Gene Action for Resistance in Sorghum to Midge, *Contarinia sorghicola*

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ABSTRACT

Gene action for resistance to sorghum midge (*Contarinia sorghicola* Coq.) was studied in a diverse array of midge-resistant and midge-susceptible females and males under natural infestation and under uniform infestation with a no-choice headcage technique. Gene action for glume and grain characteristics associated with resistance to sorghum midge was also studied to understand their role in expression of resistance to this insect. Gene action for resistance to midge is largely governed by additive gene action. Genotype × environment interaction was significant for midge damage rating under natural infestation but nonsignificant under no-choice headcage screening. The GCA effects of midge-resistant cytoplasmic male-sterile (CMS) females (PM 7061 A and PM 7068 A) were significant and negative, and such effects for the midge-susceptible CMS females ICSA 42 and 296 A were positive. Similar results were observed for the males (except for CS 3541 and MR 750 for midge damage in one out of two seasons). Dominance (mid-parent heterosis) was also important for midge resistance in some cross combinations. For genotypic nonpreference by the midge females, the SCA effects were greater than the GCA effects. The SCA effects for genotypic nonpreference were negative for PM 7061 A. The GCA effects were significant and negative for glume length in PM 7061 B, glume hardness for 296 B, and glume hairiness for PM 7061 B. The GCA effects were significant and positive for glume length, glume hairiness, and glume hardness of ICSB 42. Resistance is needed in both the parents to produce midge-resistant hybrids.

SORGHUM [*Sorghum bicolor* (L.) Moench] is one of the most important crops in the semiarid tropics. It is damaged by several insect pests, of which sorghum midge (Diptera: Cecidomyiidae) is the most damaging pest worldwide (Harris, 1976). Host plant resistance is an effective means of controlling the midge populations, and considerable genetic variability exists in sorghum for resistance to this insect (Sharma et al., 1991). Resistance to sorghum midge has been transferred into agronomically adapted high-yielding cultivars (Wiseman et al., 1973; Johnson et al., 1973; Agrawal et al., 1987; Sharma et al., 1993).

Inheritance of resistance to midge in sorghum has been studied by Patil and Thombre (1982), Widstrom et al. (1984), Boozaya-Angoon et al. (1984), Henzell et al. (1986), and Agrawal et al. (1988) under natural infestation. Because of day-to-day fluctuation in midge populations, staggered flowering of sorghum genotypes, and the differences in the parental material used, different patterns have been reported for inheritance of resistance to sorghum midge.

Recent efforts in breeding for resistance to sorghum midge are largely focused on developing midge-resistant hybrids based on genetic cytoplasmic male-sterility (CMS). At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), resistance to sorghum midge has been transferred to two midge-resistant CMS females, PM 7061 A and PM 7068 A (Sharma et al., 1993). There is no information on the inheritance of midge resistance involving midge-resistant CMS females and midge-resistant and midge-susceptible restorers. Also, none of the earlier studies were based on a screening under uniform insect infestation. Since future breeding efforts will largely focus on high yielding midge-resistant hybrids, it is important to understand the mechanisms and inheritance of resistance involving CMS females. The objective of this study was to determine gene action in crosses involving two midge-resistant and two midge-susceptible CMS females with four midge-resistant and five midge-susceptible males selected at random from the restorer collection maintained at ICRISAT.

MATERIALS AND METHODS

Gene action for midge resistance was studied on two midge-resistant (PM 7061 A and PM 7068 A) and two midge-susceptible CMS females (296 A and ICSA 42). Sterility of all the CMS females was based on milo-cytoplasm. Four diverse midge-resistant (ICSV 745, PM 15908-3, PM 17422-3, and PM 17592-1) and five agronomically elite midge-susceptible (CS 3541, MR 750, MR 836, MR 844, and MR 923) genotypes were used as males. Four females were crossed with nine males in a line × tester mating design. Thirty-six F_1 hybrids and their parents were evaluated during the 1990 rainy season [June–October; 11- to 12-h daylength, 20–31°C, and 60–94% relative humidity (RH)] and 1991 post-rainy season (January–April; 10- to 11-h daylength, 16 to 37°C, and 23 to 92% RH) at ICRISAT Center, Andhra Pradesh, India.

