

Genetic studies on shoot fly resistance in sorghum [*Sorghum bicolor* (L.) Moench.]

■ SANJEEV K. DESHPANDE, B.D. BIRADAR, PRAKASH I. GANGASHETTY AND P.M. SALIMATH

SUMMARY

An investigation was carried out to elicit the information on the inheritance pattern of resistance to shoot fly in *Rabi* sorghum using six parameter model of generation mean analysis. The resistances to shoot fly resistant (IS2312) and susceptible (RS 29) lines were crossed separately. Back crossing to both the parents was practiced. Segregating and non-segregating material generated (*viz.*, P₁, P₂, F₁, F₂, BC₁ and BC₂) was evaluated under replicated trials and data obtained for various relevant traits were subjected for generation mean analysis. The symptoms expressed by shoot fly infection are taken at appropriate time. With respect to shoot fly inheritance studies, susceptibility was found to be dominant over resistance in the cross RS29 x IS2312. Based on gene effects, dominance component (*h*) was found prominent for inheritance of various traits like egg count, dead heart percentage, seedling height, recovery resistance, number of effective tillers etc. Additive effect was evidenced for trichome density indicating that the resistance brought through selection for increased number of trichomes per unit leaf area is fixable. Among interaction effects, dominance x dominance effects (*l*) were prominent. Epistasis of duplicate nature revealed possibility of obtaining transgressive variants for shoot fly resistance in subsequent generations of cross RS29 x GRS1.

Key Words : Shoot fly, Sorghum, Inheritance, Studies, Gene effects

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Sorghum [*Sorghum bicolor* (L.) Moench.] is widely grown throughout the world (Asia, Africa, North and Central America and Europe) for food, feed and fodder. In Peninsular India, particularly the Deccan plateau, covering

Maharashtra, Karnataka, Andhra Pradesh, parts of Madhya Pradesh and Tamil nadu, sorghum is a major crop as a source of food and fodder for a large section of people inhabited in semi-arid tropics. But grain yield levels are considerably low compared to those with the developed world. So, relevant research on improving sorghum genetically is essential.

In north Karnataka, sorghum is an important food crop grown mainly under rainfed condition in post-monsoon season. Apart from the grain flour used for *roti* making, *Rabi* sorghum also gains importance for its alternate by-products, *viz.*, semolina, snack foods (pop types used in rural areas), infant mixes, breakfast foods like *dosa* and *idli*, malted foods with high enzyme activity. Considering the regional importance of *Rabi* sorghum as a major food crop as much as wheat and rice and its fodder quality much valued than other cereals, the production levels are still marginalized compared to wheat and rice.

In sorghum, of the 150 insect species causing damage to the crop the sorghum shoot fly [*Atherigona soccata*

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(Rondani.)] has become the major seedling pest. Shoot fly infestation alone is found to cause yield losses of 80 per cent in grain sorghum. Breeding for pest resistance is one of the practical approaches against shoot fly menace. Complete host immunity for shoot fly is absent in grain sorghum (Kamtar, 2000). Moreover, the major sources of resistance is limited to Indian sub- continent and confined to *Rabi* sorghum genotypes. The degree of resistance to shoot fly is a complex character which depends on number of componential characters and varied physiological response of shoot fly to different sorghum genotypes. Information on the inheritance of resistance in relation to varying levels of shoot fly infestation is limited. Further, no hybrids and varieties in sorghum display stable resistance to shoot fly. Few resistant genotypes also exhibit differential response to shoot fly attack depending upon the pest population during the period. In this context, understanding the genetics of resistance to shoot fly helps in the development of new varieties and hybrids with enhanced levels of resistance in sorghum. Keeping the situations in mind, the present investigation was carried out to study the inheritance of shoot fly tolerance in sorghum.

MATERIALS AND METHODS

The experiment was conducted at College of Agriculture and Regional Agriculture Research Station, Bijapur. In order to investigate the inheritance pattern of tolerance to shoot fly, the resistant (R) and susceptible (S) lines were crossed. Back crossing to both the parents was practiced. Segregating and non-segregating material generated (*viz.*, P₁, P₂, F₁, F₂, BC₁ and BC₂) was evaluated under replicated trials and data obtained for various relevant traits was subjected for generation mean analysis followed by Hayman (1958). To ensure high shoot fly selection pressure under field conditions inter row fish meal technique (Taneja and Leuschner, 1985) was used. Susceptible infester rows (*viz.*, DJ6514) were grown after every ten rows to increase the incidence. The observations are recorded on the following characters *viz.*, number of eggs per plant (7, 14 and 21 DAE), dead heart percentage (14, 21 and 28 DAE), number of trichomes per unit leaf area, plant height (14, 21, 28 DAE and at maturity), recovery resistance, tillers per plant, number of effective tillers, grain yield per plant, aphid tolerance studies. Aphid population per sq cm leaf area (at 51, 58, 65, 72, 79, 86, 93 DAE and at maturity) and grain yield per plant.

