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Mechanisms of resistance to shoot fly, *Atherigona soccata* in sorghum

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Summary

Sorghum shoot fly, *Atherigona soccata* (Rondani) is an important pest of sorghum in Asia, Africa, and Mediterranean Europe, and host plant resistance is an important component for the management of this pest. The levels of resistance in the cultivated germplasm are low to moderate, and therefore, it is important to identify genotypes with different mechanisms of resistance to pyramid the resistance genes. We studied the antixenosis for oviposition, antibiosis, and tolerance components of resistance in a diverse array of shoot fly-resistant and -susceptible genotypes. The main plants and tillers of SFCR 151, ICSV 705, SFCR 125, and, IS 18551 experienced lower shoot fly deadhearts at 28 days after seedling emergence, produced more number of productive tillers. The insects fed on these genotypes also exhibited longer larval period (10.1–11.0 days compared to 9.3 days on Swarna), lower larval survival and adult emergence (54.7–67.8 and 46.7–52.2% compared to 73.3 and 60.6% on Swarna, respectively), and lower growth and adult emergence indices as compared to the susceptible check, Swarna. Physico-chemical traits such as leaf glossiness, trichome density, and plumule and leaf sheath pigmentation were found to be associated with resistance, and chlorophyll content, leaf surface wetness, seedling vigor, and waxy bloom with susceptibility to shoot fly and explained 88.5% of the total variation in deadhearts. Step-wise regression indicated that 90.4% of the total variation in deadhearts was due to leaf glossiness and trichome density. The direct and indirect effects, correlation coefficients, multiple and step-wise regression analysis suggested that deadhearts, plants with eggs, leaf glossiness, trichomes on the abaxial surface of the leaf, and leaf sheath pigmentation can be used as marker traits to select for resistance to shoot fly, *A. soccata* in sorghum.

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is one of the most important cereal crops in the semi-arid tropics. The yield penalties to sorghum are very high starting from seedling stage to harvest, and are allotted maximally to biotic stresses. More than 150 species of insects have been recorded as pests of sorghum, of which sorghum shoot fly, *Atherigona soccata* (Rondani) is an important pest in Asia, Africa, and the Mediterranean Europe. Insect pests cause nearly 32% of the total loss to the actual produce in India (Borad & Mittal, 1983), 20% in Africa and Latin America, 9% in USA (Wiseman & Morrison, 1981). Shoot flies of the genus *Atherigona* are known to cause 'deadhearts' in a number of tropical grass species (Deeming, 1971; Pont, 1972) and wheat (Pont & Deeming, 2001). Sorghum shoot fly causes an average loss of 50% in India (Jotwani, 1982), but the infestations at times may be over 90% (Rao & Gowda, 1967). The adult fly lays white, elongated, cigar shaped eggs singly on the undersurface of the leaves, parallel to the midrib. After egg hatch, the larvae crawl to the plant whorl and move downward between the folds of the young leaves till they reach the growing point. They cut the growing tip resulting in deadheart formation.

Host plant resistance is one of the most effective means of keeping shoot fly population below economic

threshold levels, as it does not involve any cost input by the farmers. A number of genotypes with resistance to shoot fly have been identified, but the levels of resistance are low to moderate (Jotwani, 1978; Taneja & Leuschner, 1985; Sharma et al., 2003). Plant resistance to sorghum shoot fly appears to be complex character and depends on the interplay of number of componential characters, which finally sum up in the expression of resistance to shoot fly (Dhillon, 2004). So, it is important to identify genotypes with different mechanisms to increase the levels and diversify the bases of resistance to this insect. Therefore, the present studies were carried out on a diverse array of sorghum genotypes to identify plant characteristics influencing resistance/susceptibility to *A. soccata*.

Materials and methods

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 a total of eight shoot fly-resistant (IS 18551, ICSV 705, ICSV 700, ICSV 708, SFCR 151, SFCR 125, ICSV 91011, and PS 30710) and four shoot fly-susceptible (ICSV 745, MR 750, CS 3541, and Swarna) sorghum genotypes. Genotypes IS 18551 and Swarna were used as resistant and susceptible checks, respectively.

Expression and contribution of different components of resistance under multi-choice conditions in the field

The test material was planted during the rainy 2002 and 2003 (last week of July), 2003 early postrainy (mid-September), and the 2003 postrainy (mid-October) seasons. Each genotype was sown in four row plots of 2 m row length, and the rows were 75 cm apart. There were three replications in a randomized complete block design (RCBD). The seed was sown with a four-cone planter at a depth of 5 cm below the soil surface. The field was irrigated immediately after sowing during the postrainy season, while the soil moisture was optimum during the rainy and early postrainy seasons. One week after seedling emergence, thinning was carried out to maintain a spacing of 10 cm between the plants. Shoot fly infestation was optimized through the use of interlard fish-meal technique (Soto, 1974). Normal agronomic practices were followed for raising the sorghum crop, and no insecticide was applied in the experimental plots. The infester rows were chopped off 30 days after emergence in the main plots to avoid shading effect in the test plots.

Data were recorded on number of eggs and numbers of plants with eggs at 14 and 21 days after seedling emergence (DAE), and plants with deadhearts at 14, 21, and 28 DAE from the central two rows. The data on number of eggs was expressed as number of eggs per 10 plants, and plants with eggs and deadhearts in terms of percentage of the total number of plants. Recovery resistance was assessed at 28 DAE in terms of percentage tillers with deadhearts. At crop maturity, data were also recorded on total number of tillers and number of tillers having panicles with grains, and expressed as percentage productive tillers. The recovery resistance was assessed on a scale of 1–9 based on productive tillers, uniformity in tiller height and maturity (1 = most of the damaged plants with two to three uniform and productive panicles, and 9 = <20% plants with productive tillers) (Dhillon et al., 2004).

