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Compensation in grain weight and volume in sorghum is associated with expression of resistance to sorghum midge, *Stenodiplosis sorghicola*

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Summary

Sorghum midge, *Stenodiplosis sorghicola* (Coquillett) is one of the most important pests of grain sorghum worldwide. We studied the inheritance of resistance to sorghum midge and compensation in grain weight and volume in panicles of sorghum hybrids and their parents under uniform infestation (40 midges per panicle for two consecutive days). Sorghum midge damage ranged from 8.2 to 82.4% in the maintainer lines (B-lines) of the females parents (A-lines), and 9.0 to 67% in the male parents (restorer lines). Hybrids involving resistant × resistant parents were highly resistant, while those involving resistant × susceptible and susceptible × resistant parents showed moderate susceptibility. Susceptible × susceptible hybrids were susceptible. Compensation in (percentage increase) grain weight and volume in midge-infested panicles of midge-resistant parents and their F_1 hybrids was greater than in midge-susceptible parents and hybrids. General combining ability effects for midge damage, and grain weight and volume were significant and negative for the midge-resistant females (ICSA 88019 and ICSA 88020), whereas those for the midge-susceptible females (ICSA 42 and 296 A) were significant and positive. However, the reverse was true in case of compensation in grain weight and volume. Inheritance of compensation in grain weight and volume and resistance to sorghum midge is controlled by quantitative gene action with some cytoplasmic effects. Resistance is needed in both parents to realize full potential of midge-resistant hybrids.

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is an important cereal crop in the semi-arid tropics. It is damaged by over 150 insect species at different stages of crop growth, of which sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Diptera: Cecidomyiidae) is the most destructive pest worldwide (Harris, 1976). Host plant resistance is one of the most effective and economic means of controlling sorghum midge (Sharma, 1993), and considerable progress has been made in screening and breeding for resistance to this insect (Johnson et al., 1973; Wiseman et al., 1973, 1988; Peterson et al., 1988; Sharma et al., 1993a). Resistance to sorghum midge has also been transferred into male-sterile lines based on the milo-cytoplasmic male-sterility system (Sharma et al., 1993a; Agrawal et al., 1996), providing new opportunities to develop midge-resistant hybrids, and exploit heterosis to increase the productivity potential of this crop.

Resistance to sorghum midge is controlled by quantitative gene action, and some cytoplasmic effects (Widstrom et al., 1984; Agrawal et al., 1988; Sharma et al., 1994, 1996). Susceptibility to sorghum midge is completely or incompletely dominant in some parents (Boozaya-Angoon et al., 1984; Rossetto & Igue, 1983). Both general and specific combining ability of the parents is important (Patil & Thombre, 1985). Resistance is needed in both parents to produce midge-resistant hybrids (Sharma et al., 1996). Antixenosis for oviposition (Franzmann, 1993; Rosetto et al., 1984; Sharma et al., 1990; Waquil et al., 1986a) and to visiting adults (Sharma & Vidyasagar, 1994; Waquil et al., 1986b), and antibiosis (Sharma et al., 1993b; Waquilet al., 1986b) are the major components of resistance to sorghum midge. Manual removal of spikelets from up to one-third of the sorghum panicle at the half-anthesis stage does not result in a significant reduction in grain yield (Henzell & Gillieron, 1973). However, Harris (1961) found no correlation between percentage sorghum midge damage and weight of surviving kernels. Montoya (1965) reported slight compensation in grain weight due to damage by the sorghum midge. However, Hallman et al. (1984) observed a significant inverse relationship between sorghum midge damage and weight of surviving kernels in two of three susceptible hybrids, and three of seven midge-resistant hybrids that were evaluated. Franzmann & Butler (1993) and Waquil & Teetes (1990) did not observe any differences in grain weight between resistant and susceptible genotypes following midge damage. Keeping these interactions in mind, we studied the compensation in grain weight and volume of midge-resistant and midge-susceptible hybrids and their parents in sorghum panicles infested with sorghum midge under no choice headcage conditions.

