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INFLUENCE OF CYTOPLASMIC MALE-STERILITY ON EXPRESSION OF PHYSICO-CHEMICAL TRAITS ASSOCIATED WITH RESISTANCE TO SORGHUM SHOOT FLY, *Atherigona soccata* (Rondani)

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SUMMARY

Sorghum is damaged by several insect species, of which the shoot fly, *Atherigona soccata,* is important in Asia and Africa. Host plant resistance is an effective component for the management of this pest under subsistence farming conditions. With the discovery of the cytoplasmic male-sterility (CMS) system (*Milo* cytoplasm), there is an increasing emphasis to develop sorghum hybrids to increase the productivity of this crop. In order to develop sorghum hybrids with broad based resistance to shoot fly, it is important to identify CMS, maintainer, and restorer lines with different mechanisms of resistance to this pest. Therefore, the expression of resistance and the components associated with resistance to sorghum shoot fly in a diverse array of shoot fly-resistant and -susceptible CMS and maintainer lines were studied for three years (2002-2004). The shoot fly-resistant CMS lines were preferred for oviposition by the shoot fly females than the corresponding maintainer lines (78.5 to 82.8% versus 71.5 to 79.9% plants with eggs), and had more deadhearts (47.6 to 79.3% versus 41.6 to 74.0%). The shoot fly-susceptible CMS and maintainers were equally susceptible to shoot fly damage. Shoot fly-resistant maintainer lines showed better recovery than the CMS lines. The expression of trichomes on abaxial and adaxial leaf surfaces was more in the maintainer lines than the CMS lines. Leaf glossiness, trichome density, and plumule and leaf sheath pigmentation showed negative associations with oviposition and deadhearts, while leaf surface wetness, chlorophyll content, and waxy bloom were associated with susceptibility. Plants with eggs, deadhearts, leaf surface wetness, leaf sheath pigmentation, leaf glossiness, trichomes on the adaxial surface of the leaf, and waxy bloom can be used as marker traits to select for resistance to *A. soccata*. The results suggested that the resistance to *A. soccata* is influenced by factors associated with cytoplasmic male-sterility and the interaction between cytoplasmic and nuclear genes.

Key words: *Atherigona soccata*, cytoplasmic male-sterility, physico-chemical traits, resistance mechanisms, sorghum.

Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop in the semi-arid tropics (SAT). It is attacked by over 150 insect species, of which the sorghum shoot fly, *Atherigona soccata* (Rondani) (Diptera: Muscidae) is an important pest in Asia, Africa, and the Mediterranean Europe (Deeming, 1971; Pont, 1972; Pont and Deeming, 2001). Host plant resistance is an important component for pest management as it does not involve

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any additional cost to the farmers. Several sources of resistance to shoot fly have been identified in sorghum germplasm collection, and resistance has also been transferred into improved varieties, and maintainer and restorer lines (Sharma *et al.*, 1992, 2003). Resistance to shoot fly is associated with a number of physico-chemical traits (Sharma and Nwanze, 1997), while the interactions between different components determine the genotypic resistance/susceptibility to this pest (Dhillon, 2004).

The discovery of cytoplasmic male-sterility (CMS) in sorghum and its subsequent exploitation for hybrid production has provided an important tool for introgression of traits of interest into the high yielding hybrids. In recent years, CMS has been recognized as a potential danger to crop production because of the possibility of insect pest and disease outbreaks due to lack of genetic diversity in the resulting cultivars grown (Yang *et al.*, 1989; Sharma *et al.*, 2003, 2004). Therefore, it is important to identify CMS, maintainer, and restorer lines with resistance to insects to develop hybrids with resistance to the target insect species. There is limited information on the reaction of CMS and maintainer lines in sorghum to shoot fly. Therefore, the present studies were undertaken on a diverse array of shoot fly-resistant and -susceptible CMS and maintainer lines.

MATERIALS AND METHODS

The experiments were conducted under natural infestation at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India (545 m amsl, 17° 32' N, 78° 16'E) between 2002-2004. The experiments were planted on deep black Vertisols under rainfed conditions during the rainy season (July-October), and under irrigated conditions during the post-rainy season (October-February). The test materials consisted of twelve CMS and their maintainer lines (seven pairs of resistant and five pairs of susceptible genotypes) (Table 1). These test materials were planted along with shoot fly-resistant (IS 18551) and -susceptible (Swarna) controls in three replications in a randomized complete block design (RCBD). Each plot had four rows 2 m long, and the rows were 75 cm apart. The seeds were sown with a 4-cone planter at 5 cm below the soil surface under optimum moisture conditions. The field was irrigated immediately after planting during the post-rainy season. One week after seedling emergence, thinning was undertaken to maintain a spacing of 10 cm between plants. The optimum level of shoot fly population was maintained by manipulating the sowing dates (late planting during the rainy season), use of infester rows, and spreading moist fish-meal (a shoot fly attractant) in the test material (interlard fish-meal technique) (Sharma *et al.*, 1992). The plants were given a basal application of diammonium phosphate (150 kg ha^{-1}) and a top dressing of urea (100 kg ha^{-1}) at 30 days after seedling emergence. There was no insecticidal application in the experimental plots. The panicles were covered with muslin cloth bags to protect the grains from bird damage.

Oviposition and deadheart formation

Observations on egg laying, "deadheart" formation, and recovery resistance (in response to damage to the main plant) were recorded from the central two rows. The number of eggs and number of plants with eggs were recorded at 14 days after seedling emergence (DAE). Numbers of plants with deadhearts were recorded at 14, 21, and 28 DAE, and expressed as percentage of the total number of plants. Observations on tillers with deadhearts were recorded at 28 DAE from the central two rows in the same plants where the observations on main plant deadhearts were recorded. The healthy plants were

tagged one month after seedling emergence. At crop maturity, data were recorded on total number of tillers and the tillers having panicles with grain, and expressed as percentage productive tillers. Recovery resistance (uniformity in tillers and number of tillers with productive panicles) was also evaluated at crop maturity on a scale of 1 to 9 (1= > 80% plants with 2 to 3 uniform productive tillers; and 9 = <20% damaged plants with 1 to 2 productive tillers).