Data were also recorded on plant traits such as leaf glossiness, trichome density on abaxial (lower) and adaxial (upper) surfaces of the leaf, seedling vigor, leaf surface wetness, plumule and leaf sheath pigmentation, chlorophyll content, and waxy bloom. The leaf glossiness was evaluated on a 1–5 rating at 10 DAE in the early morning hours when there was maximum reflection of light from the leaf surfaces (1 = highly glossy, light green, shining, narrow and erect leaves; and 5 = non-glossy, dark green, dull, broad and drooping leaves). To record data on trichome density, central-portion of the fifth leaf (from the base) was taken from three seedlings selected at random. The leaf pieces (approximately 2 cm^2) were placed in acetic acid and alcohol solution (2:1) in a stoppered glass vial (10 ml capacity). The leaf pieces were kept in this solution for 24 h and thereafter transferred into lactic acid (90%). Leaf segments cleared of the chlorophyll content were observed for the trichome density. The leaf sections were mounted on a slide in a drop of lactic acid and observed under stereomicroscope at a magnification of 10×. The trichomes on both abaxial and adaxial surfaces of the leaf were counted in microscopic fields selected at random, and expressed as number of trichomes/10× microscopic field. The seedling vigor was recorded at 10 DAE on 1–5 rating scale (1 = highly vigorous, more number of fully expanded leaves, good adaptation and robust seedling; and 5 = poor seedling vigor, plants showing poor growth, and weak seedlings). The leaf surface wetness of the leaf blade of central whorl was measured on the test genotypes planted in plastic cups (10 cm diameter). The observations were recorded

between 0430 and 0630 h. The seedlings at fifth leaf stage (12 DAE) were brought to the laboratory, and central whorl was opened and mounted on a slide with sticky tape and observed under the microscope (10× magnification) for leaf surface wetness. Leaf surface wetness was rated on a 1–5 scale (1 = leaf blade without water droplets; and 5 = entire leaf blade densely covered with water droplets). The chlorophyll content of the flag leaf of 80 days old plants was measured with the help of chlorophyll meter (SPAD-502, Minolta Corporation) and expressed in g m^{-2}. The pink colored pigment on plumule and leaf sheath both, were visually scored at 5 DAE on a 1–5 rating scale (1 = plumule or leaf sheath with dark pink pigment; and 5 = plumule or leaf sheath with green color). The waxy bloom was recorded on a rating scale of 1–5 (1 = the stem and leaves without wax; and 5 = the stem and leaves covered with a fully waxy layer at 50% flowering).

Expression and contribution of different components of resistance under greenhouse conditions

Insect culture

The shoot fly females were collected in fish-meal baited traps in the sorghum fields having sorghum crop at the seedling stage. The fish-meal in the jars was replaced every 4 days. The shoot flies were collected in the morning between 07:30 and 08:30 h in 200 ml plastic bottles with the help of an aspirator, and released inside wire-mesh screened cages (30 cm × 30 cm × 30 cm) in the greenhouse (28 ± 2 °C and 75 ± 5% relative humidity). The females of *A. soccata* were separated from other flies, and released in a separate cage. The shoot fly females were provided with 20% sucrose solution on a cotton swab, and a mixture of brewer's yeast and glucose (1:1) in a petridish. The sucrose solution was changed daily, while the yeast powder–glucose mixture was changed every 3 days.

Oviposition non-preference under dual- and no-choice conditions

Oviposition preference was studied under dual- and no-choice conditions in a wire-mesh screened cage. The containment cage consisted of two plastic trays, one for planting the test material, while the other fitted with wire-mesh screen on the sides (10 cm × 15 cm) and at the top (10 cm × 15 cm) was clamped on to the tray with sorghum seedlings. The wire-mesh 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 genotypes were planted in plastic trays (40 cm × 30 cm × 14 cm) having a potting mixture consisted of black soil and farmyard manure (3:1). Diammonium phosphate 20 g (per tray) was mixed with the soil before sowing. Each genotype had four rows, and there were 40 seedlings in each tray. For no-choice tests, only one genotype was planted in each tray. For dual-choice tests, there were two rows of the test genotype and two rows of resistant or susceptible check. There were six replications for dual-choice tests, and three replications for no-choice tests in a completely randomized design (CRD). The seedlings were exposed to shoot fly females (@ 16 flies per 40 plants) at 9 days after seedling emergence (at the fifth leaf stage) for 24 h. After 24 h, the shoot fly females were removed from the trays, and data were recorded on the number of eggs and plants with eggs. Five days after infestation, data were recorded on the number of plants with deadhearts, and expressed as percentage deadhearts.

