significant except dominance (h) and dominance × dominance gene effects (l). Presence of opposite but observed for both the dominance (h) and dominance × dominance gene effects (l) imply the duplicate epistasis for the expression of this trait. Into second cross only dominance (h) and dominance × dominance gene effects (l) were found significant with opposite signs indicating duplicate gene interaction for this trait. Similar reports were made by Keshava Reddy, 2007, Sunil Puranik, 2013 and Rama Reddy, *et al.,* 2014. With respect to TRM, dominance and dominance × dominance gene effects are significantly predominant with duplicate gene interaction in both the crosses. This shows clearly trait is in control of dominance gene action with dispersion of genes. The heterosis breeding will be best method for improvement of this trait. This is because selection may not be effective in improving genetic gain for these traits as dominance and dominance × dominance gene effects

are non-fixable. Similar reports were made by Shalaby (2013). For this trait expression, mean effect (m) was found significant (48.00) in first cross. Among the gene effects only dominance (h) and dominance × dominance gene effects (l) effects were found significant. The observation on presence of similar signs for the components 'h' and 'l' indicated the complementary epistasis for the trait. And into second cross all components of this traits were found significant except additive × dominance effect (j). The opposite signs for the components 'h' and 'l' indicated the duplicate epistasis for the trait. SPAD reading at booting stage (SPADB) shows significance for mean, dominance × dominance gene effects in the cross GS-23 × K260. Mean effect was more predominant followed by dominance × dominance and dominant gene effects indicating dominant gene action play major role controlling the trait. Same sign of dominant and dominance × dominance gene effects indicate the complementary gene action involved in controlling of the trait. Similarly, mean effect was more predominant followed by dominant gene effects and dominance × dominance indicating dominant gene action play major role controlling the trait in the cross GS-23 × K359w. In the second cross the trait shows duplicate gene interaction. With respect to genetic control, all the gene effects were found significant for this trait. The additive × dominance effect (j) was manifested in positive direction. The observation on presence of contrasting signs for the components 'h' and 'l' indicates the duplicate epistasis for the trait. And with respect of second cross expect to additive effect (d) all the gene effects were found significant. The contrasting signs observed in dominance (h) and dominance × dominance (l) gene effects indicated the duplicate gene interaction. SPAD reading at maturity stage (SPADM) shows significance for all the gene effects in both the cross GS-23 × K260 and GS-23 × K359w. Mean effect was more predominant followed by dominance, dominance × dominance and additive × dominance gene effects respectively. This indicates that dominant gene action and non- allelic gene interaction play major role controlling the trait. Duplicate epistasis found controlling trait expression. Presence of duplicate type of epistasis interaction tends to reduce the trait expression hence development of hybrid varieties is not desirable. The duplicate epistasis controlling SPAD value was earlier reported by Sunil Puranik, 2013. Regarding first cross mean effect (m) was found to be significant for the trait (8.88). Among the different gene effects, only dominance effects (h) significant with positive sign. The opposite signs observed for dominance and dominance × dominance gene effects indicated the duplicate gene interaction. For second cross mean effect was observed (7.49) with respect to gene effect additive × additive (i) effect was found significant. And the opposite sign observed in 'h' and 'l' components indicating duplicate gene interaction. Total number of green leaves at booting (GLB), F_1 mean was on par with the mean value of the P_2 (K260 and K359w) in both the crosses, this revealed that trait is controlled by dominant genes. This also supported by significance and predominance of dominant gene effects in both the crosses. Significance and the opposite sign of dominance and dominance × dominance gene interaction in cross 1 indicate duplicate epistasis play major role in control of this trait. The heterosis breeding will be effective for improving this trait as dominance and dominance × dominance play major role in control of this trait. The mean effect (m) for this trait was found to be significant (3.94) in first cross. With respect to gene effects, additive (d), additive × additive (i) and additive × dominance gene effects were found non-significant. The opposite signs noticed for dominance and dominance × dominance gene effects indicated duplicate epistasis for this trait. For second cross dominance and dominance × dominance gene effects were found significant with opposite direction showing duplicate epispastics for this trait. Total number of green leaves at maturity (GLM) is an important key trait associated with stay greenness. For this trait, the mean of F_1 generation for the trait exceeding the better parental mean of P_2 (K260 and K359w) in both crosses GS-23 × K260 and GS-23 × K359w indicating presence of non-additive gene action and stay green trait is dominant over non-stay green trait. With respect to gene effects mean and dominance gene effect played an important role in both the crosses however in the second cross GS-23 × K359w this is in negative direction. Hence this trait can be incorporated in inbreeds and can be exploited for breeding drought tolerant sorghum hybrids. Similar reports were made by Keshava Reddy, 2007 and Sunil Puranik 2013. Significant mean effect (m) was observed (42.23) for per cent green leaves retained at maturity in first cross. Dominance effect (h) was significant and played a major role in this trait. Among the epistatic interactions, additive × dominance effect was found significant while it was in negative direction. Further, duplicate epistasis was evident based on opposite signs of 'h' and 'l' effects. With respect of second cross mean effect was also significant. While additive × additive effect was found significant but it was in negative direction. The opposite sign was observed in 'h' and 'I' gene effect indicating duplicate gene interaction for this trait. The higher the value of PGLM indicates higher retention of green leaves during maturity stage which indirectly depicts the stay green plant types. The mean of F_1 is superior to the better parents in both the crosses indicating involvement of non- additive gene action in controlling the trait expression. With respect to gene action dominance, additive × additive and dominance × dominance was predominant in the both crosses GS-23 × K260 and GS-23 × K359w evaluated in the experiment. Further, dominance gene effect and dominance × dominance gene effect were significant with opposite direction and clearly trait is under the control of duplicate gene interaction. Hence, the selection for this trait will be effective in later stages of line development. Similar reports were reported by Keshava Reddy, 2007 and Sunil Puranik (2013). The mean effect (m) for the green leaves area at booting stage was found significant (4559.71) in first cross. With respect of gene effects all gene effects