Table 1. Pedigrees and reaction of cytoplasmic male-sterile (A) and maintainer (B) lines of sorghum to shoot fly (ICRISAT, Patancheru, India).

Genotypes	Pedigree	Year
Shoot fly-resistant CMS/maintainer lines		
SPSFR 94011A/B	[(((BTx 623 x ((SC108-3 x GPR 148)-18-4-1)) x B lines bulk) -5-1-2-5) x ((PS 21194 x SPV 351)-3-1-2-3-3)]-13-3-1-1	1998
SPSFR 94006A/B	[(((BTx 623 x ((SC 108-3 x GPR 148)-18-4-1)) x B lines bulk) -5-1-2-5) x ((PS 21194 x SPV 351)-3-1-2-3-3)]-13-2-2-1-1	1998
SPSFR 94007A/B	[(((BTx 623 x ((SC 108-3 x GPR 148)-18-4-1)) x B lines bulk) -5-1-2-5) x ((PS 21194 x SPV 351)-3-1-2-3-3)]-13-3-2-2-1	1998
SPSFR 94010A/B	[(((((BTx 623 x ((SC 108-3 x GPR 148)-18-4-1)) x B lines bulk) -5-1-2-5) x PS 30715-1) x PS 19349B]-2-4-1	1998
SPSFR 94034A/B	[((Indian Synthetic 89-2 x Rs/R 20-682)-5-4-2) x ((PS 21194 x SPV 391)-3-1-2-3-1-1)]-4-2-1-1	1998
SP 55299A/B	(PS 21303 x SPV 386)-3-2-2-2-1	1998
SP 55301A/B	[(((((BTx 623 x ((SC108-3 x GPR 148)-18-4-1)) x B lines bulk) -5-1-2-5) x ((PS 21194 x SPV 351)-3-1-2-3-3) x PS 19349B]-10	1998
Shoot fly-susceptible CMS/maintainer lines		
SPSFR 94012A/B	[(((BTx 623 x ((SC 108-3 x GPR 148)-18-4-1)) x B lines bulk)-5-1-2-5) x ((PS 21194 x SPV 351)-3-1-2-3-3)]-13-3-1-4	1998
296A/B	IS 3922 x Karad local	-
Tx 623A/B	IS 40583 (kafir) x IS 21807 (caudatum)	-
CK 60A/B	Day milo x Black hull kafir	-
ICSA 42A/B	[(BTx 623 x ((SC 108-3 x GPR 148)-18-4-1)) x B lines bulk]-5-3-6-3	1984

Morphological traits associated with resistance to sorghum shoot fly

The influence of CMS on expression of plant traits such as leaf glossiness, trichome density, seedling vigor, and leaf surface wetness (which are associated with resistance to shoot fly) was studied under natural conditions in the field. The leaf glossiness was evaluated on a 1 to 5 rating scale at 10 DAE in the morning hours when there was maximum reflection of light from the leaf surfaces (1= highly glossy- light green, shiny, narrow, and erect leaves; 5= non-glossy- dark green, dull, broad, and drooping leaves). Trichome density was recorded on the central portion of the 5th leaf (from the base) in three seedlings selected at random in each plot. The leaf pieces (approximately 2 cm^2) were cut with scissors and placed in an acetic acid and alcohol solution (2:1) in stopper glass vials (10 ml capacity) for 24 h. The leaf samples were then transferred to lactic acid (90%). Leaf

segments cleared of chlorophyll were observed for trichome density under a microscope. The leaf sections were mounted on a slide in a drop of lactic acid and observed under a stereomicroscope at a magnification of 10x. The trichomes on both abaxial (lower leaf surface) and adaxial (upper leaf surface) surfaces were counted in three microscopic fields selected at random and expressed as number of trichomes per microscopic field. Seedling vigor was recorded at 10 DAE on 1 to 5 rating scale (1= highly vigorous- plants showing maximum height, more fully expanded leaves, good adaptation, and robust seedlings; 5= poor seedling vigor- plants showing poor growth and weak seedlings). The leaf surface wetness on the central whorl leaf was recorded in test genotypes planted in plastic cups (10 cm dia.) and kept in the open outside the greenhouse. The seedlings at 5th leaf stage (12 DAE) were brought to the laboratory in the early morning hours (0430 to 0630 h). The central whorl leaf was pulled out and mounted on a slide with a sticky tape and observed under the microscope (10x magnification) for recording leaf surface wetness. Leaf surface wetness was rated on a 1 to 5 scale (1= leaf blade without water droplets; and 5= entire leaf blade densely covered with water droplets).

Chlorophyll content, plumule and leaf sheath pigmentation, and waxy bloom

Influence of CMS on expression of chlorophyll content, plumule and leaf sheath pigmentation, and waxy bloom was studied under natural conditions. The chlorophyll content of the seedlings at 10 DAE and at the flag leaf stage at 80 DAE was measured with the help of a chlorophyll meter (SPAD-502® Minolta Corporation) and expressed as g m^{-2}. The pink pigmentation on the plumule and leaf sheath was scored visually at 5 DAE on a 1 to 5 rating scale (1= plumule and leaf sheath with deep pink pigment; and 5= plumule and leaf sheath green colored) (Figure 1). The waxy bloom was recorded on a rating scale of 1 to 5 (1= stem and leaves without a wax cover; and 5 = stem and leaves fully covered with a wax layer) at the 50% flowering (80 DAE) stage.

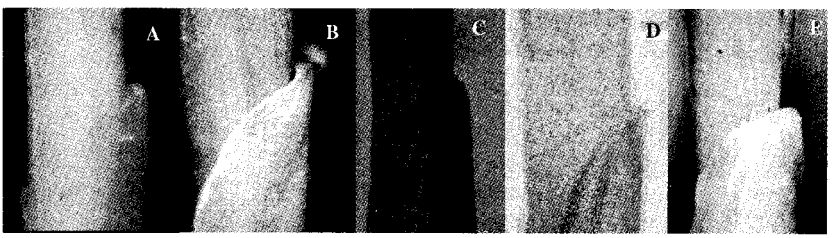

Figure 1. Plumule and leaf sheath purple pigmentation scores of sorghum genotypes at 5 days after seedling emergence. [A= 1 (dark pink); B= 2 (pink); C= 3 (light pink); D= 4 (very light pink); E= 5 (green)].

