Influence of Cytoplasmic Male Sterility on Expression of Different Mechanisms of Resistance in Sorghum to *Atherigona soccata* (Diptera: Muscidae)

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J. Econ. Entomol. 99(4): 1452–1461 (2006)

ABSTRACT *Atherigona soccata* (Rondani) (Diptera: Muscidae) is one of the most important pests of sorghum, *Sorghum bicolor* (L.) Moench, in Asia, Africa, and the Mediterranean Europe. Exploitation of cytoplasmic male sterility (CMS) for hybrid production has resulted in considerable narrowing of the genetic base and may increase the vulnerability of this crop to insect pests. Therefore, we studied the expression of different mechanisms of resistance in sorghum to *A. soccata* in CMS (A) and maintainer (B) lines of 12 genotypes under field and greenhouse conditions. The CMS lines of *A. soccata*-resistant genotypes were preferred for oviposition (78.5 versus 71.5% plants with eggs) and suffered greater deadheart incidence (47.6 versus 41.6%) than the corresponding maintainer lines, whereas such differences were not apparent in CMS lines belonging to the susceptible genotypes (92.7 versus 92.3% plants with eggs and 75.6 versus 74.6% deadhearts) under multichoice field conditions. Similar differences also were observed under controlled conditions in the greenhouse. The larval period (9.0 versus 8.8 d) and pupal mortality (18.4 versus 13.4%) were greater on maintainer lines than that on the CMS lines in the resistant group. The male and female pupal weights, fecundity, and antibiosis index were greater on the CMS than on the maintainer lines. The maintainer lines showed better recovery resistance than the CMS lines, but no such differences were observed in tiller deadhearts. The differences in susceptibility to *A. soccata* were greater in the *A. soccata* resistant CMS and maintainer lines than in the CMS and maintainer lines belonging to susceptible genotypes. Conversion of *A. soccata*-resistant genotypes into alternate less susceptible cytoplasmic backgrounds may be undertaken for developing sorghum hybrids with stable resistance to *A. soccata*.

KEY WORDS *Atherigona soccata*, cytoplasmic male sterility, mechanisms of resistance

Sorghum, *Sorghum bicolor* (L.) Moench, is one of the most important cereal crops in the semiarid tropics. It is grown in nearly 86 countries covering an area of ≈43.66 million ha with a grain production of 62.83 million tons and an average productivity of 1.45 tons/ha, of which 30% of the total global area and production is in Asia (FAO 2002). The yield penalties to sorghum are very high, starting from seedling stage to harvest, and are largely the result of biotic stresses. Among the biotic constraints, insect pests are predominant, causing nearly 32% of the total loss to the actual produce in India (Borad and Mittal 1983), 20% in Africa and Latin America, and 9% in United States (Wiseman and Morrison 1981). Insect pests cause losses of >$1 billion in grain and forage yield of sorghum worldwide.

Atherigona soccata (Rondani) (Diptera: Muscidae) is one of the most important pests of sorghum in Asia, Africa, and the Mediterranean Europe. The adult fly lays white, elongated, cigar-shaped eggs singly on the undersurface of the leaves, parallel to the midrib. After hatching the larvae crawl to the plant whorl and move downward between the folds of the young leaves until they reach the growing point. They cut the growing tip and feed on the decaying leaf tissues, resulting in "deadheart" formation. Shoot flies of the genus *Atherigona* are also known to cause deadhearts in several tropical grass species (Deeming 1971, Pont 1972) and wheat (Pont and Deeming 2001). *A. soccata* infestation levels in sorghum can be very high and vary from 0 to 90% (Hiremath and Renukarya 1966, Rao and Gowda 1967), which at times may cause 100% damage under severe outbreak.

Host plant resistance is one of the most effective means of keeping *A. soccata* populations below economic threshold levels, because it does not involve any cost input by the farmers. Plant resistance to *A. soccata* seems to be a complex character and depends on the interplay of number of componential characters, which finally sum up in the expression of resistance to *A. soccata.* Several genotypes with resistance to

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0022-0493/06/1452–1461$04.00/0

A. soccata have been identified, but the levels of resistance are low to moderate (Jotwani 1978, Taneja and Leuschner 1985, Sharma et al. 1992). Therefore, it is important to identify and transfer genes for different mechanisms of resistance into the same genetic background. The discovery of cytoplasmic male sterility (CMS) in sorghum and its subsequent exploitation for hybrid production has revolutionized sorghum production worldwide. Stephens and Holland (1954) reported the first usable sources of CMS resulting from introduction of *Kafir* genes into *Milo* cytoplasm. Effective use of CMS has made it easier to incorporate the desired characters into hybrid parents (House 1985). Most of the hybrids grown in India are based on *Milo* cytoplasm (A_1 cytoplasm). However, CMS has recently been recognized as a potential danger to the stability of crop production as a result of greater susceptibility to insect pests. Such effects of *Milo* cytoplasm have recently been reported for *Stenodiplosis sorghicola* (Coquillett); *A. soccata;* and sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Sharma 2001, Sharma et al. 2004, Dhillon et al. 2005a). However, there is no information on the expression of different mechanisms of resistance to *A. soccata* in CMS (A) and maintainer (B) lines with different levels of resistance/susceptibility to this insect. Therefore, the present studies were carried out to study the effects of CMS on expression of different mechanisms of resistance in sorghum to this pest.

Materials and Methods

Test Material. The experiments were conducted at the International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India, between 2002 and 2003. The experimental material consisted of CMS and maintainer lines of 12 sorghum genotypes (SPSFR 94011, SPSFR 94012, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, SP 55301, Tx 623, 296, CK 60, and ICSA 42) along with resistant (IS 18551) and susceptible (Swarna) checks.