Antibiosis

To quantify antibiosis component of resistance data were recorded on deadheart formation under no-choice conditions at 12 h intervals to determine the time taken by the larvae to reach the growing point, and to have an assessment of larval survival. The deadhearts were labeled for the time of appearance. Four days after deadheart formation, 15 deadhearts of same age per replication were uprooted and placed in 20 ml glass vials individually. Observations were recorded on larval and pupal periods, percentage pupation, pupal weight, adult emergence, and fecundity. There were three replications in CRD. The deadhearts collected in glass vials were observed daily after 6 days of deadheart formation to record time to pupation. Data were recorded on the duration of larval and pupal development, percentage pupation, adult emergence, and fecundity. The number of days from deadheart appearance to pupation plus 1 day (because it takes nearly 1 day for deadheart formation after egg hatching) was recorded as the larval period (Meksongsee et al., 1981). The pupae were placed in moist sand to avoid the water loss and pupal mortality because of desiccation. The pupae were sorted into males and females and the pupal weights were recorded separately for each sex within 24 h after pupation. Mortality during the pupal stage was also recorded. For fecundity studies, five pairs of shoot flies emerging from the larvae reared on a genotype were released in wire-framed cages 30 cm diameter covered with a nylon bags (60 mesh). The adults were provided with 20% sucrose solution and brewer's yeast + glucose (1:1) as described above. Ten sorghum

seedlings (planted in plastic pots of 10 cm diameter) of the same genotype on which the larvae were reared, were provided to the shoot flies for oviposition till all the females died. The seedlings were changed on alternate days, and data were recorded on number of eggs laid per female.

Statistical analysis

Data were subjected to analysis of variance, and the significance of differences between the genotypes was tested by *F*-tests, while the treatment means were compared by least significant differences (LSD) at $P = 0.05$. For the dual-choice tests, pair *t*-test ($P = 0.05$) was used to test the significance of differences. Data were also subjected to correlation, regression, and path coefficients analysis to understand the direct and indirect effects of various plant characteristics on oviposition and damage by *Atherigona soccata*.

Results

Relative susceptibility of different genotypes to shoot fly damage under multi-choice and no-choice conditions

There was a significant variation in shoot fly deadhearts in different genotypes under multi-choice conditions in the field (Table 1). The 14-, 21-, and 28-day-old seedlings of IS 18551, ICSV 705, SFCR 151, SFCR 125, ICSV 708, ICSV 700, and PS 30710 suffered significantly less damage (deadhearts) than the susceptible check, Swarna. Genotypes ICSV 91011 and PS 30710 showed moderate levels of resistance to shoot fly across observation intervals and seasons. At 28 DAE, SFCR 151 and ICSV 705 were as resistant as the resistant check, IS 18551. The genotypes ICSV 705, SFCR 151, ICSV 708, and ICSV 700 were also on par with the resistant check, IS 18551 under dual-choice conditions (Table 2). However, there were no significant differences in deadheart formation among the genotypes tested under no-choice conditions in the greenhouse (Table 1), suggesting the breakdown of resistance to shoot fly under no-choice conditions.

Oviposition non-preference

The seedlings of sorghum genotypes ICSV 745, CS 3541, MR 750, and Swarna (susceptible check) were significantly more preferred for oviposition (90.3–94.4% plants with eggs and 11.9–16.9 eggs plants^{-10}) as compared to resistant check, IS 18551 (68.9% plants with eggs and 8.6 eggs plants^{-10}) at 14 DAE under multi-choice conditions in the field (Table 1). At 21 DAE, IS 18551, ICSV 705, SFCR 151, SFCR 125, ICSV 708, and ICSV 700 were significantly less

Table 1. Oviposition preference and damage by the shoot fly, *Atherigona soccata* females on 12 sorghum genotypes under multi-choice field and no-choice conditions in the greenhouse (ICRISAT, Patancheru 2002–2003)

	Eggs plants^{-10}*			Plants with eggs (%)*			Deadhearts (%)			
	Multi-choice		No-choice	Multi-choice		No-choice	Multi-choice			No-choice
Genotypes	14 DAE	21 DAE	(10 DAE)	14 DAE	21 DAE	(10 DAE)	14 DAE	21 DAE	28 DAE	(14 DAE)
ICSV 745	15.7d	12.4c	34.0a	94.4f	96.2d	100.0a	73.9efg	87.2ef	93.3d	92.2a
ICSV 700	10.2abc	10.8b	38.0a	80.0c	85.8bc	96.3a	42.9bc	73.4bc	82.4c	81.3a
ICSV 708	9.7ab	8.9ab	38.0a	74.1abc	82.8bc	95.7a	41.6abc	68.0bc	78.7bc	83.5a
PS 30710	10.4abc	11.8c	33.0a	81.1bcd	90.2cd	90.6a	41.3abc	75.6cd	84.1c	77.7a
SFCR 151	8.5a	9.0ab	36.0a	71.6ab	81.1abc	95.7a	34.2a	67.3bc	72.7a	88.1a
SFCR 125	11.5b	9.6ab	42.0a	74.6abc	82.7b	98.3a	46.7cd	74.8cd	79.5bc	90.8a
ICSV 91011	12.5c	10.3abc	37.0a	83.9cde	90.1cd	100.0a	53.9d	82.4de	92.4d	91.7a
CS 3541	16.9d	11.8c	38.0a	90.3df	96.3d	93.2a	66.4e	90.6ef	95.4d	71.5a
MR 750	11.9b	10.7b	40.0a	92.3ef	97.8d	97.8a	75.3fg	92.6f	98.0d	89.2a
IS 18551	8.6a	9.3a	43.0a	68.9a	80.1ab	95.8a	33.4a	66.1b	71.7ab	80.5a
ICSV 705	9.2ab	8.5a	25.0a	69.9a	72.1a	91.3a	35.3ab	57.5a	64.7a	80.0a
Swarna	12.9c	11.8c	34.0a	92.3ef	97.2d	100.0a	78.6g	93.5f	96.1d	91.1a
LSD ($P = 0.05$)	2.72	2.14	19.70	9.78	9.58	21.15	8.18	8.29	8.08	21.64

Note. DAE, Days after seedling emergence. The values in the columns following different letters are significantly different.
*Values are the means of the four seasons.