Statistical analysis

The data were subjected to analysis of variance using a factorial analysis to estimate the effects of cytoplasms, genotypes, and their interaction. The differences between the treatment means were compared using the least significant difference (LSD). The diversity among the test genotypes was determined through principal component analysis based on oviposition, deadhearts, and physico-chemical traits associated with resistance to sorghum shoot fly. Correlation coefficients and multiple linear and stepwise regressions for each trait were computed separately for oviposition and deadhearts. The

path coefficient analysis was used to assess the direct and indirect effects of oviposition and physico-chemical traits on deadhearts.

RESULTS

Influence of CMS on damage by sorghum shoot fly

There were significant differences between the CMS and the maintainer lines for oviposition and deadhearts formation. The numbers of eggs laid on CMS and their maintainer lines varied from 8.8 to 17.6 and 8.6 to 17.8 eggs per 10 plants, respectively (Table 2). The percentage plants with eggs in the CMS and maintainer lines varied from 74.5 to 97.5% and 65.9 to 96.7%, respectively. The CMS lines of the genotypes SPSFR 94011, SPSFR 94006, SPSFR 94010, SPSFR 94034, SP 55299, and 296 had significantly more eggs than the respective maintainer lines. The genotypes SPSFR 94012, 296, Tx 623, CK 60, and ICSA 42 were preferred for oviposition, and were at par with the susceptible check, Swarna. The shoot fly deadhearts on CMS and maintainer lines ranged from 37.9 to 85.3% and 37.7 to 83.0% at 14 DAE, 66.1 to 95.9% and 58.0 to 96.6% at 21 DAE, and 73.2 to 97.6% and 65.8 to 98.0% at 28 DAE (Table 3). The CMS lines showed more shoot fly deadhearts than the respective maintainer lines, although there were a few exceptions. The genotypes SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 had significantly lower percentage of deadhearts than the susceptible check, Swarna. SPSFR 94012, 296, Tx 623, CK 60, and ICSA 42 showed a susceptible reaction to sorghum shoot fly across observation dates. There were no significant differences among the CMS and maintainer lines in tiller deadhearts, productive tillers, and recovery resistance (Table 4).

Influence of CMS on expression of morphological traits associated with resistance to sorghum shoot fly

The CMS and maintainer lines SPSFR 94011, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 had moderate levels of leaf glossiness as compared to the resistant check, IS 18551. The CMS and maintainer lines of the genotypes SPSFR 94012, Tx 623, 296, CK 60, and ICSA 42 were non-glossy as was the susceptible check, Swarna. The numbers of trichomes on both abaxial and adaxial leaf surfaces of CMS lines were lower than of the respective maintainer lines (except in case of SPSFR 94006 and SP 55299). The numbers of trichomes were greater on the adaxial leaf surface as compared to abaxial leaf surface. Both A- and B-lines of SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 were glossy and trichomed, while SPSFR 94012, 296, Tx 623, CK 60, and ICSA 42 were non-glossy and trichomeless (Table 5). The CMS lines were numerically more vigorous than the respective maintainer lines, except in the case of CK 60, although the interaction effects were nonsignificant. The line 296, which has been exploited extensively for hybrid production in India, exhibited poor seedling vigor (Table 5). The CMS lines of the genotypes SPSFR 94007, SPSFR 94010, SP 55299, Tx 623, and ICSA 42 showed greater leaf surface wetness, while those of SPSFR 94012 and SPSFR 94034 showed lower leaf surface wetness than their respective maintainer lines (Table 5). In general, the leaf surface wetness of CMS lines was greater than the maintainer lines.

Table 2. Oviposition by sorghum shoot fly at different plant growth stages on 12 cytoplasmic male-sterile (A) and maintainer (B) lines under multi-choice conditions in the field (ICRISAT, Patancheru, India; 2002-2003).

Genotypes	Eggs plants^{-10}				Plants with eggs (%)			
	14 DAE		21 DAE		14 DAE		21 DAE	
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	11.2	9.5	9.5	9.6	83.1	70.0	85.2	80.4
SPSFR 94012	13.8	12.0	10.1	10.6	85.8	87.4	92.6	88.6
SPSFR 94006	10.3	9.6	10.0	9.0	78.4	73.5	83.8	86.7
SPSFR 94007	8.8	9.4	8.7	7.8	76.1	78.1	77.1	77.5
SPSFR 94010	12.6	10.7	11.1	10.6	86.7	75.2	89.3	84.1
SPSFR 94034	10.4	9.3	9.5	9.0	74.5	69.4	82.9	79.6
SP 55299	10.2	8.6	10.0	8.1	75.5	68.4	80.5	76.8
SP 55301	9.3	9.1	9.2	8.5	74.9	65.9	80.7	74.2
296	17.6	16.2	11.7	12.6	93.4	90.8	97.0	96.2
Tx 623	15.8	15.4	10.7	10.7	97.5	96.7	98.0	98.3
CK 60	15.5	17.8	12.3	11.3	91.3	93.6	91.6	94.5
ICSA 42	15.1	14.9	11.8	11.4	95.6	93.0	97.8	97.6
Mean	12.5	11.9	10.4	10.0	84.4	80.2	88.0	86.2
Controls*								
IS 18551 (R)	9.3		9.1		71.6		77.4	
Swarna (S)	14.5		11.7		92.6		96.8	
For comparing	LSD	Fp	LSD	Fp	LSD	Fp	LSD	Fp
Cytoplasms (C)	0.68	0.050	NS	0.090	2.27	<0.001	NS	0.124
Genotypes (G)	1.66	<0.001	1.21	<0.001	5.56	<0.001	5.72	<0.001
G x C	NS	0.426	NS	0.693	NS	0.073	NS	0.833

* Controls were not included in the analysis of variance. R =Resistant. S = Susceptible. NS = Nonsignificant at P = 0.05. LSD = Least significant difference for comparing means at P = 0.05. Fp = F-probability. DAE = Days after seedling emergence.

