Wild relatives of sorghum as sources of resistance to sorghum shoot fly, *Atherigona soccata*

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Abstract

The levels of resistance to shoot fly, *Atherigona soccata* in sorghum germplasm are low to moderate and therefore, we evaluated 17 wild relatives of sorghum under field and greenhouse conditions as an alternate source of genes for resistance to this pest. Thirty-two accessions belonging to *Parasorghum*, *Stiposorghum* and *Heterosorghum* did not suffer any shoot fly damage under multi-choice conditions in the field, while one accession each of *Heterosorghum* (*Sorghum laxiflorum*) and *Chaetosorghum* (*S. macrospermum*) suffered very low shoot fly damage. Accessions belonging to *S. exstans* (TRC 243601), *S. stipoideum* (TRC 243399) and *S. matarankense* (TRC 243576) showed absolute non-preference for oviposition under no-choice conditions. Accessions belonging to *Heterosorghum*, *Parasorghum* and *Stiposorghum* were preferred for oviposition, but suffered low deadheart formation. Manual infestation of seedlings with shoot fly eggs did not result in deadheart formation in some of the accessions belonging to *S. exstans* (TRC 243601), *S. stipoideum* (TRC 243399), *S. matarankense* (TRC 243576) and *S. purpureosericeum* (IS 18944). Larval mortality was recorded in main stems of the *Parasorghums*. Within section *Sorghum*, accessions belonging to *S. bicolor* ssp. *verticilliflorum* were highly susceptible to shoot fly, as were those of *S. halepense*. However, a few accessions such as IS 18226 (race *arundinaceum*) and IS 14212 (*S. halepense*) resulted in reduced survival and fecundity. Wild relatives of sorghum exhibited very high levels of antibiosis to *A. soccata*, while only low levels of antibiosis have been observed in the cultivated germplasm. Therefore, wild relatives with different mechanisms of resistance can be used as a source of alternate genes to increase the levels and diversify the basis of resistance to shoot fly, *A. soccata*.

Key words: *Atherigona soccata* — wild sorghums — host plant resistance — resistance mechanisms — shoot fly

Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop in the semiarid tropics. In India, which is the secondary centre of diversity, sorghum is third in importance after rice and wheat, and is currently grown on 8.7 million hectares with an annual production of 7.2 million tons [Food and Agriculture Organization (FAO) 2006]. The productivity levels under subsistence farming conditions are quite low (500–800 kg/ha) mainly because of biotic and abiotic constraints. In sorghum, the insects cause an estimated loss of over US$ 1 billion annually (Sharma et al. 2005). Around 150 arthropod species have been reported as pests on sorghum, of which shoot fly, *Atherigona soccata* (Rondani) is the most important biotic constraint in sorghum production in Asia, Africa and the Mediterranean Europe (Sharma 1993). In India, average yield losses of 5% have been reported (Jotwani 1982), but the infestations at times may be over 90% (Rao and Gowda 1967). The shoot fly larvae infest the sorghum seedling in the first to fourth week after emergence. The larvae damage the growing point resulting in drying of the central leaf, producing a deadheart.

Cultivation of plant genotypes resistant to insect pests has been the principal method of pest control and several sources of resistance have been identified in sorghum (Sharma et al. 1992, 2003). However, levels of resistance to sorghum shoot fly in cultivated germplasm are low to moderate (Sharma 1993) and increased insect pressure combined with changing virulence patterns of the pest often cause breakdown of resistance. This underscores the need to develop cultivars with broad-based resistance utilizing genes from diverse sources. The genetic potential of wild species, particularly in resistance breeding, is well documented for cereals such as wheat, rice, maize and barley (Goodman et al. 1987). By contrast, the potential of wild sorghums in sorghum improvement has not been fully explored with only a few isolated reports on resistance screening. *Sorghum purpureosericeum* and *S. versicolor* of Indian and African origin, respectively, have been reported to possess high levels of resistance to the shoot fly [Bapat and Mote 1982, Mote 1984, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) 1995], while some Australian species of sorghum have been shown to possess high levels of resistance to the sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Harris 1979, Sharma and Franzmann 2001). Most of the green bug [*Schizaphis graminum* (Rondani) (biotype C)] resistant hybrids grown in the USA have been derived from the race *virgatum* of *S. bicolor* ssp. *verticilliflorum*, and highest levels of antibiosis to biotype E were found in *S. halepense* (Duncan et al. 1991). To identify accessions that could serve as alternate sources of resistance genes for the long-term control of sorghum shoot fly, we assessed the response of 17 sorghum species to the sorghum shoot fly under field and greenhouse conditions and also studied the non-preference and antibiosis components of resistance to this pest.

