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Genetics of traits associated with shoot fly resistance in post-rainy season sorghum (*Sorghum bicolor* L.)

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Abstract

Generation mean analyses were carried out to study genetics of traits associated with shoot fly resistance in three crosses using male sterile susceptible female and resistant male parents (104B x IS18551, 104B x IS2312 and 104B x RSE03) during 2006-07 at two locations. The mean performance of families showed that resistance as indicated by lower deadheart percentage is governed by recessive genes. Both additive and nonadditive gene actions were important for resistance, and this trait is influenced by environment. The line RSE 03 was a better source of resistance with relatively simple genetics for shoot fly resistance and component traits. Indirect selection through the component traits such as glossiness and seedling height which were under the control of additive genes would be effective for developing sorghum varieties resistant to shoot fly infestation.

Key words : Epistasis, additive-dominance model, generation mean analysis, shoot fly resistance, *Sorghum bicolor* (L.)

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is unique in its adaptation to extreme environmental conditions. In India, there are two distinct growing seasons for sorghum *i.e.* rainy (*kharif)* and post-rainy (*rabi*) seasons. *Rabi* sorghum is highly valued for consumption purpose due to the excellent quality of grain, which matures during rain-free cool climate. Hence, this grain fetches high market price, almost double that of *kharif* grain. But the average productivity of *rabi* sorghum (727 kg/ha) is much less compared to *kharif* sorghum (992 kg/ha) [1]. The main reasons for low productivity of *rabi* sorghum are low genetic diversity and higher susceptibility to shoot fly. Therefore, there is a need to increase the productivity by focusing on the development of improved shoot fly resistant lines.

The shoot fly larvae cuts the growing tip, resulting in deadheart formation which ultimately leads to considerable damage to the crop. Worldwide, the yield losses were estimated to be 274 million US dollars [2]. Resistance breeding requires identification of the resistant genetic stocks, understanding the genetics of resistance and associated traits and transfer of useful genes to susceptible genotypes. The grain yield of the identified resistant sources is low due to their physiologically inefficient plant type. Hence, the primary objective of sorghum breeding programmes is to transfer such types of resistance into an improved agronomical background. Characters such as leaf glossiness, seedling vigour, trichome density and plants with fewer shoot fly eggs confer resistance to shoot fly and can be used as marker traits to select against shoot fly [3-6]. Seedling height as a trait also contribute to shoot fly resistance in sorghum [7].

Knowledge of the nature of gene interaction is important to a plant breeder in deciding appropriate methodologies for plant improvement [8]. The primary objective of this study was to evaluate the relative importance of additive, dominance and epistatic effects for shoot fly resistance for determining the most efficient breeding procedure to develop shoot fly resistant sorghum genotypes. A secondary objective was to identify the better resistant source(s) for use in breeding programme.

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Material and methods

Plant material

One elite male-sterile line, 104B (with low resistance to shoot fly) and three shoot fly resistant lines (IS18551, IS2312 and RSE03) were used in the present study to understand the genetics of traits associated with shoot fly resistance in *rabi* sorghum. The important features of the lines used in the study are given in Table 1. The three shoot fly resistant lines used are of diverse origin. Three crosses, 104B x IS18551 (cross 1), 104B x IS2312 (cross 2) and 104B x RSE03 (cross 3), and their F_1, F_2 and F_3 families were raised for the study. The crosses were made during *rabi* 2004, and the F_1 and F_2s were raised during *kharif* 2005 and *rabi* 2005 respectively, and seed was harvested from 70 individual F_2 plants of each cross to get F_3 families. Five families (P_1, P_2, F_1, F_2 and F_3) for each cross were generated and were grown in a randomized block design with three replications during *rabi* 2006-07 at two locations: Directorate of Sorghum Research (DSR), Hyderabad, and Centre for Rabi Sorghum (CRS), Solapur. Plot size varied for different families. For each cross, parental lines and the F_1s were grown in single row plots; F_2 population in 6 rows, and each of the 70 F_3 families were grown in two rows of 4 m length. To attain uniform and high shoot fly pressure, the interlard fish meal technique [9] was adopted. All the recommended agronomic practices except plant protection measures were followed to ascertain good crop stand.

