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Pattern of genetic inheritance of morphological and agronomic traits of sorghum associated with resistance to sorghum shoot fly, *Atherigona soccata*

Riyazaddin Mohammed · Ashok Kumar Are · Rajendra S. Munghate · Anil Gaddameedi · Kavi Kishor Polavarapu Bilhan · Hari C. Sharma

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Abstract Sorghum shoot fly, *Atherigona soccata* is an important pest of sorghum during the seedling stage, which influences both fodder and grain yield. To understand the nature of inheritance of shoot fly resistance in sorghum, we performed generation mean analysis using two crosses IS 18551 × Swarna and M 35-1 × ICSV 700 during the 2013–2014 cropping seasons. The F_1, F_2, BC_1 and BC_2 progenies, along with the parental lines were evaluated for agronomic and morphological traits associated with resistance/susceptibility to sorghum shoot fly, *A. soccata*. The cross IS 18551 × Swarna exhibited significant differences between the parents for shoot fly deadhearts (%) in the postrainy season. The progenies of this cross exhibited lower shoot fly damage, suggesting that at least one of the parents should have genes for resistance to develop shoot fly-resistant hybrids. Leaf glossiness, leafsheath pigmentation and plant vigor score during the seedling stage exhibited non-allelic gene interactions with dominant gene action, whereas 100 seed weight showed both additive and dominant gene interactions. Presence of awns showed recessive nature of the awned gene. Generation mean analysis suggested that both additive and dominance gene effects were important for most of the traits evaluated in this study, but dominance had a more pronounced effect.

Keywords Sorghum shoot fly resistance · *Atherigona soccata* · Genetic inheritance · Generation mean analysis

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R. Mohammed · A. K. Are · A. Gaddameedi · H. C. Sharma (✉)
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Medak, Patancheru, Telangana 502 324, India
e-mail: h.sharma@cgiar.org

R. Mohammed · A. Gaddameedi · K. K. Polavarapu Bilhan
Department of Genetics, Osmania University, Hyderabad, Telangana 500 007, India

R. Mohammed
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT-Sahelian Centre), BP-12404, Niamey, Niger

R. S. Munghate
Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Krishinagar, Akola, Maharashtra 444104, India

H. C. Sharma
Dr YS Parmar University of Horticulture and Forestry, Nauni, Himachal Pradesh 173230, India

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important drought tolerant cereal crop after maize, rice, wheat, and barley (Doggett 2008). It is adapted to the tropical and subtropical climates of the semi-arid regions, and is the staple food for millions of people living in these regions. According to Food and Agriculture organization (FAO 2014), the grain sorghum area in India is about 5.82 m ha, with a production of 5.39 million tonnes of grain sorghum, with a productivity of 926.1 kg/ha. It is a multipurpose crop that can be utilised as food, feed, fodder, and presently, it is emerging as a bio-fuel crop (House 1985; Doggett 1988; Rooney and Waniska 2000). It is vulnerable to several biotic and abiotic constraints, resulting in decreased grain yields, and consequently leading to decline in the sorghum area under cultivation. Hence, it is important to increase the grain yields within the existing area to feed the growing population in the semi-arid regions of Asia and Africa.

During the process of breeding for high yielding sorghums, no attention was paid for insect pest resistance and as a result, most of the high yielding sorghum cultivars are susceptible to insect pests. Therefore, it is important to focus attention on the constraints that result in grain yield loss than on genetic improvement for grain yield per se. About 150 insect pests attack sorghum from seedling to physiological maturity stage. Of these, sorghum shoot fly, *Atherigona soccata* (Rondani) is one of the serious insect pests that attack sorghum at the seedling stage. Shoot fly infestation results in severe economic loss to the farmers (Sharma 1993; Riyazaddin et al. 2015). Sorghum shoot fly, *A. soccata* infests sorghum at the early seedling stage i.e., from 7 to 30 days after seedling emergence (DAE). Host plant resistance (HPR) is one of the effective methods for controlling shoot fly, *A. soccata*. A number of genotypes with resistance to shoot fly have been identified, but the levels of resistance are low to moderate (Pradhan and Jotwani 1978; Taneja and Leuschner 1985; Sharma et al. 2003).

The genotypes exhibiting resistance to sorghum shoot fly, *A. soccata* generally have poor grain type, low productivity and physiologically inefficient plant type, which were undesirable. Whereas, the hybrids developed for high grain yield have lower genetic diversity, and are highly susceptible to sorghum shoot fly. Low genetic diversity seen in the sorghum hybrids is because of usage of the available germplasm lines within the region. Even though high yielding hybrids were developed, but because of their susceptibility to sorghum shoot fly, there has been little improvement in grain yield.

The choice of selection and breeding strategies for genetic improvement of sorghum or any other crop largely depend on the type, and relative importance of genetic components, and presence of non-allelic interactions. In view of the potential economic and environmental constraints associated with insecticide use, breeding of crop varieties with resistance to shoot fly is a promising method to control the insect pests (Sharma 1993). Hence, transferring the resistance from agronomically undesirable genotypes (resistant genotypes) into the high-yielding hybrids is essential (Rana et al. 1981) for sustainable sorghum production.

Understanding the genetic inheritance of shoot fly resistance and the agronomic, and morphological traits associated with resistance/susceptibility to shoot fly damage will be helpful in breeding sorghums with high grain yields that are acceptable to the farmers. Genetic improvement depends primarily on the effectiveness of selection among the progenies that differ in genetic value. Generation means provides information on genetic inheritance of the quantitative traits. Most of the researchers working on shoot fly resistance have focused mainly on inheritance of shoot fly resistant traits, with little information on agronomic and morphological traits. An understanding of genetic inheritance of resistance to shoot fly, *A. soccata,* and as well as the agronomic, morphological traits will be useful to breed sorghums with shoot fly resistance and desirable agronomic traits. Hence, the present study was aimed at understanding the type of gene interactions governing inheritance of shoot fly resistance, and the agronomic and morphological traits associated with shoot fly resistance.

Materials and methods

Experiments were conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Medak, Telangana, India, which is situated at 17°53′N latitude, 78°27′E longitude and at an altitude of 545 m.

Experimental material

The experimental material consisted of six generations of two crosses of M 35-1 × ICSV 700, and IS 18551 × Swarna. One of the crosses involved a shoot fly-resistant (IS 18551, P_1) and the susceptible (Swarna, P_2) genotypes. Back cross progenies were obtained by crossing the F_1 progeny with either of the parents [BC_1 (F_1 crossed with P_1), and BC_2 (F_1 crossed with P_2)]. The F_1's were selfed to obtain the F_2 progenies. Hence, segregating and non-segregating material was generated (viz. P_1, P_2, F_1, F_2, BC_1 and BC_2). All the six generations were evaluated in replicated trials using randomized complete block design (RCBD), during the rainy and postrainy seasons. The test material was sown with parents in two rows, F_1's in a single row, F_2's in 10 rows, and back cross progenies in four rows, with a row length of 2.0 m, row to row distance of 75 cm, and a distance of 10 cm in between the plants. A basal dose of ammonium phosphate was applied to the field @ 100 kg/ha. Normal agronomic practices were followed in raising the crop. Earthing up and top dressing with urea at 100 kg/ha was done 30 days after seedling emergence. During the postrainy season, the test plots were irrigated at 30 day intervals. Interlard fish meal technique as described by Soto (1974) and Sharma (1993) was followed for multiplication of shoot fly population and even exposure of the test genotypes to shoot fly infestation. One set of the replicated test material was grown under protected conditions by periodical spraying with cypermethrin, and applying the carbofuran 3G granules in the leaf whorls to protect the seedlings from shoot fly damage for recording data on morphological, agronomic, panicle traits, and grain yield.

Observations

Data on shoot fly damage was recorded by observing the number of shoot fly deadhearts in a test plot at 21 DAE, and expressed as percentages. The data on the agronomic, morphological and panicle traits were recorded based on the sorghum descriptors (IBPGR and ICRISAT 1993), from seedling to the harvesting stage with slight modifications (Supplementary Table 1). Days to 50% flowering was recorded when half of the panicle, and 50% of the plants in the experimental plot attained the anthesis stage, while plant height of three randomly selected plants within a plot was recorded at maturity. Data on 100 seed weight and grain yield were recorded from the protected test plots after harvesting and threshing the panicles.