Materials and Methods

Plant material: Fifty accessions of wild relatives of sorghum representing 17 species belonging to sections *Parasorghum*, *Heterosorghum*,

Chaetosorghum, *Stiposorghum* and *Sorghum* were evaluated for resistance to sorghum shoot fly, *A. soccata* under field and greenhouse conditions.

Multi-choice conditions (field screening): The test entries along with five cultivated checks (CSH 1 and ICSV 112 – susceptible checks; IS 1054, IS 18551 and IS 2146 – resistant checks) (Sharma et al. 2005) were field screened for resistance to sorghum shoot fly during the 1998 and 1999 rainy seasons. The experiment was laid out in a randomized complete block design with three replications. Each accession was planted in two rows, 2 m long, with an inter-row spacing of 75 cm. The plants were thinned to a spacing of 10 cm within a row at 10 days after seedling emergence. Recommended agronomic practices were followed for raising the crop. Interlard fishmeal technique was used to ensure high and uniform shoot fly infestation in the test plots (Taneja and Leuschner 1985, Sharma et al. 1992). Observations on shoot fly damage (14 and 21 days after seedling emergence) were recorded in terms of number of plants with eggs, number of eggs per plant and number of plants with deadhearts.

Mechanisms of resistance to shoot fly, *Atherigona soccata*: Twenty-two accessions belonging to 14 species were selected based on the field screening for in-depth studies on antixenosis (oviposition non-preference) and antibiosis components of resistance under greenhouse conditions (27 ± 2°C and 85 ± 5% RH).

Non-preference for oviposition (antixenosis): Non-preference for oviposition was studied under no-choice conditions in the greenhouse using the top-cage technique (Sharma et al. 1992). The system consisted of two plastic trays (40 × 30 × 14 cm), one for sowing the test material and the other fitted with a fine wire-mesh clamped over the first tray to serve as a cage. The experiment was laid out in completely randomized design with three replications. The plants were thinned to 50 plants per tray at 10 days after seedling emergence. Urea (5 g per tray) was applied to the seedlings at 10 days after seedling emergence. Shoot flies for infesting the sorghum seedlings in the greenhouse were collected in fish-meal baited traps in the morning hours in the field (Taneja and Leuschner 1985). The *A. soccata* females were separated from the other species and confined with the sorghum seedlings for 2 days. The shoot fly females were provided with glucose and brewers' yeast (1 : 1) in a Petri dish and water on a cotton swab. When the seedlings were at the four to five leaf stage (15 to 18-day old for wild sorghums and 10-day old for the cultivated types), 25 shoot fly females were released inside each cage. The flies were removed after 3 days and the data were recorded on number of plants with eggs (oviposition) and number of eggs per plant. Data on deadhearts were recorded 1 week after infestation.

Antibiosis: To assess antibiosis component of resistance, seedlings of the 22 accessions were raised in plastic trays as described above. Each plant was infested artificially by gently placing two shoot fly eggs into the central leaf whorl for 15–18 days after seedling emergence to have uniform level of infestation across genotypes. The eggs were obtained by allowing gravid shoot fly females to lay eggs on the susceptible cultivar, CSH-1 placed inside a wooden cage fitted with a wire mesh. The eggs were gently dislodged from the leaves with a camel hair brush and used for infesting the test entries. Data on number of plants with deadhearts were recorded at 4 days after egg infestation. Plants with deadhearts were removed from the trays and transferred into plastic jars with moist sand. Data were recorded on duration of postembryonic development and numbers of adults emerged. In case of accessions where no deadhearts were observed, the experiment was repeated and 10 plants per accession were dissected to record larval survival/mortality at 4–5 days after egg infestation.