RESULTS AND DISCUSSION

Shoot fly is one of the important biotic stresses in sorghum (Kamtar and Salimath, 2003). Resistance breeding thus, requires understanding of inheritance pattern of tolerance to these biotic stresses. In this context, an attempt was made to know the inheritance of tolerance to shoot fly in sorghum through generation mean analysis.

For this, firstly a resistant parent was crossed to a susceptible parent, like wise, totally three separate crosses were attempted, each cross representing a particular biotic stress. Further, in each cross six generations, *viz.*, P₁, P₂, F₁, F₂, BC₁ and BC₂ were produced. These segregating (F₂, BC₁ and BC₂) and non-segregating (P₁, P₂ and F₁) generations were evaluated at a time and data on various characters determining resistance was generated. The data was subjected for scaling tests (Mather, 1949), joint scaling tests (Cavalli, 1952) and six generation mean analysis (Hayman, 1958) in order to study inheritance pattern of tolerance to shoot fly. To understand the inheritance pattern underlying shoot fly tolerance, susceptible (S) x resistance (R) cross was attempted between the lines RS29 and IS2312, respectively. The resultant populations, namely, P₁, P₂, F₁, F₂, BC₁ and BC₂ were used for analysis. In the study, to estimate the gene effects, scaling and joint scaling tests, six generation means was carried out; generation means and their variances were calculated.

Scaling tests and joint scaling test :

The tests revealed that simple additive-dominance model was inadequate to explain the gene action operating with respect to all the seventeen characters as revealed by higher magnitude of calculated 't' value in case of scaling tests and higher chi-square values in joint scaling test. The parameters A, B, C (scaling tests) and m, d, h (joint scaling test) cannot explain the possible presence of non-allelic gene interactions, as revealed by significance of 't' values and chi-square test at both 5 per cent and 1 per cent levels, respectively. Further, six parameter model (Hayman, 1958) was used to explain the results.

In the present study, IS2312 as a resistant line was crossed to a susceptible line RS29. The six generations, namely, P₁, P₂, F₁, F₂, BC₁ and BC₂ were produced and evaluated at a time. Agrawal and House (1982) reported resistance to be polygenic. In the present investigation also, no discrete variation was evident. Hence, quantitative analysis of different characters conferring resistance or susceptibility based on gene effects was carried out to study the inheritance pattern. Significance of different parameters in scaling tests (A, B, C) revealed possibility of non-allelic interaction effects. So, six parameter model of Hayman (1958) was used to estimate gene effects (m, d, h, i, j and l) in different characters. Results obtained are discussed character wise as below.

Number of eggs per plant (7, 14 and 21 days after emergence (DAE), The mean of F₁ and BC₁ generations for the trait tended more towards susceptible parent for number of eggs per plant, more pronounced at 21 DAE (Table 1). This inferred that least egg counts (associated with resistance) was recessive over high egg counts (associated with susceptibility). Jayanthi *et al.* (2000) also reported recessive nature of lower egg counts. Though all the genetic parameters were significant, based on relative magnitude dominance effect

(*h*) and dominance x dominance gene effects (*l*) were found important in genetic control of the trait. Kulkarni (2002) made similar conclusions. While, importance of both additive and non-additive gene effects for egg counts was narrated by Dabholkar *et al.* (1989).

For dead heart percentage (14, 21 and 28 DAE), Jayanthi *et al.* (2000) described recessive nature of resistance for the trait. It is also quite clear that F₁ mean and BC₁ mean tended more towards the recessive parent P₁ (RS 29). This revealed that susceptibility to shoot fly is dominant over resistance based on percentage of dead hearts observed. Contrarily, Borikar and Chopde (1981) obtained dominance for resistance when shootfly population was low. Further, estimation of gene effects depicted that although both additive (*d*) and non-additive effects (*h*) were found important, predominance of additive effects (*d*) was observed for inheritance of the character. Similar reports of prominence of additive gene action were made by Borikar and Chopde (1981) and Ravindrababu

et al. (1997). Contrarily, Nimbalkar and Bapat (1987) revealed prominence of non-additive gene action for the trait. Considering non-allelic interactions, dominance x dominance effects played a major role for genetic control of the trait. Significance of epistatic effects for the trait was also narrated by Ravindrababu and Pathak (2000a).

Number of trichomes per unit leaf area for trichome density on abaxial leaf surface is an important parameter positively correlated with shoot fly resistance. Gibson and Maiti (1983) reported that trichome presence was a recessive trait controlled by a single locus. But quantitative estimation of trichome density makes it a polygenic character with susceptible cultivar possessing comparatively less number of trichomes per unit area than resistant ones and resistance based on trichome density is a recessive trait (Halalli *et al.*, 1982). On similar lines, in the present study, perusal of data indicated that mean values of F₁ and BC₁ generations for trichome density were more inclined towards susceptible

Table 1: Generation means and variances in respect of characters associated with shoot fly tolerance studies in sorghum
Cross : RS29 (S) x IS2312 (R)

