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Expression of resistance to *Atherigona soccata* in F_1 hybrids involving shoot fly-resistant and susceptible cytoplasmic male-sterile and restorer lines of sorghum

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With 5 tables

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Abstract

In recent years, cytoplasmic male-sterility (CMS) has been recognized as a potential danger to the stability of crop production and resistance to insect pests in sorghum. Therefore, the influence of CMS on the expression of resistance to sorghum shoot fly was studied at the ICRISAT, Patancheru, India using the interlard fishmeal technique. The experimental material consisted of 12 restorer, 12 CMS and the maintainer lines, and their 144 F_1 hybrids. Shoot fly-resistant CMS lines were preferred for oviposition and had more damage because of deadhearts than the corresponding maintainer lines. The hybrids based on shoot fly-resistant CMS × resistant restorer lines were significantly less preferred for oviposition than the hybrids based on other cross combinations and exhibited the highest frequency (69.1%) of shoot fly-resistant hybrids. The hybrids based on glossy and trichomed parents had the highest frequency (> 90%) of hybrids with glossy and trichome traits, emphasizing the need to transfer these traits into both parents for better expression in the F_1 hybrids. The expression pattern of trichome density, leaf glossiness and leaf sheath pigmentation in the F_1 hybrids and their parents suggested that the interactions between cytoplasmic and nuclear genes possibly control the expression of traits associated with resistance to sorghum shoot fly in the F_1 hybrids.

Key words: *Sorghum bicolor* — *Atherigona soccata* — CMS — physico-chemical traits — mechanisms of resistance

The first usable source of cytoplasmic-nuclear male-sterility (CMS) in sorghum, *Sorghum bicolor* (L.) Moench, was developed by Stephens and Holland (1954) from the crosses involving 'Day milo' with 'Kafir', and 'Milo' with 'Black hull kafir'. Since then, a large number of hybrids developed on this cytoplasm (called A_1 cytoplasm) have been deployed on a large scale worldwide. But in recent years, cytoplasmic male-sterility has been recognized as a potential danger to the stability of crop production (Sharma et al. 2004, Dhillon et al. 2005a). The CMS in sorghum has been reported to be associated with increased susceptibility to sorghum midge, *Stenodiplosis sorghicola* Coquillett, shoot fly, *Atherigona soccata* (Rondani) and sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Sharma et al. 1996, 2004, Sharma 2001).

A number of sorghum genotypes with resistance to shoot fly, *A. soccata*, an important pest of sorghum during the seedling stage, have been identified, but the levels of resistance are only low to moderate (Jotwani 1978, Taneja and Leuschner 1985, Sharma et al. 2003). As most of the sorghum area is being planted with hybrids, it is important to identify and transfer genes conferring resistance to shoot fly into CMS (A-lines), maintainer (B-lines), and restorer (R-lines) lines. However, there is little information on the interaction between shoot fly-resistant and -susceptible A-, B- and R-lines of sorghum and the expression of resistance to *A. soccata*. The present studies were therefore carried out to determine the resistance/susceptibility reaction of *milo-kafir*-based CMS, maintainer, and restorer lines and their F_1 hybrids to sorghum shoot fly. Physico-chemical traits such as leaf glossiness, trichome density, plumule and leaf sheath pigmentation, chlorophyll content, leaf surface wetness, seedling vigour and waxy bloom associated with resistance/susceptibility to shoot fly were also studied in the F_1 hybrids.

Materials and Methods

Plant materials: The experimental material consisted of 12 CMS maintainer, and 12 restorer lines (Table 1) of sorghum, *Sorghum bicolor* (L.) Moench and their 144 F_1 hybrids. The 144 F_1 hybrids were produced by crossing 12 A-lines with 12 R-lines using a line × tester mating design. The experiments were conducted under natural infestation at the research farm of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, for three cropping seasons between 2003 and 2004. The test material was planted on deep black Vertisols under rainfed conditions during the rainy season (July to October), and under irrigated conditions during the post-rainy season (October to February). The material was planted in a randomized complete block design (RCBD), and there were three replications. Genotypes IS 18551 and Swarna were included in the trials as resistant and susceptible checks, respectively. Each plot had four rows of 2 m length, and the rows were 75 cm apart. The seed was sown with a 4-cone planter, 5 cm below the soil surface, and the field was irrigated immediately after planting. One week after seedling emergence, thinning was carried out to maintain a spacing of 10 cm between the plants. The interlard fishmeal technique (Sharma et al. 1992) was adopted to provide an optimum level of shoot fly infestation in the experimental material. No insecticide was used in the experimental plots. Data were recorded from the central two rows in each plot.