Experimental Procedures and Observations

Seeds of the F_1 hybrids and parental females were produced during the 1990 post-rainy season. Hybrids and their parents were planted in the Alfisols (red laterite light sandy soils) in a 7 × 7 triple lattice design. The crop was planted on 10 July during the 1990 rainy season and on 1 Nov. and 5 Jan. during the 1991 post-rainy season. Each entry was planted in a two-row plot, 4 m long. Rows were spaced 75 cm apart, and the plants were spaced at 10 cm within a row. The seeds were drilled with carbofuran 3G (2,3-dihydro-2,3-dimethylbenzofuran-7-yl methylcarbamate; 1.2 kg a.i. per ha) to protect the seedlings against sorghum shoot fly (*Atherigona soccata* Rond.). No insecticide was applied during the reproductive phase of the crop. The crop was grown under rainfed conditions during the rainy season and under irrigation (furrow irrigation at 15-d intervals) during the post-rainy season.

Four infester rows of the early flowering midge-susceptible line IS 802 were planted after every 16 rows of the test material. The infester rows were inoculated with midge-infested chaffy

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Abbreviations: GCA, general combining ability; SCA, specific combining ability; CMS, cytoplasmic male-sterile; ICRISAT, International Crops Research Inst. for the Semi-Arid Tropics; RH, relative humidity; DR, damage rating; MD-C, midge damage under headcage; DR-C, damage rating under headcage; DR-N, damage rating under natural infestation. *,** Significant at the 0.05 and 0.01 probability levels, respectively.

panicles to augment natural midge populations for screening under natural infestation (Sharma et al., 1988a). To overcome the problem of day-to-day variation in midge populations and the differential flowering dates of sorghum genotypes, five panicles marked at random were screened under uniform insect pressure in each plot with the headcage technique (Sharma et al., 1988b). Each panicle was infested with 40 midges per panicle for two consecutive days at the half-anthesis stage.

Data were recorded on percentage midge damage at maturity in panicles infested under headcage (from a sample of 500 spikelets drawn at random from five panicles in each replication; Sharma et al., 1988b). Grain mass per 1000 grains, 100-grain volume, and grain yield were also recorded at maturity. Before recording the percentage midge damage, the infested panicles were also rated visually for midge damage on a 1 to 9 scale [1 = <10% spikelets with midge damage (sterile flowers because of midge damage) and 9 = >80% spikelets with midge damage]. Midge damage was also rated visually in panicles exposed to natural midge infestation. During the 1991 post-rainy season, midge damage was rated visually under natural infestation in the second planting only, because natural infestation in the first planting was very low. Data on grain yield were not recorded during the 1990 rainy season because of heavy shoot fly and head bug infestation.

Cultivar nonpreference by midge females towards different genotypes was assessed in terms of number of midges attracted to each genotype at the half-anthesis stage in the second planting during the 1991 post-rainy season. The number of midges per panicle were recorded on panicles selected at random between 0900 and 1000 for five consecutive days. The panicles were at the same stage of flowering.

Data were also recorded on glume length, glume hardness, and glume hairiness at panicle emergence. Glume length was measured under an ocular micrometer (Sharma et al., 1990). Glume hardness was rated on a 1 to 5 scale (1 = glumes tight and hard when pressed between the thumb and finger, 2 = glumes moderately tight and hard when pressed, 3 = glumes moderately soft, 4 = glumes soft and slightly collapse when pressed, and 5 = glumes highly soft and collapse when pressed). Glume hairiness was evaluated visually on a 1 to 5 scale (1 = glumes glabrous, smooth, and shining, 2 = glumes with some hairs on the margins and most of the glume surface smooth and shining, 3 = nearly 50% of the glume surface covered with hairs, 4 = nearly 75% glume surface covered with hairs, and 5 = glumes covered with long hairs and dull in appearance).