Sr. No.	Generation	1		2		3		4	5	6
		Number of eggs per plant (7 DAE)		Number of eggs per plant (14 DAE)		Number of eggs per plant (21 DAE)		Dead heart percentage (14 DAE)	Dead heart percentage (21 DAE)	Dead heart percentage (28 DAE)
		Mean	Variance	Mean	Variance	Mean	Variance	Mean	Mean	Mean
1.	P ₁	0.72 ± 0.004	0.001	0.92 ± 0.001	0.001	1.10 ± 0.001	0.002	66.05 ± 0.04 (54.37 ± 0.02)	75.20 ± 0.06 (60.14 ± 0.02)	79.88 ± 0.01 (63.37 ± 0.006)
2.	P ₂	0.28 ± 0.003	0.002	0.57 ± 0.001	0.003	0.71 ± 0.001	0.01	22.38 ± 0.09 (28.25 ± 0.06)	26.00 ± 0.04 (30.66 ± 0.03)	32.35 ± 0.02 (34.67 ± 0.014)
3.	F ₁	0.59 ± 0.001	0.001	0.73 ± 0.001	0.001	0.90 ± 0.001	0.002	55.38 ± 0.03 (48.10 ± 0.01)	66.38 ± 0.01 (54.57 ± 0.01)	70.15 ± 0.006 (56.88 ± 0.003)
4.	F ₂	0.49 ± 0.003	0.03	0.69 ± 0.003	0.04	0.83 ± 0.002	0.06	53.5 ± 0.16 (47.01 ± 0.11)	61.00 ± 0.08 (51.36 ± 0.07)	68.15 ± 0.07 (55.64 ± 0.05)
5.	BC ₁	0.67 ± 0.001	0.01	0.82 ± 0.001	0.02	0.94 ± 0.002	0.03	59 ± 0.11 (50.19 ± 0.06)	67.75 ± 0.09 (55.40 ± 0.05)	77.85 ± 0.05 (61.93 ± 0.04)
6.	BC ₂	0.58 ± 0.003	0.02	0.77 ± 0.001	0.02	0.86 ± 0.001	0.04	54.75 ± 0.11 (47.73 ± 0.07)	65.50 ± 0.10 (54.03 ± 0.06)	70.5 ± 0.06 (57.11 ± 0.04)

Table 1: Contd.....

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Sr. No.	Generation	7		8		9		10	
		Number of trichomes per unit leaf area (mm ²)		Plant height (14 DAE) (cm)		Plant height (21 DAE) (cm)		Plant height (28 DAE) (cm)	
		Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
1.	P ₁	10.82 ± 0.03	0.06	10.85 ± 0.03	0.06	16.35 ± 0.03	0.06	21.25 ± 0.04	0.25
2.	P ₂	41.28 ± 0.04	0.39	24.8 ± 0.08	0.29	31.1 ± 0.04	0.25	36.1 ± 0.04	0.06
3.	F ₁	19.52 ± 0.01	0.01	12.25 ± 0.01	0.01	16.25 ± 0.02	0.02	21 ± 0.01	0.01
4.	F ₂	18.23 ± 0.15	1.06	20.5 ± 0.15	1.06	25.5 ± 0.08	0.57	30.5 ± 0.10	1.01
5.	BC ₁	25.75 ± 0.06	0.41	9.5 ± 0.04	0.39	16.25 ± 0.07	0.26	21.5 ± 0.05	0.16
6.	BC ₂	16.75 ± 0.08	0.29	15.5 ± 0.06	0.41	20.25 ± 0.08	0.57	25.6 ± 0.07	0.26

Note: Figures in the parenthesis are Arcsin transformations

parent P₁ (RS29). This confirmed that resistance based on this character was recessive to susceptibility. Further, continuous variation in F₂ and test cross generation (BC₂) revealed polygenic inheritance of trichome density. Based on estimation of gene effects in the present study, additive component (*d*) was found to be prominent than non-additive component (*h*). Halalli *et al.* (1982), Shivanna *et al.* (1996) and Kamtar (2000) also revealed the importance of additive gene action compared to non-additive gene action for inheritance of the trait. While, Jayanthi *et al.* (2000) reported that inheritance of trichome density appeared to be more complex from additivity to complete dominance depending upon parents involved and seasonal effect. Duplicate epistasis was evident for inheritance of the trait.

Seedling height (14, 21 and 28 DAE) :

Seedling height predicts the shoot length and is an important parameter to determine seedling vigour at early stages in sorghum. Krishna Kumar *et al.* (2000) reported that seedling vigour is an inherent seed character determining seedling resistance against establishment of shoot fly larvae. In the present study, based on the average values of F₁ and BC₁ generations, the resistance based on seedling vigour was found to be a recessive trait. This observation was in accordance with the studies made by Jayanthi *et al.* (2002). Further, six generation mean analysis depicted that dominance component (*h*) was more important towards inheritance of the trait. Borikar and Chopde (1981) proposed similar findings, while Kamtar (2000) obtained additive effects for seedling height. Among interaction effects, dominance x dominance gene effects (*l*) and additive x additive effects (*i*) played a major role. Epistasis was found to be governed by duplicate genes.