Leaf glossiness was visually scored on a 1–5 scale at 10–12 DAE (fifth leaf stage), when the expression of this trait is most apparent, in the morning hours, when there was maximum reflection of light from the leaf surface (Sharma and Nwanze 1997), leafsheath pigmentation was visually scored on a 1–3 rating scale at 7 DAE (Dhillon et al. 2006), and seedling vigor at 10 DAE on a 1–3 scale (Sharma and Nwanze 1997). Data were also recorded on waxy bloom, plant color, inflorescence exsertion, panicle compactness, panicle shape, glume color, glume coverage, awns, grain color, and grain lustre (Supplementary Table 1).

Statistical analysis

The data were subjected to the analysis of variance (ANOVA) using GenStat, 14th edition (GenStat 2010). *F*-test was used to test the significance of differences between the test genotypes, while least significance differences (LSD) was used to compare the genotypic means at $P \leq 0.05$. Data obtained for various morphological, agronomic and panicle traits were subjected to generation mean analysis followed by Mather (1949) and Hayman and Mather (1955) for scaling test, and Hayman (1958) approach to find the significant inter-allelic interactions, using Windostat (Indostat 2004) software.

Results

Mean performance of crosses across seasons

Analysis of variance for various agronomic, morphological, and panicle traits for the rainy and postrainy seasons are presented in Tables 1 and 2. The *F*-values due to generations were significant at $P \leq 0.01$ for days to 50% flowering, 100 seed weight, grain yield, glume color and glume cover across seasons for both the crosses; while plant height, waxy bloom, grain lustre and awns showed significant *F*-values for the cross IS 18551 × Swarna across seasons. The cross M 35-1 × ICSV 700 showed non-significant variation for these traits, which exhibit moderate levels of resistance to shoot fly. Plant color exhibited significant *F*-value at $P \leq 0.01$ for the cross M 35-1 × ICSV 700

Table 1 Mean performance of two crosses with respect to various agronomic and morphological traits of sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

Pedigree	Generation	Shoot fly deadhearts (%)		Leaf glossy score	Leaf sheath pigmentation	Plant vigor score	Days to 50% flowering		Plant height (cm)	
		2013R	2013PR	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700										
M 35-1	P_1	70.54	7.89	1.67	1.00	1.67	74.33	72.80	306.70	182.00
M 35-1 × ICSV 700	F_1	78.15	13.46	1.00	1.00	2.00	67.47	68.93	312.70	212.70
M 35-1 × ICSV 700	F_2	71.34	8.23	2.06	1.57	1.57	69.82	71.15	301.90	207.60
{M 35-1 × ICSV 700} × M 35-1	BC_1	71.33	9.98	2.02	1.78	1.54	70.22	70.56	301.20	200.50
{M 35-1 × ICSV 700} × ICSV 700	BC_2	45.20	16.90	1.81	1.46	1.51	71.70	71.39	314.80	206.50
ICSV 700	P_2	64.68	20.99	1.33	1.00	1.00	78.33	75.47	295.30	213.30
Mean		66.87	12.90	1.65	1.30	1.55	71.98	71.70	305.43	203.80
SE±		7.39	3.51	0.31	0.10	0.16	0.97	0.78	7.71	8.79
Vr (10, 5)		2.40	2.22	1.81	13.11**	4.36*	15.86**	8.20**	0.92	1.75
LSD (*P* 0.05)		NS	NS	NS	0.30	0.49	3.05	2.45	NS	NS
Cross IS 18551 × Swarna										
IS 18551	P_1	51.87	3.60	1.00	1.00	1.00	79.73	76.67	325.30	210.70
IS 18551 × Swarna	F_1	68.15	17.68	3.00	1.00	2.00	64.80	66.13	312.70	215.30
IS 18551 × Swarna	F_2	82.44	24.27	3.06	1.70	1.51	68.29	66.68	280.50	203.60
{IS 18551 × Swarna} × IS 18551	BC_1	81.90	16.22	2.68	1.48	1.70	70.56	70.56	303.30	212.90
{IS 18551 × Swarna} × Swarna	BC_2	91.89	38.26	4.18	1.57	1.83	69.07	64.04	252.50	194.10
Swarna	P_2	59.61	54.31	5.00	1.67	2.00	65.67	62.33	169.30	130.70
Mean		72.64	25.70	3.15	1.40	1.67	69.69	67.70	273.96	194.50
SE±		10.71	3.44	0.09	0.14	0.10	0.85	0.67	3.90	7.96
Vr (10, 5)		2.05	27.46**	253.45**	5.34**	13.58**	39.95**	60.06**	215.83**	16.37**
LSD (*P* 0.05)		NS	10.83	0.27	0.44	0.32	2.68	2.11	12.30	25.09

Table 1 continued

Pedigree	Generation	100 seed weight (g)		Grain yield (t/ha)		Waxy bloom		Plant color	
		2013R	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700									
M 35-1	P_1	2.31	3.56	2.51	6.56	2.00	2.67	1.00	1.00
M 35-1 × ICSV 700	F_1	3.12	3.96	5.17	12.24	1.67	2.67	1.00	1.00
M 35-1 × ICSV 700	F_2	2.54	3.64	2.87	8.96	1.08	2.26	1.42	1.37
{M 35-1 × ICSV 700} × M 35-1	BC_1	2.70	3.97	4.23	11.85	1.32	2.31	1.05	1.08
{M 35-1 × ICSV 700} × ICSV 700	BC_2	2.44	3.44	3.55	10.63	1.12	2.20	1.43	1.57
ICSV 700	P_2	2.14	2.43	1.03	5.68	1.33	2.00	2.00	2.00
Mean		2.54	3.50	3.23	9.32	1.42	2.40	1.32	1.30
SE±		0.13	0.05	0.46	0.61	0.22	0.21	0.06	0.03
Vr (10, 5)		6.79**	161.97**	9.86**	20.11**	2.69	1.59	37.89**	155.39**
LSD (*P* 0.05)		0.41	0.14	1.44	1.93	NS	NS	0.20	0.10
Cross IS 18551 × Swarna									
IS 18551	P_1	1.57	2.21	1.20	4.77	1.00	2.00	1.00	1.00
IS 18551 × Swarna	F_1	2.73	3.18	4.42	10.13	2.67	3.00	1.00	1.00
IS 18551 × Swarna	F_2	2.39	3.12	2.55	7.93	1.99	2.68	1.04	1.00
{IS 18551 × Swarna} × IS 18551	BC_1	2.34	2.78	3.14	9.19	1.43	2.24	1.16	1.00
{IS 18551 × Swarna} × Swarna	BC_2	2.98	3.63	4.02	8.50	2.73	2.91	1.00	1.00
Swarna	P_2	3.00	3.36	4.57	3.64	3.00	3.00	1.00	1.00
Mean		2.50	3.05	3.32	7.36	2.14	2.60	1.03	1.00
SE±		0.10	0.06	0.29	0.30	0.14	0.06	0.04	0.00
Vr (10, 5)		30.29**	65.48**	19.62**	71.67**	31.52**	53.96**	2.22	1.00
LSD (*P* 0.05)		0.31	0.19	0.92	0.96	0.45	0.18	NS	NS

NS non-significant

*, ***F* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

Table 2 Mean performance of two crosses with respect to various panicle traits of sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