Statistical analyses: Data on insect numbers and percentage deadhearts were transformed to log $(x + 1)$ and angular values, respectively, and subjected to analysis of variance (ANOVA). The level of significance was similar with the transformed and untransformed data

and therefore, results from untransformed data are presented in this paper. Significance of differences between the treatments was tested by using F-test while the treatment means were compared by using least significant difference (LSD) at P = 0.05.

Results

Reaction of wild relatives of sorghum to shoot fly, *Atherigona soccata*, under multi-choice field conditions

Significant differences were observed among different accessions of wild relatives of sorghum in response to *A. soccata* infestation (Table 1). Thirty-two accessions belonging to *Parasorghum* (*S. australiense, S. purpureosericeum, S. brevicallosum, S. timorense, S. versicolor, S. matarankense, S. nitidum*), *Stiposorghum* (*S. angustum, S. ecarinatum, S. exstans, S. intrans, S. interjectum, S. stipoideum*) and *Heterosorghum* (*S. laxiflorum*) did not suffer any shoot fly damage under multi-choice conditions in the field, while one accession each of *S. laxiflorum* (TRC 243486) and *Chaetosorghum* (*S. macrospermum*) showed very low shoot fly damage. Within section *Sorghum*, the 16 accessions representing *S. halepense* and *S. bicolor* ssp. *verticilliflorum* were highly susceptible to shoot fly.

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

Oviposition non-preference (antixenosis)

The 22 accessions belonging to 14 species, that were highly resistant under multi-choice conditions in the field, showed varying levels of non-preference for oviposition and deadheart formation under no-choice conditions in the greenhouse (Table 2). Accessions belonging to *Heterosorghum* (*S. laxiflorum*) and *Chaetosorghum* (*S. macrospermum*) had more egg laying under no-choice conditions in the greenhouse as compared with multi-choice conditions in the field. *Sorghum macrospermum* (TRC 241162) of *Chaetosorghum* was as susceptible as the susceptible check, CSH 1 in terms of egg laying and deadheart formation. Accessions belonging to *Heterosorghum* had significantly lower deadheart incidence compared to the resistant check, IS 18551, despite high oviposition (61.3–80.5% plants with eggs). Among the *Para-* and *Stiposorghums*, the accessions could be categorized into three groups based on egg-laying under no-choice conditions: (i) no egg-laying (absolute non-preference) as in *S. exstans* (TRC 243601), *S. stipoideum* (TRC 243399) and *S. matarankense* (TRC 243576); (ii) very low egg laying as in case of *S. australiense* (IS 18955, IS 18956), *S. angustum* (TRC 243499), *S. ecarinatum* (TRC 243574), *S. intrans* (TRC 243571), *S. interjectum* (TRC 243461), *S. versicolor* (IS 14262) and *S. purpureosericeum* (IS 18944, IS 18955 and RN 285) and (iii) egg-laying similar to that on the susceptible check as in *S. timorense* (TRC 243498), *S. nitidum* (TRC 243514), *S. purpureosericeum* (IS 18943 and IS 18947) and *S. versicolor* (IS 14275 and IS 23177). Some accessions, although preferred for oviposition, had lower deadheart incidence than the resistant check, IS 18551. There were no deadhearts in one accession of *S. versicolor* (IS 14262) despite having 2.1% plants with eggs.

Antibiosis

When the plants were infested artificially with shoot fly eggs in the greenhouse, significant differences were observed among the accessions for percentage deadheart formation and adult emergence (Table 3). *Stiposorghums* suffered least deadheart

Table 1: Oviposition and deadheart formation by shoot fly, *Atherigona soccata* in wild relatives of sorghum under multi-choice field conditions (ICRISAT, Patancheru, 1998–99)