Field Studies. *Screening Technique.* The test material was planted in four-row plots of 2-m row length, with rows 75 cm apart, in a randomized complete block design in three replications. The seed was planted with a four-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. *A. soccata* infestation was optimized through the use of interlard fish-meal technique (Sharma et al. 1992). Normal agronomic practices were followed for raising the sorghum crop. There was no insecticide application in the experimental plots. The infester rows were chopped off 30 d after seedling emergence in the test plots to avoid shading and competition. Data were recorded on oviposition nonpreference, deadheart formation, and recovery resistance.

Relative Susceptibility of CMS and Maintainer Lines to A. soccata under Multichoice Conditions in the Field. Total numbers of plants with eggs and deadhearts under multichoice conditions in the field were recorded in the central two rows at 14 d after seedling emergence (DAE) and expressed as percentage of the total number of plants with eggs and deadhearts.

Recovery Resistance. The number of tillers with deadhearts was recorded at 28 DAE from the central two rows and computed as percentage of the total number of tillers with deadhearts. The healthy plants were tagged 1 mo after seedling emergence. At crop maturity, total number of tillers and the tillers having panicles with grain were recorded and expressed as percentage productive tillers. The recovery resistance was scored on a scale of 1–9 by taking into account the number of productive tillers at maturity, their height, and panicle size in comparison with main plant (1, >80% plants with two to three uniform productive tillers; and 9, <20% damaged plants with one to two productive tillers).

Greenhouse Studies. *Insect Culture. A. soccata* culture was maintained in the greenhouse from the *A. soccata* females collected from fish-meal-baited traps in the field. The traps were placed 50 cm apart in fields having sorghum crop at the seedling stage. A plastic jar filled with moist fish-meal was kept inside a plastic bucket with 0.5-cm-diameter holes (spaced 10 cm apart). The fish-meal in the jars was replaced with fresh moist fish-meal every 4 d. The flies were collected in the morning between 0730 and 0830 hours in collection bottles by using an aspirator and released inside wire mesh screened cages (30 by 30 by 30 cm) in the greenhouse. Female *A. soccata* were separated from other flies and released in a separate cage. Female *A. soccata* were provided with 20% sucrose solution on a cotton swab, and a mixture of brewer's yeast and glucose (1:1) in a petri dish. The sucrose solution was changed daily, whereas the yeast powder–glucose mixture was changed every 3 d.

Relative Susceptibility of CMS and Maintainer Lines to A. soccata *under Greenhouse Conditions.* Oviposition nonpreference and deadheart formation in the test material was studied under no-, dual-, and multichoice conditions in the greenhouse in a wire mesh, screened plastic cage (40 by 30 by 28 cm). The plastic cage consisted of two plastic trays: one tray for planting the test material, and a second tray fitted with a wire mesh screen on the sides (10 by 15 cm) and at the top (10 by 15 cm). The screen on the top of the plastic tray had a 5-cm-diameter hole, which was blocked with a 20-ml plastic cup. The test entries were planted in the plastic trays (40 by 30 by 14 cm) (half filled with potting mixture of black soil and farmyard manure (3:1) + 15–20 g of diammonium phosphate per tray before planting) in four rows accommodating 40 plants per tray. For no-choice tests, only one test entry was planted in each tray. For dual-choice tests, two rows of the CMS (10 plants each) and two rows of the respective maintainer lines were planted in each tray. There were six replications for dual-choice and three replications for no-choice

tests in a completely randomized design (CRD). The plastic tray with screened wire mesh was clamped on to the tray with sorghum seedlings. The test material was exposed to *A. soccata* females (two flies per five plants or 16 flies per 40 plants) at 9 d after seedling emergence (at the fifth-leaf stage) for 24 h. After 24 h, *A. soccata* females were removed from the trays, and data were recorded on the number of plants with eggs. Five days after infestation, data were recorded on the number of plants with deadhearts. Data on plants with eggs and plants with deadhearts were expressed as percentage of the total number of plants.

Antibiosis. To quantify antibiosis component of resistance, appearance of deadhearts in the no-choice tests was monitored at 12-h intervals to determine the time taken by the larvae to reach the growing point, so as to have an indication of the larval survival. The deadhearts were labeled for the time of appearance. Four days after deadheart formation, 15 deadhearts of same age in each replication were uprooted and placed in 20-ml glass vials individually. Observations were recorded on larval and pupal periods, pupation, pupal weight, adult emergence, and fecundity. There were three replications in a CRD. The deadhearts collected in glass vials were observed daily after 6 d of deadheart formation to record time to pupation. Number of days from deadheart appearance to pupation plus 1 d (because it takes 1 d for deadheart realization after egg hatching) was recorded as the larval period. Larval period was recorded for each insect separately, and the mean larval period for each replication was computed for the surviving larvae (out of 15 larvae). Data also were recorded on the number of surviving larvae and expressed as percentage larval survival. The pupal period was recorded separately for each insect, and the mean pupal period per replication was calculated for the surviving pupae. Pupal weight (milligrams) was measured for individual pupa on an electronic balance within 24 h after pupation. The pupae were sorted into males and females, and the pupal weights were recorded separately for each sex. The pupae were placed in moist sand to avoid the water loss and pupal mortality because of desiccation. For fecundity studies, five pairs of shoot flies emerging from larvae reared on each genotype were released in metal cages (30 cm in diameter and 30 cm in height) covered with a nylon bags (60 mesh). The adult flies were provided with 20% sucrose solution in a cotton swab, and brewer's yeast + glucose (1: 1) in a petri dish. Ten sorghum seedlings (planted in plastic 10-cm-diameter pots) of the same entry, on which the larvae were fed, were provided to *A. soccata* throughout the adult life span for oviposition. The seedlings were changed on alternate days, and data were recorded on number of eggs laid. Data on different biological parameters were used for computing various indices, such as development index, weight index, adult emergence index, Howe's growth index, fecundity index, and antibiosis index as suggested by Dhillon et al. (2005a,b).