Pedigree	Generation	Inflorescence exertion		Panicle compactness		Panicle shape	Glume color		Glume coverage	
		2013R	2013PR	2013R	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700										
M 35-1	P_1	2.00	2.00	2.00	3.00	4.00	3.00	3.00	1.00	1.00
M 35-1 × ICSV 700	F_1	1.33	3.00	2.00	3.00	4.00	3.00	3.00	1.00	1.00
M 35-1 × ICSV 700	F_2	1.73	2.40	2.00	2.86	3.58	2.66	2.76	1.69	1.27
{M 35-1 × ICSV 700} × M 35-1	BC_1	2.23	2.40	2.00	2.99	3.96	2.78	2.81	1.27	1.00
{M 35-1 × ICSV 700} × ICSV 700	BC_2	2.08	2.59	2.00	2.95	3.84	2.50	2.28	2.53	1.40
ICSV 700	P_2	2.33	2.00	2.00	3.00	4.00	2.00	2.00	3.67	3.00
Mean		1.95	2.40	–	3.00	3.90	2.66	2.60	1.86	1.40
SE±		0.21	0.09	–	0.01	0.04	0.06	0.06	0.34	0.07
Vr		3.17	18.11**	–	15.68**	15.42**	39.74**	43.69**	9.57**	137.28**
LSD (*P* 0.05)		NS	0.28	–	0.05	0.13	0.19	0.20	1.08	0.21
Cross IS 18551 × Swarna										
IS 18551	P_1	1.67	2.00	2.00	3.00	4.00	3.00	3.00	9.00	6.33
IS 18551 × Swarna	F_1	1.00	1.00	2.00	2.00	1.00	3.00	4.00	5.00	3.67
IS 18551 × Swarna	F_2	1.31	1.70	2.00	2.46	2.42	3.86	3.80	5.03	4.96
{IS 18551 × Swarna} × IS 18551	BC_1	1.57	1.73	2.00	2.80	3.40	3.32	3.87	6.39	6.33
{IS 18551 × Swarna} × Swarna	BC_2	1.36	1.32	2.00	2.36	2.10	4.44	3.67	1.80	2.44
Swarna	P_2	1.00	1.00	2.00	2.00	1.00	6.00	4.00	1.00	1.00
Mean		1.32	1.50	–	2.40	2.30	3.94	3.70	4.70	4.10
SE±		0.15	0.10	–	0.04	0.12	0.19	0.06	0.19	1.16
Vr		3.63*	18.19**	–	97.12**	97.11**	37.71**	36.36**	238.02**	3.45*
LSD (*P* 0.05)		0.46	0.31	–	0.13	0.39	0.59	0.20	0.60	3.66

Pedigree	Generation	Grain color		Grain lustre		Awns	
		2013R	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700							
M 35-1	P_1	1.00	1.00	2.00	2.00	2.00	2.00
M 35-1 × ICSV 700	F_1	1.00	1.00	2.00	2.00	2.00	2.00
M 35-1 × ICSV 700	F_2	1.00	1.00	2.00	2.00	2.00	2.00
{M 35-1 × ICSV 700} × M 35-1	BC_1	1.00	1.00	2.00	2.00	2.00	2.00
{M 35-1 × ICSV 700} × ICSV 700	BC_2	1.00	1.00	2.00	2.00	2.00	2.00
ICSV 700	P_2	1.00	1.00	2.00	2.00	2.00	2.00
Mean		–	–	–	–	–	–
SE±		–	–	–	–	–	–
Vr		–	–	–	–	–	–
LSD (*P* 0.05)		–	–	–	–	–	–
Cross IS 18551 × Swarna							
IS 18551	P_1	1.00	1.00	1.00	1.00	2.00	2.00
IS 18551 × Swarna	F_1	1.00	1.00	2.00	2.00	1.00	1.00
IS 18551 × Swarna	F_2	1.00	1.00	1.84	1.92	1.13	1.11
{IS 18551 × Swarna} × IS 18551	BC_1	1.00	1.00	1.72	1.84	1.27	1.50
{IS 18551 × Swarna} × Swarna	BC_2	1.00	1.00	2.00	1.99	1.00	1.00

Table 2 continued

Pedigree	Generation	Grain color		Grain lustre		Awns	
		2013R	2013PR	2013R	2013PR	2013R	2013PR
Swarna	P_2	1.00	1.00	2.00	2.00	1.00	1.00
Mean		–	–	1.76	1.8	1.2	1.30
SE±		–	–	0.01	0.01	0.02	0.02
Vr		–	–	789.75**	1110.02**	281.83**	295.43**
LSD (*P* 0.05)		–	–	0.04	0.04	0.07	0.07

NS non-significant

*, ***F* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

across seasons. Inflorescence exsertion showed significant differences between the parents of the two crosses across seasons, except for M 35-1 × ICSV 700 during the rainy season. Leaf glossy score, leafsheath pigmentation and plant vigor score, which were recorded during postrainy season, exhibited significant differences between the parents for both the crosses, except leaf glossy score, which was non-significant for the cross M 35-1 × ICSV 700. The traits that had shown non-significant differences between the generations were not subjected to generation mean analysis.

The per se performance of the parents and their generations are given in Tables 1 and 2. The order of the generations presented in the tables is as follows P_1, F_1, F_2, BC_1, BC_2, and P_2; where P_1 and P_2 were the female and male parents, respectively. The performances of different generations is discussed below.

Shoot fly deadhearts

The parents of the cross IS 18551 × Swarna exhibited significant differences for percentage shoot fly deadhearts in the postrainy season (Table 1). The susceptible parent, Swarna suffered greater shoot fly damage (54.31%) as compared to the resistant parent, IS 18551 (3.60%). The progenies F_1 and BC_1 exhibited lower shoot fly deadhearts (17.68 and 16.22%, respectively), and were nearer to the resistant parent, IS 18551; whereas F_2 and BC_2 generations exhibited higher numbers of deadhearts (24.27 and 38.26%, respectively), and were closer to the susceptible parent, Swarna.

Days to 50% flowering

Days to 50% flowering exhibited significant differences between the parents across seasons (Table 1). Both the crosses flowered at the same time with a mean flowering period of 71.98 ± 0.97 and 71.70 ± 0.78 for the cross M 35-1 × ICSV 700, and 69.69 ± 0.85 and 67.70 ± 0.67 days for the cross IS 18551 × Swarna, respectively, during the rainy and postrainy seasons. In both the crosses, the mean performances of the progenies were on par with the early flowering parent.

Plant height

The cross M 35-1 × ICSV 700 exhibited non-significant differences between the generations for plant height because of equal height attained by the parents, and their progenies across seasons (Table 1). The cross IS 18551 × Swarna showed significant differences, with a mean performance of 273.96 ± 3.90 and 194.50 ± 7.96 cm, respectively, in the rainy and postrainy seasons. The F_1, F_2, and BC_1 exhibited plant height towards IS 18551, while the BC_2 exhibited moderate plant height. In both the crosses, the parents attained different heights across the seasons, with longer plants in the rainy season.

100 seed weight

There were significant differences between the generations for 100 seed weight (Table 1). In the cross M 35-1 × ICSV 700, F_1 has attained highest 100 seed weight of 3.12 and 3.96 g in the rainy and postrainy seasons, respectively. The remaining generations had higher 100 seed weight than the parent M 35-1 (2.31 and 3.56 g respectively, in the rainy and postrainy seasons). In the cross IS 18551 × Swarna the female parent IS 18551 recorded lower 100 seed weight of 1.57 and 2.21 g than the male parent Swarna 3.00 and 3.36 g respectively, in the rainy and postrainy seasons. The other generations recorded 100 seed weight towards the male parent, Swarna.

Grain yield

Significant differences were observed between the parents for grain yield across seasons (Table 1). In M 35-1 × ICSV 700, the per se performance of M 35-1 was 2.51 and 6.56 t/ha, and of ICSV 700 1.03 and 5.68 t/ha, respectively, in the rainy and postrainy season. The per se performance of the F_1's was greater than the better parent. The other generations also recorded more grain yield, tilting towards the parent with high grain yield.

Waxy bloom and plant color

There were no significant differences in waxy bloom among the parents of the cross M 35-1 × ICSV 700 across seasons (Table 1), but both the parents in the cross IS 18551 × Swarna exhibited significant differences for waxy bloom across seasons. The progenies had greater amounts of waxy bloom than the female parent, IS 18551.

The parents of the cross IS 18551 × Swarna were nontan type and their progenies also showed the nontan plant color (Table 1), but in the cross M35-1 × ICSV 700, the parent M 35-1 was non tan, and ICSV 700 was tan type and the F_1 progenies of their cross were non-tan.