Species	Accessions	Plants with eggs (%)			Eggs/plant			Deadhearts (%)		
		1998	1999	Pooled	1998	1999	Pooled	1998	1999	Pooled
Chaetosorghum										
S. macrospermum	TRC 241162 (Australia)	3.3	28.0	15.7	0.0	0.4	0.2	3.3	10.1	6.7
Heterosorghum										
S. laxiflorum	TRC 243486 (Australia)	6.7	0.0	3.3	0.1	0.0	0.0	6.7	0.0	3.3
	TRC 243492, IS 18958 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parasorghum										
S. australiense	IS 18954, IS 18955, IS 18956 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. brevicallosum	TRC 243491, IS 18957 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. matarankense	TRC 243576, RN 341 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. nitidum	TRC 243514 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. purpureosericeum	RN 285, IS 18947, IS 18951 (India) IS 18943, IS 18944, IS 18945 (Africa)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. timorense	TRC 243437, TRC 243498 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. versicolor	IS 14262, IS 14275, IS 18926, IS 18940, IS 18941, IS 23177 (Africa)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stiposorghum										
S. angustum	TRC 243598, TRC 243499 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. ecarinatum	TRC 243574 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. exstans	TRC 243601 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. interjectum	TRC 243461 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. intrans	TRC 243571, TRC 243602 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. stipoideum	TRC 243399 (Australia)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sorghum										
S. bicolor ssp. *verticilliflorum*										
Race *aethiopicum*	IS 27584 (Africa)	98.3	100.0	99.2	1.0	1.9	1.5	88.3	89.5	88.9
	IS 18819 (Africa)	85.0	100.0	92.5	0.9	2.8	1.8	85.0	100.0	92.5
	IS 14564 (Africa)	97.2	100.0	98.6	0.9	1.9	1.4	97.2	100.0	98.6
Race *arundinaceum*	IS 18883 (Africa)	79.8	100.0	89.9	0.8	1.6	1.2	74.2	95.6	84.9
	IS 18826 (Africa)	86.7	100.0	93.3	0.9	1.8	1.3	78.3	100.0	89.2
	IS 18830 (Africa)	96.3	100.0	98.2	1.2	2.7	2.0	84.4	100.0	92.2
Race *verticilliflorum*	IS 18865 (Africa)	91.7	100.0	95.8	1.0	2.4	1.7	83.3	100.0	91.7
	IS 14717 (Africa)	90.2	100.0	95.1	0.9	2.8	1.9	85.1	100.0	92.5
	IS 20995 (Africa)	95.4	100.0	97.7	1.0	3.2	2.1	91.7	100.0	95.8
Race *virgatum*	IS 18803 (Africa)	97.8	100.0	98.9	1.0	1.6	1.3	97.8	86.7	92.2
	IS 18813 (Africa)	90.4	100.0	95.2	1.0	2.6	1.8	85.0	100.0	92.5
S. halepense	IS 18891 (USA)	86.1	97.0	91.5	1.1	2.3	1.7	73.9	89.4	81.6
	IS 14299 (Africa)	85.2	100.0	92.6	0.9	1.3	1.1	74.7	88.9	81.8
	IS 14212 (Africa)	80.5	92.3	86.4	0.8	1.5	1.1	53.3	88.1	70.7
	IS 18845 (India)	93.3	100.0	96.7	1.1	1.8	1.4	89.4	88.9	89.2
	IS 18849 (India)	81.7	100.0	90.8	1.0	1.6	1.3	73.3	81.7	77.5
S. bicolor (SC)	CSH 1	96.7	100.0	98.3	1.0	2.0	1.5	93.3	100.0	96.7
S. bicolor (SC)	ICSV 112	100.0	100.0	100.0	1.1	1.7	1.4	86.7	100.0	93.3
S. bicolor (MRC)	IS 1054	76.9	100.0	88.5	0.8	1.6	1.2	47.6	85.2	66.4
S. bicolor (RC)	IS 18551	45.8	50.6	48.2	0.5	0.5	0.5	32.3	30.6	31.4
S. bicolor (RC)	IS 2146	40.2	51.8	46.0	0.4	0.5	0.5	30.2	32.5	31.4
F*p*		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
LSD (5%)		2.98	5.05	3.02	0.16	0.58	0.32	13.36	13.53	9.67