Statistical Analysis. Data were subjected to analysis of variance (ANOVA) by using GENSTAT release 8.0. The multichoice and no-choice data were analyzed by factorial analysis in a randomized complete block design. The significance of differences between the treatments was measured by *F*-test, whereas the treatment means were compared using Tukey's honestly significant difference (HSD) test at $P = 0.05$. For the dual-choice tests, paired *t*-tests were used to test the significance of differences at $P = 0.05$. The number of resistant and susceptible genotypes were estimated as resistant = $\leq B + X$ and susceptible = $\geq B + 2X$ [$X = (A - B)/2$, where A is deadhearts (percentage) in the susceptible check, and B is deadhearts (percentage) in the resistant check]. The resistant and susceptible CMS and the maintainer lines were separately averaged, and the CMS and the maintainer lines in different groups were then compared for antixenosis, antibiosis, and recovery mechanisms of resistance to *A. soccata.*

Table 1. Relative resistance/susceptibility of 12 CMS (A) and maintainer (B) lines of sorghum to *A. soccata* under multi-choice conditions in the field (ICRISAT, Patancheru 2002–2003)

Breeding line	Plants with eggs (%)		Deadhearts (%)	
	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	83.1 ± 3.99bc**	70.0 ± 7.51abc*	42.4 ± 6.55ab*	45.9 ± 8.55b**
SPSFR 94012	85.8 ± 5.86cd*	87.4 ± 4.29e*	71.8 ± 7.33e**	66.2 ± 7.89c*
SPSFR 94006	78.4 ± 5.76ab**	73.5 ± 6.31bcd*	52.6 ± 8.14cd**	45.0 ± 7.43ab*
SPSFR 94007	76.1 ± 5.75a*	78.1 ± 6.74d*	51.5 ± 7.70c**	40.6 ± 7.46ab*
SPSFR 94010	86.7 ± 2.66cd**	75.2 ± 5.75cd*	59.4 ± 5.84de**	40.2 ± 6.85ab*
SPSFR 94034	74.5 ± 6.86a**	69.4 ± 8.81ab*	40.2 ± 6.83a**	37.7 ± 7.97a*
SP 55299	75.5 ± 7.56a**	68.4 ± 7.05ab*	49.5 ± 7.98bc**	38.3 ± 6.71a*
SP 55301	74.9 ± 4.85a**	65.9 ± 7.73a*	37.9 ± 6.67a*	43.6 ± 7.51ab**
296	93.4 ± 1.82ef**	90.8 ± 3.24ef*	67.8 ± 8.42e*	71.8 ± 7.34cd**
Tx 623	97.5 ± 1.34f*	96.7 ± 1.13g*	85.3 ± 3.47f*	83.0 ± 3.73e*
CK 60	91.3 ± 3.91de*	93.6 ± 2.87fg*	69.0 ± 9.16e*	75.5 ± 6.67d**
ICSA 42	95.6 ± 1.80ef*	93.0 ± 2.36fg*	83.9 ± 4.60f**	74.0 ± 5.90d*
Checks[a]				
IS 18551 (R)	68.9 ± 6.98		33.4 ± 6.63	
Swarna (S)	92.3 ± 2.63		78.6 ± 5.98	

Values followed by the same letter within a column are not significantly different (Tukey's HSD; $P = 0.05$). The A- and B-lines in a row within a parameter having same number of asterisks are not significantly different (Tukey's HSD; $P = 0.05$).

[a] Checks were not included in the analysis of variance. R, Resistant. S, susceptible.

Table 2. Relative resistance/susceptibility of 12 CMS (A) and maintainer (B) lines of sorghum to *A. soccata* under no-choice conditions in the greenhouse (ICRISAT, Patancheru 2002–2003)

Breeding line	Plants with eggs (%)		Deadhearts (%)	
	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	96.1 ± 2.00bcd**	82.4 ± 2.89bcd*	90.8 ± 5.83a**	62.1 ± 10.21a*
SPSFR 94012	81.6 ± 17.11a**	69.0 ± 12.29a*	79.8 ± 17.55a**	65.4 ± 12.61ab*
SPSFR 94006	99.2 ± 0.83d**	87.4 ± 8.88d*	90.0 ± 5.00a**	77.7 ± 8.58bc*
SPSFR 94007	94.1 ± 4.69abcd**	73.9 ± 1.07abc*	86.9 ± 5.76a**	71.3 ± 1.05abc*
SPSFR 94010	84.8 ± 12.68abc*	89.3 ± 4.32d*	81.4 ± 13.72a*	81.1 ± 7.71c*
SPSFR 94034	91.5 ± 4.45abcd*	91.7 ± 3.33d*	86.2 ± 6.11a**	75.0 ± 3.82abc*
SP 55299	85.7 ± 4.11abc*	87.0 ± 3.92cd*	82.3 ± 3.90a**	73.8 ± 6.40abc*
SP 55301	97.4 ± 1.48cd**	88.8 ± 5.03d*	91.8 ± 1.73a**	81.5 ± 5.37c*
296	87.3 ± 6.58abcd*	83.4 ± 3.78bcd*	87.3 ± 6.58a**	77.5 ± 3.33bc*
Tx 623	81.9 ± 10.36a*	81.7 ± 8.82abc*	80.1 ± 8.34a**	73.3 ± 7.27abc*
CK 60	91.5 ± 2.41abcd**	72.5 ± 5.20ab*	89.0 ± 1.79a**	71.7 ± 4.41abc*
ICSA 42	83.3 ± 5.92ab*	93.0 ± 0.93d**	82.4 ± 5.08a*	80.9 ± 2.06c*
Checks[a]				
IS 18551 (R)	95.8 ± 3.01		80.5 ± 8.99	
Swarna (S)	100.0 ± 0.00		91.1 ± 5.88	

Values followed by the same letter within a column are not significantly different (Tukey's HSD; $P = 0.05$). The A- and B-lines in a row within a parameter having same number of asterisks are not significantly different (Tukey's HSD; $P = 0.05$).