Statistical Analysis

Data for each season were analyzed separately. The combining ability analysis was done following Kempthorne (1957). The original data on percentage midge damage were transformed to Arcsin square root of percentage values before statistical analysis. Simple correlations were computed for glume and grain characteristics with midge damage under headcage screening and natural infestation for parental lines and hybrids. The sum of squares due to F_1 hybrids was partitioned into sum of squares due to females, males, and their interaction components, which was used to estimate the additive and nonadditive components of the variation. Also, the contribution of females, males, and their interactions towards total variability for each character was computed for assessing their relative importance.

The main effects of males and females are equivalent to general combining ability (GCA), and female interaction with a specific male is equivalent to specific combining ability (SCA; Hallauer and Miranda, 1981). Standard errors for GCA for females and males were calculated to test the significance of these effects.

Heterosis for susceptibility-resistance to midge in the F_1 hybrids was computed over mid-parent (MP) value for percentage midge damage and visual damage rating. Heterosis values were estimated for percentage damage and damage ratings (averaged across two seasons) under headcage screening for 36 crosses,

$$\text{Heterosis (\%)} = 100[(F_1 - MP)/MP]$$

where MP was the mid-parent value for midge damage for the respective cross.

RESULTS

Analysis of Variance

Midge Damage

B-lines of the midge-resistant females (PM 7061 B and PM 7068 B) were significantly less damaged than the B-lines of midge-susceptible females (ICSB 42 and 296 B). For midge-resistant females, midge damage under headcage (MD-C) ranged from 8.2 to 17.5%, and visual damage rating under headcage (DR-C) and damage rating under natural infestation (DR-N) ranged from 1.7 to 3.3. For the midge-susceptible females, the MD-C ranged from 59.0 to 82.4% and DR-C and DR-N from 6.0 to 9.0 (Table 1). Midge-resistant males ICSV 745, PM 17422-3, PM 15908-3, and PM 17592-1 suffered <16.5% damage and showed a damage rating (DR) <4.0 (except DR-C in PM 17422-3 and DR-N in PM 15908-3 during 1990). Midge-susceptible males CS 3541, MR 750, MR 836, MR 844, and MR 923 suffered >20% damage (except CS 3541 in 1991 and MR 750 in 1990) and showed a DR >5 (except DR-N for CS 3541 in 1991).

Differences in midge damage among parents, parents vs. crosses (except DR-C during the 1990 and MD-C and DR-N during the 1991 season), females, and males were significant ($P < 0.01$) under natural infestation and no-choice headcage screening (Table 2), indicating the presence of variability among hybrids and their parents for susceptibility to midge. Difference for females × males were significant only for DR-C during the 1991 post-rainy season. Estimates for variance were greater during the 1990–1991 post-rainy season than the 1990 rainy season for MD-C and DR-C (except for parents).

Cultivar Nonpreference

The PM 15908-3 genotype had significantly fewer midge flies (per five panicles) at the half-anthesis stage compared with ICSV 745 (Table 1). For genotypic preference by midge females (i.e., number of midges per five panicles at the half-anthesis stage), the variance components were significant for females, males, and parents vs. crosses (Table 2). However, the variance components for parents and females × males were not significant.

Table 1. Midge damage, genotypic nonpreference, and yield of four females and nine males of sorghum (ICRISAT Center, 1990–1991).