Table 3. Relative susceptibility of 12 cytoplasmic male-sterile (A) and their maintainer (B) lines to sorghum shoot fly at different plant growth stages under multi-choice conditions in the field (ICRISAT, Patancheru, India; 2002-2003).

Genotypes	Deadhearts (%)					
	14 DAE		21 DAE		28 DAE	
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	42.4	45.9	74.2	69.3	81.1	75.6
SPSFR 94012	71.8	66.2	84.3	83.5	88.1	88.7
SPSFR 94006	52.6	45.0	71.6	69.0	77.6	76.8
SPSFR 94007	51.5	40.6	67.8	62.0	73.2	72.4
SPSFR 94010	59.4	40.2	82.5	70.6	88.4	80.4
SPSFR 94034	40.2	37.7	70.7	66.3	83.0	74.4
SP 55299	49.5	38.3	72.8	59.2	77.4	65.8
SP 55301	37.9	43.6	66.1	58.0	74.5	72.8
296	67.8	71.8	91.1	91.2	97.4	96.0
Tx 623	85.3	83.0	95.4	96.6	97.1	98.0
CK 60	69.0	75.5	90.0	91.2	95.1	95.3
ICSA 42	83.9	74.0	95.9	91.1	97.6	96.6
Mean	59.3	55.2	80.2	75.7	85.9	82.7
Controls*						
IS 18551 (R)	30.5		62.7		68.3	
Swarna (S)	79.2		93.4		95.9	
For comparing	LSD	Fp	LSD	Fp	LSD	Fp
Cytoplasms (C)	2.98	0.007	2.34	<0.001	2.13	0.004
Genotypes (G)	7.29	<0.001	5.74	<0.001	5.22	<0.001
G x C	10.31	0.010	NS	0.195	NS	0.260

* Controls were not included in the analysis of variance. R =Resistant. S = Susceptible. NS = Nonsignificant at P = 0.05. LSD = Least significant difference for comparing means at P = 0.05. Fp = F-probability. DAE = Days after seedling emergence.

Table 4. Tiller deadhearts, productive tillers, and recovery resistance of 12 cytoplasmic male-sterile (A) and maintainer (B) lines of sorghum (ICRISAT, Patancheru, India; 2002-2003).

Genotypes	Tiller deadhearts (%)		Productive tillers (%)		Recovery resistance	
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	32.7	35.4	42.2	42.3	5.7	4.8
SPSFR 94012	49.7	50.6	54.1	52.7	5.5	5.3
SPSFR 94006	49.5	40.7	50.4	58.5	5.5	5.5
SPSFR 94007	41.8	44.0	50.1	59.7	6.3	5.2
SPSFR 94010	51.0	48.3	58.8	46.8	5.5	5.8
SPSFR 94034	40.0	42.6	50.1	51.3	6.1	5.0
SP 55299	46.5	42.7	49.5	50.3	6.2	5.7
SP 55301	39.0	44.7	56.8	54.6	5.1	5.2
296	47.8	54.0	25.7	22.6	6.8	7.3
Tx 623	58.8	55.1	47.3	52.5	7.8	7.4
CK 60	54.1	58.1	55.5	52.2	6.0	7.5
ICSA 42	58.3	51.8	49.2	44.3	7.9	7.2
Mean	47.4	47.3	49.1	49.0	6.2	6.0
Controls*						
IS 18551 (R)	41.5		31.2		4.3	
Swarna (S)	60.8		58.0		6.7	
For comparing	LSD	Fp	LSD	Fp	LSD	Fp
Cytoplasms (C)	NS	0.943	NS	0.938	NS	0.178
Genotypes (G)	7.21	<0.001	9.80	<0.001	0.72	<0.001
G x C	NS	0.556	NS	0.737	1.02	0.019

* Controls were not included in the analysis of variance. R =Resistant. S = Susceptible. NS = Nonsignificant at P = 0.05. LSD = Least significant difference for comparing means at P = 0.05. Fp = F-probability.

Table 5. Expression of leaf glossiness, trichome density, seedling vigor, and leaf surface wetness in 12 cytoplasmic male-sterile (A) and maintainer (B) lines of sorghum (ICRISAT, Patancheru, India; 2002-2003).

Genotypes	Leaf glossiness score		Trichome density				Seedling vigor		Leaf surface wetness	
			Abaxial		Adaxial					
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	2.4	2.5	61.1	79.0	122.1	139.6	2.0	2.8	1.0	1.0
SPSFR 94012	4.7	5.0	0.0	6.9	0.0	15.0	2.5	2.7	4.0	5.0
SPSFR 94006	2.5	2.4	63.8	75.4	132.9	127.5	2.3	3.0	1.3	1.5
SPSFR 94007	2.6	2.5	56.2	60.4	94.2	101.7	2.7	2.7	1.5	1.0
SPSFR 94010	3.0	2.6	12.6	46.7	19.3	85.9	2.3	2.7	2.2	1.0
SPSFR 94034	2.5	2.6	89.6	114.6	137.5	157.9	3.0	3.0	1.0	2.5
SP 55299	2.3	2.0	69.0	87.5	130.8	113.8	2.7	3.0	1.8	1.0
SP 55301	2.3	2.7	50.8	53.3	77.1	107.1	2.8	2.7	1.0	1.2
296	5.0	4.8	0.0	0.0	0.2	0.0	3.7	4.0	5.0	5.0
Tx 623	5.0	4.9	0.0	0.0	0.4	0.0	2.3	2.5	4.3	3.7
CK 60	4.8	4.8	0.7	0.0	0.8	1.3	3.0	2.7	3.0	3.0
ICSA 42	4.8	4.9	0.0	10.4	0.0	23.3	2.7	3.0	5.0	3.0
Mean	3.5	3.5	33.6	44.5	59.6	72.8	2.7	2.9	2.6	2.4
Controls*										
IS 18551 (R)	1.2		83.8		130.4		2.0		1.0	
Swarna (S)	4.8		7.9		24.7		3.0		5.0	
For comparing	LSD	Fp	LSD	Fp	LSD	Fp	LSD	Fp	LSD	Fp
Cytoplasms (C)	NS	0.787	4.66	<0.001	6.03	<0.001	0.21	0.041	0.16	0.019
Genotypes (G)	0.25	<0.001	11.41	<0.001	14.78	<0.001	0.52	<0.001	0.40	<0.001
G x C	NS	0.129	16.13	0.051	20.90	<0.001	NS	0.632	0.56	<0.001