Table 2. Relative resistance in sorghum genotypes to *Atherigona soccata* under dual-choice conditions (in relation to resistant check, IS 18551) in the greenhouse (ICRISAT, Patancheru 2002–2003)

	Eggs plants^{-10}			Plants with eggs (%)			Deadhearts (%)		
Genotypes	Test entry	IS 18551	*t*-value	Test entry	IS 18551	*t*-value	Test entry	IS 18551	*t*-value
ICSV 745	27.3	18.3	2.15	95.4	78.2	2.23*	92.8	64.6	4.22**
ICSV 700	24.7	26.7	1.26	85.0	81.7	1.58	78.3	70.0	1.39
ICSV 708	18.5	17.5	0.21	84.1	72.6	0.73	79.1	62.4	1.17
PS 30710	12.8	12.0	1.11	83.3	80.0	0.47	80.0	53.3	4.34**
SFCR 151	26.8	18.7	5.24**	98.3	82.8	2.23*	91.1	76.1	2.09
SFCR 125	15.0	14.0	0.49	84.0	79.6	0.63	76.9	59.1	2.92*
ICSV 91011	28.5	17.2	5.54**	96.5	85.0	1.43	94.8	71.7	3.43**
CS 3541	19.2	11.8	3.48**	84.1	56.7	1.96	79.8	48.3	3.03*
MR 750	18.0	9.8	3.64**	91.7	73.3	1.75	84.8	55.0	4.76**
ICSV 705	22.0	25.3	1.01	83.3	90.0	1.58	71.7	65.0	1.39
Swarna	19.8	13.0	3.38**	91.7	70.5	2.72	85.0	44.8	5.00**

*t-value significant at $P = 0.05$.
**t-value significant at $P = 0.01$.

preferred for egg laying (72.1–85.8% plants with eggs, and 8.5–10.8 eggs plants^{-10}) as compared to susceptible check, Swarna (97.2% plants with eggs and 11.8 eggs plants^{-10}). Genotypes PS 30710 and ICSV 91011 showed moderate levels of oviposition preference under multi-choice conditions in the field. However, there were no significant differences in numbers of eggs laid and the percentage plants with eggs under no-choice conditions in the greenhouse (Table 1). In dual-choice tests in relation to the resistant check, IS 18551, the genotypes ICSV 745, SFCR 151, ICSV 91011, CS 3541, MR 750, and Swarna had significantly more number of eggs than IS 18551 (Table 2).

Recovery resistance

The tillers of ICSV 700, ICSV 708, ICSV 705, PS 30710, SFCR 151, and SFCR 125 had significantly lower deadhearts at 28 DAE as compared to susceptible check, Swarna, and were on par with the resistant check, IS 18551 (Table 3). Genotypes ICSV 708, PS 30710, and SFCR 151 had more number of productive tillers, and showed better recovery resistance (recovery resistance score <4) as compared to other genotypes tested. Swarna, though susceptible produced more number of tillers following shoot fly damage on the main plants, but had poor recovery resistance. The tillers of IS 18551 showed less deadheart formation and high recovery resistance, indicating the presence of induced resistance.

Table 3. Tiller damage, productive tillers, and recovery resistance in 12 sorghum genotypes in response to shoot fly, *Atherigona soccata* damage (ICRISAT, Patancheru 2002–2003)

Genotypes	Tiller deadhearts (%) (28 DAE)	Productive tillers (%)	Recovery resistance score
ICSV 745	58.0bcd	37.5ab	7.2g
ICSV 700	49.2abc	40.9ab	3.4a
ICSV 708	47.3abc	59.6e	3.5ab
PS 30710	48.6abc	56.1de	3.9abc
SFCR 151	44.7ab	56.3de	4.5bcd
SFCR 125	45.8ab	50.7cde	5.1de
ICSV 91011	52.6bcd	51.0cde	4.8cde
CS 3541	49.2abc	51.4cde	6.2fg
MR 750	60.9d	41.7abc	6.9g
IS 18551	40.3a	35.4a	4.3abcd
ICSV 705	49.0ab	47.5bcd	5.8ef
Swarna	58.9cd	59.2e	6.8fg
LSD ($P = 0.05$)	11.58	11.37	1.01

Note. The values in the columns following different letters are significantly different.
*Values are the means of the four seasons. DAE, days after seedling emergence.

Antibiosis

The larval period was longer on IS 18551, ICSV 705, SFCR 125, and SFCR 151 (10.1–11.0 days) as compared to susceptible check, Swarna (9.3 days) (Table 4). The differences in pupal period were nonsignificant.

