

Original Research Article

Estimation of gene interaction for grain yield and yield traits in *rabi* sorghum [*Sorghum bicolor* (L.) Moench]

Abstract

Generation mean analysis is the potent tool to provide information about different types of gene actions and interactions. To determine the inheritance pattern and gene action of 10 grain yield and grain related quantitative traits, six generations of the four cross combinations *viz.*, BJV44 × DSMR8, BJV44 × DSMR4, PKV Kranti × DSMR8 and PKV Kranti × DSMR4 were studied employing generation mean analysis during *rabi* of 2020. Interestingly, both additive and dominant gene action were prevalent for all the traits in the cross BJV44 × DSMR8, whereas the other three crosses exhibited additive for some traits and dominant gene action for some traits. Most of the traits in the majority of the crosses displayed the duplicate type of gene interaction and realized their suitability for the population improvement program. Some crosses *viz.*, BJV44 × DSMR4 and PKV Kranti × DSMR4 exhibited complementary gene interaction and were found suitable for heterosis breeding for grain yield/plant.

Keywords; Sorghum, grain size, grain yield, genetic interaction, generation mean analysis

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is a C₄ plant with higher photosynthetic efficiency and shows tolerance to abiotic stress (Reddy *et al.*, 2009). Sorghum originated in Africa and adapted to a diverse set of environments ranging from arid and semiarid to tropical across the world. After wheat, rice, maize, barley, and sorghum is the major cereal crop with respect to production. Sorghum is significant for providing micronutrients at a low cost, in addition to serving as a food and fodder crop (Rao *et al.*, 2010). Sorghum is an often cross pollinated crop with an average of 5 to 10 percent cross pollination and it may exceed up to 40 percent (Barnaud *et al.*, 2008).

Grain size and other grain related traits *viz.*, grain width, grain length, grain thickness, 100 grain weight, grain volume, grain density, number of grains/panicle, and days to flowering

exhibited positive and significant association with grain yield (Kariyannanavaret *al*, 2022). Path analysis also showed a positive and significant direct & indirect effect on grain yield (Verma and Biradar, 2021). Therefore, a genetic study was planned and executed to know the underlying gene action, inheritance pattern, and trait heritability so that these traits can be exploited for crop improvement.

Knowledge of gene actions and the inheritance of these traits is critical to harnessing the large variability available in sorghum. Generation mean analysis informs about the relative importance of additive effects, dominance deviations, and effects due to epistatic interactions, in determining the genotypic worth of the individuals and, consequently, means genotypic values of families and generations.

Material and methods

In this study, each of the two promising varieties *viz.*, BJV44 and PKV Kranti were crossed with each of the two strong restorers on *maldandi* male sterile source *viz.*, DSMR-8 and DSMR-4 (Verma *et al.*, 2022) to generate four crosses namely, BJV44 × DSMR8, BJV44 × DSMR4, PKV Kranti × DSMR8, and PKV Kranti × DSMR4. Six generations, *i e.*, P₁, P₂, F₁, F₂, B₁, and B₂ were generated for each cross combination during *the summer* and *Kharif* seasons-2020. The F₁'s of all the four crosses developed in summer-2020 and Kharif-2020, each of the F₁ was backcrossed with their P₁ and P₂ parents to develop B₁ and B₂ populations, respectively. At the same time, each F₁ advanced to produce F₂ populations. Since the development of six generations in four different crosses was time consuming process and there were not enough seeds for multiple seasons/year evaluation. Therefore, the six generations were evaluated only during the post rainy season-2020 at Botany Garden, College of Agriculture, UAS, Dharwad, Karnataka, India.

To evaluate the six generations of all the four crosses, an experiment was carried out without replications; the population size and characteristics of the parents used are given in Table 1. All the recommended packages of practices were followed to raise a healthy crop. The grain size related traits *viz.*, grain length (mm), grain width (mm), grain thickness (mm), were measured using the vernier caliper while the volume of the 100 grains was measured based on the water displacement method.