* = Controls were not included in the analysis of variance. R = Resistant. S = Susceptible. NS = Nonsignificant at P = 0.05. LSD = Least significant difference for comparing means at P = 0.05. Fp = F-probability.

Influence of CMS on expression of biochemical traits associated with resistance to sorghum shoot fly

The pigmentation scores for plumule and leaf sheath were numerically greater in the maintainer lines than in the CMS lines, although there were a few exceptions (Table 6). The leaf sheath pigmentation in the CMS lines SPSFR 94034, SP 55299, and 296 was significantly greater than in their respective maintainer lines. The genotypes SPSFR 94011, SPSFR 94012, and SP 55299 showed similar levels of pigmentation in the plumule. The genotypes SP 55301, Tx 623, CK 60, and ICSA 42 were tan type (non-pigmented).

Chlorophyll content of the CMS and maintainer lines varied from 31.3 to 38.5 g m^{-2} and 33.5 to 37.0 g m^{-2} at 10 DAE; and 40.2 to 53.0 g m^{-2} and 37.4 to 53.8 g m^{-2} at 80 DAE, respectively (Table 6). The chlorophyll content of CMS lines was relatively lower than of the maintainer lines at 10 DAE, while the opposite was true at 80 DAE, except in SPSFR 94012, SP 55299, SP 55301, Tx 623, CK 60, and ICSA 42. Waxy scores of the CMS and maintainer lines were similar to the susceptible check, Swarna, except in SPSFR 94007, SP 55299, and SP 55301 (Table 6). The resistant check, IS 18551, had significantly less wax covering on leaves and stem as compared to the CMS and maintainer lines tested.

Table 6. Plumule and leaf sheath pigmentation, waxy bloom, and chlorophyll content of cytoplasmic male-sterile (A) and maintainer (B) lines of sorghum (ICRISAT, Patancheru, India; 2002-2003).

Genotypes	Pigmentation score				Chlorophyll (g m^{-2})				Waxy bloom score	
	Plumule		Leaf sheath		10 DAE		80 DAE			
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	1.7	2.0	3.0	2.7	34.7	35.4	44.8	42.6	4.4	5.0
SPSFR 94012	1.3	2.3	3.0	3.0	34.0	33.5	45.4	44.1	5.0	5.0
SPSFR 94006	3.0	2.3	3.0	3.0	33.0	34.2	41.9	40.7	4.2	4.0
SPSFR 94007	2.7	2.2	3.0	3.0	31.3	35.1	42.7	40.7	3.9	3.9
SPSFR 94010	2.7	2.7	3.3	2.8	33.1	34.3	47.3	37.4	4.5	5.0
SPSFR 94034	2.3	3.0	3.3	4.0	33.4	35.2	44.6	38.8	4.4	5.0
SP 55299	2.0	2.0	2.3	3.3	37.0	36.1	41.4	43.0	3.7	3.7
SP 55301	4.3	5.0	5.0	5.0	33.9	33.5	40.2	45.0	3.7	3.9
296	3.7	3.7	3.0	4.0	37.2	34.7	48.4	40.2	5.0	5.0
Tx 623	4.3	4.7	4.7	4.7	38.5	37.0	48.1	51.5	5.0	5.0
CK 60	4.7	4.7	5.0	5.0	37.7	36.9	53.0	53.8	5.0	5.0
ICSA 42	4.0	5.0	4.7	5.0	32.9	34.9	43.6	46.3	5.0	5.0
Mean	3.1	3.3	3.6	3.8	34.7	35.1	45.1	43.7	4.5	4.6
Controls*										
IS 18551 (R)	1.3		2.2		32.8		42.9		3.2	
Swarna (S)	1.7		3.3		33.8		48.4		5.0	
For comparing	LSD	Fp	LSD	Fp	LSD	Fp	LSD	Fp	LSD	Fp
Cytoplasms (C)	NS	0.160	0.19	0.058	NS	0.307	NS	0.121	NS	0.153
Genotypes (G)	0.81	<0.001	0.46	<0.001	1.63	<0.001	4.51	<0.001	0.23	<0.001
G x C	NS	0.573	0.65	0.03	2.31	0.024	6.38	0.041	NS	0.621

* = Controls were not included in the analysis of variance. R = Resistant. S = Susceptible. NS = Nonsignificant at P = 0.05. LSD = Least significant difference for comparing means at P = 0.05. Fp = F-probability. DAE = Days after seedling emergence.

Association of physico-chemical traits with resistance to sorghum shoot fly

Leaf glossiness, trichome density, and plumule and leaf sheath pigmentation were significantly and negatively associated with eggs plants^{-10}, percentage plants with eggs, and deadhearts (Table 7). The chlorophyll content, leaf surface wetness, and waxy bloom were positively associated with susceptibility to shoot fly. Multiple linear regression analysis revealed that these physico-chemical traits explained 83.4% of the total variation in eggs plants^{-10}, 79.8% of the variation in plants with eggs, and 82.4% of the variation in deadhearts (Table 7). Stepwise regression analysis indicated that the trichome density (adaxial) (X_8) and waxy bloom (X_9) explained 84.9% variation in eggs plants^{-10} (R^2= 84.9%) and 85.1% of the total variation in percentage plants with eggs (R^2= 85.1%). Leaf glossiness (X_2) explained 81.0% of the total variation in percentage plants with deadhearts (R^2= 81.0%).