Table 4. Expression of antibiosis component of shoot fly, *Atherigona soccata* resistance on 12 genotypes of sorghum under greenhouse conditions (ICRISAT, Patancheru 2002–2003)

Genotypes	Larval period (days)	Larval survival (%)	Pupal period (days)	Pupal mortality (%)	Adult emergence (%)	Pupal weight (mg)	Fecundity female^{-1}	Sex ratio M:F		Adult emergence index*	Fecundity index**	Growth index***
								Male	Female			
ICSV 745	9.3ab	79.6d	7.1ab	18.3f	61.3bcd	3.89a	5.45ab	90.1a	1:1.03a	1.16de	0.96ab	15.2e
ICSV 700	9.1a	67.8bc	7.4b	15.6e	52.2abc	3.86a	5.29ab	67.9a	1:0.93a	0.99c	0.72a	14.0d
ICSV 708	9.6abc	76.4cd	7.1ab	13.5cd	62.9bcd	3.68a	4.84a	113.3ab	1:1.05a	1.15de	1.20cd	14.5de
PS 30710	9.4abc	79.0d	7.0ab	8.8a	70.2d	3.60a	4.84a	94.9ab	1:1.92bcd	1.23e	1.01c	15.0e
SFCR 125	10.3c	62.6ab	6.8ab	11.3b	51.3abc	3.68a	4.75a	131.6bc	1:1.53abc	0.94bc	1.40de	12.7bc
SFCR 151	10.8de	60.1ab	7.0ab	11.7bc	48.4ab	4.00a	5.44ab	135.9bcd	1:1.92bcd	0.90ab	1.44de	12.2ab
ICSV 91011	9.5abc	76.7cd	7.2ab	15.4de	61.3bcd	3.58a	5.05a	178.6cd	1:1.57abc	1.14d	1.90f	14.7de
CS 3541	9.8abc	66.1b	6.8ab	11.7bc	54.4bcd	3.94a	5.04a	139.6bcd	1:1.14ab	0.99c	1.48e	13.3c
MR 750	9.8abc	78.8cd	7.1ab	12.7b	66.1cd	3.99a	5.94b	97.6ab	1:1.99cd	1.20de	1.04bc	14.6de
IS 18551	11.0e	54.7a	6.5a	8.0a	46.7a	3.87a	4.84a	185.5d	1:1.47abc	0.84a	1.97f	11.6a
ICSV 705	10.1bcd	76.7cd	6.7ab	16.5ef	60.2bcd	3.60a	5.06a	128.6bc	1:1.07a	1.13d	1.37de	14.2d
Swarna	9.3ab	73.3cd	7.3ab	12.7bc	60.6bcd	3.89a	5.81b	94.1ab	1:2.44d	1.00c	1.00bc	14.5de
LSD ($P = 0.05$)	0.85	11.09	0.83	1.94	17.04	0.89	0.71	51.77	0.79	0.08	0.24	0.74

Note. The values in the columns following different letters are significantly different. M, males. F, females.

*Adult emergence index: adult emergence on the test genotype/adult emergence on the susceptible check.

**Fecundity index: total eggs laid by the insect reared on test genotype/total eggs laid by the insect reared on susceptible check.

***Growth index: mean percent pupation/mean larval period.

Larval survival (60.1–67.8%), and adult emergence (48.4–52.2%) were significantly lower on SFCR 125, SFCR 151, and ICSV 700 as compared to other genotypes tested, and on par with resistant check, IS 18551 (54.7% larval survival and 46.7% adult emergence). The growth and adult emergence indices were significantly lower on IS 18551, SFCR 151, and SFCR 125 as compared to other genotypes tested. There was little variation in the male pupal weights on the genotypes tested. Female pupal weight was significantly lower on ICSV 708, IS 18551, ICSV 705, SFCR 125, PS 30710, ICSV 91011, and CS 3541 as compared to susceptible check, Swarna. The female pupae were heavier than the male pupae on all the genotypes tested (Table 4). Fecundity was highest on the resistant check, IS 18551 (185.5 eggs female^{-1}), which was on par with SFCR 151, ICSV 91011, and CS 3541. Highest disturbance in sex ratio was observed on the susceptible check, Swarna, which was on par with PS 30710, SFCR 151, and MR 750. The fecundity index was significantly greater on ICSV 91011and IS 18551 as compared to other genotypes tested (Table 4).

Physico-chemical characteristics

Leaf glossiness of ICSV 705, ICSV 700, ICSV 708, SFCR 151, SFCR 125, and ICSV 91011 was comparable to the resistant check, IS 18551. Genotypes ICSV 745, CS 3541, MR 750, and Swarna were non-glossy and non-trichomed (Table 5), while PS 30710 exhibited intermediate level of leaf glossiness and ICSV 91011 was non-trichomed, but glossy. The trichome density varied from 78.7 to 115.8 (abaxial) and 112.1–166.8 (adaxial) in a 10× microscopic field (Table 5). The susceptible check, Swarna considered as non-trichomed earlier, showed a few trichomes on abaxial (7.9 trichomes) and adaxial (18.5 trichomes) leaf surfaces. Numbers of trichomes on the adaxial surface were greater as compared to the abaxial leaf surface. The seedlings of ICSV 700, ICSV 708, PS 30710, ICSV 91011, CS 3541, MR 750 and Swarna were less vigorous compared to IS 18551. Chlorophyll content was significantly lower in IS 18551, ICSV 705, ICSV 91011, SFCR 151, ICSV 700, and ICSV 745 as compared to susceptible check, Swarna at 80 DAE. In general, the shoot fly-susceptible genotypes had more chlorophyll content than the resistant check, IS 18551. The leaf surface wetness in ICSV 705, SFCR 121, SFCR 151, and PS 30710 was low at 12 DAE, and these were on par with the resistant check, IS 18551 (Table 5). Leaf surface wetness score of the susceptible check, Swarna was the highest, and that of the resistant check, IS 18551 was lowest. The plumule and leaf sheath pigmentation scores varied from 1 to 4.7 and 2 to 5 at 5 DAE, respectively (Table 5). Expression of pigmentation was better in plumule than in the leaf sheath. Plumule and leaf sheath pigmentation started fading 5 days after seedling emergence. The leaf sheaths of ICSV 700, ICSV 708, PS 30710, SFCR 151, and SFCR 125 were highly pigmented (non-tan type), and were on par with the resistant check, IS 18551. Pigmentation in PS 30710, MR 750, and ICSV 705 was of intermediate intensity; while ICSV 745, CS 3541 and ICSV 91011 were non-pigmented. The genotypes ICSV 700, IS 18551, and ICSV 705 were less waxy, whereas the other genotypes were fully covered with waxy bloom.