Genotype	1990 MD-C†	1991 MD-C	1990 DR-C‡	1991 DR-C	1990 DR-N§	1991 DR-N	1991 MF¶	1991 yield/10 panicles
	%		DR††					kg
Females								
PM 7061 B	17.5	8.2	3.2	1.8	3.3	1.7	7.7	0.354
PM 7068 B	13.8	12.3	2.0	2.3	3.3	2.0	9.3	0.349
ICSB 42	70.5	82.4	9.0	9.0	9.0	7.3	5.7	0.403
296 B	61.9	59.5	6.0	8.8	7.5	7.0	10.0	0.633
Males								
ICSV 745	8.7	9.0	2.7	4.1	3.7	2.0	10.3	0.551
PM 15908-3	12.7	15.9	4.0	2.0	4.3	2.0	4.3	0.535
PM 17422-3	16.5	10.2	5.3	1.8	4.0	2.0	7.0	0.647
PM 17592-1	14.1	14.9	4.3	3.1	4.0	2.0	6.7	0.627
CS 3541	21.8	18.7	5.5	5.1	4.0	3.0	9.7	0.588
MR 750	15.1	32.7	6.5	7.3	6.3	4.3	8.7	0.494
MR 836	20.3	36.9	5.0	8.7	4.7	3.7	6.7	0.347
MR 844	46.2	52.1	8.5	9.0	6.5	5.0	8.7	0.357
MR 923	23.6	67.0	8.0	9.0	7.3	3.7	6.3	0.389
LSD (0.05)	24.6	16.3	2.8	2.0	2.4	1.9	5.2	0.188
CV, %	58.3	34.3	23.9	21.1	25.8	34.2	33.0	20.3

† MD-C = midge damage under headcage.
‡ DR-C = damage rating (1 = <10% midge damage and 9 = >80% midge damage) under headcage.
§ DR-N = damage rating under natural infestation.
¶ MF = number of midge flies per five panicles (showing genotypic nonpreference).
†† DR = damage rating.

Grain Yield

Grain yield of 296 B was higher than that of ICSB 42, PM 7068 B, and PM 7061 B (Table 1). The males ICSV 745, PM 15908-3, PM 17422-3, and PM 17592-1 yielded more than MR 750, MR 836, MR 844, and MR 923 under midge infestation. Parents, females, males, parents vs. crosses, and females × males differed significantly for grain yield (Table 2).

Genotype × Environment Interaction

The mean squares for percentage midge damage were significant for genotypes [1404**, degrees of freedom (df) = 48], environments (4304**, df = 1), and genotype × environment (231*, df = 48). The mean squares for midge damage rating under no-choice headcage screening were significant for genotype (27*, df = 48), and genotype × environment (6*, df = 48), but nonsignificant for environment (0.1, df = 1). Under natural infestation, the mean squares were significant for genotype (13*, df = 48), environment (456*, df = 1), and genotype × environment (3*, df = 48). Genotype × environment interactions were significant for midge damage under headcage screening and natural infestation. Studies on inheritance of resistance to midge should be based on uniform insect infestation to draw the right conclusions.

General Combining Ability

Midge Damage

General combining ability effects of midge-resistant females (PM 7061 A and PM 7068 A) were significant and negative ($P < 0.01$) for midge susceptibility (except for DR-N during the 1990 rainy season; Table 3), while those of the susceptible females (ICSA 42 and 296 A) were positive (except for percentage midge damage during the 1990 rainy season). Thus, midge-resistant females contributed towards the production of midge-resistant hybrids while hybrids based on midge-susceptible females were highly susceptible to sorghum midge.

General combining ability effects for the males were significant and negative for ICSV 745, PM 15908-3 (except for MD-C during the 1990 rainy season), and PM 17422-3. Genotypes CS 3541, MR 750, MR 836, MR 844, and MR 923 showed positive GCA effects for midge susceptibility (except CS 3541 for MD-C and MR

Table 2. Mean squares for eight parameters in sorghum for midge resistance (ICRISAT Center, 1990–1991).