Material and methods

The studies were conducted during the 1990/91 post-rainy season at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India. The crop was raised under irrigated conditions during the post-rainy season on Alfisols (shallow red-laterite soils). The expression of resistance to sorghum midge and compensation in grain weight was studied on two midge-resistant (ICSA 88019 and ICSA 88020) (Agrawal et al., 1996) and two midge-susceptible commercial male-sterile lines (296 A and ICSA 42). Nine genotypes selected at random (ICSV 745; PM 15908-3, PM 17422-3, PM 175921, CS 3541, MR 750, MR 836, MR 844, and MR 923) were used as male parents (restorer lines) to produce the F_1 hybrids in combination with all the four male-sterile lines. Thirty-six hybrids and their parents were planted in a 7×7 triple lattice design during the 1990/91 post-rainy season. The rows were spaced 75 cm apart, and each entry planted in a 2-row plot, 4 m long. Plants were thinned to a spacing of 10 cm within the row 15 days after germination. The seeds were planted with a 4-cone planter with carbofuran 3G (@ 1.2 kg ai per ha) to control sorghum shoot fly, *Atherigona soccata* Rondani, at the seedling stage. No insecticide was applied during the reproductive phase of the crop.

At flowering, six random panicles were tagged in each plot and covered with muslin cloth bags to prevent natural midge infestation. Three of these panicles were infested with sorghum midge, while the other three panicles were left as un-infested controls. The former were covered with a wire-framed cage at 50% flowering, and infested with 40 sorghum midge females for two consecutive days (Sharma et al., 1988). Because the midge females only lay eggs in spikelets at the flowering stage, the spikelets which had flowered the previous day at the tip of the panicle, and those at the bottom of the panicle which may not flower even the next day were removed with scissors, thus retaining nearly 70% of the spikelets at the mid-portion of the panicle for infestation with sorghum midge females. Since sorghum midge females die after oviposition (4 to 6 h after emergence), the panicles were infested for two consecutive days to ensure that all the spikelets were exposed to midge females at the flowering stage for oviposition. The cages were removed after 15 days, and the midge-infested panicles were covered with muslin cloth bags. At maturity, data were recorded on percentage midge damage in a sample of 250 random spikelets taken from infested panicles. After recording data on midge damage, the infested and non-infested panicles were threshed separately for each replication. The grain was equilibrated for moisture content at 35 °C for 24 h, and data were recorded on 1,000 grain weight and 100 grain volume. Grain volume was recorded by a placing a 100 grain sample in a 25 ml measuring cylinder containing 10 ml of ethanol. The level of ethanol in the measuring cylinder over the 10 ml mark was taken as the 100 grain volume. Compensation in grain weight and volume in panicles infested with sorghum midge was calculated as follows:

Compensation in grain weight/volume =

$$\frac{\begin{array}{c}\text{Wt/volume of grains in}\\ \text{the infested panicles}\end{array} - \begin{array}{c}\text{Wt/volume of grains in}\\ \text{the uninfested panicles}\end{array}}{\text{Wt/volume of grains on the uninfested panicles}} \times 100$$

Statistical analysis

Data on percentage midge damage, and grain weight and volume were subjected to analysis of variance. Significance of differences between the treatment means was judged by the F-test, and the treatment means were compared using least significant difference (LSD) at $p = 0.05$. Compensation in grain weight and volume in the F_1 hybrids and their parents was analyzed in relation to sorghum midge damage. The combining ability analysis was carried out according to Kempthorne (1957). The sum of squares due to F_1 hybrids was partitioned into sum of squares due to females, males, and interaction components, which were used to estimate additive and nonadditive components of the variation. The contribution of females, males, and interactions towards total variability for each character was computed for assessing their relative importance. The main effects of the females and males are equal to general combining ability (GCA), and female parent interaction with a specific male parent is equivalent to specific combining ability (SCA) (Hallauer & Miranda, 1981). Standard errors of GCA for females and males were calculated to test the significance of these effects. Heterosis was computed over the lower or higher parent to gain an understanding of the nature of gene action for resistance to sorghum midge, grain weight and volume, and compensation in grain weight and volume in panicles infested with sorghum midge.