were found significant. Further, the observation on opposite signs of 'h' and 'l' gene effects indicated the expression of the trait under the control of duplicate epistasis. Into second cross contrasting gene effect was observed in 'h' and 'I' with opposite sign indicate the expression of these traits under control of duplicate epistasis. Green leaf area at booting (GLAB), the mean of F_1 generation for the trait exceeding the better parental means of K260 and K359w indicating presence of non-additive gene action in the both the crosses GS-23 × K260 and GS-23 × K359w. The dominance effect for the GLAB indicated a significant predominant effect compared with all other assessed gene and epistatic effects in cross 1 (GS-23 × K260). Dominance × dominance epistasis was significant with predominant followed by dominance effect in cross 2 cross (GS-23 × K359w). The cross-wise direct genetic and interaction effects revealed that in both crosses has duplicate gene interaction. Duplicate epistasis signifies dispersion of alleles at the interacting loci and will decrease variation in S_2 or F_2 and subsequent generations and will delay the pace of progress through selection. Similar reports were made by Keshava Reddy, 2007 and Sunil Puranik, 2013. Regarding first cross significant mean effect (m) was noticed for this trait (2834.71). All gene effects were found significant for this trait. The opposite signs noticed for dominance (h) and dominance × dominance gene effects (l) indicated evidence of duplicate epistasis for this trait. With respect of second cross mean effect (m) was observed (2530.94) and all the components for this cross also found significant. The observation on opposite signs of 'h' and 'l' gene effects indicated the expression of the trait under the control of duplicate epistasis. Green leaf area at maturity (GLAM) is key trait that determines the drought tolerance during post maturity stage. The trait with higher GLAM more photosynthetically efficient compared to genotype having higher leaf senescence. As regards to GLAM trait all the six parameters were significant in the two crosses. The opposite sign of the parameters h and l revealed the duplicate epistasis in both the crosses. In cross 1 significant mean (m) effect (61.78) was recorded for the trait. The estimates of dominance effects (h) and additive × additive (i), additive × dominance effect (j) was significant with positive signs. Among the epistatic effects, dominance (h) and dominance × dominance effects (l) and were significant but opposite sign indicating duplicate gene interaction for this trait. In the cross 2 significant mean (m) play a major role effect (58.99) additive effect (d) significant but negative signs. The parameter 'h' and 'l' significant but opposite sign indicating the presence of duplicate gene action for this trait. These findings were in conformity with the reports of Sunil Puranik 2013. With respect to days to rate of leaf senescence**,** all the gene effects showed significance at the 5 per cent levels. With respect to the interaction effects, additive × additive effects (i) and additive × dominance effect (j) was found with significant negative values. Dominance (h) and dominance × dominance effects (l) observed with opposite directions indicating duplicate nature of gene action for the trait. And with respect of second cross all the gene effects were significant at 5% level except additive effect (d). The mean effect (m) (15.54) was recorded for this trait. The parameter 'h' and 'l' found with opposite sign indicating the presence of duplicate gene action for this trait. Rate of leaf senescence reveals the number of days taken between a stay green and non-stay green genotypes. For this trait, the mean of F_1 generation for the trait place near to the mid parent value in both the crosses, indicating presence of additive gene action in controlling trait expression. These results are in line with the reports of Pavan and Gangaprasad (2022).

Stay green inheritance studies

Stay green inheritance studies in the Table 6 showed the presence of dark green colour in the F_1 progenies of the cross GS-23×K260 which is inherited from parent P_1 indicating that the presence of dominant effect of stay green trait. Phenotypic segregation of F_2 of the cross GS-23×K260 for colour of leaf in the Table 6 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the trait colour of leaf. Similarly phenotypic segregation of F_2 of the cross GS-23× K260 for stay green at maturity in the Table 6 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the stay green trait at maturity.