Association and effects of physico-chemical traits with resistance to A. soccata

The correlation coefficients of leaf glossiness, leaf surface wetness, and leaf sheath pigmentation were significant and positive ($P = 0.05$) for eggs plants^{-10} ($r = 0.57$–0.79), percentage plants with eggs ($r = 0.67$–0.91), and deadhearts ($r = 0.58$–0.94), while for trichome density, these correlation coefficients were significant and negative ($r = -0.79$ to -0.88) (Table 6). The correlation coefficients for leaf sheath pigmentation, chlorophyll content, seedling vigor, and waxy bloom were positive, but nonsignificant. Physico-chemical traits such as leaf glossiness, trichome density, and plumule and leaf sheath pigmentation were found to be associated with resistance, and chlorophyll content, leaf surface wetness, seedling vigor, and waxy bloom with susceptibility to shoot fly.

Multiple linear regression analysis indicated that morpho-chemcial traits explained 46.4% of the total variation in eggs plants^{-10}, 57.6% of the variation in plants with eggs, and 88.5% of the variation in deadhearts. Step-wise regression analysis indicated that leaf glossiness and leaf sheath pigmentation accounted for 75.4% of the total variation in eggs plants^{-10}; whereas the leaf glossiness and trichome density on abaxial leaf surface explained 86.4% of variation in plants with eggs, and 90.4% of the variation in deadhearts (Table 6).

The path coefficient analysis for deadhearts, eggs plants^{-10}, plants with eggs, and the plant traits suggested that plants with eggs, chlorophyll content, leaf surface wetness, leaf sheath pigmentation, leaf glossiness, trichomes on the abaxial surface of the leaf, and waxy bloom had the correlation and direct effects in the

Table 5. Plant characteristics of 12 sorghum genotypes associated with resistance/susceptibility to *Atherigona soccata* (ICRISAT, Patancheru 2002–2003)

Genotypes	Leaf glossiness* (10 DAE)	Trichome density (10× mf)* (12 DAE)		Chlorophyll content (g^{-2}) (80 DAE)	Seedling vigor (10 DAE)	Leaf surface wetness (12 DAE)	Waxy bloom at 50% flowering	Pigmentation score	
		Abaxial	Adaxial					Plumule (5 DAE)	Leaf sheath (5 DAE)
ICSV 745	4.6e	0.0a	0.0a	41.6ab	2.0a	2.3cd	5.0e	4.7e	5.0c
ICSV 700	2.1bcd	94.9bc	146.3d	43.2abc	2.8bc	1.8bc	3.4ab	1.3ab	2.7ab
ICSV 708	1.9bc	78.7b	166.8e	45.6bcd	3.3c	2.0bc	4.4cd	2.0abc	2.0a
PS 30710	2.5d	92.8bc	124.8c	46.9bcde	3.0bc	1.7abc	4.5de	2.7cd	2.7ab
SFCR 151	1.7ab	109.0cd	148.6de	39.2a	2.3ab	1.3ab	4.5de	2.3bcd	2.3a
SFCR 125	1.8abc	115.8d	149.5de	53.7e	2.0a	1.7abc	5.0e	1.3ab	2.0a
ICSV 91011	2.2cd	0.0a	0.0a	44.3abcd	3.0bc	2.0bc	5.0e	4.7e	5.0c
CS 3541	4.8e	0.0a	0.0a	46.1bcd	3.0bc	3.0d	4.5de	3.3d	4.3c
MR 750	4.8e	0.0a	0.0a	51.0de	3.0bc	3.0d	3.9bc	1.0a	3.0b
IS 18551	1.4a	83.6b	114.8c	42.9abc	2.0a	1.0a	3.2a	1.3ab	2.2a
ICSV 705	2.0bc	88.9b	112.1c	45.1abcd	2.7ac	1.5ab	3.5ab	2.7cd	3.3b
Swarna	4.8e	7.9a	18.5b	48.4cde	3.0bc	5.0e	5.0e	1.7abc	3.3b
LSD ($P = 0.05$)	0.42	20.28	18.32	6.15	0.71	0.74	0.45	1.02	0.71

Note. The values in the columns following different letters are significantly different. mf, microscopic field. DAE, days after seedling emergence.
*Values are means across four seasons.