With respect to plant height (at maturity) (cm), the mean value of F₁ generation exceeded the better parental mean of P₂ indicating over dominance for plant height in the cross RS29 x IS2312 (Table 2). Although, the additive and non-additive gene effects were found important, based on relative magnitude of (*d*) and (*h*), the dominance effect was found to play a major role for genetic control of the trait. Similar observations were evidenced by Gururaj Rao (1992). Among the interaction effects, additive x additive (*i*) and dominance x dominance effects (*l*) were found most important. Duplicate epistasis was evident for inheritance of the trait.

Recovery resistance (%) :

Recovery resistance percentage is an inbuilt capacity of a plant to recover from shoot fly infestation and give economic yield levels. It is an important parameter of evaluation for resistance. Genotypes are known to show differences for recovery resistance. It is partially related to tillering.

In this study, it is interesting to note that, mean value of recovery resistance in F₁ (43.77%) was found highest among all six generations and even exceeded the resistant parent P₂ (39.72%). This depicted over dominance effects for recovery resistance percentage in the cross RS29 x IS2312. Borikar and Chopde (1980) also obtained similar kind of over- dominance for the trait. This is desirable as hybrids developed using one of the parents with high recovery resistance like IS 2312 will confer at least some amount of partial resistance to shoot fly through this trait. Based on estimation of genes effects, dominance effect (*h*) and dominance x dominance effect (*l*) were found to be most important for inheritance of the trait. Contrarily, Shivanna *et al.* (1996) obtained preponderance of additive effects for the trait.

Tillers per plant (29 DAE) with respect to number of

Table 2: Generation means and variances in respect of characters associated with shoot fly tolerance studies in sorghum

Sr. No.	Generation	11		12		13		14		15	
		Plant height (at maturity) (cm)		Recovery resistance (%)		Tillers per plant (29 DAE)		Number of effective tillers		Grain yield per plant (g)	
		Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
1.	P ₁	127.80 ± 0.19	3.69	27.65 ± 0.07 (31.75 ± 0.04)		0.88 ± 0.001	0.007	0.44 ± 0.001	0.006	26.60 ± 0.15	4.31
2.	P ₂	162.25 ± 0.52	21.43	40.85 ± 0.09 (39.73 ± 0.04)		1.62 ± 0.002	0.005	0.76 ± 0.002	0.002	39.32 ± 0.26	6.96
3.	F ₁	178.90 ± 0.03	2.04	47.85 ± 0.06 (43.77 ± 0.03)		1.66 ± 0.001	0.003	0.77 ± 0.001	0.003	79.63 ± 0.13	2.79
4.	F ₂	126.40 ± 1.29	83.57	31.00 ± 0.16 (33.83 ± 0.11)		1.52 ± 0.10	0.73	0.69 ± 0.002	0.250	37.63 ± 0.69	38.30
5.	BC ₁	145.30 ± 0.39	71.45	43.50 ± 0.07 (41.27 ± 0.05)		1.49 ± 0.02	0.52	0.53 ± 0.001	0.180	52.65 ± 0.60	18.00
6.	BC ₂	162.50 ± 0.95	30.40	43.00 ± 0.11 (40.98 ± 0.06)		0.85 ± 0.01	0.45	0.71 ± 0.003	0.150	59.65 ± 0.35	10.05

Note: Figures in the parenthesis are Arcsin transformations

tillers per plant, both additive (d) and dominance (h) effects were found important. But, predominance of dominance component (h) was evident based on relative magnitudes. Similar findings were registered by Borikar and Chopde (1982). Contrarily, Shivanna *et al.* (1996) reported prominence of additive effects for the trait. Among interaction effects, dominance x dominance effect (l) played a major role for inheritance of the trait. Epistasis was found to be governed by duplicate genes.

Number of effective tillers determines the inbuilt capacity of a genotype to give productive tillers with good panicle size and seed set. Therefore it is an important parameter determining resistance. Both additive (d) and non-additive (h) gene effects were found important for the genetic control of the trait with predominance of non-additive component (h), while Shivanna *et al.* (1996) noticed preponderance of additive effects (i) were found to play a major role.

Grain yield per plant mean of F_1 generation (79.63 g) exceeded the better parent GRS1 (39.32 g) for grain yield per plant depicting over dominance for the trait. This provided scope for improvement of the trait by use of the cross RS 29 x GRS1 in heterosis breeding programme. Based on the study of six generation mean analysis in the above cross, the dominance effects (h) were found to be relatively of higher magnitude compared to other gene effects depicting the major role of non-additive gene action for grain yield per plant. Similarly, Subba Rao and Aruna (1997) and Bhavsar and Borikar (2002) also reported prominence of non-additive gene action for the trait. Among epistatic effects, additive x additive (i) and dominance x dominance (l) effects were prominent for genetic control of the trait in the above cross. Epistasis of duplicate type was observed, thus providing scope for selection of desirable transgressive segregants for the trait in advanced generations.