Breeding behavior in F_3 families of the cross GS-23 × K260 for leaf colour in the Table 6 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the trait colour of leaf. Similarly, breeding behavior in F_3 families of the cross GS-23 × K260 for stay green at maturity in the Table 6 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the stay green trait at maturity. Joint segregation of leaf colour and stay green colour of leaf in F_2 generation of the cross GS-23 × K260 showed that the calculated chi-square value was lesser than the Table value (7.815) at 5 per cent level and 3 degrees of freedom indicating that the characters under the study are independent. Stay green inheritance studies showed the presence of dark green colour in the F_1 progenies of the cross GS-23×K359w. Which is inherited from parent P_2, indicating that the presence of dominant effect of stay green trait. Previously, similar studies were conducted and reports were made by Keshava Reddy 2007 and Sunil Puranik, 2013.

Phenotypic segregation of F_2 of the cross GS-23 × K359w for colour of leaf in the Table 7 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the trait colour of leaf.

Similarly, phenotypic segregation of F_2 of the cross GS-23 × K359w for stay green at maturity in the Table 7 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the stay green trait at maturity. Breeding behavior in F_3 families of the cross GS-23 × K359w for leaf colour in the Table 8 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the trait colour of leaf. Similarly, phenotypic segregation of F_2 of the cross GS-23 × K359w for stay green at maturity in the Table 7 showed that the calculated chi square value was lesser than the Table value (3.841) at 5 per cent level and 1 degree of freedom, indicating that the chi square value is non-significant and the presumed ratio is good fit for the stay green trait at maturity. Joint segregation of leaf colour and stay green colour of leaf in F_2 generation of the cross GS-23 × K359 in the Table 8 showed that the calculated chi-square value was lesser than the Table value (7.815) at 5 percent level and 3 degrees of freedom indicating that the characters under the study are independent. The contrasting phenotypes for leaf colour were dark green and green colour and in F_1 dark green was found dominant over green. In F_2 of both the crosses 3:1 ratio of dark green to green was obtained which meant that different single pair of alleles controlled this character.

Stay green colour was studied in the cross GS-23×K260 and GS-23×K359w. The contrasting phenotypes for stay green present at maturity and stay green absent at maturity and in F_1 presence of stay green was found dominant over absent. In F_2 of the both the crosses 3:1 ratio of stay green presence and absence was obtained which meant that different single pair of alleles is controlling this trait. Thus, making the sorghum plants to stay green at maturity level to with stand drought stress. Similar reports were made by Keshava Reddy 2007 and Sunil Puranik, 2017 with respect to stay green trait in sorghum.

CONCLUSIONS

The dominant gene action is significant and predominant for canopy temperature and leaf temperature in both crosses and also the F_1 mean of both the crosses on par with the better parents (K260 and K359w) indicate dominant genes play role in trait expression. Photosynthetic rate at booting and maturity the mean of F_1 generation for the trait on par with the better parental means of K260 and K359w indicating presence of dominant gene action in the both the crosses GS-23×K260 and GS-23 × K359w. For PRB, apart from mean effect, dominance and additive × dominance gene effects are significantly predominant among all the gene effects. With respect to grain yield component traits scaling test revealed presence of epistasis for all the traits except days to 50% flowering. Days to booting all the gene effects were significant in cross 1 (GS-23 × K260). With respect to gene effects additive, dominance, additive×dominance and dominance×dominance effects were significant indicate their predominant role in controlling the trait. Days to maturity, duplicate epistasis involved in the controlling of the trait in the cross GS-23 × K260 and complementary epistasis involved in the controlling of the trait in other cross GS-23 × K359w. Plant height, panicle length and panicle width, the mean of F_1, BC_1 and BC_2 generation is more inclined toward the better parents indicating the trait is under control of dominance gene action. Further, the dominance and dominance×dominance gene actions are predominant in trait expression and they are under duplicate epistasis. Grain yield per plant with respect to gene effects, except additive gene effect, all other gene effects are significant in first cross (GS-23 × K260) and mean effect followed by dominance and dominance × dominance gene effects are predominant in controlling the trait. Whereas in second cross additive and additive × dominance gene interaction is non-significant (GS-23 × K359w) and mean effect followed by dominance and additive × additive gene effects are predominant in controlling the trait. The additive × dominance is significant and the value is near to the mean indicating the major involvement of additive × dominance gene effect in trait expression of fodder yield per plant. Thousand seed weight and grain number per panicle all the gene effects are significant with predominance of dominance and dominance × dominance gene effect with opposite sign values indicating duplicate epistasis involved in trait expression. For harvest index per panicle mean and all gene effects are significant dominance mean and additive × dominance are predominant in trait expression. Whereas in the second cross (GS-23 × K359w), dominance, mean and dominance × dominance is predominant in trait expression.

Leaf colour was controlled by two dominant independent genes *viz.*, *Dg1* and *Dg2*. Whereas stay green trait was controlled by two independent dominant genes *STG3A* and *STG3B.* Stay green inheritance studies in F_1, F_2 and F_3 breeding behavior showed that the dominant gene action plays major role in controlling the stay green trait in both the crosses and stay green trait is dominant across generations in nature of expressing at maturity level too, thus giving the sorghum crop to with stand physiological stress under drought conditions by staying green.

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