Table 6. Association of nine physico-chemical traits of 12 sorghum genotypes with eggs plants^{-10}, percentage plants with eggs, and deadhearts at 14 days after seedling emergence by sorghum shoot fly, *Atherigona soccata* under field conditions (ICRISAT, Patancheru 2002–2003)

	Physico-chemical traits								
Characters	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9
Eggs plants^{-10}	79.0**	−0.79**	−0.79**	0.57*	0.17	0.08	0.53	0.76**	0.50
Plants with eggs (%)	0.91**	−0.88**	−0.87**	0.77**	0.24	0.20	0.36	0.67*	0.54
Deadhearts (%)	0.94**	−0.87**	−0.85**	0.85**	0.34	0.26	0.21	0.58*	0.47

Note. X_1, leaf glossiness; X_2, trichome density (abaxial leaf surface); X_3, trichome density (adaxial leaf surface); X_4, leaf surface wetness; X_5, chlorophyll content 80 DAE; X_6, seedling vigor 10 DAE; X_7, plumule pigmentation at 5 DAE; X_8, leaf sheath pigmentation at 5 DAE; X_9, waxy bloom. Number of eggs per plant with physico-chemical traits: multiple linear regression equation; eggs plants$^{-10} = -0.77 + 0.17X_1 - 0.003X_2 + 0.004X_3 - 0.06X_4 + 0.02X_5 - 0.10X_6 + 0.17X_7 + 0.04X_8 - 0.01X_9$ ($R^2 = 46.4\%$); step-wise regression equation: eggs plants$^{-10} = 0.97 + 0.11X_1 + 0.12X_7$ ($R^2 = 75.4\%$). Percentage plants with eggs with physico-chemical traits: multiple linear regression equation; plants with eggs (%) $= 54.9 - 0.18X_1 - 0.06X_2 + 0.001X_3 + 3.56X_4 + 0.12X_5 - 1.25X_6 - 0.82X_7 + 2.40X_8 + 3.41X_9$ ($R^2 = 57.6\%$); step-wise regression equation; plants with eggs (%) $= 75.3 + 3.80X_1 - 0.09X_2$ ($R^2 = 86.4\%$). Percentage deadhearts with physico-chemical traits: multiple linear regression equation; deadhearts (%) $= 6.6 - 8.07X_1 - 0.31X_2 + 0.16X_3 + 4.07X_4 + 0.38X_5 - 8.23X_6 + 0.96X_7 + 10.71X_8 + 7.61X_9$ ($R^2 = 88.5\%$); step-wise regression equation; deadhearts (%) $= 35.62 + 8.40X_1 - 0.11X_2$ ($R^2 = 90.4\%$).

*Correlation coefficients significant at $P = 0.05$.

**Correlation coefficients significant at $P = 0.01$.

Table 7. Direct and indirect path coefficients for deadhearts *via* eggs per plant, plants with eggs, and nine independent variables of 12 sorghum genotypes under field conditions (ICRISAT, Patancheru 2002–2003)

Characters	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	r
Eggs plants^{-10} (x_1)	**−0.15**	0.43	0.02	0.04	−0.01	0.49	−0.26	0.16	0.63	−0.61	0.08	0.81**
Plants with eggs (x_2)	−0.13	**0.51**	0.03	0.06	−0.06	0.43	−0.18	0.18	0.71	−0.67	0.08	0.96**
Chlorophyll content (x_3)	−0.03	0.12	**0.12**	0.03	−0.04	−0.14	0.21	0.05	0.06	−0.08	0.04	0.34
Leaf surface wetness (x_4)	−0.08	0.39	0.05	**0.08**	−0.10	0.21	0.02	0.17	0.54	−0.48	0.06	0.85**
Seedling vigor (x_5)	−0.01	0.13	0.02	0.03	**−0.24**	0.06	0.00	0.05	0.24	−0.12	0.04	0.20
Leaf sheath pigmentation (x_6)	−0.11	0.34	−0.03	0.03	−0.02	**0.64**	−0.41	0.10	0.64	−0.65	0.05	0.58*
Plumule pigmentation (x_7)	−0.08	0.18	−0.05	0.00	0.00	0.55	**−0.49**	0.03	0.38	−0.38	0.07	0.21
Leaf glossiness (x_8)	−0.12	0.46	0.03	0.07	−0.05	0.32	−0.06	**0.20**	0.64	−0.60	0.06	0.94**
Trichome (Abaxial) (x_9)	0.12	−0.45	−0.01	−0.05	0.07	−0.51	0.23	−0.16	**−0.80**	0.75	−0.05	−0.87**
Trichome (Adaxial) (x_{10})	0.12	−0.45	−0.01	−0.05	0.04	−0.54	0.24	−0.16	−0.77	**0.78**	−0.05	−0.85**
Waxy bloom (x_{11})	−0.08	0.27	0.03	0.03	−0.06	0.22	−0.22	0.08	0.28	−0.26	**0.15**	0.47

Note. Path coefficient equation: deadhearts (%) $= -5125 - 0.15x_1 + 0.51x_2 + 0.12x_3 + 0.08x_4 - 0.24x_5 + 0.64x_6 - 0.49x_7 + 0.20x_8 - 0.80x_9 + 0.78x_{10} + 0.15x_{11}$ (residual variance = 0.0). The diagonal values in bold are the direct effects and rest of the values are indirect effects of independent variables on the deadheart formation.

*Correlation coefficients (r) significant at $P = 0.05$.

**Correlation coefficients (r) significant at $P = 0.01$.

same direction for deadhearts, and hence, these can be used as marker traits to select for resistance to shoot fly (Table 7). The indirect effects of leaf surface wetness, leaf glossiness, and waxy bloom on shoot fly deadhearts were largely through trichomes on the abaxial surface of the leaf, leaf sheath pigmentation, and plants with eggs. The direct and indirect effects, correlation coefficients, multiple and step-wise regressions suggested that plants with eggs, leaf glossiness, trichomes on the abaxial surface of the leaf, and leaf sheath pigmentation are the reliable parameters to select sorghums for resistance to shoot fly.