Considering the various important traits determining resistance or susceptibility to shoot fly, namely, egg counts (at 7, 14 and 21 DAE), dead heart percentage (at 14, 21 and 28 DAE), trichome density per unit leaf area (mm^2), seedling plant height (at 14, 21 and 28 DAE) *etc.*, it was found that resistance to shootfly was recessive to susceptibility. Further, the individual plant values in the F_2 and test cross segregating generations revealed that continuous variation existed for all the traits like egg counts, trichome density, seedling vigour, tiller number and effective tillers depicting polygenic inheritance of these traits determining resistance. Based on gene effects, compared to additive component, dominance component (h) was found prominent for inheritance of various traits except trichome density. For trichome density, additive effect (d) was found to be of much importance.

Among interaction effects, dominance x dominance (l) effect was found to be predominant followed by additive x additive effect (i) for most of the traits studied. Epistasis governed by duplicate genes was found to be responsible for

inheritance of resistance to shootfly. This indicated the possibility of obtaining transgressive variants for shoot fly resistance in the subsequent generations of the cross RS29 x GRS 1. Different shapes of panicles were evidenced in the six generations depicting variation among them. Further, curved peduncle, a desirable trait to avoid bird damage observed in the resistant parent, IS2312 was found to be recessive to straight peduncle based on the phenotypes of F_1 and susceptible parent, Rs.29.

Generation means and variances :

The mean values and variances for trait wise explained in the following paragraphs.

The number of eggs per plant (7 DAE) highest mean value for the trait was noticed in the susceptible parent P_1 (0.75) followed by BC_1 (0.67). F_1 generation also displayed considerably high mean value for the trait in undesirable direction (0.59). P_2 exhibited least mean value (0.28) displaying resistance. Variance was highest in the F_2 generation (0.03) followed by BC_2 (0.02). Lower level of variation for the trait was noticed in P_1 and F_1 generations (0.001). For number of eggs per plant (14 DAE), compared to resistant parent P_2 (0.57), P_1 , BC_1 and F_1 generations expressed higher mean values for the trait (0.92, 0.82 and 0.73, respectively). F_2 variance was highest followed by BC_1 and BC_2 populations. The number of eggs per plant (21 DAE) has highest mean value for the trait in unfavourable direction was recorded by susceptible parent P_1 (1.10), BC_1 (0.94) and F_1 (0.90) generations. While, resistant parent, P_2 displayed least mean value for the trait. Variance was highest in the F_2 generation followed by BC_2 and BC_1 . Lowest level of variance was evidenced by F_1 and P_1 . The dead heart percentage (14 DAE) considerably, increased magnitude of dead heart percentage at 14 DAE was observed in P_1 (54.37%) followed by BC_1 (50.19%) and F_1 (48.10%) generations, while lowest mean value for the trait was noticed in the resistant parent, P_2 (28.55%). For dead heart percentage (21 DAE) mean value was highest for the trait in P_1 (60.14%) followed by BC_1 (55.40%) generation. F_1 generation also evidenced considerably higher mean value (54.57%). Dead heart percentage (28 DAE) has wide range of mean values was noticed among the parents for the trait (from 34.67 to 63.37%). F_1 generation expressed considerably higher mean value in considerable direction (56.88%). This revealed that resistance was found to be recessive to susceptibility in the cross. Among the segregating generations highest average values were noticed in BC_1 (61.93%) followed by BC_2 (57.11%).

The number of trichomes per unit leaf area (mm^2) was Highest number of trichomes per unit leaf area was observed in the resistant parent P_2 (41.28) followed by BC_1 (25.75). Least mean value for the trait was observed in susceptible parent P_1 (10.82). Trichome number was also found to be reduced in F_1 (19.52) and F_2 (18.23) generations. F_2 variance for the trait was of higher magnitude. While, F_1 generation showed least variance

Table 3: Scaling test and joint scaling test in respect of characters associated with shoot fly tolerance in sorghum