[a] Checks were not included in the analysis of variance. R, Resistant; S, susceptible.

Results

Evaluation of A- and B-lines for Oviposition Nonpreference and Deadheart Formation. There were significant differences for oviposition preference among CMS and the maintainer cytoplasms ($F = 13.37$; df = 1, 184; $P = 0.001$) and different genotypes ($F = 23.59$; df = 11, 184; $P = 0.001$), whereas the genotypes × cytoplasm interaction ($F = 1.70$; df = 11, 184; $P = 0.077$) was nonsignificant under multichoice conditions in the field. Under no-choice conditions, there were significant differences among CMS and the maintainer cytoplasms for oviposition ($F = 5.36$; df = 1, 46; $P = 0.025$) and deadhearts ($F = 17.21$; df = 1, 46; $P = 0.001$), whereas for different genotypes ($F = 1.28$; df = 1, 46; $P = 0.266$ for oviposition and $F = 0.61$; df = 11, 46; $P = 0.811$ for deadhearts) and genotypes × cytoplasm interaction ($F = 1.06$; df = 11, 46; $P = 0.413$ for oviposition and $F = 0.62$; df = 11, 46; $P = 0.801$ for deadhearts) were nonsignificant. The oviposition preference for CMS and maintainer lines ranged from 65.9 to 97.5% plants with eggs at 14 DAE under field conditions (Table 1), from 69.0 to 99.2% under no-choice conditions (Table 2), and from 38.5 to 90.0% under dual-choice conditions (Table 3) at 10 DAE in the greenhouse. The CMS lines were more preferred for oviposition than the maintainer lines under multichoice field conditions (except SPSFR 94012, SPSFR 94007, and CK 60), no-choice (except SPSFR 94010, SPSFR 94034, SP 55299, and ICSA 42), and dual-choice (except ICSA 42) greenhouse conditions. The genotypes SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 exhibited oviposition nonpreference to *A. soccata* and were comparable with the resistant check IS 18551, whereas SPSFR 94012, 296, Tx 623, CK 60, and ICSA 42 showed a susceptible reaction and were similar to the susceptible check, Swarna in their susceptibility to *A. soccata* under multichoice field conditions.

There were significant differences for deadheart formation among CMS and the maintainer cytoplasms ($F = 7.39$; df = 1, 184; $P = 0.007$), different genotypes ($F = 38.67$; df = 11, 184; $P = 0.001$), and genotypes ×

Table 3. Relative resistance/susceptibility of 12 CMS and maintainer lines of sorghum to *A. soccata* under dual-choice conditions in the greenhouse (ICRISAT, Patancheru 2002–2003)

Breeding line	Plants with eggs (%)		*t*-value (df = 5)	Deadhearts (%)		*t*-value (df = 5)
	A-lines	B-lines		A-lines	B-lines	
SPSFR 94011	83.5	74.0	3.10 ($P = 0.027$)[a]	76.1	61.0	3.49 ($P = 0.017$)
SPSFR 94012	55.1	51.7	0.60 ($P = 0.574$)	47.1	35.0	2.13 ($P = 0.087$)
SPSFR 94006	59.2	38.5	4.44 ($P = 0.007$)	40.9	33.3	1.49 ($P = 0.197$)
SPSFR 94007	80.8	68.3	2.18 ($P = 0.081$)	75.0	60.0	4.39 ($P = 0.007$)
SPSFR 94010	73.3	65.0	1.47 ($P = 0.202$)	67.3	55.0	1.33 ($P = 0.240$)
SPSFR 94034	90.0	80.0	3.86 ($P = 0.012$)	74.7	67.5	1.81 ($P = 0.131$)
SP 55299	62.2	60.9	0.49 ($P = 0.647$)	62.2	45.5	10.41 ($P = 0.001$)
SP 55301	86.2	80.3	1.33 ($P = 0.242$)	80.6	63.3	3.60 ($P = 0.016$)
296	82.5	67.5	1.88 ($P = 0.118$)	70.0	52.5	2.41 ($P = 0.061$)
Tx 623	80.0	50.0	6.45 ($P = 0.001$)	70.0	40.0	2.82 ($P = 0.037$)
CK 60	62.5	59.0	0.56 ($P = 0.599$)	57.5	48.6	1.92 ($P = 0.113$)
ICSA 42	50.0	52.5	0.25 ($P = 0.812$)	45.0	32.5	2.61 ($P = 0.048$)

[a] *P* value within parentheses indicates the probability of significance of differences between A- and B-lines within a parameter.