Results and Discussion

Adequacy of additive-dominance model

Scaling tests were run to evaluate the effectiveness of the additive dominance model for the inheritance of traits relevant to grain size and grain yield. Except for grain density in PKV Kranti \times DSMR4, the entire studied trait's scaling test values were found to be significantly different from zero, indicating the presence of nonallelic gene interaction and the inadequacy of the additive dominance model for the inheritance of these traits (Table 2). Whereas, for the grain density in the cross PKV Kranti \times DSMR4 the additive dominant model was found to be adequate (Koubisy, 2019 and Feltaous *et al.*, 2020).

Gene effects

The nature and extent of the gene effects influencing the genetic control of the traits under study were determined using the six parameter model. Except for grain density in PKV Kranti \times DSMR4, the estimated mean effect parameter [m], which measures the contribution from the overall mean as well as the locus effects and interactions of the fixed loci, was found to be significant for all traits in all the four crosses. This finding suggests that these characters are quantitatively inherited and highlights the significance of non-allelic interactions. For grain length in BJV44 \times DSMR4, grain density in BJV44 \times DSMR8, and grain width in BJV44 \times DSMR4 & PKV Kranti \times DSMR4, the additive [d] gene effect was observed to be negative and significant. The results for grain volume in PKV Kranti \times DSMR4, grain weight in BJV44 \times DSMR8 and PKV Kranti \times DSMR4, grain width in PKV Kranti \times DSMR8, and grain density in BJV44 \times DSMR4 were all found to be non-significant.

For days to flowering, 100 grain weight, grain yield/plant, grain width, grain length, grain thickness, grain volume, grains/panicle, and plant height in all the crosses, the dominance effect [h] was found to be significant. While it wasn't significant for grain density in PKV Kranti \times DSMR8, for grain breadth and thickness in PKV Kranti \times DSMR4, respectively. Days to flowering, grain yield/plant, grain length, grain thickness, grains/panicle, and plant height exhibited significant additive \times additive interaction [i] in all the crosses. Except PKV Kranti \times DSMR4, the additive \times additive interaction [i] was found to be significant for 100 grain weight and volume in all the crosses. For grain density, the crosses PKV Kranti \times DSMR8 and BJV44 \times DSMR8 were recorded significant and the rest of the crosses were non significant for grain

density. The additive \times additive interaction [i] was found to be important for grain width in the BJV44 \times DSMR8 and BJV44 \times DSMR4, but not in other crosses. It's interesting to note that the additive \times dominance interaction [j] was significant for grain yield/plant and grains/panicle in all four crosses.

For days to flowering, grain yield/plant, 100 grain weight, grain breadth, grain thickness, 100 grain volume, grains/panicle, and plant height, the dominance \times dominance interaction [l] effect was observed significant in all the examined crosses. While it was significant in all crosses other than PKV Kranti \times DSMR8 for grain length. The dominance \times dominance interaction [l] effect was significant in all crosses other than PKV Kranti \times DSMR4 for grain thickness and grain density. For the majority of the crosses, it was discovered that dominance \times dominance interaction [l] effects were greater than additive \times dominance [j] and additive \times additive interactions [i]. These results are in harmony with the earlier reports of Gaddameedi *et al.*, 2018 and Rokade *et al.*, 2021.

Types of epistasis

Based on the signs of dominance [h] and dominance \times dominance [l] interaction, the type of epistasis is determined. The epistasis is a complementary type when these effects are in the same direction; if not, it is a duplicate type. A duplicate type of interaction was involved for most of the traits in all crosses (Table 3). It's interesting to note that duplicate gene interaction was present in all the traits of the BJV44 \times DSMR8 cross (Mohammed *et al.*, 2018).

Information about gene action, inheritance patterns, and heritability is very helpful for improving traits and, ultimately, yield. To determine the genotypic values of the individuals and, subsequently, the mean genotypic values of families and generations, Hayman's generation means analysis gives information on the relative relevance of the additive effect, dominance effect, and non-allelic gene interactions. Based on the significant values of all the scales and joint scale tests for all the traits in all the crosses except for grain density in PKV Kranti \times DSMR4 for the grain density, the current study demonstrated the existence of epistasis.