Observations

In both the environments, all observations were recorded on 10 randomly selected competitive plants from the P_1, P_2, F_1 and each of the F_3 family; and on 75 plants from the F_2 population in each replication on the following characters:

Glossiness: The leaf glossiness was recorded at 10-days after emergence (DAE) during the morning hours when there was maximum reflection of light. It was scored on a scale of 1–5, where 1 = high glossy (light green, shining, narrow and erect leaves), and 5 = non-glossy (dark green, dull, broad, and drooping leaves).

Seedling vigour: Seedling vigour was scored at 10 DAE on a scale of 1–5, where 1= high vigour (plants showing maximum height, leaf area and robustness) and 5= low vigour (plants showing minimum growth, low leaf area and poor adaptation).

Seedling height: Seedling height (cm) was measured from the soil surface to the top of the whorl of the unopened leaf at 21 DAE.

Trichome density: The central portion of the fifth leaf from the base was taken from three randomly selected seedlings at 12 DAE. Leaf samples (5 mm^2) were placed overnight in small vials having 20 ml of acetic acid: alcohol (2:1). The cleared samples were stored in 90% lactic acid. The leaf samples were observed under the microscope at a magnification of 20^x [10]. The number of trichomes was counted in three microscopic fields selected at random on both abaxial (lower) and adaxial (upper) leaf surfaces and expressed as trichome density (number/mm^2).

Deadheart percentage: The total number of plants in each row and the number of deadhearts were recorded at 28 DAE and the percentage was calculated.

While glossiness, seedling vigour and deadheart percentage were recorded at both locations, seedling height (at Solapur) and trichome density (at Hyderabad) were recorded at one location only.

Statistical analysis

Generation mean analyses were carried out for the traits studied in all the three crosses. To test the adequacy of the additive-dominance model, the individual scaling tests [11] as well as joint scaling test [12] were applied. The means of different generations were analyzed by a joint scaling test using the weighted least squares method [13, 14]. The observed generation means were used to estimate the parameters of a model consisting only of mean (m), additive (d) and dominance (h) genetic effects. The estimated parameters were used in turn to calculate the expected generation means. The goodness of fit between observed and expected values was tested; a significant chi-square indicates a significant difference between the observed and expected generation means, which implied that a simple additive-dominance model was insufficient to explain the data. In such cases, the five parameter model was applied. If a parameter was not significant in the five-parameter model then it was omitted and the best fit model was worked out using the chi-square statistic. The significance of each parameter was determined by t-test. Thus, all possible models with different combinations of epistatic parameters were tried to identify the best fit model with minimum/ non-significant parameters [13]. The analysis was carried out using the statistical software, 'Wi*ndostat* ' [15].

Results and discussion

Significance of scaling tests (C and D) reflected the presence of non-allelic interactions in the control of the traits. 'D' provides a test largely of '*i*' type of interaction (additive x additive) and C indicates '*l*' (dominance x dominance) type of interaction. Means and their standard errors for parental, F_1, F_2 and F_3 generations for the traits studied are listed in Table 2 and Table 3. The means of the parents were significantly different for all the traits in all the crosses at both the locations. The results obtained from scaling tests, joint scaling test and best fit model for shoot fly resistance and associated traits are presented in Table 4 and Table 5. Accordingly, the character-wise findings on various genetic components are described below:

Table 1. Details of the parents used in the study

Genotype	Origin	Important features
104B	India	Female parent of the high yielding post-rainy sorghum hybrids, CSH15R and CSH19R with low level of shoot fly resistance.
IS18551	Ethiopia	Shoot fly resistant germplasm line which is used as check in the All India Co-ordinated Sorghum Improvement Project(AICSIP)
IS2312	Sudan	Shoot fly resistant germplasm line which is used as check in the AICSIP
RSE03	India	An improved shoot fly resistant source developed at Rahuri, India and is used as a shoot fly resistant check in AICSIP

Genetics of glossiness: The elite parent (104B, P_1) had non glossy leaves and the resistant parents (P_2) had glossy leaves (Table 2). The mean values of F_1 were at par with P_1, and that of F_2 tended towards the non-glossy parent (P_1), indicating that glossiness is a recessive trait which confirms earlier reports [16, 17].