Oviposition and deadheart formation: Data on numbers of plants with eggs (oviposition) were recorded at 14 days after seedling emergence (DAE). After egg hatch, the larvae crawl to the plant whorl and move downwards between the folds of the young leaves till they reach the growing point. They cut the growing tip and feed on the decaying leaf tissue, resulting in 'deadheart' formation. The numbers of plants with deadhearts were recorded at 14 DAE in the central two rows, and expressed as a percentage of the total number of plants.

Table 1: Evaluation of 12 cytoplasmic male-sterile (CMS) and restorer lines of sorghum for shoot fly, *Atherigona soccata* resistance and the associated traits (ICRISAT, Patancheru, India)

Genotypes	Plants with eggs (%)	Deadhearts[3] (%)	Tiller deadhearts (%)	Leaf glossiness[1]	No. of trichomes[3]	Pigmentation[2]	
						Plumule	Leaf sheath
CMS lines							
SPSFR 94011	83.8	32.0 (R)	27.1	2.2 (G)	76.7 (T)	1.7	3.0
SPSFR 94006	74.4	44.4 (R)	45.0	2.4 (G)	65.0 (T)	3.0	3.0
SPSFR 94007	72.6	47.5 (R)	38.1	2.6 (G)	53.9 (T)	2.7	3.0
SPSFR 94010	84.9	51.9 (R)	46.8	2.7 (G)	16.8 (T)	2.7	3.3
SPSFR 94034	72.1	31.8 (R)	39.3	2.6 (G)	91.1 (T)	2.3	3.3
SP 55299	74.1	43.6 (R)	40.9	2.2 (G)	78.3 (T)	2.0	2.3
SP 55301A	72.6	29.8 (R)	37.2	2.3 (G)	57.8 (T)	4.3	5.0
296	91.8	58.1 (S)	39.5	5.0 (NG)	0.0 (NT)	3.7	3.7
CK 60	88.4	59.0 (S)	48.9	4.8 (NG)	0.9 (NT)	4.7	5.0
SPSFR 94012	82.6	65.6 (S)	45.2	4.6 (NG)	0.0 (NT)	1.3	3.0
Tx 623	97.1	83.3 (S)	55.5	5.0 (NG)	0.0 (NT)	4.3	4.7
ICSA 42	94.4	80.6 (S)	56.2	4.8 (NG)	0.0 (NT)	4.0	4.7
Restorer lines							
ICSV705	63.7	24.2 (R)	43.4	1.9 (G)	88.9 (T)	2.7	3.3
ICSV700	78.3	34.5 (R)	44.5	1.9 (G)	107.2 (T)	1.3	2.7
ICSV708	68.0	27.6 (R)	39.0	1.7 (G)	93.3 (T)	2.0	2.0
PS 30710	80.5	32.1 (R)	43.8	2.4 (G)	98.9 (T)	2.7	2.7
SFCR151	72.5	27.0 (R)	40.2	1.4 (G)	116.1 (T)	2.3	2.3
SFCR125	74.3	43.6 (R)	40.8	1.5 (G)	140.6 (T)	1.3	2.0
ICSV 91011	78.8	42.0 (R)	46.0	2.0 (G)	0.0 (NT)	4.7	5.0
IS 18551 (RC)	66.4	23.4 (R)	34.9	1.3 (G)	88.9 (T)	1.3	2.2
CS 3541	88.0	58.5 (S)	43.2	4.8 (NG)	0.0 (NT)	3.3	4.3
MR 750	90.2	69.5 (S)	54.4	4.7 (NG)	0.0 (NT)	1.0	3.0
ICSV 745	93.4	66.8 (S)	54.5	4.4 (NG)	0.0 (NT)	4.7	5.0
Swarna (SC)	90.6	73.6 (S)	54.0	4.8 (NG)	10.6 (NT)	1.7	3.3
LSD (P = 0.05)	11.22	11.25	13.64	0.46	19.21	1.09	0.91
F-value	7.55**	16.60**	2.10*	66.25**	35.85**	6.39**	6.71**

*,** Significant at P = 0.05 and P = 0.01, respectively.
[1]Leaf glossiness (1 = highly glossy and 5 = non-glossy).
[2]Pigmentation (1 = dark pink colour, and 5 = green colour). RC, resistant check. SC, susceptible check.
[3]The letters R, S, G, NG, T, and NT in parenthesis represent resistant, susceptible, glossy, non-glossy, trichomed, and non-trichomed CMS and restorer lines, respectively.