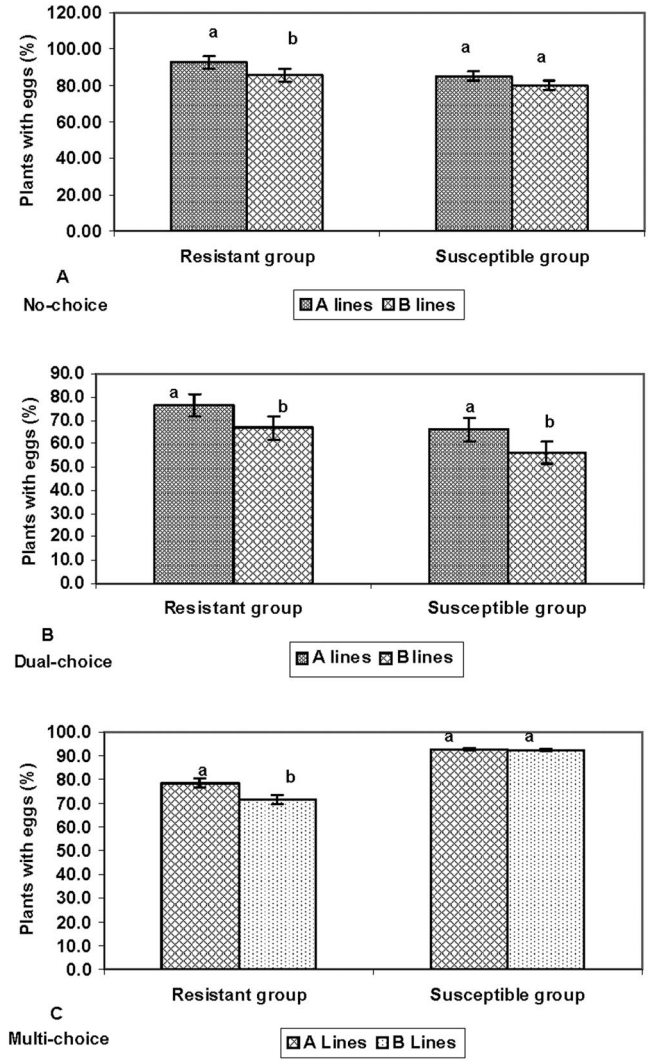

Fig. 1. Oviposition preference of *A. soccata* on resistant and susceptible CMS (A) and maintainer (B) lines of sorghum at 10 DAE under no-choice (A) and dual-choice (B) conditions in the greenhouse, and at 14 DAE (C) under multichoice field conditions. Data are means ± SE of six replications under greenhouse conditions and three replications under field conditions. Within each group, bars marked with the same letter do not differ significantly ($P = 0.05$).

cytoplasm interaction ($F = 2.33$; df = 11, 184; $P = 0.010$) under multichoice conditions in the field. Percentage of plants with *A. soccata* deadhearts ranged from 37.7 to 85.3% under multichoice conditions in the field (Table 1), from 62.1 to 91.8% under no-choice conditions (Table 2), and from 32.5 to 80.6% under dual-choice conditions (Table 3) in the greenhouse at 14 DAE. The CMS lines showed greater susceptibility to *A. soccata* damage compared with the maintainer lines under multi-, dual-, and no-choice conditions, although there were a few exceptions. The genotypes SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 were similar to the resistant check IS 18551 in their resistance/susceptibility to *A. soccata*, whereas SPSFR 94012, 296, Tx 623, CK 60, and ICSA 42 showed a susceptible reaction and were similar to the susceptible check Swarna.

The plants of *A. soccata*-resistant CMS lines were significantly more preferred by the *A. soccata* for egg laying and suffered more deadheart formation than those of the B-lines, whereas such differences between A- and B-lines of the susceptible genotypes were nonsignificant, except in case of dual-choice greenhouse conditions (Figs. 1A–C and 2A–C). However, differences in resistance/susceptibility of CMS and maintainer lines to *A. soccata* in both resistant and susceptible groups were not apparent under greenhouse conditions (Tables 2 and 3).

Recovery Resistance. The tiller deadhearts in the CMS and maintainer lines ranged from 32.7 to 58.8% at 28 DAE (Table 4). There were significant differ-

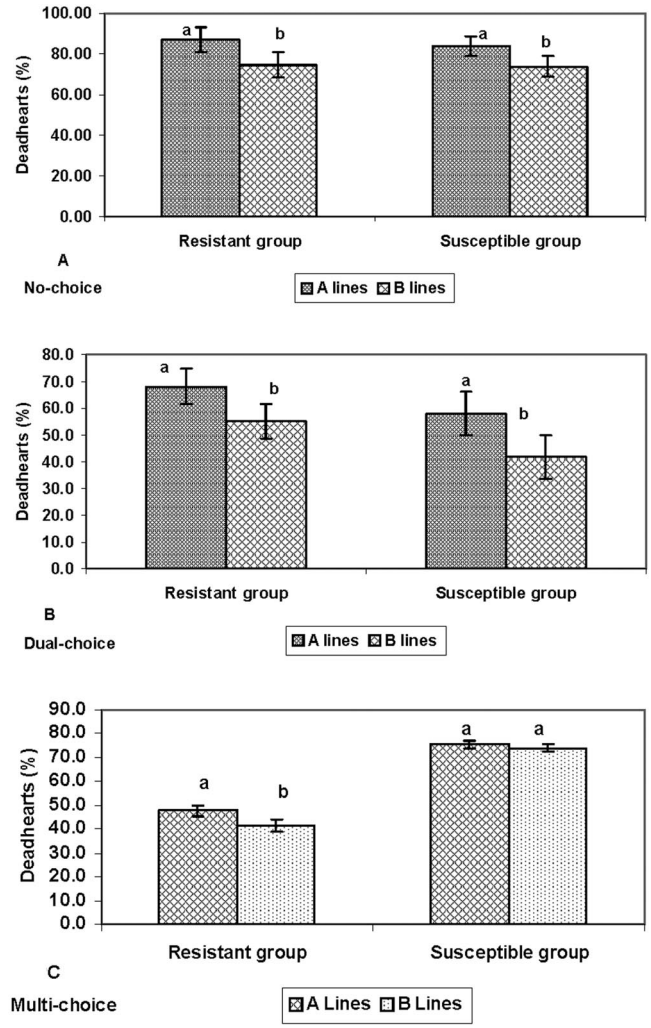

Fig. 2. *A. soccata* deadhearts in resistant and susceptible CMS (A) and maintainer (B) lines of sorghum at 14 DAE under no-choice (A) and dual-choice (B) conditions in the greenhouse and at 14 DAE (C) under multichoice field conditions. Data are means ± SE of six replications under greenhouse conditions and three replications under field conditions. Within each group, bars marked with the same letter do not differ significantly ($P = 0.05$).