Generation mean analysis for glossiness showed inadequacy of additive-dominance model and the presence of interallelic interactions in cross 1 (104B x IS18551), while additive-dominance model was adequate in cross 2 (104B x IS2312) and cross 3 (104B x RSE03) (Table 4). C and D scaling tests also confirmed the same. Since same susceptible parent has been used in each cross, any differences among the crosses would be due to the resistant parent. Hence parental line specific discussion is given rather than cross specific. In IS 18551, dominance effect [h], additive x additive [i] and dominance x dominance [l] type of gene interactions were observed at both the locations. The [h] and [l] components possessed opposite sign, indicating the presence of duplicate epistasis. In IS 2312 and

Table 2. Generation means of the families for seedling traits associated with shoot fly resistance in sorghum at two locations during 2006-07

Family	Trait	Glossiness(1-5 scale)*						Seedling vigour(1-5 scale)**						Seedling height(cm)		
		Cross1		Cross2		Cross3		Cross1		Cross2		Cross3		Cross1	Cross2	Cross3
		Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Sol	Sol	Sol
P_1	M	3.00	3.33	3.17	3.33	3.00	3.00	3.00	2.83	3.00	3.17	3.17	3.00	13.5	13.53	13.53
	SE	0.01	0.33	0.17	0.17	0.01	0.19	0.01	0.17	0.01	0.24	0.17	0.01	0.17	0.24	0.24
P_2	M	1.17	1.00	1.50	2.33	2.17	2.20	2.17	1.50	2.00	2.33	2.17	2.17	17.4	16.80	17.93
	SE	0.17	0.01	0.01	0.33	0.17	0.19	0.17	0.29	0.01	0.03	0.17	0.33	0.81	0.70	0.24
F_1	M	3.00	3.17	3.33	2.83	2.67	3.00	3.50	3.33	2.50	2.53	2.67	2.67	15.99	18.60	16.87
	SE	0.01	0.17	0.33	0.17	0.33	0.29	0.29	0.17	0.29	0.15	0.30	0.31	1.34	1.50	1.64
F_2	M	2.90	2.67	2.60	2.74	2.23	2.80	2.93	3.00	3.10	2.71	3.10	2.74	14.51	14.72	15.27
	SE	0.01	0.33	0.15	0.08	0.11	0.07	0.12	0.01	0.12	0.07	0.12	0.06	0.25	0.22	0.23
F_3	M	2.36	2.66	2.56	2.73	2.50	2.78	2.74	2.75	3.00	2.85	2.83	2.81	14.15	14.91	15.48
	SE	0.04	0.05	0.05	0.04	0.06	0.05	0.04	0.05	0.05	0.04	0.06	0.05	0.21	0.25	0.22
MP		2.08	2.16	2.33	2.83	2.58	2.60	2.58	2.16	2.50	2.75	2.67	2.58	15.4	15.16	15.73

P_1= Parent1 (104B); P_2= Parent2 (IS18551/IS2312/RSE03); M=Mean; SE=Standard error; MP=Mid-parent value; Hyd=Hyderabad; Sol=Solapur; Cross1= 104B x IS18551; Cross2= 104B x IS2312; Cross3= 104B x RSE03; Glossiness(1-5 scale)*, where 1= glossy, and 5= non-glossy; Seedling vigour (1-5 scale)**, where 1= high vigour and 5= low vigour

Table 3. Generation means of the families for shoot fly resistance and trichome density in sorghum at two locations during 2006-07

Family	Trait	Deadheart percentage						Trichome density-upper surface (no./mm^2)			Trichome density-lower surface (no./mm^2)		
		Cross1		Cross2		Cross3		Cross1	Cross2	Cross3	Cross1	Cross2	Cross3
		Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Hyd	Hyd	Hyd	Hyd	Hyd
P_1	M	57.19	45.63	55.63	47.54	54.05	47.54	57.00	57.00	57.00	13.00	13.00	13.00
	SE	0.84	2.52	5.90	2.44	2.11	2.44	3.00	3.00	3.00	1.15	1.15	1.15
P_2	M	20.52	21.78	25.39	29.06	33.59	26.03	105.0	96.33	73.83	35.33	24.34	28.23
	SE	0.52	6.41	1.12	0.78	2.86	5.90	1.53	5.39	5.61	1.20	1.67	4.06
F_1	M	65.28	49.95	61.53	60.09	58.89	51.68	73.11	85.22	76.11	18.33	16.89	24.61
	SE	1.39	8.26	3.02	2.95	4.19	3.34	3.64	4.77	4.82	3.05	1.96	3.03
F_2	M	65.52	38.36	54.27	47.33	51.88	45.11	46.36	46.92	52.63	13.76	12.52	15.90
	SE	2.40	3.90	2.91	5.29	2.76	5.88	2.11	1.40	2.00	0.65	0.46	0.76
F_3	M	47.18	37.44	50.90	43.56	49.44	38.96	59.68	48.15	50.00	16.68	13.03	17.85
	SE	1.01	1.02	1.23	1.09	1.13	1.37	1.58	1.83	2.19	0.70	0.51	0.93
MP		38.85	33.70	40.51	38.3	43.82	36.78	81.0	76.66	65.41	24.16	18.67	20.61