Leaf glossiness, leafsheath pigmentation and plant vigor

These traits were recorded only in the postrainy season, and there were significant differences between the parents, except in leaf glossy score of the cross M 35-1 × ICSV 700, as both these parents were glossy (Table 1). In the cross IS 18551 × Swarna the parent IS 18551 was highly glossy, while Swarna was non-glossy. The F_1 and F_2 progenies of these two parents was moderately glossy, with a score of 3.00 and 3.06, respectively.

Both the crosses had one of the parents with high leafsheath pigmentation, while the other had moderate levels of leafsheath pigmentation, but the F_1 progenies had high levels of leafsheath pigmentation. Some of the progenies had leafsheath pigmentation scores nearer to the moderate parent.

One of the parents had high plant vigor (1.00), whereas the other exhibited moderate vigor (2.00). The F_1 progenies had a vigor score of 2.00.

Inflorescence exsertion

The two crosses exhibited significant differences between the parents for inflorescence exsertion across seasons, except M 35-1 × ICSV 700 cross in the rainy season (Table 2). The F_1 progenies in the cross IS 18551 × Swarna exhibited good panicle exsertion, while the F_1 progenies of the cross M 35-1 × ICSV 700 did not show any particular trend.

Panicle compactness

Both the crosses did not differ significantly in panicle compactness in the rainy season, but differed significantly in panicle compactness in the postrainy season (Table 2). In the cross IS 18551 × Swarna, IS 18551 had a compact panicle (3.00), while Swarna had a semiloose panicle (2.00). The F_1 progenies had semiloose panicles (2.00).

Panicle shape

Panicle shape was recorded only in the postrainy season. The parents did not differ in panicle shape in the cross M 35-1 × ICSV 700 (Table 2). The parents in the cross IS 18551 × Swarna had the contrasting panicle shapes. Swarna had erect panicle with score of 1.00, whereas IS 18551 had elliptical panicle with a score of 4.00. Their F_1s had erect panicle with a score of 1.00.

Glume color and glume coverage of the grain

Parents differed significantly in glume color and glume coverage of the grain (Table 2). In the cross M 35-1 × ICSV 700, M 35-1 was red glumed and ICSV 700 was mahogany colored. Their F_1 progenies exhibited red glume color, indicating the dominance nature of red glumes across seasons.

M 35-1 had 25% and ICSV 700 had 50% of the grain covered with glumes. F_1 progenies were with 25% of the grain covered with the glume, indicating dominant nature of glume covering of the grain in this cross. In the cross IS 18551 × Swarna, IS 18551 grain were fully covered by the glumes, while in Swarna 25% of the grain was covered with glume, and the F_1 progenies were with 50 to 75% glume coverage.

Grain lustre and awns

There were no significant differences between the parents of the cross M 35-1 × ICSV 700 for grain lustre and awns (Table 2). In the cross IS 18551 × Swarna, the cross of non-lustrous and lustrous seed trait generated F_1 progenies with lustrous seed, indicating the dominance nature of the gene controlling grain lusture.

Awns were present in IS 18551, but absent in Swarna, F_1 progenies were awnless, indicating the recessive nature of the awned gene.

Gene effects and genetic parameters

The replicated data obtained from six generations of the two cross combinations for agronomic, morphological and panicle traits were subjected to generation mean analysis using scaling tests to test the fitness of additive–dominance model, and Hayman's six parameter model to find the significant inter-allelic interactions. Only the traits that showed significant F values were included for generation mean analysis and explained hereunder.

Leaf glossiness

The F value for leaf glossy score was non-significant for the cross M 35-1 × ICSV 700. A, B, and D scales were significant for leaf glossy score in the cross IS 18551 × Swarna, indicating the presence of non-allelic interactions for this trait (Tables 3, 4). Partitioning of the generation means showed significant mean (m) and additive (d), dominance (h), additive × additive (*i*), and dominance × dominance (*l*) components. The dominance and dominance × dominance components were in opposite direction, which suggested the presence of duplicate epistasis. The dominance variance was greater than the additive variance, indicating the predominance of dominance gene effects (Table 5). The narrow sense heritability was low and the dominance degree was negative.

Leafsheath pigmentation

The scales A, B, and C for the cross M 35-1 × ICSV 700, and all scales for the cross IS 18551 × Swarna were significant in the postrainy season (Tables 3, 4). The significance of the scales indicated the presence of non-allelic interactions. Generation means partitioned into six components using Hayman's method revealed the significance of mean for both the crosses, with significant additive and dominance × dominance interactions for the cross M 35-1 × ICSV 700; and significant dominance and additive × additive components for IS 18551 × Swarna. The variance due to dominance was greater than the additive variance in both the crosses, with higher degree of dominance (Table 5).

Plant vigor

The scales A and C for the cross M 35-1 × ICSV 700, and all the scales for IS 18551 × Swarna were significant in the postrainy season (Tables 3, 4), indicating the inadequacy of additive–dominance model and presence of non-allelic interactions. Partitioning the generation means showed significance of mean for both the crosses. The dominance component was significant for the cross M 35-1 × ICSV 700, and the dominance, dominance × dominance, and additive × additive components were significant for the cross IS 18551 × Swarna, in which the dominance and dominance × dominance components were in opposite direction, indicating the presence of duplicative epistasis. The dominance variance was high in both the crosses, which indicated the predominance of dominance gene action (Table 5).

Days to 50% flowering

M 35-1 × ICSV 700 exhibited significant scales of C and D for this trait, and the scales A, B, and D were significant for the cross IS 18551 × Swarna, indicating the inadequacy of simple additive–dominance model and the presence of epistatic interactions in the rainy season (Tables 3, 4). The partitioning of generation means and estimation of the genetic components

Table 3 Scaling tests and genetic components (Hayman's 6 parameter model) for various agronomic and morphological traits of M 35-1 × ICSV 700 in sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

	Leafsheath pigmentation	Plant vigor score	Days to 50% flowering		100 seed weight		Grain yield	
	2013PR	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR
Scales								
A	1.56 ± 0.15**	− 0.58 ± 0.19**	− 1.37 ± 1.36	− 0.61 ± 1.16	− 0.04 ± 0.14	0.42 ± 0.16**	0.79 ± 0.82	4.90 ± 0.99**
B	0.91 ± 0.15**	0.01 ± 0.12	− 2.40 ± 1.52	− 1.63 ± 1.28	− 0.37 ± 0.14**	0.49 ± 0.14**	0.90 ± 0.60	3.32 ± 0.97**
C	2.27 ± 0.18**	− 0.39 ± 0.19*	− 8.31 ± 2.10**	− 1.54 ± 1.59	− 0.55 ± 0.24*	0.64 ± 0.19**	− 2.41 ± 0.82**	− 0.88 ± 1.04
D	− 0.11 ± 0.14	0.09 ± 0.12	− 2.27 ± 1.17*	0.35 ± 0.92	− 0.07 ± 0.08	− 0.13 ± 0.11	− 2.05 ± 0.52**	− 4.55 ± 0.80**
Genetic components								
m	1.57 ± 0.04**	1.57 ± 0.04**	69.82 ± 0.40**	71.15 ± 0.27**	2.54 ± 0.03**	3.64 ± 0.03**	2.87 ± 0.13**	8.96 ± 0.23**
d	0.32 ± 0.11**	0.04 ± 0.09	− 1.483 ± 0.86	− 0.83 ± 0.75	0.25 ± 0.06**	0.53 ± 0.09**	0.68 ± 0.45	1.23 ± 0.66
h	0.21 ± 0.27	0.48 ± 0.24*	− 4.32 ± 2.44	− 5.90 ± 1.93**	1.03 ± 0.20**	1.24 ± 0.23**	7.50 ± 1.08**	15.23 ± 1.61**
l	− 2.69 ± 0.46**	0.76 ± 0.41	− 0.78 ± 4.03	2.94 ± 3.38	0.28 ± 0.34	− 1.18 ± 0.41**	− 5.78 ± 1.97**	− 17.33 ± 2.82**
i	0.21 ± 0.27	− 0.19 ± 0.23	4.54 ± 2.35*	− 0.70 ± 1.84	0.13 ± 0.17	0.27 ± 0.22	4.09 ± 1.03**	9.11 ± 1.59**
j	0.32 ± 0.11	− 0.30 ± 0.11	0.52 ± 0.93	0.51 ± 0.76	0.17 ± 0.07	− 0.04 ± 0.09	− 0.05 ± 0.46	0.79 ± 0.68

m mean, d additive gene action, h dominant gene action, *l* dominance × dominance gene interaction, *i* additive × additive gene interaction, *j* additive × dominant gene interaction