Source of variation	df	1990 MD-C†	1991 MD-C	1990 DR-C‡	1991 DR-C	1990 DR-N§	1991 DR-N	1991 MF¶	1991 yield/10 panicles
Parents	12	795.65*	1907.8**	9.59**	29.50**	10.48**	11.20**	10.13	0.43**
Parents vs. crosses	1	794.4**	325.7	7.46	6.29	28.69**	0.07	246.77**	0.452**
Males	3	1403.2**	5628.3**	32.64**	148.68**	28.89**	28.95**	53.90*	0.073
Females	8	442.3**	1536.0**	26.37**	25.02**	13.31**	7.59**	35.58*	0.127*
Males × females	24	113.6	162.9	1.87	3.23**	1.81	1.97	14.53	0.036**
Error	96	159.4	104.5	1.95	1.52	1.95	1.41	10.73	0.014

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
† MD-C = midge damage (%) under headcage.
‡ DR-C = damage rating (1 = <10% midge damage and 9 = >80% midge damage) under headcage.
§ DR-N = damage rating under natural infestation.
¶ MF = number of midge flies per five panicles.

Table 3. General combining ability effects of the females and males for eight parameters in sorghum for midge resistance (ICRISAT Center, 1990–1991).

Genotype	1990 MD-C†	1991 MD-C	1990 DR-C‡	1991 DR-C	1990 DR-N§	1991 DR-N	1991 MF¶	1991 yield/10 panicles
Females								
PM7061 B	−3.82	−13.04**	−0.87**	−2.42**	−0.45	−1.06**	−1.67**	−0.02
PM 7068 B	−6.98*	−11.94**	−1.42**	−1.58**	−1.23**	−0.72**	0.85	−0.06*
ICSB 42	12.89**	12.99**	1.32**	2.44**	1.03**	0.91**	−0.63	0.06*
296 B	−2.09	11.99**	0.96**	1.56**	0.66*	0.87**	1.45*	0.02
LSD (0.05)	7.817	5.502	0.920	0.666	0.752	0.641	1.762	0.036
Males								
ICSV 745	−7.98	−10.39**	−1.89**	−0.94*	−1.15**	−0.71*	−2.29*	−0.01
PM 15908-3	−3.76	−3.59	−2.26**	−0.99**	−1.82**	−0.88*	−1.54	0.17
PM 17422-3	−10.84*	−16.73**	−2.19**	−2.46**	−0.82*	−1.29**	−1.95*	0.02
PM 17592-1	−6.33	−2.49	−0.82	−0.26	0.02	−0.05	−0.70	0.03
CS 3541	3.83	−2.72	0.49	0.51	0.52	0.87*	1.29	−0.06
MR 750	1.62	−4.68	1.58**	−0.77*	0.69	0.45	0.79	−0.06
MR 836	7.86	17.09**	2.24**	1.59**	1.10**	0.79*	0.43	−0.13**
MR 844	9.66*	14.88**	1.87**	1.92**	1.27	0.70*	1.79	−0.02
MR 923	6.11	8.63**	0.99*	1.39**	0.19	0.12	−2.43*	−0.08*
LSD (0.05)	12.483	8.254	1.379	1.001	1.127	0.956	2.643	0.053

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
† MD-C = midge damage (%) under headcage.
‡ DR-C = damage rating (1 = <10% midge damage and 9 = >80% midge damage) under headcage.
§ DR-N = damage rating under natural infestation.
¶ MF = number of midge flies per five panicles.

750 for MD-C and DR-C during 1991). The GCA effects for CS 3541 were not significant (except for DR-N during 1991). These results indicate that additive gene action predominantly influences the expression of resistance to sorghum midge in F_1 hybrids.

Cultivar Nonpreference

The PM 7061 A genotype contributed towards nonpreference, while 296 A contributed significantly towards preference by the midge females (Table 2). Genotypes ICSV 745, PM 15908-3, PM 17422-3, and PM 17592-1 showed negative GCA effects for genotypic preference by midge females. Genotypes CS 3541, MR 750, MR 836, and MR 844 contributed towards preference by the midge females. The MR 923 genotype showed significant and negative GCA effects for cultivar preference.

Grain Yield

Midge-resistant males showed positive GCA effects for grain yield (except ICSV 745), while the midge-susceptible males showed negative GCA effects, indicating that midge-resistant males resulted in an increase in grain yield because of positive GCA effects for midge resistance (Table 3).