Results

Midge damage

The maintainer lines (B-lines) of the female parents ICSB 88019 and ICSB 88020 were resistant to sorghum midge (8.2 to 12.3% midge damage compared to 59.5 to 82.4% midge damage in 296 B and ICSB 42) (Table 1). Among the male parents; ICSV 745, PM 15908-3, PM 17422-3, PM 17592-1, and CS 3541 were resistant (R) to sorghum midge, and suffered 9.0 to 18.7% midge damage. The differences in sorghum midge damage between these genotypes were not significant. MR 750, MR 836 and MR 844 showed a susceptible reaction (S) (25.1 to 36.9% midge damage). MR 923 suffered significantly greater midge damage (67%) than the other genotypes tested, but was grouped along with the other three susceptible genotypes for purposes of comparison.

Sorghum midge damage in resistant x resistant hybrids ranged from 5.7 to 18.8%, while those involving resistant x susceptible parents suffered 13.1 to 33.3% midge damage. The susceptible × resistant hybrids suffered 16.6 to 42.6% midge damage, and susceptible × susceptible hybrids referred 33.7 to 68.3% midge damage. Sorghum midge damage in the hybrids involving midge-resistant male parents ranged from 12.2 to 26.5%, and that for the midge-susceptible male parents ranged from 24.3 to 46.0%. Sorghum midge damage in hybrids involving ICSA 88019 was 15.9%, followed by those involving ICSA 88020 (17.0%), 296 A (40.9%), and ICSA 42 (41.9%). The female parents showed a greater effect on the expression of resistance to sorghum midge than the male parents, i.e., the hybrids involving midge-resistant females in combination with midge-susceptible male parents showed greater resistance to midge than the hybrids involving midge-susceptible female parents in combination with midge-resistant male parents.

Grain weight

Grain weight per 1,000 grains in the midge-infested panicles ranged from 22.7 g in PM 17422-3 to 34.6 g in ICSV 745 among the male parents (Table 2). Among the maintainer lines of the female parents, the grain weight varied from 20.1 g in 296 B to 23.8 g in ICSB 88020. Compensation in grain weight in the midge infested panicles over the non-infested panicles was 26.9% for the hybrids based on ICSA 88019, followed by 21.6% for those based on ICSA 88020, 14.5% on 296 A and 12.1% on ICSA 42 (Table 3). Midge-resistant male parents (ICSV 745, PM 15908-3, PM 17422-3, PM 17592-1, and CS 3541) showed an average of 27.4% increase in grain weight in comparison to 5.4% increase in the grain weight in the susceptible male parents (MR 750, MR 836, MR 844, and MR 923) (Figure 1). Compensation in grain weight was 20.5% in ICSB 88019, 20.1% in ICSB 88020, 2.9% in ICSB 42, and 0.3% in 296 B (Figure 2). Hybrids based on ICSA 88019 and ICSA 88020, the midge-resistant male parents, showed 28.7 and 26.3% increase in grain weight, respectively, compared to an 18.4% increase for the hybrids based on ICSA 42 and 21.1% increase for 296 A. Hybrids involving resistant × susceptible parents showed moderate levels of compensation in grain weight (24.6% on ICSA 88019 and 15.7% on ICSA 88020). Hybrids involving susceptible parents showed poor compensation in grain weight (6.3 to 8.9%). Thus, midge-resistance influences the genotypic ability to compensate for loss in grain weight because of midge damage or physical removal of spikelets from the sorghum panicles. In the non-infested panicles, the grain weight ranged from 17.7 to 29.3 g per 1,000 grains among the male parents, and 19.7 to 21.5 g among the maintainer lines of the female parents. Grain weights of the infested

Table 1. Percentage midge damage in F_1 hybrids and their parents infested with 40 sorghum midge females under headcage (ICRISAT Centre, 1990/91 postrainy season)

Genotypes	Midge damage (%)					
	Males	Hybrids in combination with females				
		ICSA 88019	ICSA 88020	ICSA 42	296 A	Mean
ICSV 745	9.0	12.60	10.37	24.30	26.93	18.55
PM 15908-3	15.9	14.40	7.83	32.90	46.23	25.34
PM 17422-3	10.2	5.73	6.13	20.33	16.63	12.21
PM 17592-1	14.9	8.30	11.43	42.03	44.03	26.45
CS 3541	18.7	13.47	18.80	43.67	28.93	26.22
MR 750	32.7	13.63	13.07	36.60	33.73	24.26
MR 836	36.9	24.63	25.20	68.30	65.67	46.03
MR 844	25.1	29.40	27.00	52.43	66.43	43.82
MR 923	67.0	20.87	33.13	56.50	39.77	37.57
Maintainer lines of female parents	–	8.20	12.30	82.40	59.50	–
Mean	28.6	15.89	17.00	41.93	40.93	28.94
SE	±5.90					
LSD at 0.5% t	15.89					