*, ***t* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

Table 4 Scaling tests and genetic components (Hayman's 6 parameter model) for various agronomic and morphological traits of IS 18551 × Swarna in sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

	Leaf glossy score	Leafsheath pigmentation	Plant vigor score	Days to 50% flowering		Plant height	
	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Scales							
A	1.35 ± 0.26**	0.95 ± 0.15**	0.39 ± 0.12**	− 3.41 ± 1.14**	− 1.69 ± 1.27	− 31.33 ± 7.30**	− 0.22 ± 8.28
B	0.36 ± 0.17*	0.48 ± 0.19*	− 0.34 ± 0.13**	7.67 ± 1.28**	− 0.38 ± 1.18	23.07 ± 10.31*	42.22 ± 8.41**
C	0.24 ± 0.25	2.13 ± 0.22**	− 0.97 ± 0.15**	− 1.85 ± 1.42	− 4.53 ± 1.76**	2.17 ± 9.82	42.33 ± 13.40**
D	− 0.74 ± 0.20**	0.35 ± 0.14**	− 0.51 ± 0.12**	− 3.05 ± 1.00**	− 1.23 ± 1.08	5.22 ± 7.13	0.17 ± 5.25
Genetic components							
m	3.06 ± 0.06**	1.70 ± 0.05**	1.51 ± 0.04**	68.29 ± 0.29**	66.68 ± 0.37**	280.54 ± 1.99**	203.58 ± 1.69**
d	− 1.51 ± 0.16**	− 0.10 ± 0.11	− 0.13 ± 0.09	1.49 ± 0.80	6.51 ± 0.79**	50.80 ± 5.90**	18.78 ± 4.01**
h	1.47 ± 0.40**	− 1.04 ± 0.29**	1.52 ± 0.23**	− 1.80 ± 2.04	− 0.90 ± 2.21	54.90 ± 14.54**	44.33 ± 11.98**
l	− 3.19 ± 0.67**	− 0.72 ± 0.48	− 1.07 ± 0.39**	− 10.36 ± 3.51**	− 0.40 ± 3.60	18.70 ± 25.56	− 41.67 ± 20.90*
i	1.47 ± 0.40**	− 0.71 ± 0.28**	1.02 ± 0.23**	6.10 ± 1.99**	2.47 ± 2.16	− 10.43 ± 14.25	− 0.33 ± 10.50
j	0.50 ± 0.16	0.24 ± 0.12	0.37 ± 0.09	− 5.54 ± 0.82	− 0.66 ± 0.82	− 27.20 ± 6.07	− 21.22 ± 4.49

	100 seed weight		Grain yield	
	2013R	2013PR	2013R	2013PR
Scales				
A	0.38 ± 0.11**	0.17 ± 0.11	0.67 ± 0.37	3.45 ± 0.77**
B	0.22 ± 0.13	0.72 ± 0.15**	− 0.94 ± 0.57	3.21 ± 0.75**
C	− 0.49 ± 0.18**	0.56 ± 0.16**	− 4.38 ± 0.50**	3.04 ± 0.94**
D	− 0.54 ± 0.08**	− 0.17 ± 0.10	− 2.05 ± 0.34**	− 1.81 ± 0.66
Genetic components				
m	2.39 ± 0.03**	3.12 ± 0.03**	2.55 ± 0.09**	7.93 ± 0.21**
d	− 0.64 ± 0.06**	− 0.85 ± 0.08**	− 0.88 ± 0.30**	0.69 ± 0.51
h	1.53 ± 0.17**	0.73 ± 0.21**	5.64 ± 0.71**	9.54 ± 1.34**
l	− 1.68 ± 0.29**	− 1.22 ± 0.36**	− 3.83 ± 1.30**	− 10.28 ± 2.25**
i	1.09 ± 0.15**	0.33 ± 0.20	4.11 ± 0.69**	3.62 ± 1.32**
j	0.08 ± 0.07	− 0.27 ± 0.09	0.81 ± 0.33	0.12 ± 0.53

m mean, d additive gene action, h dominant gene action, *l* dominance × dominance gene interaction, *i* additive × additive gene interaction, *j* additive × dominant gene interaction

*, ***t* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

revealed highly significant positive mean values in both the crosses. In the rainy season, M 35-1 × ICSV 700 showed significant *i* type of interaction i.e., additive × additive interactions were significant and positive in the cross IS 18551 × Swarna; both *i* (additive × additive) and *l* (dominance × dominance) type of interactions were significant. The additive and dominance variances were also calculated and the estimates revealed that the additive variance ($\sigma^2 a$) was greater than the dominance variance ($\sigma^2 d$) in M 35-1 × ICSV 700, whereas IS 18551 × Swarna exhibited higher dominance variance ($\sigma^2 d$) than the additive variance (Table 5). The narrow sense heritability for M 35-1 × ICSV 700 was moderate (0.45), indicating the presence of additive nature of gene action, whereas in the cross IS 18551 × Swarna, narrow sense heritability was negative indicating dominance gene action.

In the postrainy season, the scales were non-significant for the cross M 35-1 × ICSV 700, indicating that additive dominance model explained the inheritance of this trait, whereas for the cross IS 18551 × Swarna, the scale C was significant, indicating the presence of non-allelic interactions, and inadequacy of additive dominance model (Tables 3, 4). Therefore, a six parameter model was adopted to test the presence of non-allelic interactions. Partitioning of the generation means and estimation of the genetic components revealed significance of mean (m) for the cross IS 18551 × Swarna, in which the additive component was significant, indicating the predominance of additive nature of gene action. The narrow sense heritability was 0.32, which was quite low, and the degree of dominance was negative (Table 5). The dominance variance ($\sigma^2 d$) was greater than the additive variance ($\sigma^2 a$) for both the crosses. The broadsense heritability was high (0.85) for the cross M 35-1 × ICSV 700, indicating the environmental influence on the expression of this trait.

Plant height

The F value for plant height in the cross M 35-1 × ICSV 700 was non-significant, and hence, this cross was not considered for generation mean analysis across seasons. The cross IS 18551 × Swarna exhibited significant A and B scales for plant height, indicating the inadequacy of simple additive–dominance model and presence of epistatic interactions in the rainy season (Table 4). Partitioning of generation means and estimating the genetic components revealed significant and positive mean, and significantly positive d (additive) and h (dominance) type of interactions. The dominance component was slightly higher than the additive component, and the dominance degree was > 1.00, indicating the predominance of the dominant gene action for this trait. The dominance variance ($\sigma^2 d$) was greater than the additive variance ($\sigma^2 a$), indicating the predominance of dominance gene action (Table 5).

In the postrainy season, the cross IS 18551 × Swarna exhibited significant B and C scales for plant height (Table 4), indicating the inadequacy of additive dominance model in explaining the inheritance of this trait. Partitioning of generation means revealed positive and significant mean (m), and significant additive, dominance, and dominance × dominance interactions. The dominance and dominance × dominance interactions were with opposite signs, indicating duplicate epistasis. The narrow sense heritability was negative, while the broad sense heritability was moderate (0.59) with high degree of dominance (> 1.00), indicating over-dominance type of gene action (Table 5).

100 seed weight

The scales B and C for the cross M 35-1 × ICSV 700, and A, C and D's for the cross IS 18551 × Swarna were significant, indicating the presence of non-allelic interactions for this trait in the rainy season (Tables 3, 4). To identify the type of interactions present, the generation means were partitioned into six components, and the mean (m) for both the crosses was positive and highly significant. Both additive and dominant components were significant in both the crosses, and *l* and *i* type of interactions were significant for the cross IS 18551 × Swarna. Dominant component, and dominance × dominance interactions exhibited opposite sign for the cross IS 18551 × Swarna, indicating the presence of duplicate epistasis. The narrow sense heritability was 0.42 and 0.26, respectively, in the crosses M 35-1 × ICSV 700 and IS 18551 × Swarna (Table 5). Variation in narrow sense heritability estimates might be because of differences in the parents involved in these crosses. The dominance degree for this trait was > 1.00 for the cross M 35-1 × ICSV 700, indicating the over-dominance nature of gene effects for this trait, and negative dominance degree was observed for the cross IS 18551 × Swarna.