P_1=Parent1(104B); P_2= Parent2 (IS18551/IS2312/RSE03); M=Mean; SE=Standard error; MP=Mid-parent value; Hyd= Hyderabad; Sol= Solapur; Cross1= 104B x IS18551; Cross2= 104B x IS2312; Cross3= 104B x RSE03

RSE 03, additive gene effects were found to be significant at both the locations indicating that simple selection for glossiness in F_2 and further generations would fix the trait and thus can be handled easily. Presence of additive gene action in control of glossiness was reported earlier [18]. Presence of dominance gene action and [i] and [l] epistatic interactions with duplicate epistasis in IS 18551 suggested that handling glossy trait in this parent is difficult.

Genetics of seedling vigour: The elite parent (P_1) exhibited low seedling vigour and the resistant parents (P_2) possessed high seedling vigour. F_1 mean of the cross 1 was more than both the parents, indicating the presence of overdominance for this trait in this cross. In crosses 2 and 3, the F_1 means were intermediate to both the parents, indicating the presence of incomplete dominance [3]. The mean values of F_2 and F_3 families were significantly different from the parents in all the crosses and they tended towards that of P_1.

The C and D scaling tests indicated the presence of epistatic interactions in five out of six cases (Table 4). The joint scaling test revealed that the additive-dominance model was inadequate in case of cross 1 and cross 3 at both the locations, and cross 2 at Hyderabad. The digenic epistatic model was adequate in these cases (non significant chi-squares). The [d] and [h] gene effects, and [i] interaction effects were significant at both locations in IS 18551. In case of IS 2312 at Hyderabad, [d] effects and [i] interactions were important. The predominance of additive gene effects and [i] interaction in IS 2312 and RSE 03 suggested that this trait can be fixed through simple selection in the early segregating generations. Though [d] effects and [i] interactions were predominant for seedling vigour in RSE 03, [l] gene interaction was also important for this cross at Hyderabad. This slight difference observed in the gene effects at two locations indicates the influence of environment on the expression of the trait [3]. Fixing this character in the subsequent generations may take more time in IS 18551 since dominance gene effect [h] was also involved in the expression of this trait along with [d] and [i].

Genetics of seedling height: The resistant parents (P_2) were taller than the elite parent (P_1). The F_1 means were more than the mid-parent values and not significantly different from the resistant parent (P_2). The F_2 and F_3 means were significantly different from the parental values, but at par with each other in all the crosses.

Estimation of C and D scaling tests indicated the presence of inter-allelic interactions for seedling height in cross 1. Joint scaling test also revealed the inadequacy of additive-dominance model for this trait in cross 1. The additive-dominance model was adequate

Table 4. Estimates of scaling test, joint scaling test and gene effects in the best fit model for seedling traits in sorghum at two locations during 2006-07