Table 2. Grain weight and grain volume in midge-infested and non-infested panicles of nine male parents and four maintainer lines of female parents of sorghum (ICRISAT Centre, 1990/91 postrainy season)

Genotypes	1,000 grain weight (g)		100 grain volume (cc)	
	Midge-infested panicles[a]	Non-infested panicles	Midge-infested panicles	Non-infested panicles
Males				
ICSV 745	34.6	28.6	2.77	2.10
PM 15908-3	24.4	17.7	2.13	1.43
PM 17422-3	22.7	20.2	1.87	1.57
PM 17592-1	29.5	22.9	2.43	2.00
CS 3541	28.2	21.8	2.47	1.82
MR 750	28.8	25.0	2.43	2.00
MR 836	31.0	29.3	2.63	2.23
MR 844	22.7	22.3	2.20	1.83
MR 923	24.2	22.4	2.10	1.83
Maintainer lines of female parents				
ICSB 88019	22.6	19.7	2.03	1.52
ICSB 88020	23.8	20.5	2.10	1.67
296 B	20.1	20.2	2.13	1.67
ICSB 42	22.3	21.7	1.97	1.93
SE	±1.49	±0.92	±0.10	±0.11
LSD at 5% t	4.34	2.54	0.28	0.30

[a] Panicles infested with 40 midge females for two consecutive days.

Table 3. Compensation in grain weight of F_1 hybrids and their parents in panicles infested with sorghum midge under headcage conditions (ICRISAT Centre, 1990/91 postrainy season)

Genotypes	Compensation in 1,000 grain weight (%)					
	Males	Hybrids in combination with females				
		ICSA 88019	ICSA 88020	ICSA 42	296 A	Mean
ICSV 745	21.0	29.1	20.4	5.99	21.1	20.5
PM 15908-3	38.2	44.0	35.4	25.32	16.3	30.2
PM 17422-3	14.2	34.1	25.2	28.98	37.0	31.3
PM 17592-1	29.2	15.1	34.9	5.25	19.0	18.6
CS 3541	34.6	21.3	15.7	26.67	12.3	19.0
MR 750	15.3	21.0	11.0	18.42	3.5	13.5
MR 836	5.5	19.1	15.4	7.08	3.6	11.3
MR 844	1.5	25.3	20.6	5.05	6.2	14.3
MR 923	–0.7	33.0	15.9	5.06	11.8	16.6
Maintainer lines of female parents	–	20.5	20.1	2.9	0.3	–
Mean	16.48	26.9	21.6	12.1	14.5	18.79
SE ±	7.21					
LSD at 0.5% t	20.40					

Table 4. Compensation in grain volume of F_1 hybrids and their parents in panicles infested with sorghum midge under headcage conditions (ICRISAT Centre, 1990/91 postrainy season)

Genotypes	Compensation in 1,00 grain volume (%)					
	Males	Hybrids in combination with females				
		ICSA 88019	ICSA 88020	ICSA 42	296 A	Mean
ICSV 745	32.7	35.0	33.3	21.8	16.7	26.7
PM 15908-3	50.3	62.4	52.0	27.9	31.5	43.4
PM 17422-3	20.0	50.1	49.5	35.0	50.0	46.2
PM 17592-1	21.7	26.5	56.1	24.2	27.7	33.6
CS 3541	37.7	27.8	21.0	30.4	12.9	23.0
MR 750	21.7	38.1	25.7	29.1	40.1	33.2
MR 836	19.4	16.7	28.8	8.1	8.6	15.5
MR 844	21.1	41.5	36.7	5.6	15.0	24.7
MR 923	17.2	36.5	38.1	17.9	21.6	28.5
Maintainer lines of female parents	–	39.0	27.8	1.9	31.1	–
Mean	26.87	37.2	37.9	22.2	24.9	30.5
SE ±	9.6					
LSD at 0.5% t	26.53					

and non-infested panicles were statistically different at $p = 0.05$.