The gene effect [m] revealed that all the traits in all the crosses were inherited quantitatively and exhibited the importance of epistasis. Significant [d] additive effects indicate the prospect of improvement by selection in early segregating generations for the majority of traits in the majority of crosses. Similar to this, a significant dominance impact [h] implies delaying the selection for later generations to achieve homozygosity. The findings suggested that

both additive and dominant effects contributed to the inheritance of the traits under study, raising the possibility that selection for desirable traits may be effective in early generations. However, it is preferable to postpone selection for later segregating generations.

The significance of additive \times dominance [j] and dominance \times dominance [l] gene interactions showed that additive \times dominance, dominance and non allelic interactions have a significant influence on the traits. Therefore, it is recommended to postpone selection for subsequent segregating generations until populations achieve homozygosity. According to the current research, all types of epistasis, including additive, dominance, and dominance-dominance, played a part in the expression of all the traits studied. In the current study, it is advised to postpone selection for the majority of the traits in the majority of crosses, and interestingly for all the traits in the cross BJV 44 \times DSMR8 because these were exhibiting duplicate kind of epistasis. According to this study, duplicate epistasis exists for the majority of the traits, which would reduce the range of variability (Kearsy and Pooni, 1996). Delaying selection until homozygosity is reached would be preferable to take advantage of transgressive segregants. However, it is recommended to use heterosis breeding for traits that demonstrate complementary gene interaction (Table 3). To increase grain yield/plant, it would be desirable to take advantage of heterosis in the crosses BJV44 \times DSMR4 and PKV Kranti \times DSMR4 in further breeding program.

Conclusion

The results of the current study showed that almost all traits are significantly influenced by the additive, dominance, and interaction components. Heterosis breeding can be used to exploit the crosses exhibiting complementary gene interaction, while reciprocal and biparental mating approaches can be used to accumulate favorable genes in crosses for traits that exhibit duplicate gene interaction. The findings of this study may be useful for future research on grain yield and attributes connected to grain size.

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Table 1: Parents used and population size of the different generations of different crosses

Cross-1: BJV44 × DSMR8			Cross-2: BJV44 x DSMR4	
Sl. No	Generation	Population Size	Generation	Population Size
1	P ₁ (BJV-44- High grain yield and quality)	20	P ₁ (BJV-44- High grain yield and quality)	20
2	P ₂ (DSMR-4- Strong restorer and bold seeds)	20	P ₂ (DSMR-4- Strong restorer and bold seeds)	20
3	F ₁	20	F ₁	20
4	F ₂	453	F ₂	453
5	B ₁	158	B ₁	158
6	B ₂	157	B ₂	157
Cross-3: PKV Kranti × DSMR8			Cross-4: PKV Kranti × DSMR4	
1	P ₁ (PKV Kranti- High grain yield and quality)	20	P ₁ (PKV Kranti- High grain yield and quality)	30
2	P ₂ (DSMR-8- Strong restorer and bold seeds)	22	P ₂ (DSMR-4- Strong restorer and bold seeds)	24
3	F ₁	19	F ₁	22
4	F ₂	455	F ₂	453
5	B ₁	156	B ₁	156
6	B ₂	154	B ₂	158