SC, susceptible check; MRC, moderately resistant check; RC, resistant check.

formation (0–5.4%). *Sorghum exstans* and *S. stipoideum* did not have any deadhearts. Among the *Parasorghums*, no deadhearts were recorded in *S. matarankense* (TRC 243576) and *S. purpureosericeum* (IS 18944). Deadheart incidence ranged from 12.7% to 88.9% among other accessions. The two accessions of *Heterosorghum* showed 31.2% and 50.8% deadhearts. The accession TRC 243492 of *Heterosorghum* suffered high deadheart incidence (31.2%) when the seedlings were infested artificially with shoot fly eggs. *Parasorghums* suffered greater deadheart incidence when infested artificially with shoot fly eggs under no-choice greenhouse conditions as compared to multi-choice conditions in the field. In section *Sorghum*, accessions belonging to *S. bicolor* ssp. *verticilliflorum* and *S. halepense* showed maximum deadhearts (54.8–100%). The susceptible check, CSH 1 had 98.4% plants with eggs (on par with field conditions), while the resistant check, IS 18551

had more plants with deadhearts (93.65%) under artificial egg infestation as compared to that under no-choice conditions in the greenhouse (70.2%).

Maximum adult emergence was observed in the accessions belonging to section *Sorghum* (45.8% in race *arundinaceum* to 99.5% in race *aethiopicum*) (Table 3). There was 50.8% adult emergence on the resistant check, IS 18551, compared with 79.4% on the susceptible check, CSH 1. The larval and pupal periods on the four races of section *Sorghum* were comparable with that on the susceptible check, CSH 1. The larval period ranged from 14 to 16 days on these wild races compared with 18–22 days of *S. halepense* and 14–18 days on the resistant check, IS 18551. On *Heterosorghum*, despite 31.2–50.8% plants with deadhearts, there was very low adult emergence (14.6% on TRC 243492 and 6.2% on IS 18958). Among *Parasorghums*, there was no adult emergence on *S. matarankense* (TRC

Table 2: Oviposition and deadheart formation by shoot fly, *Atherigona soccata* in wild relatives of sorghum under no-choice conditions in the greenhouse (ICRISAT, Patancheru, 1999)

Species	Accession	Plants with eggs (%)	Eggs/ plant	Deadhearts (%)
Chaetosorghum				
S. macrospermum	TRC 241162	76.6	1.9	61.5
Heterosorghum				
S. laxiflorum	TRC 243492	61.3	0.9	7.4
	IS 18958	80.5	0.9	26.4
Parasorghum				
S. australiense	IS 18955	16.6	0.2	10.1
	IS 18956	15.8	0.6	5.8
S. matarankense	TRC 243576	0.0	0.00	0.0
S. purpureosericeum	IS 18944	1.8	0.03	0.4
	IS 18945	15.2	0.3	2.8
	RN285	13.0	0.8	3.7
	IS 18943	73.2	2.3	50.3
	IS 18947	52.7	1.4	24.6
S. nitidum	TRC 243514	57.6	1.3	9.7
S. timorense	TRC 243498	100.0	2.3	21.1
S. versicolor	IS 23177	51.7	1.1	6.2
	IS 14262	2.1	0.1	0.0
	IS 14275	44.2	0.9	10.5
Stiposorghum				
S. angustum	TRC 243499	9.0	0.2	4.0
S. ecarinatum	TRC 243574	8.5	0.1	3.5
S. intrans	TRC 243571	7.1	0.1	1.1
S. exstans	TRC 243601	0.0	0.0	0.0
S. interjectum	TRC 243461	2.3	0.1	1.2
S. stipoideum	TRC 243399	0.0	0.0	0.0
Sorghum				
S. bicolor (SC)	CSH 1	100.0	2.6	97.1
S. bicolor (RC)	IS 18551	71.3	1.2	70.2
F*p*		< 0.01	< 0.01	< 0.01
LSD (5%)		30.38	1.32	19.62

SC, susceptible check; RC, resistant check.