In the postrainy season, 100 seed weight exhibited significant A, B, and C scales for the cross M 35-1 × ICSV 700, and significant B and C scales for the cross IS 18551 × Swarna, indicating the presence of non-allelic interactions (Tables 3, 4). Partitioning of generation means into six components by Hayman's method revealed significant and positive means for both the crosses. The additive, dominance, dominance × dominance components for M 35-1 × ICSV 700, and dominance, dominance × dominance, and additive × additive components for IS 18551 × Swarna were significant for this trait. In both the crosses, dominance and dominance × dominance components exhibited opposite signs, indicating the presence of duplicate epistasis for this trait. The narrow sense heritability was negative in both the crosses, with high broad sense heritabilities (Table 5). The dominance degree was > 1.00 for the cross M 35-1 × ICSV 700 and IS 18551 × Swarna, exhibiting negative dominance.

Grain yield

Scaling test for grain yield revealed that the scales C and D were significant for both the crosses in the rainy season, indicating the presence of non-allelic interactions (Tables 3, 4). Partitioning of generation means into the six components revealed positive and highly significant means (m) for both the crosses. The dominance and additive components were significant for the cross IS 18551 × Swarna with significant *l* and *i* type of interactions. Whereas for the cross M 35-1 × ICSV 700, the additive component (d) was non-significant, but dominance and *l* and *i* type of interactions were significant. The dominance component and dominance × dominance interaction was in opposite direction, indicating the presence of duplicate epistasis. The estimates of additive × additive (*i*) gene interactions was greater than dominance × dominance (*l*) interactions, suggesting predominance of additive gene action. The dominance variance was greater than the additive variance for both the crosses (Table 5). Narrow sense heritability was very low and negative in both the crosses. The dominance degree was negative for IS 18551 × Swarna, but positive and > 1.00 for M 35-1 × ICSV 700 cross, indicating over dominance nature of gene action in this cross.

M 35-1 × ICSV 700 cross exhibited significant A, B, and D scales, while A, B, and C scales in the postrainy season for the cross IS 18551 × Swarna indicated the presence of non-allelic interactions for this trait (Tables 3, 4). Partitioning of the generation means by Haymans's six parameter model revealed significant and positive mean (m), and dominance, dominance × dominance, and additive × additive components were significant for both the crosses. The dominance and dominance × dominance components exhibited opposite signs, indicating the presence of duplicate epistasis for grain yield in the postrainy season. The narrow sense heritability was low, but broad sense heritability was high, indicating the environmental influence for this trait in both the crosses (Table 5). The dominance variance ($\sigma^2 d$) was high for both the crosses, indicating the predominance of the dominant gene action. The narrow sense heritability was lower and negative with high degree (> 1.00) of dominance, indicating over-dominance nature of gene action.

Inflorescence exsertion

The *F*-value was non-significant for the cross M 35-1 × ICSV 700 in the rainy season, and hence, excluded from analysis. All the scales were significant for inflorescence exsertion in the cross IS 18551 × Swarna, indicating the presence of non-allelic interactions, and inadequacy of additive dominance model in explaining the inheritance of this trait (Tables 5, 6, 7). The Hayman's six component analysis revealed significant mean (m) value, with a significant additive component. The dominance × dominance and additive × additive gene interactions were also significant. The estimate for additive × additive component was greater than the dominance × dominance component, indicating predominance of additive gene action. The narrow sense heritability was negative (− 0.37), but broad sense heritability (0.79) was high, the dominance degree being 1.15, indicating over-dominance gene action (Table 8).

In the postrainy season, the scale C for the cross M 35-1 × ICSV 700, and all the scales for the cross IS 18551 × Swarna were significant, indicating inadequacy of the additive dominance model and presence of non-allelic interactions for inflorescence exsertion

Table 5 Estimates of various genetic parameters for different agronomic and morphological traits of two crosses of sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

Traits	Leafsheath pigmentation	Plant vigor score	Days to 50% flowering		100 seed weight		Grain yield	
	2013PR	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700								
$\sigma^2 g$	0.57	0.33	24.24	16.60	0.04	0.21	1.94	11.53
$\sigma^2 a$	− 0.03	− 0.06	13.03	− 3.02	0.06	− 0.13	− 6.46	− 7.75
$\sigma^2 d$	0.60	0.40	11.21	19.62	− 0.02	0.33	8.40	19.28
$\sigma^2 p$	0.57	0.39	28.71	19.38	0.14	0.25	2.77	12.27
h_b^2	–	0.85	0.84	0.86	0.31	0.84	0.70	0.94
${h_{ns}}^2$	− 0.04	− 0.16	0.45	− 0.16	0.42	− 0.50	− 2.34	− 0.63
Dominance degree	0.80	3.56	1.71	2.67	2.01	1.52	3.31	3.52

Traits	Leaf glossy score	Leafsheath pigmentation	Plant vigor score	Days to 50% flowering		Plant height		100 seed weight		Grain yield		Waxy bloom	
	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR	2013R	2013PR
Cross IS 18551 × Swarna													
$\sigma^2 g$	1.18	0.59	0.41	19.90	31.13	883.17	406.57	0.09	0.17	1.33	10.17	0.24	0.29
$\sigma^2 a$	− 0.20	0.14	− 0.03	− 6.14	10.64	− 691.70	− 72.46	0.04	− 0.13	− 3.30	− 0.31	0.18	0.28
$\sigma^2 d$	1.38	0.45	0.43	26.04	20.49	1574.86	479.03	0.06	0.30	4.63	10.47	0.05	0.01
$\sigma^2 p$	1.18	0.65	0.41	21.17	33.13	959.12	687.52	0.15	0.20	1.72	10.62	0.36	0.29
h_b^2	1.00	0.91	1.00	0.94	0.94	0.92	0.59	0.64	0.84	0.78	0.96	0.67	1.00
h_{ns}^2	− 0.17	0.21	− 0.07	− 0.29	0.32	− 0.72	− 0.11	0.26	− 0.68	− 1.92	− 0.03	0.52	0.98
Dominance degree	− 0.99	3.30	− 3.38	− 1.10	− 0.37	1.04	1.54	− 1.55	− 0.93	− 2.53	3.72	− 0.89	− 0.38

$\sigma^2 g$ genotypic variance, $\sigma^2 a$ additive variance, $\sigma^2 d$ dominance variance, $\sigma^2 p$ phenotypic variance, h_b^2 broadsense heritability, h_{ns}^2 narrowsense heritability; R, rainy season; PR, postrainy season

Table 6 Scaling tests and genetic components (Hayman's 6 parameter model) for panicle traits of M 35-1 × ICSV 700 in sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

	Inflorescence exsertion	Panicle compactness	Panicle shape	Glume color		Glume coverage	
	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Scales							
A	− 0.20 ± 0.17	− 0.03 ± 0.03	− 0.08 ± 0.08	− 0.43 ± 0.11**	− 0.37 ± 0.09**	0.53 ± 0.18**	–
B	0.17 ± 0.15	− 0.11 ± 0.05*	− 0.32 ± 0.16*	–	− 0.44 ± 0.10**	0.40 ± 0.43	− 1.20 ± 0.19**
C	− 0.39 ± 0.17*	− 0.58 ± 0.09**	− 1.69 ± 0.25**	− 0.38 ± 0.17*	0.04 ± 0.13	0.09 ± 0.44	− 0.90 ± 0.17**
D	− 0.18 ± 0.14	− 0.22 ± 0.05**	− 0.64 ± 0.16**	0.03 ± 0.13	0.43 ± 0.10**	− 0.42 ± 0.27	0.15 ± 0.13
Genetic components							
m	2.40 ± 0.04**	2.86 ± 0.02**	3.58 ± 0.06**	2.66 ± 0.04**	2.76 ± 0.03**	1.69 ± 0.09**	1.27 ± 0.04**
d	− 0.19 ± 0.11	0.04 ± 0.03	0.12 ± 0.09	0.28 ± 0.09**	0.53 ± 0.07**	− 1.27 ± 0.19**	− 0.40 ± 0.09**
h	1.36 ± 0.29**	0.44 ± 0.10**	1.29 ± 0.31**	0.44 ± 0.25	− 0.35 ± 0.19	− 0.49 ± 0.55	− 1.30 ± 0.25**
l	− 0.33 ± 0.49	− 0.31 ± 0.15*	− 0.89 ± 0.43*	0.49 ± 0.42	1.66 ± 0.31**	− 1.78 ± 0.90*	1.50 ± 0.41**
i	0.36 ± 0.29	0.44 ± 0.10**	1.29 ± 0.31**	− 0.06 ± 0.25	− 0.85 ± 0.19**	0.84 ± 0.53	− 0.30 ± 0.25*
j	− 0.19 ± 0.11	0.04 ± 0.03	0.12 ± 0.09	− 0.22 ± 0.10	0.03 ± 0.07	0.07 ± 0.23	0.60 ± 0.09

m mean, d additive gene action, h dominant gene action, *l* dominance × dominance gene interaction, *i* additive × additive gene interaction, *j* additive × dominant gene interaction