Table 2: Scaling test and gene effects for grain yield and grain related traits

Cross	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
1. Days to flowering				
Scaling test				
A	2.51**±0.48	0.28±0.46	1.55*±0.44	3.30**±0.43
B	-0.16±0.50	5.36**±0.47	-5.73**±0.52	3.26**±0.48
C	-3.55**±0.81	3.58**±0.82	3.07**±0.83	8.72**±0.81
D	-2.95**±0.25	-1.03**±0.31	3.63**±0.30	1.08**±0.35
Joint Scaling test	237.31**	171.29**	136.42**	270.88**
Genetic parameters				
m	67.28**±0.09	64.40**±0.13	69.55**±0.12	66.31**±0.14
d	2.99**±0.17	2.51**±0.19	4.96**±0.18	4.86**±0.21
h	4.50**±0.61	-1.64*±0.70	-7.24**±0.69	-5.34**±0.76
i	5.89**±0.49	2.06**±0.62	-7.25**±0.60	-2.16**±0.70
j	2.67**±0.55	-5.08**±0.57	7.27**±0.59	0.04±0.56
l	-8.23**±1.06	-7.70**±1.11	11.43**±1.09	-4.40**±1.17
2. Grain yield per plant (g)				
Scaling test				
A	55.15**±1.24	-15.14**±1.21	23.28**±1.36	6.22**±1.12
B	32.30**±1.26	-5.73**±1.29	-29.97**±1.29	-1.45±1.19
C	14.99**±2.17	-31.51**±2.21	50.78**±2.35	-18.43**±2.00
D	-36.24**±0.79	-5.32**±0.72	28.74**±0.82	-11.60**±0.74
Joint Scaling test	3240.99**	255.16**	2626.16**	287.83**
Genetic parameters				
m	92.52**±0.31	71.19**±0.29	118.56**±0.32	86.81**±0.28
d	11.79**±0.50	8.52**±0.43	31.66**±0.50	21.01**±0.48
h	88.01**±1.82	40.92**±1.71	-19.53**±1.91	50.75**±1.70
i	72.47**±1.58	10.64**±1.43	-57.48**±1.63	23.21**±1.49
j	22.85**±1.43	-9.41**±1.39	53.24**±1.47	7.66**±1.32
l	-159.93**±2.95	10.22**±2.80	64.17**±3.09	-27.98**±2.77
3. 100 grain weight (g)				
Scaling test				
A	0.589**±0.097	0.758**±0.118	1.807**±0.094	0.359**±0.085
B	0.620**±0.102	0.276*±0.119	0.857**±0.093	0.449**±0.089
C	-0.686**±0.172	-0.151±0.202	-0.169±0.151	0.836**±0.127
D	-0.947**±0.068	-0.592**±0.061	-1.417**±0.063	0.014±0.058
Joint Scaling test	214.96**	117.75**	717.07**	56.14**
Genetic parameters				
m	3.578**±0.028	3.681**±0.023	3.946**±0.025	4.311**±0.021
d	0.041±0.039	0.167**±0.039	0.659**±0.039	0.040±0.040
h	1.621**±0.150	0.701**±0.151	2.297**±0.138	-0.476**±0.125
i	1.894**±0.135	1.185**±0.121	2.833**±0.126	-0.027±0.115
j	-0.03±0.13	0.48**±0.13	0.95**±0.13	-0.09±0.12
l	-3.103**±0.231	-2.219**±0.255	-5.498**±0.216	-0.781**±0.204

Contd....