Specific Combining Ability

The SCA effects were not significant except for 296 A × CS 3541 for DR-N and grain yield during the 1990–1991 post-rainy season. The two midge-resistant females behaved differently in the pattern of SCA effects for genotypic nonpreference by the midge females. The SCA effects were negative for PM 7061 A × midge-resistant males (except with PM 17592-1) and positive for midge-susceptible males (except for MR 844). The reverse was true for PM 7068 A (except with CS 3541 and MR 844).

Heterosis Over Mid-Parent

Mid-parent heterosis for midge damage varied from 30 to −37% for PM 7061 B with a mean of −12% and from −27 to 44% for damage rating with a mean of 22% (Table 4). Mid-parent heterosis for hybrids based on PM 7068 B was −21 to 6% for midge damage and damage rating, respectively. For midge damage, the

Table 4. Mid-parent heterosis (%) averaged across two seasons for midge damage (MD) and damage rating (DR).

Genotype	PM 7061 A		PM 7068 A		ICSA 42		296 A	
	MD	DR†	MD	DR	MD	DR	MD	DR
	%		%		%		%	
ICSV 745	17	9	−7	−11	−32	7	−36	13
PM 15908-3	−14	−27	−43	6	21	24	−19	5
PM 17422-3	−37	25	−53	−5	−41	−8	−58	−29
PM 17592-1	−32	30	−5	−19	−9	24	−9	34
CS 3541	−18	−3	−16	24	36	26	−24	35
MR 750	−3	26	−19	−21	1	4	−38	10
MR 836	30	44	1	55	43	10	16	26
MR 844	−15	38	39	16	6	−1	1	10
MR 923	−32	2	−6	9	9	0	−38	2
Mean	−12	22	−21	6	4	10	−23	12

† Damage rating (1 = <10% midge damage and 9 = >80% midge damage).

mid-parent heterosis was −23% for hybrids based on 296 B, a midge-susceptible female. Genotypes PM 7061 A × PM 17422-3, PM 7061 A × PM 17592-1, and PM 7061 A × MR 923 showed >32% heterosis for midge susceptibility based on midge damage. Genotypes PM 7068 A × PM 15908-3, PM 7068 A × PM 17422-3, ICSA 42 × ICSV 745, ICSA 42 × PM 17422-3, 296 A × ICSV 745, 296 A × PM 17422-3, 296 A × MR 750, and 296 A × MR 923 showed negative heterosis for susceptibility to sorghum midge indicating that dominance type of expression is important for midge resistance in some hybrid combinations (Table 4).

Gene Action for Glume and Grain Characteristics

There was considerable variability for glume length between the females (1.4–3.6 mm) and males (2.3–3.6 mm; Table 5). The midge-resistant females and the males in general had smaller glumes than the susceptible ones (except PM 17422-3). Similar variability was also recorded for glume hardness (1.7–3.7), glume hairiness (1.9–4.1), 1000-grain weight (17.7–29.3 g), and volume [1.4–2.1 cm^3 (per 100 grains)].

Percentage midge damage was significantly correlated with glume length (r = 0.28**), grain weight (r = 0.40**), and grain volume (r = 0.40**). The correlation coefficients with glume hardness and glume hairiness were nonsignficant (r = 0.10). Midge damage rating under no-choice headcage screening was significantly correlated with glume length (r = 0.41**), grain weight (r = 0.60**), and grain volume (r = 0.59**). The correlations were positive but nonsignificant with glume hardness and hairiness (r = 0.15).

Mean squares were significant for glume length (except for parents vs. crosses), glume hardness for parents and females, and for grain weight and volume (Table 6). The GCA effects were significant and negative for the midge-resistant females for glume and grain characteristics (except for glume hardness and hairiness for PM 7068 A; Table 7). The GCA effects for ICSV 745 were significant for grain weight and volume. Genotypes PM 15908-3 and PM 17422-3 showed negative GCA effects (except PM 17422-3 for glume characteristics). Genotype PM 17592-1 showed positive GCA effects (except for seed volume), as did CS 3541 and MR 844 (except for glume hairiness for MR 844 and 1000-grain weight for CS 3541).