Recovery resistance: The sorghum plant produces side tillers as a result of deadheart formation in the main plant, which can, at times, also be damaged. The number of tillers with deadheart symptoms following shoot fly damage were recorded at 28 DAE and expressed as a percentage of the total number of tillers.

Physico-chemical traits associated with resistance to *Atherigona soccata*: Leaf glossiness was scored on a scale of 1–5 [1 = highly glossy (light green, shining, narrow and erect leaves) and 5 = non-glossy (dark green, dull, broad and drooping leaves)] at 10 DAE. The trichome density was estimated on the central-portion of the 5th leaf (from the base) collected from three randomly selected seedlings. The leaf pieces were cleared of chlorophyll and observed under a stereo-microscope at 10× magnification (Maiti and Bidinger 1979). The genotypes having < 50 trichomes/10× microscopic field were considered as low-trichomed. The pink pigment on the plumule and leaf sheath was scored visually at 5 DAE on a rating scale of 1–5 (1 = plumule and leaf sheath with dark pink pigment; and 5 = plumule and leaf sheath green); (Dhillon et al. 2005b).

Statistical analysis: Data were subjected to analysis of variance to test the significance of differences between the hybrids based on shoot fly-resistant and susceptible CMS and restorer lines. The hybrid parents were classified into five different categories of resistance or susceptibility to shoot fly as suggested by Sharma et al. (2003). The hybrid parents having shoot fly deadhearts $\leq (R + A)/2$ were considered as resistant, and those with $> (R + A)/2$ as susceptible so as to categorize the resistant and susceptible hybrids in the different cross combinations, where A, deadhearts (%) in the susceptible check, and R, deadhearts (%) in the resistant check.

Results

Evaluation of hybrids parents for resistance to *Atherigona soccata* and associated traits

The differences among the hybrids parents were significant at P = 0.05 or 0.01 (CMS and the restorer lines) for plants with eggs, main plant deadhearts, tiller deadhearts, leaf glossiness, number of trichomes and plumule and leaf sheath pigmentation (Table 1). The CMS lines SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299 and SP 55301; and the restorers ICSV705, ICSV700, ICSV708, PS30710, SFCR151, SPSFR125 and IS18551 were glossy, trichomed, pigmented (except SP 55301A and ICSV 91011), and showed oviposition non-preference and resistance to *A. soccata* when compared with the susceptible ones. ICSV 91011 was glossy and non-trichomed, and showed a moderate level of resistance to shoot fly. However, the shoot fly-susceptible CMS and restorer lines were non-glossy and non-trichomed (Table 1).

Expression of resistance to *Atherigona soccata* in F_1 hybrids

Oviposition preference

The F_1 hybrids based on shoot fly-resistant CMS and restorer lines (RA × RR) had a significantly lower percentage of plants with eggs when compared with the hybrids based on other cross combinations (Table 2). The highest frequency (76.7%) of hybrids with low oviposition was recorded when both the

Table 2: Damage levels and frequency of obtaining shoot fly, *Atherigona soccata*-resistant hybrids involving resistant and susceptible CMS (A) and restorer (R) lines (ICRISAT, Patancheru, India)

	Oviposition		Deadhearts		Tiller deadhearts	
Hybrid combinations	Plants with eggs (%)	Hybrids with less oviposition[2] (%)	Plants with deadhearts (%)	Resistant hybrids[2] (%)	Tiller deadhearts (%)	Resistant hybrids[2] (%)
Resistant (RA) × resistant (RR)	78.5	76.7 (30)[1]	40.8	69.1 (56)[1]	38.5	76.8 (56)[1]
Resistant (RA) × susceptible (SR)	88.4	10.0 (30)	60.8	33.3 (28)	47.5	22.5 (40)
Susceptible (SA) × resistant (RR)	93.0	9.5 (42)	69.1	14.8 (40)	49.7	21.4 (28)
Susceptible (SA) × susceptible (SR)	93.3	0.0 (42)	75.3	0.0 (20)	51.6	5.0 (20)
LSD (P = 0.05)	12.99	—	5.50	—	3.33	—

[1]Figures in parentheses are the total numbers of hybrids.
[2]Hybrids with oviposition or deadhearts less than or equal to the resistant check, IS 18551.

parents had low oviposition (Table 2). The hybrids based on shoot fly-resistant CMS × -susceptible restorer lines had 10.0% hybrids with low oviposition. The frequency of hybrids with low oviposition from the susceptible parents was nil.