Sr. No.	Characters	Scaling test (Mather, 1949)			Joint scaling test (Cavalli, 1952)		
		A	B	C	m	[d]	[h]
1.	Number of eggs per plant (7 DAE)	0.03**±0.004	0.28**±0.006	-0.24** ± 0.01	0.52**±0.002	-0.21**±0.002	0.07**±0.002
2.	Number of eggs per plant (14 DAE)	0.10±0.003	0.25**±0.004	-0.18**±0.006	0.76**±0.001	-0.15**±0.002	-0.04**±0.002
3.	Number of eggs per plant (21 DAE)	-0.12**±0.004	0.11**±0.002	-0.30**±0.005	0.92**±0.001	-0.16**±0.001	-0.03**±0.001
4.	Dead heart percentage (14 DAE)	-2.09**±0.16	19.10**±0.13	9.21** ± 0.19	47.43**±0.04	-3.92**±0.03	2.13**±0.08
5.	Dead heart percentage (21 DAE)	-3.90**±0.12	22.83**±0.09	5.49**±0.12	48.89**±0.03	-9.34**±0.03	5.77**±0.03
6.	Dead heart percentage (28 DAE)	3.60**±0.11	22.67**±0.07	10.77**±0.05	53.01**±0.01	-16.79**±0.02	3.95**±0.01
7.	Number of trichomes per unit leaf area (mm ²)	21.17**±0.11	-27.30**±0.16	-18.24**± 0.27	17.30**±0.05	-5.18**±0.03	4.80**±0.09
8.	Plant height (cm) (14 DAE)	-4.10**±0.15	-6.05**±0.16	21.85**±0.21	20.12**±0.05	6.79**±0.05	-7.59**±0.06
9.	Plant height (cm) (21 DAE)	-0.10±0.19	-6.85**±0.12	22.05**±0.22	22.30**±0.03	5.50**±0.03	-4.20**±0.07
10.	Plant height (cm) (28 DAE)	0.75**±0.11	-5.90**±0.15	22.65**± 0.26	28.89**±0.04	7.58**±0.03	-6.71**±0.06
11.	Plant height (cm) (at maturity)	-15.49**±1.9	-15.54**±1.67	-141.03**±2.06	127.46**±0.37	-0.30±0.37	48.39**±0.45
12.	Recovery resistance (%)	7.05**±0.13	-1.55** ± 0.15	-23.66**±0.23	36.33** ± 0.04	1.34**±0.04	6.86**±0.06
13.	Tillers per plant (29 DAE)	-1.57**±0.19	0.48**±0.004	0.30**± 0.01	1.26**±0.001	-0.37**±0.001	0.76**±0.002
14.	Number of effective tillers	0.07**±0.006	-0.10**± 0.003	-0.34**±0.004	0.78**±0.001	-0.03**±0.001	-0.09**±0.001
15.	Grain yield per plant (g)	13.08**±1.53	-13.65**±0.77	-74.65**±1.00	21.06**±0.23	16.85**±0.24	48.01**±0.39

* and ** indicate significance of values at P=0.05 and 0.01, respectively

for the trait. For plant height (14 DAE) resistant parent P₂ possessed a higher mean value for plant height at 14 DAE (24.80 cm) followed by F₂ generation (20.50 cm). F₁, P₁ and BC₁ generations exhibited lower values of plant height in descending order (12.25, 10.85 and 9.50 cm, respectively). Variance was found to be highest in F₂ generation and lowest in F₁ generation.

Plant height (21 DAE) resistant parent P₂ expressed highest value of 31.10 cm for the trait. Plant height at 21 DAE was considerably reduced in F₁, BC₁ generations (16.25 cm) and susceptible parent P₁ (16.35 cm). Comparatively higher magnitude of variance for the trait was observed in F₂ generation (0.57) and lowest value was recorded in F₁ (0.02). Plant height (28 DAE) for resistant parent P₂ recorded maximum

mean value for the trait (26.10 cm). The mean plant height at 28 DAE was reduced to 21.25 cm and 21.00 cm in susceptible parent P₁ and F₁ generation, respectively. F₂ population witnessed maximum variance and minimum variance was observed in F₁ generation. The plant height (at maturity) at maturity, F₁ generation exhibited maximum mean value (178.90 cm) for plant height followed by BC₂(162.50 cm) population and resistant parent P₂ (162.25 cm), respectively. While, lowest mean values for the trait was evidenced by F₂ population (126.40 cm) followed by susceptible parent P₁ (127.80 cm). Variance for plant height at maturity was of greater magnitude in F₂ (83.57) followed by BC₁ (71.45). F₁ generation obtained lowest value of variance (2.04) for the trait.

Table 4 : Gene effects for characters associated with shoot fly tolerance in sorghum