Table 7. Associations among nine physico-chemical characteristics of the sorghum genotypes tested, and eggs per 10 plants, plants with eggs, and deadhearts at 14 days after seedling emergence (ICRISAT, Patancheru, India; 2002-2003).

Characters	Correlation coefficient (r)		
	Eggs plants^{-10}	Plants with eggs (%)	Deadhearts (%)
Chlorophyll content (X_1)	0.63**	0.64**	0.63**
Leaf glossiness (X_2)	0.90**	0.88**	0.91**
Leaf sheath pigmentation (X_3)	0.53**	0.46*	0.50**
Leaf surface wetness (X_4)	0.79**	0.74**	0.78**
Plumule pigmentation (X_5)	0.45*	0.40*	0.45*
Seedling vigor (X_6)	0.24	0.04	0.04
Trichomes (abaxial) (X_7)	-0.85**	-0.89**	-0.85**
Trichomes (adaxial) (X_8)	-0.88**	-0.91**	-0.89**
Waxy bloom (X_9)	0.68**	0.59**	0.61**

*, ** Correlation coefficients significant at P = 0.05 and 0.01, respectively.

Regression equation for number of eggs per 10 plants with physico-chemical traits:
Multiple linear regression equation
Eggs plants^{-10} (Y) = $-0.56 + 0.01X_1 + 0.03X_2 + 0.06X_3 - 0.01X_4 - 0.05X_5 + 0.09X_6 + 0.0004X_7 - 0.003X_8 + 0.37X_9$ (R^2 = 83.4%)

Regression equation for plants with eggs with physico-chemical traits:
Multiple linear regression equation
Plants with eggs (Y) = $68.9 - 0.01X_1 + 1.29X_2 + 2.05X_3 - 0.43X_4 - 2.38X_5 - 2.72X_6 + 0.06X_7 - 0.17X_8 - 7.59X_9$ (R^2 = 79.8%)

Regression equation for percentage deadhearts with physico-chemical traits:
Multiple linear regression equation
Deadhearts (Y) = $57.7 - 0.61X_1 + 5.89X_2 + 6.64X_3 + 0.67X_4 - 6.02X_5 - 9.93X_6 + 0.33X_7 - 0.34X_8 + 11.01X_9$ (R^2 = 82.4%)

Direct and indirect effects of physico-chemical traits on shoot fly damage

The path-coefficient analysis (Table 8) showed that the eggs plants^{-10}, plants with eggs, leaf surface wetness, leaf sheath pigmentation, leaf glossiness, trichomes on the adaxial surface of the leaf, and waxy bloom had correlation and direct effects on deadhearts in the same direction (+ve or -ve). Conversely, the correlation coefficients and the direct effects for plumule pigmentation and trichomes on the abaxial surface of the leaf were in the opposite direction. The indirect effects of eggs plants^{-10}, plants with eggs, leaf surface wetness, leaf sheath pigmentation, and waxy bloom on deadhearts were largely through trichomes on the adaxial surface of the leaf and leaf glossiness.

Table 8. Direct and indirect effects (path coefficients) of eggs per 10 plants, plants with eggs, and nine physico-chemical traits on deadhearts due to sorghum shoot fly in cytoplasmic male-sterile and maintainer lines of sorghum (ICRISAT, Patancheru, India; 2002-2003).

Character	EP	PWG	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	r
EP	**0.29***	0.21	-0.11	0.36	0.18	0.07	-0.11	-0.06	-0.63	0.68	0.03	0.90**
PWG	0.27	**0.23**	-0.11	0.35	0.16	0.07	-0.10	-0.01	-0.65	0.70	0.02	0.92**
Chlorophyll content (X_1)	0.18	0.15	**-0.18**	0.26	0.17	0.05	-0.12	0.03	-0.43	0.49	0.02	0.63**
Leaf glossiness (X_2)	0.26	0.20	-0.12	**0.40**	0.18	0.07	-0.13	-0.04	-0.64	0.71	0.02	0.91**
LS pigmentation (X_3)	0.15	0.10	-0.09	0.21	**0.35**	0.04	-0.22	-0.05	-0.38	0.38	0.01	0.50**
Leaf surface Wetness (X_4)	0.23	0.17	-0.09	0.33	0.14	**0.09**	-0.08	-0.05	-0.56	0.59	0.02	0.78**
Plumule pigmentation (X_5)	0.13	0.09	-0.09	0.20	0.31	0.03	**-0.25**	-0.02	-0.32	0.35	0.01	0.45**
Seedling vigor (X_6)	0.07	0.01	0.02	0.07	0.07	0.02	-0.02	**-0.25**	-0.03	0.08	0.00	0.04
Trichomes (abaxial) (X_7)	-0.25	-0.20	0.10	-0.35	-0.18	-0.07	0.11	0.01	**0.74**	-0.74	-0.02	-0.85**
Trichomes (adaxial) (X_8)	-0.25	-0.21	0.11	-0.36	-0.17	-0.07	0.11	0.02	0.71	**-0.77**	-0.20	-0.89**
Waxy bloom (X_9)	0.20	0.13	-0.07	0.24	0.07	0.06	-0.03	-0.02	-0.37	0.37	**0.04**	0.61**

* Direct effects

Path coefficient equation:

Deadhearts (%) = 40.5 + 0.29 EP + 0.23 PWG - 0.18X_1 + 0.40X_2 + 0.35X_3 + 0.09X_4 - 0.25X_5 - 0.26X_6 + 0.74X_7 - 0.77X_8 + 0.04X_9 (Residual variance = 0.08)

** Correlation coefficients significant at P = 0.01. EP = Eggs plants^{-10}. PWG = Plants with eggs (%). LS = Leaf sheath. The bold values across diagonal are direct effects of a trait, while the rest of the values are indirect effects.