Cross	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
4. Grain width (mm)				
Scaling test				
A	0.654**±0.046	0.110*±0.048	-0.184**±0.048	-0.111*±0.045
B	0.398**±0.045	0.102*±0.049	-0.128**±0.044	-0.147**±0.045
C	0.180*±0.080	0.063±0.078	-0.326**±0.079	-0.292**±0.078
D	-0.436**±0.028	-0.074**±0.022	-0.007±0.027	-0.017±0.026
Joint Scaling test	367.25**	14.67**	20.11**	15.34**
Genetic parameters				
m	3.862**±0.011	4.228**±0.008	4.109**±0.011	4.199**±0.010
d	0.060**±0.017	-0.098**±0.016	-0.009±0.017	-0.040*±0.017
h	0.683**±0.065	0.402**±0.057	0.231**±0.064	0.098±0.062
i	0.872**±0.056	0.148**±0.044	0.013±0.055	0.034±0.052
j	0.26**±0.05	0.01±0.06	-0.05±0.05	0.04±0.05
l	-1.925**±0.105	-0.360**±0.100	0.299**±0.105	0.224*±0.104
5. Grain length (mm)				
Scaling test				
A	0.497**±0.057	0.154*±0.085	-0.229**±0.059	-0.067±0.055
B	0.173**±0.057	0.127±0.082	-0.360**±0.055	-0.101*±0.059
C	-0.369**±0.101	-0.424**±0.157	-0.974**±0.098	-1.440**±0.099
D	-0.519**±0.036	-0.352**±0.053	-0.193**±0.035	-0.636**±0.033
Joint Scaling test	243.09**	44.63**	104.72**	440.79**
Genetic parameters				
m	4.692**±0.014	4.887**±0.023	4.883**±0.014	4.599**±0.012
d	0.238**±0.021	-0.086**±0.028	0.179**±0.022	0.064**±0.021
h	1.132**±0.083	0.821**±0.124	0.895**±0.081	1.328**±0.078
i	1.038**±0.072	0.704**±0.106	0.385**±0.070	1.272**±0.065
j	0.32**±0.07	0.027±0.09	0.14*±0.07	0.03±0.06
l	-1.707**±0.132	-0.985**±0.192	0.203±0.132	-1.103**±0.131
6. Grain thickness				
Scaling test				
A	0.457**±0.044	0.259**±0.052	0.239**±0.046	0.058±0.046
B	0.199**±0.044	0.001±0.057	-0.105*±0.047	-0.026±0.053
C	0.098±0.076	-0.243*±0.094	-0.425**±0.078	-0.107±0.084
D	-0.279**±0.025	-0.251**±0.028	-0.280**±0.024	-0.070*±0.027
Joint Scaling test	190.87**	100.38**	192.69**	9.67*
Genetic parameters				
m	2.753**±0.010	2.758**±0.011	2.851**±0.008	2.841**±0.010
d	0.161**±0.016	0.101**±0.018	0.299**±0.017	0.167**±0.018
h	0.389**±0.060	0.470**±0.070	0.551**±0.059	-0.081±0.065
i	0.558**±0.050	0.503**±0.057	0.559**±0.047	0.140*±0.054
j	0.26**±0.05	0.26**±0.06	0.34**±0.05	0.08±0.05
l	-1.214**±0.099	-0.762**±0.119	-0.693**±0.103	-0.172±0.111

Contd....

Cross	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
7. 100 grain volume				
Scaling test				
A	1.072**±0.078	0.710**±0.079	0.706**±0.083	-0.438**±0.068
B	0.529**±0.076	0.034±0.075	0.042±0.077	-0.409**±0.080
C	-0.441**±0.128	-0.169±0.139	-0.575**±0.146	-0.719**±0.098
D	-1.021**±0.048	-0.456**±0.062	-0.661**±0.052	0.064±0.057
Joint Scaling test	515.50**	117.39**	218.06**	90.65**
Genetic parameters				
m	2.962**±0.018	3.108**±0.025	3.429**±0.021	3.608**±0.019
d	0.323**±0.032	0.157**±0.036	0.468**±0.029	0.065±0.043
h	1.861**±0.109	0.766**±0.133	1.299**±0.119	-1.197**±0.118
i	2.043**±0.096	0.912**±0.124	1.322**±0.103	-0.128±0.113
j	0.54**±0.09	0.68**±0.01	0.66**±0.09	-0.03±0.10
l	-3.644**±0.180	-1.655**±0.201	-2.070**±0.187	0.975**±0.197
8. Grain density				
Scaling test				
A	-0.159**±0.030	0.059*±0.032	0.255**±0.021	0.010±0.015
B	0.026±0.030	-0.591**±0.037	0.221**±0.020	0.022±0.016
C	0.029±0.061	-0.530**±0.058	0.304**±0.036	0.009±0.029
D	0.081**±0.022	0.001±0.017	-0.086**±0.012	-0.012±0.012
Joint Scaling test	62.12**	292.94**	207.02**	6.15 ^{NS}
Genetic parameters				
m	1.212**±0.009	1.206**±0.007	1.194**±0.005	
d	-0.099**±0.011	0.017±0.011	0.020*±0.008	
h	-0.187**±0.049	-0.419**±0.043	0.026±0.029	
i	-0.162**±0.043	-0.003±0.035	0.172**±0.025	
j	-0.18**±0.03	0.65**±0.04	0.03±0.02	
l	0.295**±0.076	0.536**±0.072	-0.648**±0.048	
9. Number of grains per panicle				
Scaling test				
A	1023.84**±22.47	-815.65**±73.16	-560.40**±22.45	-79.82**±22.45
B	452.24**±22.08	-390.23**±63.58	-1291.58**±21.26	-322.04**±23.70
C	309.68**±38.15	-855.67**±123.55	1422.39**±38.17	-930.88**±38.67
D	-583.20**±13.36	175.10**±37.17	1637.19**±12.84	-264.51**±13.77
Joint Scaling test	3200.74**	132.99**	17689.97**	772.81**
Genetic parameters				
m	2467.63**±5.22	1968.45**±14.92	3058.92**±5.129	2035.32**±5.03
d	263.86**±8.32	156.23**±22.15	398.41**±7.72	462.04**±9.40
h	1752.53**±31.12	747.56**±91.93	-1967.17**±30.31	1419.97**±32.11
i	1166.40**±26.71	-350.21**±74.34	-3274.37**±25.68	529.02**±27.55
j	571.60**±26.24	-425.41**±71.58	731.17**±25.23	242.22**±26.20
l	-2642.47**±50.63	1556.09**±152.04	5126.35**±49.11	-127.15*±53.94