Sr. No.	Characters	6 parameter model (Hayman, 1958)						Epistasis type
		<i>m</i>	[<i>d</i>]	[<i>h</i>]	[<i>i</i>]	[<i>j</i>]	[<i>l</i>]	
1.	Number of eggs per plant (7 DAE)	0.49** ± 0.002	0.10** ± 0.003	0.64**±0.01	0.55** ± 0.01	-0.13**±0.004	-0.86**±0.02	Duplicate
2.	Number of eggs per plant (14 DAE)	0.69** ± 0.001	0.05** ± 0.001	0.40**±0.005	0.42**±0.004	-0.12**±0.002	-0.67**±0.009	Duplicate
3.	Number of eggs per plant (21 DAE)	0.83** ± 0.001	0.08** ± 0.002	0.27**±0.006	0.27**±0.006	-0.11**±0.002	-0.28**±0.009	Duplicate
4.	Dead heart percentage (14 DAE)	47.01** ± 0.02	2.46** ± 0.07	14.60**±0.18	7.80**±0.16	-10.60**±0.09	-24.81**±0.33	Duplicate
5.	Dead heart percentage (21 DAE)	51.36** ± 0.02	1.37** ± 0.06	22.62**±0.16	13.44**±0.15	-13.37**±0.08	-32.37**±0.28	Duplicate
6.	Dead heart percentage (28 DAE)	55.64** ± 0.01	4.82** ± 0.06	23.37**±0.13	15.50**±0.13	-9.53**±0.07	-41.77**±0.25	Duplicate
7.	Number of trichomes per unit leaf area (mm ²)	18.23** ± 0.04	9.00** ± 0.03	5.57**±0.21	12.10**±0.19	24.23**±0.09	-5.97**±0.30	Duplicate
8.	Plant height (cm) (14 DAE)	20.50** ± 0.04	-6.00** ± 0.08	-37.58**±0.23	-32.00**±0.21	0.98**±0.11	42.15**±0.38	Duplicate
9.	Plant height (cm) (21 DAE)	25.50** ± 0.04	-4.00** ± 0.09	-36.48**±0.24	-29.00**±0.23	3.38**±0.10	35.95**±0.42	Duplicate
10.	Plant height (cm) (28 DAE)	30.50** ± 0.04	-4.10** ± 0.05	-35.48**±0.20	-27.80**±0.17	3.33**±0.06	32.95**±0.32	Duplicate
11.	Plant height (cm) (at maturity)	126.40**±0.39	-17.20**±1.08	143.27**±2.74	110.00**±2.66	0.03±1.26	-78.97**±4.78	Duplicate
12.	Recovery resistance (%)	33.83** ± 0.04	0.29** ± 0.07	37.20** ± 0.24	29.16**±0.23	4.30**±0.09	-34.66**±0.37	Duplicate
13.	Tillers per plant (29 DAE)	1.52** ± 0.003	-0.64** ± 0.10	-1.04** ± 0.19	-1.39**±0.19	-1.03**±0.10	2.48** ± 0.38	Duplicate
14.	Number of effective tillers	0.69** ± 0.001	0.12** ± 0.003	0.29** ± 0.007	0.31**±0.007	0.09**±0.003	-0.28** ± 0.01	Duplicate
15.	Grain yield per plant (g)	37.63** ± 0.15	7.00** ± 0.78	120.75**±1.71	74.08**±1.66	13.36**±0.84	-73.51**±3.27	Duplicate

* and ** indicate significance of values at P= 0.05 and 0.01, respectively

For recovery resistance (%), the number of affected plants exhibiting economic yield were counted and expressed in percentage as recovery resistance. It is clear that highest mean value of recovery resistance was expressed by F_1 (43.77%) generation. Lowest value for the trait was noticed in susceptible parent P_1 (31.75%) followed by F_2 population (33.83%). Resistant parent P_2 , BC_2 and BC_1 populations also expressed higher mean values (39.73, 40.98 and 41.27%) of recovery resistance after F_1 . The tillers per plant (29 DAE) among the parents, more number of tillers per plant was noticed in P_1 (1.62) compared to P_2 (0.88). F_1 generation recorded highest mean value (1.66) for the trait. Variance of higher magnitude for tiller per plant (29 DAE) was noticed in F_2 generation and least in F_1 . Number of effective tillers the number of tillers yielding productive panicles out of total number of tillers per plant were counted and expressed as frequency of effective tillers per plant. Highest number of effective tillers was exhibited by F_1 generation (0.77) followed by P_2 (0.76). Lowest mean value was recorded in susceptible parent P_1 (0.44). With respect to variance for the trait, segregating generations (F_2 , BC_1 and BC_2) revealed maximum values and non-segregating generations (P_1 , P_2 and F_1) obtained lower values.

Grain yield per plant compared to segregating generations (F_2 , BC_1 and BC_2) and parents (P_1 and P_2), the F_1 hybrid generation registered considerably higher mean value (79.63 g) for grain yield per plant. Among the segregating generations, BC_2 obtained maximum value for the trait (59.65 g). Susceptible parent P_1 showed lowest mean value (26.60 g) followed by F_2 population (37.63 g). Variation for grain yield per plant was found to be highest in F_2 segregating generation (38.30) and lowest in the F_1 hybrid generation (2.79).

Six generation mean analysis to estimate gene effects for shoot fly tolerance :

The results obtained regarding estimates of mean effect [m], additive effect [d], dominance effect [h], additive x additive effect [i], additive x dominance effect [j] and dominance x dominance effect [l] with respect to characters determining resistance to shoot fly follows.

Number of eggs per plant (7 DAE) :

Among the five genetic parameters d , h , i , j and l that showed significance with respect to number of eggs per plant at 7 DAE, the dominance x dominance [l] effect was found to be highest (-0.86) followed by dominance effect h (0.64). Additive effect [d] obtained least value (0.10). The parameters [h] and [l] obtained significant but opposite signs. This depicted, duplicate nature of gene action for the trait. Number of eggs per plant (14 DAE). Mean effect expressed for the trait was significant (0.69). Though all other five genetic parameters were found to be significantly important, for genetic

control of the trait, dominance x dominance effects [l] were found to be predominant (-0.67). h and l received significant values in opposite direction indicating duplicate epistasis. Number of eggs per plant (21 DAE). The mean effect [m] was found to be significant for the trait (0.83). Dominance effect [h] was of higher magnitude compared to additive effect [d]. In case of interaction effects, additive x additive gene effects [i] were found to be important (0.28) followed by dominance x dominance [l] effects (-0.27). Dominance effect [h] expressed significant positive value (0.27), while dominance x dominance [l] showed significant negative value (-0.27). This revealed duplicate nature of gene interaction for the trait.