Grain volume

Grain volume per 100 grains of the male parents ranged from 1.43 - 2.10 cc, and that of the maintainer lines of the female parents from 1.52 to 1.93 cc in non-infested panicles (Table 2). In midge infested panicles, the average grain volume was 2.34 cc compared to 1.75 cc for the non-infested panicles. Compensation in grain volume in midge-infested panicles was 37.2, 37.9, 22.2, and 24.9% for the hybrids based on ICSA 88019, ICSA 88020, ICSA 42, and 296 A, respectively (Table 4). Compensation in grain volume in the midge-infested panicles was greater for hybrids involving

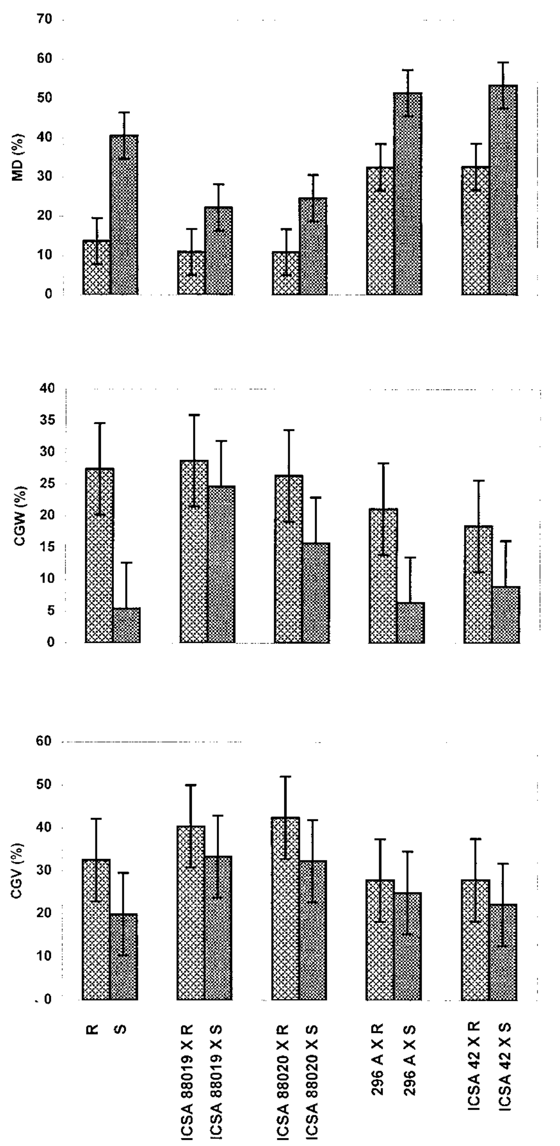

Figure 1. Sorghum midge damage (MD) and compensation grain weight (CGW) and volume (CGV) of sorghum hybrids based on four male-sterile lines in combination with midge-resistant (R) and midge-susceptible (S) male parents (ICRISAT Center, 1990/91 postrainy season).

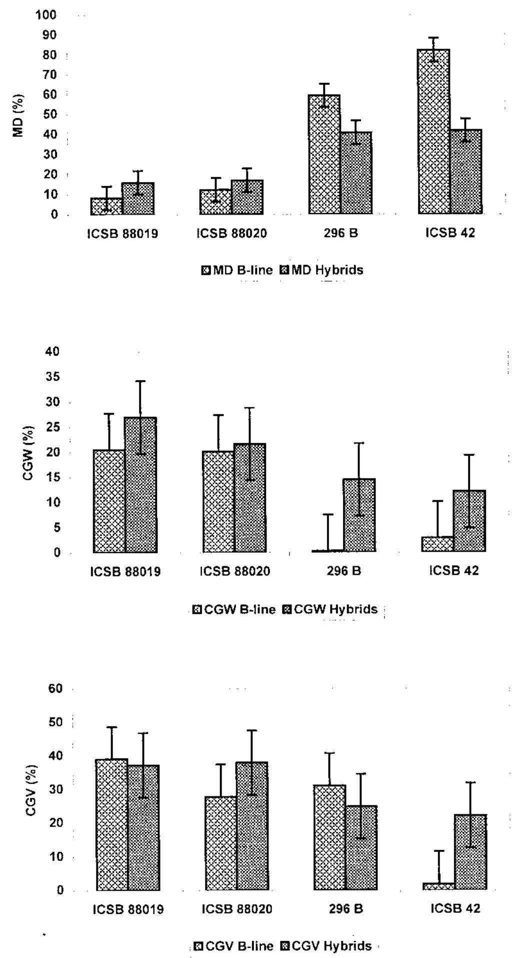

Figure 2. Sorghum midge damage and compensation grain weight (CGW) and volume (CGV) in four maintainer lines (B-lines of the male-sterile lines) and their hybrids (mean of hybrids in combination with nine males) (ICRISAT Center, 1990/91 postrainy season).