Significant SCA effects were observed for seed volume in PM 7068 A × PM 17422-3 and for glume hairiness in PM 7068 A × PM 15908-3, PM 7068 A × PM 17422-3, PM 7068 A × CS 3541, PM 7068 A × MR 750, PM 7068 A × MR 923, 296 A × PM 15908-3, 296 A × CS 3541, and 296 A × MR 923.

Table 5. Glume and grain characteristics of nine males and four females of sorghum (ICRISAT Center, 1990–1991).

Genotype	Glume length	Glume hardness†	Glume hairiness‡	1000 grain weight	Seed volume/100 grains
	mm			g	cm^3
Females					
PM 7061 B	1.4	2.2	2.1	19.6	1.5
PM 7068 B	2.1	2.7	2.6	20.7	1.7
ICSB 42	2.9	2.7	3.1	21.6	1.9
296 B	3.6	3.9	3.6	20.2	1.7
Males					
ICSV 745	2.3	2.3	3.3	28.6	2.1
PM 15908-3	2.2	1.7	2.3	17.7	1.4
PM 17422-3	3.4	3.7	4.1	20.2	1.6
PM 17592-1	2.7	2.7	2.0	22.9	2.0
CS 3541	3.1	2.8	1.9	21.8	1.8
MR 750	3.3	2.5	2.3	25.0	2.0
MR 836	3.0	1.7	1.3	29.3	2.2
MR 844	3.1	3.7	3.6	22.5	1.8
MR 923	3.6	3.2	3.1	24.5	1.8
LSD (0.05)	0.8	1.1	1.1	2.5	0.3
CV, %	16.4	20.1	23.4	6.6	10.0

† Glume hardness (1 = glume tight and hard and 5 = glume soft).
‡ Glume hairiness (1 = glume nonhairy and shining and 5 = glume covered with long hairs).

Table 6. Mean squares for five characters in sorghum associated with resistance to sorghum midge (ICRISAT Center, 1990–1991).

Source of variation	df	Glume length	Glume hardness†	Glume hairiness‡	1000 grain weight	Seed volume/100 grains
		mm			g	cm^3
Parents	12	1.34**	1.58**	2.04**	35.15**	0.17**
Parents vs. crosses	1	0.06	0.75	0.33	94.33**	0.54**
Females	3	2.13**	3.94**	3.75**	161.78**	1.17**
Males	8	0.59**	0.43	0.91	31.96**	0.27**
Females × males	24	0.23	0.54	0.69	4.18*	0.03
Error	96	0.21	0.55	0.44	2.51	0.02

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
† Glume hardness (1 = glume tight and hard and 5 = glume soft).
‡ Glume hairiness (1 = glume nonhairy and shiny and 5 = glume covered with long hairs).

Table 7. General combining ability effects of the females and males for five characters associated with resistance to sorghum midge (ICRISAT Center, 1990–1991).

Genotype	Glume length	Glume hardness†	Glume hairiness‡	1000 grain weight	Seed volume/100 grain
	mm			g	cm^3
Females					
PM 7061 B	−0.18*	−0.24	−0.35**	−1.58**	−0.15**
PM 7068 B	−0.09	0.25	0.03	−2.58**	−0.27**
ICSB 42	0.42**	0.39**	0.51**	2.39**	0.19**
296 B	−0.14	−0.40**	−0.18	1.76**	0.17**
LSD (0.05)	0.25	0.39	0.36	0.84	0.11
Males					
ICSV 745	0.13	−0.01	−0.01	1.88**	0.18**
PM 15908-3	−0.44**	−0.25	−0.06	−2.36**	−0.17**
PM 17422-3	−0.20	0.08	0.03	−2.12**	−0.24**
PM 17592-1	0.13	0.08	0.16	0.52	−0.01
CS 3541	0.09	0.28	0.59**	−0.44	0.04
MR 750	−0.13	−0.21	−0.19	−0.64	−0.07
MR 836	0.13	−0.17	−0.43*	1.88**	0.17**
MR 844	0.29*	0.25	−0.02	1.75**	0.14**
MR 923	−0.01	−0.04	−0.07	−0.47	−0.05
LSD (0.05)	0.36	0.59	0.53	1.29	0.17

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
† Glume hardness (1 = glume tight and hard and 5 = glume soft).
‡ Glume hairiness (1 = glume nonhairy and shiny and 5 = glume covered with long hairs).