Principal component analysis

Principal component analyses based on oviposition, deadhearts, and physico-chemical traits indicated that there was considerable diversity among the genotypes tested. Principal component analysis placed the CMS lines into III groups [I = SPSFR 94011A and SP 55301A; II = SPSFR 94006A, SPSFR 94007A, SPSFR 94034A, and SP 55299A; and III = SPSFR 94012A, SPSFR 94010A, 296A, Tx 623A, CK 60A, and ICSA 42A] (Figure 2). The maintainer lines were also placed in three groups, [I = SPSFR 94011B, SPSFR

94006B, SPSFR 94034B, and SP 55299B; II = SPSFR 94007B, SPSFR 94010B, and SP 55301B; and III = SPSFR 94012B, 296B, Tx 623B, CK 60B, and ICSA 42B] (Figure 3). The grouping pattern was similar for CMS and the respective maintainer lines, except in the case of SPSFR 94011, SPSFR 94007, and SPSFR 94010.

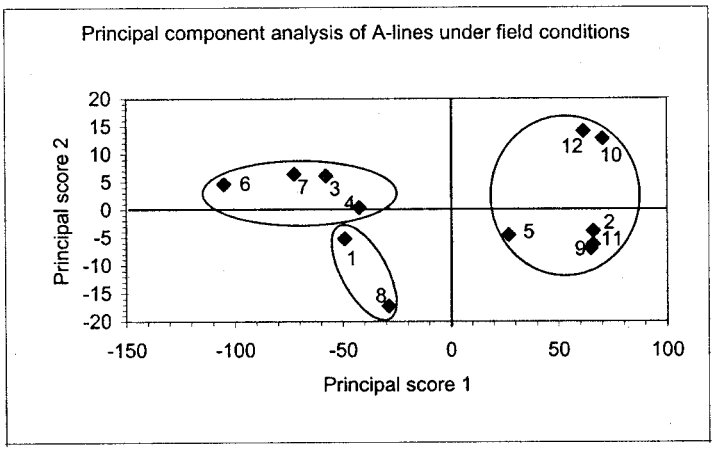

Figure 2. Principal component analysis of 12 cytoplasmic male-sterile lines of sorghum based on number of eggs per 10 plants, percentage plants with eggs, deadhearts, and physico-chemical characteristics (1= SPSFR 94011A, 2= SPSFR 94012A, 3= SPSFR 94006A, 4= SPSFR 94007A, 5= SPSFR 94010A, 6= SPSFR 94034A, 7= SP 55299A, 8= SP 55301A, 9= 296A, 10= Tx 623A, 11= CK 60A, and 12= ICSA 42A).

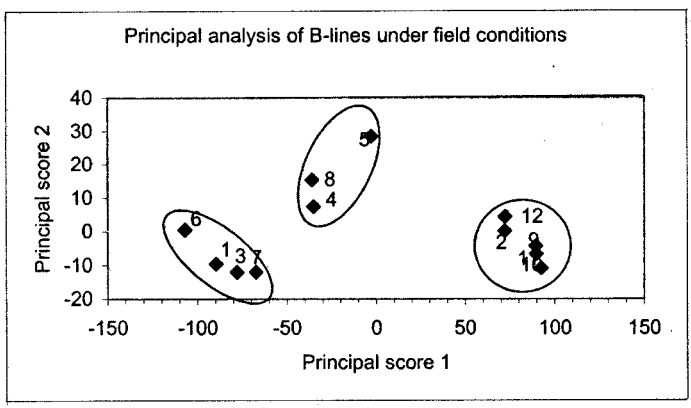

Figure 3. Principal component analysis of 12 maintainer lines of sorghum based on number of eggs per 10 plants, percentage plants with eggs, deadhearts, and physico-chemical characteristics (1= SPSFR 94011B, 2= SPSFR 94012B, 3= SPSFR 94006B, 4= SPSFR 94007B, 5= SPSFR 94010B, 6= SPSFR 94034B, 7= SP 55299B, 8= SP 55301B, 9= 296B, 10= Tx 623B, 11= CK 60B, and 12= ICSA 42B).

DISCUSSION

Oviposition non-preference (antixenosis), antibiosis, and recovery are the major components of resistance in sorghum to shoot fly, *A. soccata* (Doggett *et al.*, 1970; Raina *et al.*, 1981; Sharma and Nwanze, 1997). Non-preference for oviposition- the primary mechanism of resistance in sorghum to shoot fly, is not operative under no-choice conditions (Soto, 1974; Taneja and Leuschner, 1985; Dhillon *et al.*, 2005). Tiller development as a result of damage to the main shoot and tiller survival depend on the level of primary resistance and shoot fly abundance (Doggett *et al.*, 1970). The recovery resistance in shoot fly-resistant maintainer lines was better than in the CMS lines, while no such differences were observed for productive tillers. The shoot fly-resistant genotypes had more productive tillers than the susceptible ones (Table 9), and varieties with recovery resistance yield more under shoot fly infestation (Raina, 1985).

Table 9. Expression of resistance/susceptibility to sorghum shoot fly and physico-chemical traits in shoot fly-resistant and -susceptible genotypes of sorghum (ICRISAT, Patancheru, India; 2002-2003).