Discussion

Non-preference by insects is often projected as a property of the plant to render it unattractive for oviposition, feeding, or shelter. Oviposition non-preference is considered to be a primary mechanism of resistance to shoot fly in sorghum (Blum, 1967; Singh & Narayana,

1978; Maiti & Bidinger, 1979; Singh & Jotwani, 1980a; Taneja & Leuschner, 1985). The shoot fly-resistant genotypes had significantly lower oviposition as compared to susceptible ones (Jain & Bhatnagar, 1962). Under no-choice conditions in the cage, there were no differences in oviposition on resistant and susceptible genotypes (Soto, 1974; Taneja & Leuschner, 1985; Dhillon, 2004). The present results also indicated that though oviposition non-preference is the primary component of resistance to shoot fly under multi-choice field conditions, it breaks down under no-choice conditions in the cage, a situation akin to large-scale planting of the resistant cultivar or very heavy shoot fly density during the delayed planting in the rainy season, and early planting during the postrainy season. The initial choice of cultivars, such as CSH 1 for oviposition was random, although the time spent by female shoot flies on resistant cultivars (IS 2146, IS 3962 and IS 5613) was short (Raina et al., 1984). Shoot fly females lay eggs on non-preferred cultivars only after laying several eggs on the seedlings of susceptible cultivars. Non-preference for oviposition in sorghum is relative, since none of the known resistant cultivars were completely non-preferred for egg laying. Genotypes preferred for oviposition also show heavy deadheart formation (Rana et al., 1975; Unnithan & Reddy, 1985).

Retardation of growth and development, prolonged larval and pupal periods, and poor emergence of adults on resistant genotypes provides an evidence of antibiosis to sorghum shoot fly (Sharma et al., 1997; Singh & Jotwani, 1980b; Raina et al., 1981). Singh and Jotwani (1980b) reported prolongation of larval and pupal periods (8–15 days) on resistant cultivars. The larvae on the resistant genotypes are generally smaller, and the mortality of the first-instars was higher than on the susceptible genotypes. The mortality of the first-instars was highest (90%) in the first 24 h (Zein el Abdin, 1981). Highest larval survival has been observed on 2-week old plants, followed by very young seedlings, and lowest in >50-day-old plants (Ogwaro & Kokwaro, 1981). Antibiosis of shoot fly offers exciting possibilities of exerting biotic pressure against insect feeding and development, resulting in low-larval survival on resistant varieties (Dahms, 1969; Soto, 1974).

Tiller survival is related to rate of tiller growth, faster the tiller growth greater the chances to escape shoot fly infestation. Tall seedlings and high-plant recovery were reported as the characteristics of resistant varieties by Sharma et al. (1977), which may not have definite relation with the height of the plant, as some of the tolerant germplasm lines are dwarf, medium tall or very tall (Shivankar et al., 1989; Dhillon, 2004). The shoot fly-resistant genotypes had significantly less tiller deadhearts than the susceptible ones. Tiller development consequent to deadheart formation in the main shoot, and its survival depend on the level of primary resistance and shoot fly abundance (Doggett et al., 1970; Dhillon, 2004). Varieties with high recovery resistance yield more under shoot fly infestation (Rana et al., 1985).

Cultivars with high transpiration rate are preferred for oviposition (Mate et al., 1988). Leaf surface wetness (Nwanze et al., 1990) along with epicuticular wax (Nwanze et al., 1992) has been reported to be associated with susceptibility, and leaf glossiness with resistance to shoot fly (Blum, 1972; Agrawal & Abraham, 1985). There is negative correlation between glossiness with oviposition and deadhearts (Maiti et al., 1984; Kamatar & Salimath, 2003). The intensity of leaf glossiness at the seedling stage is positively associated with the level of resistance to shoot fly (Sharma et al., 1997). Trichomes on the abaxial surface of the sorghum leaves have been reported to be associated with resistance to shoot fly (Blum, 1968; Maiti et al., 1980); and trichome density and plant resistance to shoot fly have positive association (Gibson & Maiti, 1983; Maiti & Gibson, 1983; Omori et al., 1983). Shoot fly egg lying was significantly and negatively associated with trichomes and leaf glossiness (Omori et al., 1983). The present studies demonstrated higher level of resistance to shoot fly when leaf glossiness and trichomes occurred together in a genotype. The frequency of lines with high vigor score was greater in the resistant group than in the susceptible group (Sharma et al., 1997). Seedling vigor was significantly and negatively associated with deadhearts and oviposition (Taneja & Leuschner, 1985), but this theory does not hold true with diverse array of shoot fly-resistant and -susceptible genotypes (Dhillon, 2004). Regression analysis indicated inverse association between seedling vigor and deadhearts, and direct association with percent oviposition and egg count, suggesting direct contribution of plants with eggs with deadheart formation (Kamatar & Salimath, 2003). Trichomes and glossy trait have independent effects in reducing the incidence of shoot fly (Maiti, 1980). Although trichome density is significantly and negatively correlated with deadhearts, it does not have direct role in reducing deadhearts, but contributes to shoot fly resistance mainly through other traits (Karanjkar et al., 1992). The correlation and path coefficients, and multiple linear and step-wise regressions indicated that the plants with eggs, deadhearts, leaf glossiness, trichomes

on the abaxial surface of the leaf, and leaf sheath pigmentation are the most reliable parameters, and these can be used as marker traits to screen and select for resistance to sorghum shoot fly.

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