ences for tiller deadhearts among the genotypes ($F = 7.29$; df = 11, 184; $P = 0.001$), whereas the differences among the CMS and maintainer cytoplasms ($F = 0.01$; df = 11, 184; $P = 0.942$) and genotype × cytoplasm interaction ($F = 0.90$; df = 11, 184; $P = 0.545$) were nonsignificant. The A and B pairs of SPSFR 94011, SPSFR 94012, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 had significantly lower percentage of tillers with deadhearts than that on susceptible check Swarna and were similar to the resistant check IS 18551. The tillers of SPSFR 94012, Tx 623, 296, CK 60, and ICSA 42 were susceptible to *A. soccata* damage and were similar to the susceptible check Swarna. Productive tillers ranged from 22.6 to 59.7 per 100 plants (Table 4). The differences for productive tillers among different genotypes ($F = 6.24$; df = 11, 184; $P = 0.001$) were also significant, whereas the differences for CMS and maintainer cytoplasms ($F = 0.01$; df = 1, 184; $P = 0.937$) and genotype × cytoplasm interaction ($F = 0.71$; df = 11, 184; $P = 0.731$) were nonsignificant. The maintainer lines of SPSFR 94006, SPSFR 94007, and Tx 623 had more productive tillers than the respective CMS lines, but the reverse was true in case of ICSA 42 and SPSFR 94010. The genotypes SPSFR 94006, SPSFR 94007, SPSFR 94010, SP 55301, and CK 60 had significantly more productive tillers than the other lines tested. The recovery score (1–9) ranged from 4.8 to 7.9 (Table 4). There were significant differences among the genotypes ($F = 13.83$; df = 11, 184; $P = 0.001$) and genotype × cytoplasm interaction ($F = 2.43$; df = 11, 184; $P = 0.008$), whereas for CMS and maintainer cytoplasms ($F = 2.07$; df = 1, 184; $P = 0.151$), the differences were nonsignificant. In general, the recovery

Table 4. Recovery resistance of 12 CMS (A) and maintainer (B) lines of sorghum in response to *A. soccata* damage (averaged across seasons) under multichoice conditions in the field (ICRISAT, Patancheru 2002–2003)

Breeding line	Tiller deadhearts (%)		Productive tillers (%)		Recovery resistance	
	A-lines	B-lines	A-lines	B-lines	A-lines	B-lines
SPSFR 94011	32.7 ± 5.50a*	35.4 ± 8.41a*	42.2 ± 5.56b*	42.3 ± 3.25b*	5.7 ± 0.60abc**	4.8 ± 0.55a*
SPSFR 94012	49.7 ± 7.13ef*	50.6 ± 6.85def*	54.1 ± 7.50cd*	52.7 ± 5.90cde*	5.5 ± 0.60ab*	5.3 ± 0.43abc*
SPSFR 94006	49.5 ± 6.87ef**	40.7 ± 6.93ab*	50.4 ± 6.28bcd*	58.5 ± 5.43e**	5.5 ± 0.31ab*	5.5 ± 0.40abc*
SPSFR 94007	41.8 ± 6.89bcd*	44.0 ± 7.05bcd*	50.1 ± 6.64bcd*	59.7 ± 3.92e**	6.3 ± 0.48c**	5.2 ± 0.49abc*
SPSFR 94010	51.0 ± 5.32ef*	48.3 ± 5.49cdef*	58.8 ± 6.00d**	46.8 ± 5.39bcd*	5.5 ± 0.45ab*	5.8 ± 0.44c**
SPSFR 94034	40.0 ± 6.59bc*	42.6 ± 7.46abc*	50.1 ± 5.61bcd*	51.3 ± 4.62bcde*	6.1 ± 0.51bc**	5.0 ± 0.33ab*
SP 55299	46.5 ± 7.65cde**	42.7 ± 6.74bc*	49.5 ± 6.41bcd*	50.3 ± 7.26bcde*	6.2 ± 0.49bc**	5.7 ± 0.50bc*
SP 55301	39.0 ± 6.30ab*	44.7 ± 0.66bcde*	56.8 ± 6.63cd**	54.6 ± 6.28de*	5.1 ± 0.58a*	5.2 ± 0.51abc*
296	47.8 ± 7.57de*	54.0 ± 7.30fg**	25.7 ± 7.27a*	22.6 ± 4.20a*	6.8 ± 0.70d*	7.3 ± 0.47d**
Tx 623	58.8 ± 5.32g**	55.1 ± 7.66fg*	47.3 ± 4.47bc*	52.5 ± 5.45cde**	7.8 ± 0.31e**	7.4 ± 0.48d*
CK 60	54.1 ± 6.32fg*	58.1 ± 6.55g**	55.5 ± 7.49cd*	52.2 ± 7.21cde*	6.0 ± 0.39abc*	7.5 ± 0.36d**
ICSA 42	58.3 ± 6.89g**	51.8 ± 7.93efg*	49.2 ± 7.26bcd*	44.3 ± 5.55bc*	7.9 ± 0.36e**	7.2 ± 0.41d*
Checks[a]						
IS 18551 (R)	40.3 ± 6.96		35.3 ± 4.49		4.3 ± 0.48	
Swarna (S)	58.9 ± 8.01		59.2 ± 6.59		6.8 ± 0.51	

Values followed by the same letter within a column are not significantly different (Tukey's HSD; $P = 0.05$). The A- and B-lines in a row within a parameter having same number of asterisks are not significantly different (Tukey's HSD; $P = 0.05$).