Estimates	Glossiness						Seedling vigour						Seedling height		
	Cross1		Cross2		Cross3		Cross1		Cross2		Cross3		Cross1	Cross2	Cross3
	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Sol	Sol	Sol	Sol
Scaling test															
C	1.43± 0.43*	0.01± 0.50	-0.93± 0.91	-0.37± 0.59	-1.57± 0.81	-0.11± 0.68	-0.83± 0.76*	1.00± 0.47	0.40± 0.75	0.68± 0.70	1.73± 0.86*	0.78± 0. 73	3.18± 2.97	-2.64± 3.22	-4.12± 3.42
D	-0.52± 0.31	1.00± 0.38*	0.39± 0.33	-0.24± 0.44	0.37± 0.35	0.19± 0.35	-0.08± 0.34	0.67± 0.38*	0.80± 0.32*	0.47± 0.60	-0.22± 0.600.92± 0.2	9**	-3.32± 1.28*	-0.14± 1.32	-0.07± 1.05
Joint scaling test															
m	3.00± 0.01**	3.00± 0.01**	2.60± 0.1**	2.71± 0.07**	2.23± 0.11**	2.70± 0.1**	3.00± 0.01**	2.67± 0.3**	3.17± 0.06**	2.99± 0.08**	2.72 ± 0. 09**	2.67± 0.02**	14.88± 0.29**	14.93± 0.30**	15.70±0.16**
[d]	0.92± 0.08**	0.42± 0.08	0.83± 0.1**	0.57± 0.16*	0.42± 0.08*	0.50±0.12*	0.42± 0.08	1.17± 0.17*	0.50± 0.01	0.48± 0.27	0.50± 0.12**	0.42± 0.17	-1.43± 0.32**	-1.45± 0.33*	-2.20±0.17**
[h]	-0.44± 0.04**	-0.56± 0.20**	0.58± 0.39	0.07± 0.19	-0.42± 0.34	0.25±0.21	-0.56± 0.20**	0.36± 0.69	0.67± 0.23**	-0.60± 0.19*	0.46± 0.27-	0.44± 0.23*	-1.46± 0.82	-0.09± 0.77	-0.75±0.55
X^2	7.4*	10.3**	0.52	0.66	0.82	1.65	9.21**	8.69*	6.03*	4.26	7.04*	8.16*	11.29*	5.22	3.33
Best fit model															
m	2.90± 0.10**	2.67± 0.04**	-	-	-	-	2.93± 0.12*	3.00± 0.01	2.60± 0.15**	-	3.10± 0.12	2.74± 0.06**	14.27± 0.30**	-	-
[d]	0.92± 0.08**	-	-	-	-	-	0.42±0.08*	0.67± 0.17*	0.83± 0.08**	-	0.50± 0.12*	0.58± 0.08*	-1.95± 0.41**	-	-
[h]	1.50± 0.23**	0.33± 0.18*	-	-	-	-	0.90±0.33*	0.89± 0.16**	-	-	-	-	-	-	-
[i]	2.42± 0.27**	1.67± 0.41**	-	-	-	-	0.81± 0.38*	1.06± 0.28**	1.25± 0.49*	-	1.43± 0.45*	0.68± 0.32*	1.18±0.44**	-	-
[l]	-2.60± 0.83**	-1.33± 0.59*	-	-	-	-	-	-	-	-	-2.60± 1.36*	-	-	-	-
X^2	2.03	3.16					1.09	2.08	2.1		2.15	2.78	4.16		

*, **- Significant at p=0.05 and p=0.01 respectively; Cross1= 104B x IS18551; Cross2= 104B x IS2312; Cross3= 104B x RSE03

to explain the variation in crosses 2 and 3 and additive gene effects were more important indicating simple inheritance of the trait which can be exploited easily. In case of IS 18551, [d] gene effects and [i] interaction effects were found to be significant, which can also be fixed by early generation selections. Based on the evidence that additive gene action is the most important component of inheritance, a simple recurrent selection or backcrossing scheme should work quite well to concentrate the frequency of desirable genes for seedling height.

Genetics of trichome density: The resistant parents (P_2) were having high number of trichomes per unit area than the elite parent (P_1). In general, the trichome density was more on upper surface compared to the lower surface of the leaves in the parents, and all generations studied. The F_1 means were intermediate to both the parents in case of cross 1 and cross 2, while it was on par with the resistant parent (P_2) in case of cross 3 for trichome density on both the surfaces.

The joint scaling test indicated the inadequacy of additive-dominance model with significant χ^2 values for 3-parameter model. Analysis through five parameter model suggested the adequacy of digenic interaction model for trichome density in all the three crosses at both the locations. In case of IS 18551, [d], [h] and [l] effects were significant. The opposite signs of [h] and [l] indicated the predominance of duplicate type of gene action for this trait. The [d] and [i] effects were significant in IS 2312 for trichome density on both the surfaces, in addition to significant [l] interaction for trichome density on upper surface. In RSE 03, [d], [i] and [l] for trichomes on upper surface, and [d], [h] and [l] for trichomes on lower surface were contributing for the expression of the trait.