midge-resistant female parents than those involving midge-susceptible female parents (Figure 2). Hybrids involving midge-resistant male parents showed a 34.6% increase in grain volume compared to a 30.5% increase for those hybrids involving midge-susceptible male parents. Midge-resistant male parents showed a greater increase in grain volume (32.5%) than midge-susceptible male parents (19.9%) (Figure 1). Hybrids involving resistant ‘X’ resistant combinations showed 40.4 to 42.4% compensation in grain volume compared to 22.2 to 24.9% compensation in hybrids involving susceptible parents. Hybrids based on resistant × susceptible parents showed 27.8 to 33.3% increases in grain volume.

Association between sorghum midge damage and compensation in grain weight and volume

Susceptibility to sorghum midge was positively associated with grain weight (r = 0.46) and volume (r = 0.52) of non-infested panicles, but poorly associated with grain weight and volume of midge-infested pan-

Table 5. Correlation coefficients between midge damage, grain weight and volume, and compensation in grain weight and volume in F_1 hybrids and their parents in sorghum (ICRISAT Centre, 1990/91 postrainy season)

Trait	MD	1000 GM-IP	100 GV-IP	1000 GM-NP	100 GV-NP	CGM	CGV
MD	1.00						
1000 GW-IP	–0.05	1.00					
100 GV-IP	0.01	0.88**	1.00				
1000 GW-NP	0.46*	0.72**	0.67**	1.00			
100 GV-NP	0.52*	0.65**	0.64**	0.93**	1.00		
CGM	–0.70**	0.21	0.13	–0.51*	–0.51*	1.00	
CGV	–0.65**	–0.06	0.06	–0.59**	–0.72**	0.77**	1.00

MD = Midge damage, GM = grain weight, GV = grain volume, CGM = compensation in grain weight, CGV = compensation in grain volume, IP = panicles infested with sorghum midge, and NP = Non-infested panicles.
*, ** = Correlation coefficients significant at $p = 0.05$ and 0.01, respectively.

icles (r = 0.01 to –0.05) (Table 5). However, susceptibility to sorghum midge was negatively associated with compensation in grain weight (r = –0.70) and volume (r = –0.65), suggesting that midge-resistant genotypes have a better capability to compensate for loss of grain due to sorghum midge damage and/or reduced sink size due to other factors. Grain weight and volume of the non-infested panicles showed a positive association (r = 0.64 to 0.72) with grain weight and volume of the midge infested panicles. Grain weight and volume of non-infested panicles were negatively associated with compensation in grain weight and volume (r = –0.51 to –0.72). This could be due to smaller grain volume of midge-resistant female parents, and the positive association between grain volume and susceptibility to sorghum midge.

Inheritance of resistance to sorghum midge, grain weight and volume

Differences in sorghum midge damage, grain weight and volume, and compensation in grain weight and volume for the parents, parents versus crosses, females, and males (except for % increase in grain volume for parents and parents vs. crosses) were significant, indicating the presence of variability among the hybrids and their parents for these parameters. Mean squares for females × males were not significant (Table 6). The contribution of general combining ability (GCA) effects was greater than specific combining ability (SCA) effects, indicating that inheritance of resistance to sorghum midge, grain weight and volume, and compensation in grain weight and volume are largely governed by additive gene action. The proportional contribution of females was greater than that of the males for midge damage, and for grain weight and volume. However, the contribution of males was greater than females for compensation in grain weight and volume, and the contribution of the interaction effects was also high.