*, ***t* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

Table 7 Scaling tests and genetic components (Hayman's 6 parameter model) for various morphological and panicle traits of IS 18551 × Swarna in sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

	Waxy bloom		Inflorescence exsertion		Panicle compactness	Panicle shape	Glume color		Glume coverage	
	2013R	2013PR	2013R	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Scales										
A	− 0.81 ± 0.18**	− 0.51 ± 0.10**	0.48 ± 0.19**	0.47 ± 0.16**	0.60 ± 0.09**	1.80 ± 0.25**	0.64 ± 0.22**	0.73 ± 0.24**	− 1.23 ± 0.58*	2.67 ± 1.16*
B	− 0.2 ± 0.17	− 0.18 ± 0.06**	0.72 ± 0.13**	0.64 ± 0.13**	0.71 ± 0.10**	2.20 ± 0.30**	− 0.12 ± 0.35	− 0.67 ± 0.14**	− 2.40 ± 0.30**	0.22 ± 0.43
C	− 1.38 ± 0.30**	− 0.28 ± 0.14*	0.58 ± 0.19**	1.78 ± 0.21**	0.85 ± 0.13**	2.68 ± 0.38**	0.45 ± 0.35	0.22 ± 0.26	0.13 ± 0.62	5.17 ± 1.31**
D	− 0.19 ± 0.11	0.20 ± 0.09*	− 0.31 ± 0.12**	0.34 ± 0.15*	− 0.23 ± 0.09**	− 0.66 ± 0.27*	− 0.04 ± 0.27	0.08 ± 0.19	1.88 ± 0.45**	1.14 ± 0.46**
Genetic components										
m	1.99 ± 0.04**	2.68 ± 0.04**	1.31 ± 0.03**	1.70 ± 0.05**	2.46 ± 0.03**	2.42 ± 0.10**	3.86 ± 0.09**	3.80 ± 0.07**	5.03 ± 0.16**	4.96 ± 0.17**
d	− 1.31 ± 0.08**	− 0.67 ± 0.06**	0.21 ± 0.10*	0.41 ± 0.10**	0.44 ± 0.07**	1.30 ± 0.20**	− 1.12 ± 0.21**	0.20 ± 0.14	4.59 ± 0.33**	3.89 ± 0.31**
h	1.04 ± 0.26**	0.09 ± 0.18	0.28 ± 0.24	− 1.17 ± 0.29**	− 0.04 ± 0.19	− 0.18 ± 0.55	− 1.43 ± 0.54**	0.35 ± 0.38	− 3.76 ± 0.90**	− 2.28 ± 1.07*
l	0.64 ± 0.45	1.09 ± 0.27**	− 1.82 ± 0.42**	− 0.44 ± 0.46	− 1.77 ± 0.29**	− 5.32 ± 0.88**	− 0.59 ± 0.89	0.08 ± 0.62	7.39 ± 1.45**	− 0.611 ± 1.8
i	0.37 ± 0.23	− 0.41 ± 0.18*	0.62 ± 0.23**	− 0.67 ± 0.29*	0.46 ± 0.19**	1.32 ± 0.55*	0.07 ± 0.54	− 0.15 ± 0.38	− 3.76 ± 0.90**	− 2.28 ± 0.91*
j	− 0.31 ± 0.08	− 0.17 ± 0.06	− 0.12 ± 0.11	− 0.09 ± 0.10	− 0.06 ± 0.07	− 0.20 ± 0.20	0.38 ± 0.21	0.70 ± 0.14	0.59 ± 0.33	1.22 ± 0.59

m mean, d additive gene action, h dominant gene action, *l* dominance × dominance gene interaction, *i* additive × additive gene interaction, *j* additive × dominant gene interaction

*, ***t* test significant at *P* 0.05 and 0.01, respectively; R, rainy season; PR, postrainy season

(Tables 6, 7). Partitioning of the generation means using the six parameter model revealed significant and positive mean (m). The dominance (h) component was significant for the cross M 35-1 × ICSV 700, and the additive, dominance and additive × additive gene interactions were significant in the cross IS 18551 × Swarna. The additive component was greater than the dominance component, indicating the predominance of additive gene action for this trait in the cross IS 18551 × Swarna. The narrow sense heritability was low, while the dominance degree was negative in both the crosses (Table 8).

Waxy bloom

The scaling test for this trait in the cross IS 18551 × Swarna exhibited significant A and C scales in the rainy season (Table 7), indicating the presence of non-allelic interactions, and inadequacy of additive–dominance model in explaining the inheritance of this trait. Partitioning of the generation means into the six components revealed positive and highly significant mean (m). The dominance and additive components were also significant. The dominance component was high as compared to the additive component, but the additive variance was greater than the dominance variance. The trait exhibited moderate narrow sense heritability (0.52), and dominance degree was negative (Table 8).

The *F*-value of this trait was non-significant for the cross M 35-1 × ICSV 700 in the postrainy season, and hence, not included for calculating the generation means. All the scales were significant for the cross IS 18551 × Swarna, indicating inadequacy of additive–dominance model in explaining the inheritance of this trait, and presence of non-allelic interactions (Table 7). Partitioning of the generation means into six parameter model revealed significant mean (m), while the components additive, dominance × dominance, additive × additive were also significant. The additive variance was high (0.28), and the narrow sense heritability (0.98) was also high (Table 8).

Table 8 Estimates of various genetic parameters for different panicle traits of two crosses of sorghum across seasons (ICRISAT, Patancheru, 2013–2014)

Traits	Inflorescence exertion		Panicle compactness	Panicle shape	Glume color		Glume coverage	
	2013PR		2013PR	2013PR	2013R	2013PR	2013R	2013PR
Cross M 35-1 × ICSV 700								
$\sigma^2 g$	0.51		0.12	1.09	0.31	0.30	1.25	0.51
$\sigma^2 a$	0.04		0.18	1.60	0.05	0.23	0.70	0.36
$\sigma^2 d$	0.47		− 0.06	− 0.51	0.26	0.06	0.56	0.14
$\sigma^2 p$	0.51		0.12	1.09	0.31	0.30	1.49	0.51
h^2_b	–		–	–	1.00	1.00	0.84	1.00
h^2_{ns}	0.09		1.48	1.47	0.16	0.79	0.47	0.71
Dominance degree	− 2.70		3.33	3.28	1.25	− 0.81	0.62	1.80
Traits	Inflorescence exertion		Panicle compactness	Panicle shape	Glume color		Glume coverage	
	2013PR	2013PR	2013PR	2013PR	2013R	2013PR	2013R	2013PR
Cross IS 18551 × Swarna								
$\sigma^2 g$	0.22	0.69	0.25	2.19	1.85	1.04	5.76	2.49
$\sigma^2 a$	− 0.11	0.47	0.11	0.87	0.56	0.32	3.52	5.01
$\sigma^2 d$	0.33	0.22	0.14	1.32	1.30	0.72	2.24	− 2.52
$\sigma^2 p$	0.28	0.69	0.25	2.19	1.85	1.04	5.76	6.78
h^2_b	0.79	1.00	1.00	1.00	1.00	1.00	1.00	0.37
h^2_{ns}	− 0.37	0.68	0.42	0.40	0.30	0.31	0.61	0.74
Dominance degree	1.15	− 1.69	− 0.30	− 0.38	1.13	1.32	− 0.91	− 0.77