The gene effects for trichome density on upper and lower surfaces of

Table 5. Estimates of scaling test, joint scaling test and gene effects in the best fit model for shoot fly resistance and trichome density in sorghum at two locations during 2006-07

Estim	Deadheart percentage						Trichome density (upper)			Trichome density (lower)		
	Cross1		Cross2		Cross3		Cross1	Cross2	Cross3	Cross1	Cross2	Cross3
	Hyd	Sol	Hyd	Sol	Hyd	Sol	Hyd	Hyd	Hyd	Hyd	Hyd	Hyd
Scaling test												
C	53.80±10.1**	32.81±24.1	34.21±10.46*	-7.48±22.1	3.27±30.0	-4.49±33.3	-122.8±11.6**	-136.1±12.67**	-72.53±14.04**	-29.96±6.85**	-21.04±4. 80**	-26.86±7.99**
D	-20.0±6.37*	-116.5±12.6**	19.60±7.21*	27.01±11.7*	28.0±5.40**	34.07±14.5*	-15.99±8.30*	-94.56±9.97**	-36.09±11.55*	-9.11±3.52*	-10.27±3. 03**	-1.65±5.83
Joint scaling test												
m	39.26±0.47**	6.68±2.49**	50.47±1.18**	39.98±1.07**	45.53±0.83**	41.86±2.44**	71.94±1.38**	47.68±2.11**	53.19±2.29**	22.20±0.70**	15.12±0 .68**	17.75±1.27**
[d]	18.51±0.49**	15.94±3.84**	24.38±1.55**	10.60±1.15**	9.73±0.88	7.16±2.84*	-29.33±1.58**	-4.39±2.85	-1.63±2.93	-11.09±0.83**	-4.42±0.98* *	-5.18±1.55
[h]	28.42± 1.42**	20.74± 7.88*	15.93± 3.39*	22.66± 3.12*	34.09±3.52	10.17±9.09	-25.63±3.58**	3.92±4.75	6.35±5.14	-15.98±1.88**	-4.56±1.65*	-1.36±2.91
X^2	29.4**	85.2**	14.73*	6.40*	29.0**	8.17*	133.5**	179.2**	37.5**	12.6*	26.58**	12.01*
Best fit model												
m	38.62±0.49**	-27.90±4.92**	52.30±1.28**	46.12±1.48**	54.88±2.29**	45.51±1.32**	79.69±1.54**	32.60±1.79**	45.69±2.12**	23.14±0.73**	12.87 ±0.34**	20.18±1.45**
[d]	18.23±0.49**	-	15.12±3.0**	9.24±1.28**	10.23±0.89**	10.76±3.19*	-24.77±1.63*	-19.67±3.08**	-8.42±3.18*	-11.13±0.83**	-5.67±1.01**	-7.25 ±1.66**
[h]	58.10±6.87**	207.2±29.9**	11.35±3.62*	-	-	-	-135.0±10.25**	-	-	-35.23±4.72**	-	-21.78±6.64**
[i]	-	60.94±6.20**	-11.8±3.26*	-7.82±1.96**	-11.1±1.00**	-8.72±3.46*	-	44.06±3.57**	19.73±3.82**	-	5.80±1.07**	-
[l]	-31.4±7.12**	-149.3±29.3**	-	13.87±3.67**	-		128.4±11.27**	53.98±5.84**	29.97±6.04**	30.41±6.84**	-	26.21±7.66**
X^2	9.89	4.70	1.69	0.66	1.44	1.81	3.71	0.85	0.15	6.71	4.84	0.08

*, **- Significant at p= 0.05 and p= 0.01 respectively; Cross 1= 104 B x IS 18551; Cross 2= 104 B x IS 2312; Cross 3= 104 B x RSE 03

Genetics of deadheart percentage: The deadheart percentage was found to be lower in resistant parents (P_2) and higher in the P_1. The F_1s had high mean values compared to the parents, indicating their susceptibility to shoot fly. F_2 and F_3 means were significantly different from the parents and were more than the mid-parent values. The mean values of F_1 and F_2 families for deadheart percentage tended towards the susceptible parent (P_1), indicating that resistance is governed by recessive genes, thus confirming earlier reports [18, 19]. Dominant genetic effects for deadheart percentage were positive and significant which also suggests dominance of susceptibility.