General combining ability effects for midge damage and grain weight and volume were negative and significant for the midge-resistant females (ICSA 88019 and ICSA 88020), whereas those for the midge-susceptible females (ICSA 42 and 296 A), the GCA effects were significant and positive (Table 7). However, the reverse was true in the case of percentage increase in grain weight and volume in sorghum midge-infested panicles. Among the males, ICSV 745 and PM 17592-1 showed significant and negative GCA effects for susceptibility to sorghum midge, whereas MR 836, MR 844 and MR 923 showed positive and significant GCA effects. For grain weight and volume, ICSV 745, MR 844, and MR 836 showed positive and significant GCA effects, whereas PM 15908-3 and PM 17422-3 showed negative GCA effects. For percentage increase in grain weight and volume, PM 15908-3 and PM 17422-3 showed significant and positive GCA effects. The SCA effects in general were low and non-significant (except ICSA 42 × ICSV 745 and ICSA 88020 × PM 174223 for grain weight; and ICSA 88020 × PM 17592-1 and ICSA 42 × CS 3541 for percentage increase in grain weight). Heterosis for susceptibility to sorghum midge in the F_1 hybrids over the lower or higher parent was positive, except for ICSA 88019 × PM 17422-3 (–30%), ICSA 88020 × PM 15908-3 (–36%), ICSA 88020 × PM 17422-3 (–50%), ICSA 42 × MR 923 (–16%), and 296 A × MR 923 (–33%), suggesting that overdominance may also contribute to inheritance of resistance to sorghum midge in some cross combinations. Codominance effects were important in crosses such as ICSA 88019 ×

Table 6. Analysis of variance with mean squares for sorghum midge damage, and grain weight and volume in sorghum (ICRISAT Centre, 1990/91 postrainy season)

Source of variation	df	Midge damage (%)	Grain weight (g)	Grain volume (cc)	Compensation in grain weight (%)	Compensation in grain volume (%)
Parents	12	1907.8**	35.1**	0.17**	564.4**	446.9
Parents vs. crosses	32	325.7**	94.3**	0.54**	484.8*	511.3
Males	3	5628.3**	161.7**	1.17**	1218.2**	1762.0**
Females	8	1536.0**	31.9**	0.27**	679.9**	1140.5**
Males × females	24	162.9	4.2	0.03	204.5	242.6
Error	96	104.5	2.51	0.037	163.3	277.1
Relative contribution of GCA and SCA:						
GCA		34.5	38.6	43.3	5.96	7.26
SCA		9.4	6	9.9	3.33	4.70
GCA/SCA		3.6	5.1	4.4	1.79	1.54
Proportional contribution (%) of:						
Males		51.8	57.7	55.6	26.1	26.12
Females		37.1	30.4	34.1	38.8	45.10
Males × Females		11.8	11.9	10.3	35.0	28.70

*,** = Significant at $p = 0.05$ and $p = 0.01$ probability levels, respectively.
GCA = General combining ability effects, and SCA = Specific combining ability effects.

Table 7. General combining ability effects (GCA) of the female and male parents for sorghum midge damage, grain weight and volume, and compensation in grain weight and volume in midge infested panicles (ICRISAT Centre, 1990–91 postrainy season)

Source of variation	Midge damage (%)	Grain weight (g)	Grain volume (cc)	Compensation in grain weight (%)	Compensation in grain volume (%)
Females					
ICSA 88019	–13.0*	–1.58*	–0.15*	8.1*	7.30*
ICSA 88020	–11.9*	–2.58*	–0.20*	2.8	7.30*
ICSA 42	13.0*	2.40*	0.19*	–6.7*	–8.2*
296A	12.0*	1.76*	0.17*	–4.2	–5.7
SE (gi)	1.96	0.305	0.037	2.45	3.20
SE (gi-gj)	2.78	0.432	0.052	3.48	4.53
Males					
ICSV 745	–10.4*	1.88*	0.19*	0.4	–3.8
PM 15908-3	–3.6	–2.36*	–0.17*	11.4*	12.9*
PM 17422-3	–16.7*	–2.12*	–0.24*	12.5*	15.6*
PM 17592-1	–2.5	0.52	–0.01	–1.4	3.0
CS 3541	–2.7	–0.44	0.04	0.3	–7.3
MR 750	–4.7	–0.64	–0.07	–5.3	2.7
MR 836	17.1*	1.88*	0.17*	–10.2*	–15.1*
MR 844	14.9*	1.75*	0.14*	–4.5	–6.0
MR 923	8.6*	–0.47	–0.05	–3.2	–2.1
SE(gi)	2.95	0.458	0.055	3.69	4.81
SE(gi-gi)	4.17	0.647	0.078	5.23	6.79

* GCA effects significant from zero at $p = 0.05$.