[a] Checks were not included in the analysis of variance. R, resistant; S, susceptible.

resistance was poor in the CMS lines compared with the respective maintainer lines, but statistically the differences among CMS and the maintainer lines were nonsignificant. The B-lines had more productive tillers (Fig. 3B) and showed better recovery resistance (Fig. 4) than the A-lines, but such differences were

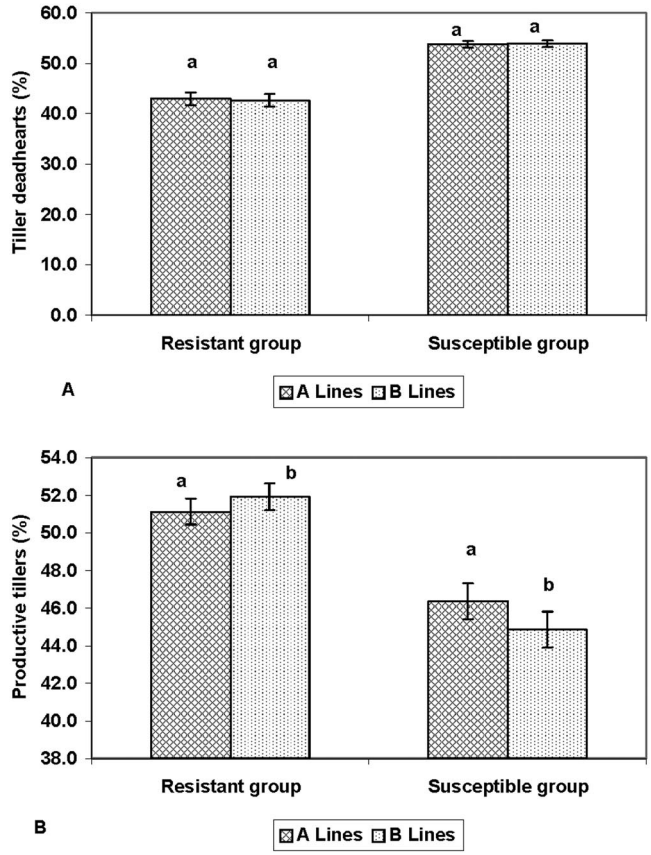

Fig. 3. Tiller deadhearts caused by *A. soccata* at 28 DAE (A) and productive tillers at maturity (B) in the resistant and susceptible CMS (A) and maintainer (B) lines of sorghum. Data are means ± SE of three replications. Within each group, bars marked with the same letter do not differ significantly ($P = 0.05$).

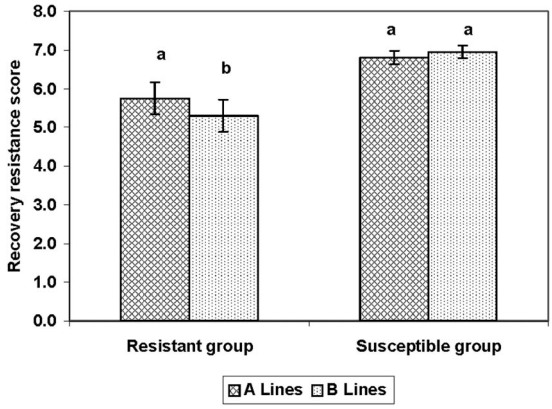

Fig. 4. Recovery resistance scores of resistant and susceptible CMS (A) and maintainer (B) lines of sorghum after damage by *A. soccata*. Data are means ± SE of three replications. Within each group, bars marked with the same letter do not differ significantly ($P = 0.05$).

not evident in case of tiller deadhearts (Fig. 3A). The *A. soccata*-resistant A/B-lines exhibited less tiller deadhearts and more productive tillers, resulting in high recovery than the susceptible lines (Figs. 3 and 4).

Antibiosis. There were considerable differences among CMS and the maintainer lines for larval period, larval survival, pupal mortality, adult emergence, and fecundity. The larval period, larval survival, pupal mortality, adult emergence, and fecundity on CMS and maintainer lines ranged from 7.6 to 9.1 d, 81.7 to 97.2%, 4.5 to 38.0%, 52.0 to 89.2%, and 81.0 to 174.6 eggs per female, respectively.

The larval period, larval survival, pupal mortality, adult emergence, and fecundity for the resistant group of CMS and maintainer lines were 8.8 versus 9.0 d, 90.6 versus 86.9%, 13.4 versus 18.4%, 77.2 versus 68.5%, and 132.4 versus 124.0 eggs per female, respectively (Table 5). Larval period and pupal mortality were greater on the maintainer lines than that on the CMS lines. Larval survival, adult emergence, pupal weights, and fecundity were greater on the CMS lines than on the maintainer lines in the resistant group, whereas such differences were not observed in the susceptible group. Similarly, adult emergence, fecundity, and antibiosis indices were greater on CMS lines than on the maintainer lines. The differences between CMS and the maintainer lines for the antibiosis parameters were more apparent in resistant than in the susceptible genotypes.

Discussion

Host plant resistance to *A. soccata* has largely been attributed to oviposition nonpreference and is considered as a primary mechanism of resistance to this insect (Blum 1967, 1969; Sharma et al. 1977; Singh and Narayana 1978; Maiti and Bidinger 1979; Singh and Jotwani 1980a; Taneja and Leuschner 1985; Unnithan and Reddy 1985). Plants without deadhearts despite oviposition can be selected for strengthening antibiosis component of resistance (Sharma and Rana 1983). In the present study, A and B pairs of SPSFR 94011, SPSFR 94006, SPSFR 94007, SPSFR 94010, SPSFR 94034, SP 55299, and SP 55301 showed oviposition nonpreference and suffered low deadheart formation. Under greenhouse conditions, the differences in oviposition preference and deadheart formation were much smaller, indicating the breakdown of oviposition nonpreference mechanism of resistance to *A. soccata* under no-choice conditions or high levels of insect density. The CMS lines were more preferred for oviposition and exhibited more susceptibility to *A. soccata* damage than the B-lines. Greater susceptibility of A-lines than the corresponding B-lines also has been observed in *S. sorghicola* (Sharma et al. 1994, Sharma 2001). The results suggested that resistance/susceptibility reaction to *A. soccata* was influenced by the CMS. However, there were a few exceptions, which may be because of differences in interaction between cytoplasmic and nuclear genes of particular CMS line or incomplete conversion of the maintainer lines into CMS lines. The resistance/susceptibility to bacterial blight in rice is influenced not only by the cytoplasm but also by the nuclear