Presence of inter-allelic interactions in all the three crosses at both the locations was indicated by C and D scaling tests. The joint scaling test also indicated the inadequacy of additive-dominance model in all the cases for deadheart percentage. Digenic interactions were observed in all the cases and the predominant gene interactions were found to be varying between the two locations in each cross. This variation in the magnitude of gene effects would be due to high influence of environment the leaf were found to be different indicating the possible involvement of different set of genes for trichomes on upper and lower surfaces. The presence of dominance and epistasis for trichome density especially in IS 18551 and RSE 03 would tend to slow down the pace of progress in incorporation of the trait through early generation selection. It may be necessary to have a lenient selection pressure in early selfed generations, which has to be intensified on approaching homozygosity. The role of both additive and non-additive genes in the control of trichome density was reported earlier [5].

in the expression of this trait. High G x E interactions for deadheart percentage was reported earlier [20, 21]. The best fit model for deadheart percentage in IS 18551 indicated that [d] and [h] gene effects, and [i], [l] gene interactions were significant. The [h] and [l] gene effects possessed opposite signs indicating the presence of duplicate type of epistasis. In case of IS 2312, [d], [h] and [i] gene effects at Hyderabad, and [d], [i] and [l] effects at Solapur were significant. On the contrary, [d] gene effects and [i] interactions were important in the expression of deadheart percentage in RSE 03.

Both additive and non-additive gene actions were found to be important in the control of shoot fly resistance [22] in IS 18551 and IS 2312. Presence of dominance and [l] type of interactions delays the progress of selection for shoot fly resistance in these crosses. Presence of duplicate type of epistasis in IS 18551 makes the situation more complicated for improving the shoot fly resistance. Non-allelic interactions are known to either reduce or enhance the extent of heterosis depending on their direction and magnitude of action. Higher magnitude of dominance gene effects and [l] interactions could not be exploited for heterosis breeding due to presence of duplicate epistasis in the crosses as it minimizes the manifestation of heterosis [14]. In case of RSE 03, additive gene action was playing a predominant role in the expression of the trait. The negative estimates of [i] in the IS 2312 and RSE 03 suggested that additive loci contributed towards low deadheart percentage i.e., resistance to shoot fly, and hence the selection for resistance in the progenies of IS 2312 and RSE 03 will be easier.

Since the susceptible parent (104B) was common in all the three crosses, the observed differences in gene effects were due to the different genes in the three resistant parents used in the study. By carefully selecting the source of resistance, one could greatly improve the effectiveness of the breeding programme [24]. In general, inheritance was more complex in the cross involving IS18551 as parent (cross1). The greater amount of epistasis present in this cross, however, could be due to the nondirectional distribution of alleles in the two parents. The shoot fly resistance can be handled relatively easily in the cross involving RSE03 as a parent (cross3) because additive gene action was found to be predominant for the component traits like glossiness, seedling vigour, seedling height and deadheart percentage. Earlier study indicated that the line RSE03 was a good combiner for glossiness, deadheart percentage and trichome density, and it is genetically diverse from the shoot fly resistant germplasm lines, IS18551 and IS2312 [5]. Hence, this line may be utilized as gene source in breeding programmes aimed at stable and long lasting resistance to shoot fly.

Earlier studies showed that the genetic improvement for shoot fly resistance would be easier through indirect selection for component traits like glossiness, seedling vigour, seedling height and trichome density than through direct selection for resistance itself [4]. However, the presence of dominance and epistatic effects for most of the traits in all the crosses would slow down the progress of selection. Because neither the simple nor the epistatic dominance gene effects can be fixed in homozygous lines, it may be necessary for selection pressure to be lenient in early selfed generations and be intensified when homozygosity is approached. To develop an inbred line with increased resistance to shoot fly, bi-parental crossing between two F_2 derivatives and advancing to F_6 would be more effective and less time consuming than direct pedigree selection and /or back-cross methods. This is because bi-parental mating (crossing among desirable segregants) helps in accumulating the minor genes that may be distributed in different segregants and thus provides an opportunity in obtaining desirable selections. Further, this approach is likely to break some undesirable linkages, resulting in the establishment of rare, useful combinations.

The study thus revealed that the shoot fly resistance is under the control of both additive and non-additive genes and hence direct selection for resistance may not be effective. Presence of dominance and epistatic interactions for resistance and associated traits suggested that simple selection for these traits is difficult and these gene effects could be exploited by breeding methods like biparental mating followed by selections in segregating generations. Crossing between the resistant or moderately resistant lines endowed with different resistant mechanisms is likely to produce stable lines with desirable traits.

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