Contd....

Cross	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
10. Plant height				
Scaling test				
A	21.84**±1.41	-17.99**±1.96	31.31**±1.69	-20.25**±1.56
B	-3.70*±1.46	-9.92**±2.09	-14.20**±1.62	-22.38**±1.76
C	58.25**±2.32	-9.00**±3.28	25.21**±2.77	-74.04**±2.69
D	20.06**±0.79	9.45**±1.11	4.05**±0.85	-15.71**±0.93
Joint Scaling test	1205.93**	125.73**	690.91**	823.51**
Genetic parameters				
m	270.38**±0.28	262.27**±0.40	270.44**±0.31	253.41**±0.33
d	32.39**±0.55	20.39**±0.77	46.34**±0.59	33.00**±0.66
h	-51.35**±1.87	-10.12**±2.64	-29.45**±2.11	40.17**±2.19
i	-40.11**±1.57	-18.90**±2.23	-8.10**±1.70	31.41**±1.85
j	25.54**±1.69	-8.07**±2.43	45.51±1.84	2.13±1.96
l	21.98**±3.20	46.80**±4.49	-9.02*±3.64	11.22**±3.76

Table 3: Different gene interaction for the traits under study in four different crosses

Sl. No.	Crosses	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
	Characters				
1.	Days to flowering	Duplicate	Complementary	Duplicate	Complementary
2.	Grain yield / plant (g)	Duplicate	Complementary	Duplicate	Duplicate
3.	100 grain weight (g)	Duplicate	Duplicate	Duplicate	Complementary
4.	Grains/ panicle	Duplicate	Complementary	Duplicate	Duplicate
5.	100 grains volume (cc)	Duplicate	Duplicate	Duplicate	Duplicate
6.	Grain density	Duplicate	Duplicate	Duplicate	No interaction
7.	Grain length (mm)	Duplicate	Duplicate	Complementary	Duplicate
8.	Grain width (mm)	Duplicate	Duplicate	Complementary	Complementary
9.	Grain thickness (mm)	Duplicate	Duplicate	Duplicate	Complementary
10.	Plant height (cm)	Duplicate	Duplicate	Complementary	complementary

Table 4: Gene actions recorded for the different traits in different crosses

Traits	BJV44 × DSMR8	BJV 44 × DSMR-4	PKV Kranti × DSMR8	PKV Kranti × DSMR4
Days to flowering	A and D	D	D	D
Grain yield per plant	A and D	A and D	D	A and D
100 grain weight	A and D	A and D	A and D	D
Grain width	A and D	D	D	D
Grain length	A and D	D	A and D	A and D
Grain thickness	A and D	A and D	A and D	D
100 Grain volume	A and D	A and D	A and D	D
Grain density	A and D	D	A and D	*
Number of grains per panicle	A and D	A and D	D	A and D
Plant height	D	D	D	D

* Trait showed absence of non allelic interaction.

Where,

A- Additive gene action, D- Dominance gene action and A & D- both Additive and Dominance gene action.