PM 17592-1 and MR 844; ICSA 88020 × ICSV 745, MR 750, and MR 844; ICSA 42 × MR 750; and 296A × MR 750, MR 836, and MR 844. Heterosis for 1,000 grain weight in non-infested panicles ranged from 7 to 25% for the hybrids based on ICSA 88019, 1 to 15% on ICSA 88020, 11 to 43% on ICSA 42, and 11 to 66% on 296 A. Thus, additive gene action largely influenced the expression of resistance to sorghum midge, and inheritance of grain weight and volume, and compensation in grain weight and volume in the midge infested panicles.

Discussion

Hybrids involving resistant × resistant parents showed a resistant reaction, whereas those involving resistant × susceptible parents showed moderately resistant/susceptible reactions. Hybrids involving susceptible parents were susceptible. Hybrids based on ICSA 88019 and ICSA 88020 suffered significantly less midge damage than those based on ICSA 42 and 296A. Thus, female parents have a greater effect on the response to sorghum midge damage than the male parents. Midge-resistant males showed 27.4% increase in grain weight in midge-infested panicles compared to 5.4% increase for midge-susceptible males. Similarly, the increase in grain weight and volume was greater in panicles of hybrids involving midge-resistant females than hybrids involving midge-susceptible females. Thus, midge-resistant genotypes have a better ability to compensate for the loss of grain than midge susceptible genotypes. Grain weight and volume in non-infested panicles were negatively associated with genotypic ability for compensation in grain weight and volume, suggesting that genotypes with larger grains have a poor ability to compensate for loss of grain due to midge damage or other factors.

Resistance to sorghum midge is associated with short, tight, and hard glumes, faster rate of grain development, and high tannin content (Sharma et al., 1990). A faster rate of grain development immediately after pollination in the midge-resistant genotypes may be responsible for their better ability to compensate for loss of grain due damage by sorghum midge or other factors. Compensation in grain weight is closely associated with resistance to sorghum midge. Thus, midge-resistant cultivars not only suffer less damage, but also have a better ability to compensate for loss of grains. The level of damage in midge-resistant genotypes is less than that in midge-susceptible genotypes. Thus, it may be difficult to infer that panicles suffering higher midge damage will have a proportional increase in grain weight as the physical removal of spikelets or reduction in sink size may produce different types of effects than the actual damage by the sorghum midge (Hallman et al., 1984; Sharma, 1997).

Compensation in grain weight has been observed in sorghum genotypes following damage by the sorghum midge (Franzmann & Butler, 1993; Waquil & Teetes, 1990). However, compensation in grain weight is not apparent at damage levels below 40% (Hallman et al., 1984). The extent of compensation in grain weight is greater in panicles suffering low midge damage than in panicles suffering high midge damage (Sharma, 1997). Thus, compensation in grain weight seems to be influenced by sink size, midge damage, and genotypic resistance to sorghum midge. Some of the observed variation in compensation in grain weight in different studies may be due to differences in environmental factors during grain development, in addition to genotypic differences in their ability to compensate for midge damage.

The contribution of GCA effects was greater than the SCA effects indicating that inheritance of resistance to midge, and grain weight and volume is largely governed by additive gene action. The proportional contribution of females was greater than that of the males for midge damage and grain weight and volume, whereas the reverse was true for compensation in grain weight and volume. General combining ability effects for midge damage, and grain weight and volume were negative and significant for the midge-resistant females and significant and positive for midge-susceptible females. However, the reverse was true for compensation in grain weight and volume. Heritability of resistance to sorghum midge is high (Agrawal et al., 1988) and resistance is apparently controlled by different numbers of genes in different genotypes (Patil & Thombre, 1982; Rossetto & Igue, 1983; Widstrom et al., 1984; Boozaya-Angoon et al., 1984). Thus, to develop midge-resistant hybrids, it is important that both parents be resistant (Sharma et al., 1996). Midge-resistant cultivars, in addition to showing resistance to midge damage, also have a better ability to compensate for loss of grain due to either mechanical factors or midge damage.

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