243576), *S. nitidum* (TRC 243514), *S. purpureosericeum* (IS 18944 and IS 18955) and *S. versicolor* (IS 14262). In IS 23177 (*S. versicolor*), there were 25.9% plants with deadhearts when infested with eggs artificially under greenhouse conditions, as compared with 6.2% plants with deadhearts when the shoot flies were allowed to oviposit on seedlings under no-choice conditions and no deadheart incidence under field conditions. Adult emergence was also very low (26.3%) on this accession under greenhouse conditions. There was no adult emergence on *S. nitidum* and *S. versicolor* (IS 14262) in spite of 51.8% and 19.4% plants with deadhearts, respectively. Similarly, no adult emergence was recorded on *Stiposorghums* despite 3–5% plants with deadhearts. Dissection of plants with deadhearts did not reveal the presence of any larvae near the growing point. In *Heterosorghum*, only a few plants had live larvae at the growing point. Larval mortality was also recorded in accessions belonging to *Parasorghums* (*S. versicolor*, *S. purpureosericeum*, *S. timorense* and *S. nitidum*). Larval and pupal duration ranged from 15 to 19 days on *Heterosorghums* and from 13 to 24 days on *Parasorghums*, suggesting that reduced survival and prolonged development were the major components of resistance to *A. soccata* in these species, in addition to strong oviposition non-preference.

Discussion

Very high levels of resistance to the sorghum shoot fly, *A. soccata* were observed in the wild relatives of sorghum. Resistance to

sorghum shoot fly in 12 species namely, *S. brevicallosum*, *S. timorense*, *S. matarankense*, *S. nitidum*, *S. angustum*, *S. ecarinatum*, *S. exstans*, *S. intrans*, *S. interjectum*, *S. stipoideum*, *S. laxiflorum* and *S. macrospermum* has been studied for the first time. These species are from Australia, where shoot fly is not known to occur. While resistance to the shoot fly has earlier been reported in accessions of *S. australiense*, *S. purpureosericeum* and *S. versicolor* (Bapat and Mote 1982, Mote 1984, ICRISAT 1995), four new accessions in each of the latter two species have been identified to be highly resistant to this pest.

Within section *Sorghum*, *S. bicolor* ssp. *verticilliflorum* accessions (races *aethiopicum*, *arundinaceum*, *verticilliflorum* and *virgatum*) were highly susceptible to shoot fly, as were those of *S. halepense*. Earlier studies have reported that these species are common wild hosts of the shoot fly (Starks et al. 1970, Delobel and Unnithan 1981). Shoot fly damage in the cultivated sorghums varied across seasons, but there was not much variation in the reaction of *Hetero-*, *Stipo-* and *Parasorghums*, suggesting that levels of resistance to shoot fly in these wild relatives were quite stable across seasons. The 22 accessions belonging to *Parasorghum*, *Heterosorghum* and *Stiposorghum*, which were non-preferred under multi-choice conditions in the field, showed varying levels of non-preference for oviposition under no-choice conditions in the greenhouse. Accessions belonging to *Heterosorghum* (*S. laxiflorum*) and *Chaetosorghum* (*S. macrospermum*) had more egg-laying under no-choice conditions in the greenhouse as compared to field conditions. Both the resistant, IS 18551 and the susceptible, CSH 1 checks were equally preferred for egg-laying under no-choice conditions in greenhouse. In the cultivated sorghum, oviposition non-preference as a resistance mechanism is ineffective under no-choice conditions (Soto 1974, Singh and Narayana 1978, Dhillon et al. 2005). However, oviposition non-preference as a mechanism of resistance was quite stable in three accessions (TRC 243576, TRC 243601 and TRC 243399), while 10 accessions showed very high levels of oviposition under no-choice tests in the greenhouse. Oviposition non-preference exhibited by the wild species may be due to absence of attractants or presence of certain repellant compounds. Shoot fly susceptible genotypes are reported to emit volatile substances that guide the shoot fly females to their hosts for oviposition (Nwanze et al. 1998). Lwande and Bentley (1987) identified (2) 3 Hexene-1-ol acetate as the major volatile from the seedlings of *S. bicolor* (var. 'Serena') that elicits a behavioural response in some phytophagous insects. A study of the qualitative or quantitative differences in blends of volatile compounds in sorghum and its wild relatives will be useful to understand shoot fly–sorghum plant interactions, especially the biochemical mechanisms of oviposition non-preference.