Deadhearts

The hybrids based on shoot fly-resistant CMS and restorer lines had a significantly lower proportion of plants with deadhearts than the hybrids based on other cross combinations (40.8% vs. 60.8–75.3% plants with deadhearts) at 14 DAE (Table 2). The hybrids based on resistant CMS and restorer lines suffered lower shoot fly damage when compared with the hybrids based on susceptible CMS and resistant or susceptible restorer lines, suggesting that CMS influences the expression of resistance to shoot fly in sorghum. The shoot fly-resistant maintainer lines showed better resistance to shoot fly damage (32.5%) than the CMS lines (40.1%). However, no such differences were observed between the shoot fly-susceptible CMS and the maintainer lines (64.5 vs. 67.4% plants with deadhearts). Resistance was required in both the parents to develop shoot fly-resistant hybrids. The highest frequency (69.1%) of shoot fly-resistant hybrids was observed when both the parents were resistant to *A. soccata* (Table 2). The hybrids based on shoot fly-resistant CMS × -susceptible restorer lines produced 33.3% shoot fly-resistant hybrids. The frequency of shoot fly-resistant hybrids involving susceptible parents was nil.

Recovery resistance

The numbers of tiller deadhearts were significantly lower in hybrids based on shoot fly-resistant CMS and restorer lines (38.5%) than in the hybrids based on other cross combinations (47.5–51.6%; Table 2). The frequency of hybrids with low tiller deadhearts was greater when both the parents had low tiller deadhearts (Table 2). The hybrids based on shoot fly-resistant CMS × -susceptible restorer lines produced 76.8% shoot fly-resistant hybrids. However, there was no variation in frequency of hybrids with low tiller deadhearts when both of the parents showed greater susceptibility to shoot fly. The frequency of hybrids with low tiller deadhearts was 5% when both the parent showed a susceptible reaction to shoot fly damage in the main plants.

Expression of physico-chemical traits associated with resistance to *Atherigona soccata*

The hybrids based on glossy CMS and restorer lines showed the same level of glossiness as the parents, while the hybrids based on the non-glossy CMS and glossy or non-glossy restorer lines were non-glossy (Table 3). However, the hybrids based on glossy CMS with non-glossy restorer lines were intermediate in expression of leaf glossiness. The frequency of hybrids with the glossy trait was 94.6% when both the parents were glossy (Table 3). The hybrids based on glossy CMS × non-glossy restorer lines showed 10.7% frequency of hybrids with the glossy trait. These results suggested that expression of leaf glossiness was influenced more by the female than the male parent.

The hybrids based on trichomed CMS and restorer lines showed greater trichome density (94.5 trichomes in a 10× microscopic field), and a high frequency (93.9%) of trichomed hybrids (Table 4) compared to the hybrids based on other cross combinations. Hybrids based on non-trichomed CMS and trichomed restorer lines had a lower trichome density than

Table 3: Leaf glossiness intensity and frequency of glossy hybrids in crosses involving glossy and non-glossy CMS (A) and restorer (R) lines (ICRISAT, Patancheru, India)

Hybrid combinations	No. hybrids	Leaf glossiness score[1]	Frequency of hybrids with glossy trait (%)
GA × GR[2]	56	2.2	94.6
GA × NGR	28	3.9	10.7
NGR × GR	40	4.5	0.0
NGA × NGR	40	4.7	0.0
LSD (P = 0.05)	—	0.54	—

[1]Leaf glossiness score (1 = Glossy, and 5 = Non-glossy).
[2]GA, glossy CMS; NGA, non-glossy CMS; GR, glossy restorer; NGR, non-glossy restorer.

Table 4: Trichome density and frequency of trichomed hybrids involving trichomed and non-trichomed CMS (A) and restorer (R) lines (ICRISAT, Patancheru, India)

Hybrid combinations	No. hybrids	Trichome density (10× microscopic field)	Frequency of trichomed hybrids (%)
TA × TR[1]	49	94.5	93.9
TA × NTR	35	19.8	8.6
NTA × TR	35	32.3	22.9
NTA × NTR	25	1.2	0.0
LSD (P = 0.05)	—	12.35	—

[1]TA, trichomed CMS; NTA, non-trichomed CMS; TR, trichomed restorer; NTR, non-trichomed restorer.