Table 5. Survival and development of *A. soccata* on 12 CMS (A) and maintainer (B) lines of sorghum under greenhouse conditions (ICRISAT, Patancheru 2002–2003)

Biological measure	Resistant group[a] (mean ± SE, $n = 7$, $r = 3$)		Susceptible group[b] (mean ± SE, $n = 5$, $r = 3$)	
	A-lines	B-lines	A-lines	B-lines
Larval period (d)	8.8 ± 0.07	9.0 ± 0.07	8.4 ± 0.03	8.5 ± 0.03
Pupal period (d)	8.1 ± 0.01	8.1 ± 0.01	7.9 ± 0.01	7.9 ± 0.01
Larval survival (%)	90.6 ± 1.86	86.9 ± 1.86	90.9 ± 0.05	91.0 ± 0.05
Pupal mortality (%)	13.4 ± 2.52	18.4 ± 2.52	10.3 ± 0.36	9.6 ± 0.36
Adult emergence (%)	77.2 ± 1.86	68.5 ± 1.86	80.6 ± 0.42	81.5 ± 0.42
Male pupal wt (mg/pupa)	4.35 ± 0.04	4.27 ± 0.04	4.42 ± 0.06	4.31 ± 0.06
Female pupal wt (mg/pupa)	6.44 ± 0.03	6.50 ± 0.03	6.82 ± 0.11	6.60 ± 0.11
Fecundity/female	132.4 ± 4.2	124.0 ± 4.2	111.4 ± 4.4	102.6 ± 4.4
Adult emergence index	1.27 ± 0.07	1.13 ± 0.07	1.33 ± 0.01	1.34 ± 0.01
Fecundity index	1.41 ± 0.05	1.32 ± 0.05	1.18 ± 0.05	1.09 ± 0.05
Antibiosis index	4.92 ± 0.12	4.69 ± 0.12	4.77 ± 0.05	4.67 ± 0.05

[a] Values based on mean of seven *A. soccata*-resistant sorghum genotypes in three replications.
[b] Values based on mean of five *A. soccata*-susceptible sorghum genotypes in three replications.

genes (Xu and Song 1997, Xu et al. 1998). The plants of *A. soccata*-resistant CMS lines were significantly more preferred by female *A. soccata* for egg laying and suffered more deadheart formation than those of the B-lines, whereas such differences between A- and B-lines of the susceptible group of genotypes were not apparent. Similar results also have been reported for oviposition preference of *S. sorghicola* (Sharma 2001). Genotypes preferred for oviposition, in general, also showed high degree of deadheart formation (Rana et al. 1975).

Retardation of growth and development, prolonged larval and pupal periods, and low adult emergence on resistant varieties are important components of antibiosis mechanism of resistance to *A. soccata* in sorghum (Sharma et al. 1977, Singh and Jotwani 1980b, Raina et al. 1981; Dhillon et al. 2005b). Singh and Jotwani (1980b) reported prolongation in larval and pupal periods (8–15 d) on resistant cultivars. The larval period was longer and larval survival was significantly lower on *A. soccata*-resistant CMS and maintainer lines than on the susceptible lines (Table 5). Similar differences in larval survival on resistant and susceptible genotypes have been reported by Jadhav and Mote (1986). Pupal period was comparatively longer and the fecundity was greater, whereas adult emergence and pupal weights were lower on *A. soccata*-resistant A/B-lines than on the susceptible A/B-lines. The fecundity of >63 eggs per female was reported by Ogwaro (1978), whereas 17–239 eggs per female were recorded by Raina (1982). The adult emergence index was lower, and fecundity and antibiosis indices were higher on *A. soccata*-resistant A/B-lines than on the susceptible lines. Antibiosis to *A. soccata* offers exciting possibilities of exerting biotic pressure against larval feeding (Dahms 1969), resulting in low larval survival on resistant varieties (Soto 1974), and thus reducing population density of the pest in the ecosystem.

Tiller survival in sorghum is related to the rate of plant growth. Faster the tiller growth, greater the chances to avoid infestation by *A. soccata* (Blum 1972). Tiller development consequent to deadheart formation in the main shoot and subsequent survival depends on the level of primary resistance and *A. soccata* abundance (Doggett et al. 1970). The CMS lines have more number of effective panicles per plant than the maintainer lines in barley (Sun 1995) and wheat (Murai 1997) under uninfested conditions. The B-lines produced more productive tillers and showed better recovery resistance than the A-lines in response to *A. soccata* damage on the main plants in sorghum. The *A. soccata*-resistant A/B-lines had less tiller deadhearts and more productive tillers, resulting in better recovery than the susceptible lines, and varieties with high recovery resistance yield more under *A. soccata* infestation (Rana et al. 1985). In conclusion, the CMS lines were more preferred for oviposition, suffered more deadheart formation, had less antibiosis effect, and showed poor recovery than the maintainer lines, suggesting that CMS influences the expression of different mechanisms of resistance to *A. soccata* in sorghum.

Acknowledgments

We thank G. T. Gujar, Indian Agricultural Research Institute, Pusa, New Delhi, India, for critical comments on the manuscript; Suri Sehgal Foundation for extending funds for these studies; B.V.S. Reddy for providing the seeds of some of the CMS and the maintainer lines; Messers J. Raja Rao, V. Venkateshwara Rao, K. Hareendranath, Madhu Sudhan Reddy, S.V.N. Chandra, and Ponnamma for help in these studies; and S. Chandra and Prasanth for help in statistical analysis of the data.

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Received 11 September 2005; accepted 8 March 2006.