DISCUSSION

There was considerable variability among the parents in susceptibility to midge. The variance components for females, males, parents, parents vs. crosses, and females × males were significant. However, the proportional contribution of variance components differed significantly across seasons and between natural infestation and headcage screening. The seasonal differences may be because of the variation in midge populations, and the environmental influences on the expression of resistance to sorghum midge (Sharma et al., 1988a,b). The differences in variance components between natural and headcage screening exist largely because of variation in midge infestation on different genotypes, and the elimination of nonpreference component of resistance under no-choice screening under headcage (Sharma et al., 1988b). Thus, it is important to study the inheritance of resistance to insects under uniform insect pressure. The observed differences in the proportional contribution of various components across seasons and between natural and cage screening may also explain different patterns of gene action reported by different researchers in the past.

Heritability of midge resistance is fairly high (Agrawal et al., 1988). Resistance is controlled by different numbers of genes in different genotypes (Deokar and Cruz, 1962; Rossetto and Igue, 1983; Johnson, 1974; Boozaya-Angoon et al., 1984). The GCA effects were significant and negative for midge susceptibility for the midge-resistant females and males. Thus, both the parents contribute towards midge resistance in F_1 hybrids. A good correspondence was observed between resistant parents and their GCA effects for susceptibility to midge. The SCA effects for midge susceptibility were nonsignificant, although there were definite trends in the nature of gene action for different females and males.

Cultivar nonpreference is one of the components of resistance to midge in germplasm accessions and CMS females (Sharma et al., 1988b). Variance components and GCA effects were also significant for the nonpreference component of resistance, and hence, this component of resistance can be combined with other factors associated with resistance to sorghum midge.

Some of the variance components for glume and grain characteristics were significant for parents, parents vs. crosses, females, males, and females × males. Glume and grain characteristics showed significant and negative GCA effects for midge-resistant females (except for glume hardness and hairiness for PM 7068 B). These differences in the nature of gene action for glume and grain characteristics between PM 7068 B and PM 7061 B may account for the differences in GCA and SCA effects observed for midge damage and cultivar nonpreference for these genotypes. Short and tight glumes and faster rate of grain development are associated with resistance to midge in sorghum and can be used as a criterion to select for resistance to this insect (Sharma et al., 1990, 1991). The present studies indicated that glume length and grain weight and volume were associated with resistance to sorghum midge, and their GCA effects were significant in crosses involving midge-resistant and midge-susceptible males and females.

Johnson (1977) observed that resistant × susceptible hybrids are less damaged than susceptible × susceptible hybrids, and the dominance nature of resistance has been reported by Faris et al. (1976), Agrawal et al. (1988), and Widstrom et al. (1984). Both additive (Patil and Thombre, 1982) and dominance genetic effects are important for midge resistance. Additive × additive genetic effects are less important compared with other types of interactions (Agrawal et al., 1988). Dominance is important in expression of resistance to sorghum midge in some cross combinations.

The present studies conducted under uniform midge infestation clearly indicated that resistance to sorghum midge is controlled by additive gene action. Dominance (MP heterosis) is also important in some cross combinations. When both the parents were resistant to sorghum midge, the resulting hybrids showed high levels of resistance. Some of the hybrids based on midge-resistant females were moderately susceptible, but all the hybrids based on midge-susceptible females were highly susceptible. Thus, it is important to transfer midge resistance into both the parents (CMS lines and pollinators) to develop midge-resistant hybrids.

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