Table 5: Intensity of plumule and leaf sheath pigmentation, and frequency of obtaining pigmented hybrids involving pigmented and non-pigmented CMS (A) and restorer (R) lines (ICRISAT, Patancheru, India)

Hybrid combinations	No. hybrids	Plumule pigmentation score[1]	Frequency of hybrids with pigmented plumule (%)	Leaf sheath pigmentation score[1]	Frequency of hybrids with pigmented leaf sheath (%)
PA × PR[2]	63	2.2	95.2	2.9	87.3
PA × NPR	21	2.7	95.2	3.8	14.3
NPA × PR	45	2.1	91.2	3.0	68.9
NPA × NPR	15	3.1	40.0	4.0	26.7
LSD (P = 0.05)	—	0.67	—	0.61	—

[1]Plumule/leaf sheath pigmentation (1 = plumule/leaf sheath with intense expression of pink pigment, and 5 = plumule/leaf sheath of tan type, i.e. of light green colour).
[2]PA, pigmented CMS; NPA, non-pigmented CMS; PR, pigmented restorer; NPR, non-pigmented restorer.

the hybrids with both trichomed parents. The hybrids based on non-trichomed CMS and restorer lines were non-trichomed. Hybrids involving trichomed CMS and non-trichomed restorer lines had an 8.6%, and non-trichomed CMS × trichomed restorer lines a 22.9% frequency of trichomed hybrids, suggesting a greater influence of the male parent on the expression of trichomes in the F_1 hybrids (Table 4).

The hybrids based on pigmented CMS and restorer lines had greater plumule (score 2.2) and of leaf sheath pigmentation (score 2.9) intensity, and showed a high frequency of hybrids with pigmented plumules (95.2%) and leaf sheaths (87.3%) compared with the hybrids based on other cross combinations (Table 5). However, the hybrids based on non-pigmented CMS and pigmented restorer lines, and the hybrids based on both parents with a pigmented plumule and leaf sheath had similar pigmentation intensities, and a high frequency of hybrids with pigmented plumules (91.2%) and leaf sheaths (68.9%), suggesting greater influence of restorer lines on the expression of plumule and leaf sheath pigmentation in the F_1 hybrids (Table 5).

Discussion

Oviposition by sorghum shoot fly is significantly and negatively associated with trichome density and leaf glossiness (Omori et al. 1983, Dhillon et al. 2005b). The glossy trait was influenced more by the CMS lines, while the restorer lines showed greater influence on the expression of trichomes in the F_1 hybrids. Trichomes and leaf glossiness are independently inherited and apparently have an additive effect in reducing shoot fly damage (Maiti et al. 1984, Dhillon et al. 2006). The CMS lines were preferred for oviposition and had more deadhearts than the maintainer lines (Dhillon et al. 2006). Greater shoot fly damage on CMS lines was reported earlier in the case of sorghum midge (Sharma et al. 1994, Sharma 2001). Hybrids based on sorghum midge-resistant CMS × -susceptible restorer lines have been found to be more resistant to sorghum midge than the hybrids based on susceptible CMS × susceptible restorer lines (Johnson 1977, Sharma et al. 1996). The reactions of the F_1 hybrids based on shoot fly-resistant and/or -susceptible CMS and restorer lines to shoot fly damage suggested that factors in the cytoplasm influence the expression of resistance to shoot fly in the F_1 sorghum hybrids.

Resistance is needed in both parents to develop shoot fly-resistant hybrids. The greater susceptibility of CMS lines based on *milo* cytoplasm necessitates the incorporation of shoot fly-resistance traits into the alternate CMS systems (Dhillon et al. 2005a). The tillers of shoot fly-resistant CMS and restorer lines had fewer deadhearts than those of the susceptible CMS and restorer lines, and the hybrids based on such parents. Recovery resistance is partially related to the tillering response to shoot fly damage (Jotwani and Srivastava 1970), level of primary resistance, and productive tillers (Blum 1969, Doggett et al. 1970). The hybrids based on glossy and trichomed parents showed better resistance to sorghum shoot fly. The level of resistance to shoot fly has been reported to be better when both glossy and trichome traits occurred together (Agrawal and House 1982, Dhillon et al. 2005b). The restorer lines were dominant over CMS lines for plant colour (Torres-Montalvo et al. 1992). Purple-pigmented sorghum genotypes have been reported to be tolerant to shoot fly damage (Singh et al. 1981), but genetically diverse sorghum material tested in these studies did not support this hypothesis. Resistance/susceptibility in sorghum to shoot fly is influenced not only by the cytoplasm, but also by nuclear genes (Dhillon et al. 2006). It is difficult to separate the effects of cytoplasmic and nuclear genes, as CMS itself is the result of interaction of cytoplasmic and nuclear genes. It is desirable to have resistance in both CMS and restorer lines to develop hybrids with resistance to shoot fly.

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