Components of resistance	Resistant group		Susceptible group	
	A-lines	B-lines	A-lines	B-lines
Eggs plants^{-10} (14 DAE)	10.4± 0.28	9.5± 0.28	15.6± 0.48	15.3± 0.48
Plants with eggs (%) 14 DAE	78.5± 2.02	71.5± 2.02	92.7± 0.64	92.3± 0.64
Deadhearts (%) 14 DAE	47.6± 2.47	41.6± 2.47	75.6± 1.79	74.1± 1.79
Deadhearts (%) 21 DAE	72.2± 2.12	64.9± 2.12	91.3± 0.62	90.7± 0.62
Deadhearts (%) 28 DAE	79.3± 1.54	74.0± 1.54	95.1± 0.04	94.9± 0.04
Tiller deadhearts (%) 28 DAE	42.9± 1.21	42.6± 1.21	53.7± 0.69	53.9± 0.69
Productive tillers (%)	51.1± 0.71	51.9± 0.71	46.3± 0.95	44.9± 0.95
Recovery resistance score	5.8± 0.41	5.3± 0.41	6.8± 0.17	7.0± 0.17
Leaf glossiness	2.5± 0.20	2.5± 0.20	4.9± 0.21	4.9± 0.21
Trichomes density (Abaxial)	57.6± 10.78	73.8± 10.78	0.1± 0.97	3.5± 0.97
Trichomes density (Adaxial)	102.0± 10.30	119.1± 10.30	0.3± 2.21	7.9± 2.21
Leaf surface wetness	1.4± 0.20	1.3± 0.20	4.3± 0.05	3.9± 0.05
Seedling vigor	2.5± 0.15	2.8± 0.15	2.8± 0.10	3.0± 0.10
Pigmentation (plumule)	2.7± 0.00	2.7± 0.00	3.6± 0.25	4.1± 0.25
Pigmentation (leaf sheath)	3.3± 0.05	3.4± 0.05	4.1± 0.10	4.3± 0.10
Waxy bloom	4.1± 0.15	4.4± 0.15	5.0± 0.00	5.0± 0.00
Chlorophyll content (gm^{-2}) 10 DAE	33.8± 0.52	34.8± 0.52	36.1± 0.32	35.4± 0.32
Chlorophyll content (gm^{-2}) 80 DAE	43.3± 1.05	41.2± 1.05	47.7± 0.25	47.2± 0.25

The values are Mean ± SE at P = 0.05 (based on mean of seven genotypes in the shoot fly-resistant and five in the shoot fly-susceptible groups across three replications).

The shoot fly-resistant CMS lines were preferred for oviposition and had more deadhearts as compared to the respective maintainer lines, while the maintainer lines of the shoot fly-susceptible parents were as susceptible as the CMS lines (Table 9). Similar findings have earlier been reported for sorghum midge, *Stenodiplosis sorghicola* (Coq.), where the midge-resistant CMS lines suffered more midge damage than the respective maintainer lines (Sharma *et al.*, 1994; Sharma, 2001). Ergot (*Claviceps fusiformis*) severity in pearl millet A-lines has also been found to be greater than in the B-lines and in the open pollinated varieties (Thakur *et al.*, 1989). Cytoplasmic male-sterility also influences the reactions to the pathogens *Pyricularia oryzae* and *Xanthomonas compestris* pv. *oryzae* in rice (Yang *et al.*, 1989).

The intensity of leaf glossiness at the seedling stage and trichomes on the adaxial surface of leaves are associated with expression of resistance in sorghum to shoot fly (Blum, 1968; Maiti and Gibson, 1983; Maiti *et al.*, 1984; Kamatar and Salimath, 2003; Dhillon *et al.*, 2005). Trichomes on the shoot fly-resistant genotypes possibly deter the movement of the young larvae in the whorl (Gibson and Maiti, 1983; Raina, 1985). Sorghum genotypes with resistance to shoot fly were glossy, but non-glossy lines were more vigorous than the glossy lines (Omori *et al.*, 1983). The shoot fly-resistant genotypes had more plumule and leaf sheath pigmentation and less chlorophyll content than the susceptible genotypes. Purple-pigmented plant types and low levels of chlorophyll content have significant and positive associations with resistance to sorghum shoot fly. Singh *et al.* (1981) and Kamatar *et al.* (2002) also reported the similar effects of these traits on genotypic reaction to shoot fly damage. Cultivars with a high transpiration rate and chlorophyll content are preferred for oviposition (Mate *et al.*, 1996). Low chlorophyll content was associated with the expression of the glossy trait in sorghum seedlings, and there are distinct differences in surface wax structure (Nwanze *et al.*, 1992) and wax composition of glossy and non-glossy genotypes (Woodhead, 1987). The reflection of light from the leaf surface and chemicals on the leaf surface might influence oviposition and deadheart formation. Refai *et al.* (1955) reported that the amounts of sugars in wheat plants infested with Hessian fly, *Maytiola destructor* (Say), were double than those in healthy plants, which may be due to inhibition of phosphorylase enzyme by insect secretions or due to greater concentration of chlorophyll in certain leaves of infested plants than in the healthy plants. A smooth amorphous wax layer and sparse wax crystals characterize shoot fly-resistant and moderately-resistant genotypes, while susceptible genotypes possess a dense mesh of crystalline epicuticular wax (Nwanze *et al.*, 1992). The shoot fly-resistant A- and B-lines had relatively less leaf surface wetness (LSW score <2.5) than the susceptible lines (score >3 to 5) (Table 9). A highly waxy leaf may retain more water as droplets than a non-waxy leaf and vice-versa, and leaf surface wetness is associated with susceptibility to sorghum shoot fly (Nwanze *et al.*, 1990a, b).

CONCLUSIONS

The resistance/susceptibility to shoot fly is influenced not only by the cytoplasm, but also by the nuclear genes. Similar observations have been reported in the case of genotypic susceptibility to sorghum midge, *S. sorghicola* (Sharma, 2001), and bacterial leaf blight, *X. oryzae* pv. *oryzae* in rice (Xu and Song, 1997; Xu *et al.*, 1998). It is difficult to separate the effects of cytoplasmic and nuclear genes, as CMS itself is the result of interaction between cytoplasmic and nuclear genes. The present findings suggest that the

resistance/susceptibility to shoot fly is influenced by the factors associated with cytoplasmic male-sterility. However, there were few exceptions, which may be because of differences in the level of interaction between cytoplasmic and nuclear genes of a particular CMS line. Correlation, path coefficient, and multiple linear and stepwise regression analyses indicated that leaf surface wetness, leaf sheath pigmentation, leaf glossiness, trichomes on the adaxial surface of the leaf, and waxy bloom are associated with resistance/susceptibility to *A. soccata*. These traits have high narrow sense heritability (13 to 61%, except for trichome density) and additive type of gene action (Dhillon *et al.*, 2006), and thus can be used as marker traits to select sorghum with resistance to this insect. There is a need to transfer the traits associated with resistance to sorghum shoot fly (Dhillon *et al.*, 2006) into CMS, maintainer, and restorer lines to develop sorghum hybrids with resistance to this insect pest for sustainable crop production.

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