$\sigma^2 g$ genotypic variance, $\sigma^2 a$ additive variance, $\sigma^2 d$ dominance variance, $\sigma^2 p$ phenotypic variance, h^2_b broadsense heritability, h^2_{ns} narrowsense heritability; R, rainy season; PR, postrainy season

Panicle compactness

The *F*-value for panicle compactness was non-significant in the rainy season for both the crosses, and hence, excluded from the analysis. B, C, and D scales for M 35-1 × ICSV 700 cross, and all the scales for the cross IS 18551 × Swarna were significant, indicating the presence of the non-allelic interactions in the inheritance of this trait in the postrainy season (Tables 6, 7). Partition of the generation means using the Haymans' six parameter model revealed significant and positive mean (m) for both the crosses. The components h, *l,* and *i* were significant for M 35-1 × ICSV 700, indicating the presence of epistatic interactions. The dominant and dominant × dominant components were with opposite signs, indicating presence of duplicate epistasis in the postrainy season. IS 18551 × Swarna showed significant mean (m), and significant d, *l,* and *i* components. High narrow sense heritabilities were observed for this trait in both the crosses, with high dominance degree (3.33) for M 35-1 × ICSV 700, but low and negative dominance degree for the cross IS 18551 × Swarna (Table 8).

Panicle shape

The B, C, and D scales for the cross M 35-1 × ICSV 700, and all the scales for IS 18551 × Swarna were significant in the postrainy season (Tables 6, 7). The significance of the scales indicated the presence of the non-allelic interactions. In order to know the type of interactions, the generation means were partitioned into six parameters, which revealed that the mean was significant for both the crosses. Dominance, dominance × dominance, and additive × additive components were significant for the cross M 35-1 × ICSV 700, while additive, dominance × dominance, and additive × additive interactions were significant for the cross IS 18551 × Swarna. The dominance variance was high in the cross IS 18551 × Swarna, but high additive variance was recorded for the cross M 35-1 × ICSV 700, with high dominance degree in the cross M 35-1 × ICSV 700, and negative dominance degree in the cross IS 18551 × Swarna (Table 8).

Glume color

The A and C scales were significant for the cross M 35-1 × ICSV 700, while scale A was significant for the cross IS 18551 × Swarna, indicating that additive dominance model was inadequate in explaining the inheritance of this trait in the rainy season (Tables 6, 7). Hayman's method revealed positive and highly significant mean (m) in both the crosses. The additive component in the cross M 35-1 × ICSV 700, and additive and dominance component in the cross IS 18551 × Swarna was found to be significant. The narrow sense heritability for this trait was low in both the crosses, with high dominance degree (Table 6). The dominance variance was high in both the crosses.

The scales A, B, and D and A, B were significant, respectively, for the crosses M 35-1 × ICSV 700 and IS 18551 × Swarna in the postrainy season (Tables 6, 7), indicating the presence of non-allelic interactions in the inheritance of this trait in the postrainy season. Partitioning of the generation means revealed the positive significant mean (m) in both the crosses. The additive, dominance × dominance, and additive × additive components were significant for the cross M 35-1 × ICSV 700, and none of the components was significant for the cross IS 18551 × Swarna. The additive variance was greater for the cross M 35-1 × ICSV 700, while dominance variance was greater for the cross IS 18551 × Swarna (Table 8). The cross M 35-1 × ICSV 700 exhibited higher narrow sense heritability (0.79) with negative dominance degree. The cross IS 18551 × Swarna showed lower narrow sense heritability with high dominance degree (1.32), indicating over dominance type of gene action.

Glume coverage

The scaling test for this trait in the rainy season revealed significant A scale for the cross M 35-1 × ICSV 700, and significant A and C scale for the cross IS 18551 × Swarna indicating non-allelic interactions, and inadequacy of additive–dominance model in explaining the inheritance of this trait (Tables 6, 7). Partitioning of the generation means into six components, and estimation of the genetic components revealed positive and significant means (m) for both the crosses. The additive and dominance × dominance interactions were significant for the cross M 35-1 × ICSV 700, while in IS 18551 × Swarna exhibited significant dominance and additive components, and significant dominance × dominance and additive × additive gene interactions. The dominance and dominance × dominance interactions had opposite signs, indicating complementary gene action. The additive component was greater than the dominance component, whereas dominance × dominance interaction was greater in magnitude than the additive × additive gene interactions. The narrow sense heritability estimates were 0.45 and 0.61, respectively, for the crosses M 35-1 × ICSV 700 and IS 18551 × Swarna (Table 8). The dominance degree for the cross M 35-1 × ICSV 700 was 0.62 indicating partial dominance, whereas the cross IS 18551 × Swarna exhibited negative dominance degree.

In the postrainy season, glume coverage of the grain exhibited significant B, C scales for the cross M 35-1 × ICSV 700, while the cross IS 18551 × Swarna exhibited significant A, C, and D scales, indicating the presence of non-allelic interactions (Tables 6, 7). Partitioning of generation means using Hayman's six parameter model revealed significant and positive mean for both the crosses. The additive, dominance, dominance × dominance, and additive × additive interactions were significant for the cross M 35-1 × ICSV 700, while additive, dominance, and additive × additive components were significant for IS 18551 × Swarna. The dominance and dominance × dominance components were opposite in sign, indicating the presence of duplicative epistasis for the cross M 35-1 × ICSV 700. The additive variance was high for both the crosses, while the cross M 35-1 × ICSV 700 exhibited higher dominance degree, whereas the cross IS 18551 × Swarna exhibited negative dominance degree (Table 8).

Discussion

Sorghum shoot fly, *A. soccata* is an economically important pest that has a significant bearing on grain yield in sorghum. The present studies were aimed at understanding genetic parameters for different traits including the traits associated with shoot fly resistance using generation mean analysis to detect the major gene effects (additive and dominance), and their digenic (additive × additive, additive × dominance, and dominance × dominance) interactions for inheritance of quantitative traits (Kearsey and Pooni 1996). Generation mean analysis helps us in understanding the performance of the parents used in crosses, and the potential of crosses to be used either for heterosis exploitation or pedigree selection (Sharma and Sain 2003). Susceptibility/resistance of the progenies of the cross IS 18551 × Swarna, and the performance of the progenies indicated that one of the parents should have genes for shoot fly resistance (IS 18551) to develop shoot fly-resistant sorghums. The non-allelic interactions between the genes for component traits such as leafsheath pigmentation and plant vigor suggested that proper care should be taken while selecting the sorghum genotypes for the crossing program, based on these traits. Predominance of dominant gene action has been reported for the leaf glossiness, leafsheath pigmentation and plant vigor, whereas Riyazaddin et al. (2016) and Aruna et al. (2011) reported additive type of gene action for these traits. The results showed dominant nature of gene action for early flowering and early maturity. The cross between the tall and dwarf sorghum genotypes generated the progenies with tall plants, indicating the dominance nature of the tallness gene in sorghum. The morphological traits such as grain lustre and red glume color also showed dominant gene action. The cross between the awned and awnless parents produced the awnless F_1 progeny, indicating the recessive nature of the gene action for presence of awns. The earlier studies of Ravindrababu and Pathak (2000) reported that additive, dominance, and epistatic (additive × dominance) effects were important for resistance to shoot fly. The results suggested that delayed selection is the best approach for the traits governed by dominance and epistasis effects. However, the traits that were governed by additive effects should undergo thorough selection at an early stage.

Conclusion

The present studies indicated that at least one of the parents involved in the crossing program should possess genes for resistance to shoot fly to develop high-yielding shoot fly-resistant sorghum. Both the non-allelic and predominance of dominance gene action for the component traits indicated that heterosis breeding is ideal for improving shoot fly resistance in sorghum genotypes. The additive nature of gene action for most of the traits indicated the importance of heterosis breeding, followed by simple selection for developing shoot fly-resistant sorghums.

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