Dead heart percentage (14, 21 and 28 DAE) :

Mean effect was found to be significant with respect to dead heart per cent at all the four intervals, namely, 14, 21 and 28 DAE. All the other genetic parameters, namely, [d], [h], [i], [j] and [l] were found to be significantly important. However, with respect to dead heart percentage recorded at all the four intervals, compared to additive gene action, dominance gene action [h] exhibited greater effects. Dominance x dominance gene effects [l] with significant negative values exceeded other non-allelic interaction effects except in case of dead heart percentage at 7 DAE. With respect to dead heart percentage at 7 DAE additive x dominance effect [j] played a major role. Dominance x dominance [l] gene effects followed by dominance effects [h] were found to control the inheritance of the trait in the S x R cross RS29 x IS2312.

Number of trichomes per unit leaf area has significant mean effect [m] for the trait (18.23) was observed. Both additive [d] and non-additive gene effects [h] were found to be significantly important for the trait. However, higher magnitude of additive gene action (9.00) was registered compared to non-additive gene action (5.57). Among the interaction effects, though all the three parameters were found significant, additive x dominance gene action [j] displayed considerably higher effects (24.23) compared to additive x additive (12.10) and dominance x dominance gene effects (-5.97). The genetic parameter [j] followed by [i], [d], [l] and [h] gene effects were found to control the inheritance of the trait in the cross. Further, duplicate epistasis was evident based on opposite signs of [h] and [l].

Plant height (at 14, 21, 28 DAE and at maturity) estimates of all the six gene effects were found to be highly significant for plant height at 14, 21, 28 DAE and at maturity. However, compared to additive gene action [d], non-additive gene action [h] was found to possess significantly higher values [h] displayed significant negative values with respect to plant height at 14, 21 and 28 DAE (-37.58, -36.48 and -35.48,, respectively) and positive sign in case of plant height at maturity (143.27). Among the interaction effects dominance x dominance effects [l] played a major role compared to [i] and [j] in case of plant height at 14, 21 and 28 DAE. While, additive x additive effect [i] was predominant among the interaction

effects in case of plant height at maturity. Among all the five gene effects estimated, dominance effect [h] with highest magnitude was found to be the major parameter with respect to inheritance of plant height throughout the crop growth period in the S x R cross RS29 x IS2312. Further the parameters [h] and [l] with opposite signs revealed duplicate nature of gene action for plant height at different stages of plant height, namely, 14, 21 and 28 DAE and at maturity.

Recovery resistance for the three types of gene effects, namely, additive, dominance and epistasis were found to play significantly important role in the inheritance of the trait. The six parameter model indicated high level of significance of both additive [d] and dominance [h] effects in the crops. However, dominance [h] effect (37.20) was found to be predominant followed by dominance x dominance [l] effect (-34.66) and additive x additive effect (29.16) for inheritance of the trait. [h] and [l] possessed positive and negative values, respectively. This indicated duplicate epistasis in the cross.

Tillers per plant (29 DAE), with respect to tillers per plant, all the genetic parameters showed significance at both 5 per cent and 1 per cent levels. Both additive [d] and dominance [h] gene effects exhibited significant but negative values with higher magnitude of dominance effects [h]. With respect to interaction effects, dominance x dominance effects was found to be predominant with significant positive value (2.48). Negative values of [h] and positive value of [l] depicted duplicate nature of gene action for the trait. For number of effective tillers both additive [d] and dominance [h] gene effects were positive and significant. However, magnitude of [h] was higher compared to [d] gene effects in the cross. Although, all the interaction effects expressed significance, additive x additive gene effect (0.31) followed by dominance x dominance effects (-0.28) were found to be of major important for the trait. The opposite signs of [h] and [l] displayed duplicate epistasis in the cross.

Grain yield per plant with respect to grain yield per plant all the six parameters showed significant values depicting adequacy of digenic interaction model to explain the gene action in the cross. Significant higher magnitude of [h] gene effects (120.75) was evidenced for the trait followed by [i] (74.08) and [l] (-73.51). This suggested predominance of dominance effects [h] followed by additive x additive [i] and dominance x dominance [l] gene effects for genetic control of the trait in the S x R cross RS29 x IS2312. Duplicate nature of non-allelic interaction effects was observed in the cross based on positive and negative values with respect to [h] and [l].

Conclusion :

With respect to shoot fly inheritance studies, susceptibility was found to be dominant over resistance in the cross RS29 x IS2312. Based on gene effects, dominance component (h) was found prominent for inheritance of various traits like egg count, dead heart percentage, seedling height,

recovery resistance, number of effective tillers *etc.* Additive effect was evidenced for trichome density indicating that the resistance brought through selection for increased number of trichomes per unit leaf area is fixable. Among interaction effect, dominance x dominance effects (l) were prominent. Epistasis of duplicate nature revealed possibility of obtaining transgressive variants for shoot fly resistance in subsequent generations of cross RS29 x GRS1.

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