Besides volatile substances, morphological traits may also contribute to oviposition non-preference. In most of the accessions of wild relatives displaying high levels of resistance to sorghum shoot fly, medium to high density of hairiness was observed on both abaxial and adaxial surfaces of the leaves. In addition, the leaf blades were pubescent, while ligule had a membrane with or without long hairs. In cultivated sorghum, trichomes on undersurface of leaf are associated with oviposition non-preference by *A. soccata* (Maiti et al. 1980, Bapat and Mote 1982, Sharma and Nwanze 1997). Glossy leaf trait at the seedling stage (Maiti and Bidinger 1979), leaf surface wetness, epicuticular wax structure (Nwanze et al. 1992), silica deposition and lignification (Ponnaiya 1951, Blum 1968) are associated with resistance to *A. soccata*. These factors need to

Table 3: Deadheart formation, adult emergence, and duration of postembryonic development of shoot fly, *Atherigona soccata* on seedlings of wild relatives of sorghum infested artificially with shoot fly eggs (ICRISAT, Patancheru, 1999)

Species	Accession	Deadhearts (%)	Adult emergence (%)	Days to adult emergence
Heterosorghum				
S. laxiflorum	TRC 243492	31.2	14.6	15–19
	IS 18958	50.8	6.2	15–19
Parasorghum				
S. australiense	IS 18955	28.8	4.2	17.00
	IS 18956	30.4	6.1	15–19
S. matarankense	TRC 243576	0.0	0.0	–
S. nitidum	TRC 243514	51.8	0.0	–
S. purpureosericeum	RN 285	88.9	32.3	13–16
	IS 18943	36.9	44.8	13–16
	IS 18944	0.0	0.0	–
	IS 18945	12.7	0.0	–
	IS 18947	61.4	43.5	15–19
S. timorense	TRC 243498	42.4	45.8	15–19
S. versicolor	IS 23177	25.9	26.3	15–24
	IS 14262	19.4	0.0	
	IS 14275	37.4	31.9	15–24
Stiposorghum				
S. angustum	TRC 243499	4.8	0.0	–
S. ecarinatum	TRC 243574	5.4	0.0	–
S. exstans	TRC 243601	0.0	0.0	–
S. interjectum	TRC 243461	4.1	0.0	–
S. intrans	TRC 243571	3.1	0.0	–
S. stipoideum	TRC 243399	0.0	0.0	–
Sorghum				
S. bicolor subsp. *verticilliflorum*				
Race *aethiopicum*	IS 14564	98.4	99.5	14–16
Race *arundinaceum*	IS 18826	54.8	45.8	14–16
Race *verticilliflorum*	IS 18865	98.4	78.5	14–16
Race *virgatum*	IS 18808	100.0	89.0	14–16
S. halepense	IS 14212	95.1	68.9	18–22
S. bicolor (R)	IS 18551	93.7	50.8	14–18
S. bicolor (S)	CSH 1	98.4	79.4	14–16
F*p*		< 0.01	< 0.01	
LSD (5%)		14.87	18.97	

–, no adult emergence; S, susceptible check; R, resistant check.

be evaluated in greater detail in the wild species resistant to shoot fly to obtain a better understanding of their role on host plant resistance to this insect.

A significantly low proportion of plants exhibited deadheart symptoms in accessions belonging to *Heterosorghum*, *Parasorghum* and *Stiposorghum* in comparison to the resistant check, IS 18551. In contrast, accessions belonging to section *Sorghum* had similar proportion of plants with both eggs and deadhearts. When seedlings of *Heterosorghum*, *Parasorghum* and *Stiposorghum* were infested manually with shoot fly eggs, some of the accessions belonging to *S. exstans*, *S. stipoideum*, *S. matarankense* and *S. purpureosericeum* did not produce any deadhearts. There was no adult emergence from deadhearts in accessions belonging to *Stiposorghum* and *Heterosorghum*, suggesting that the larvae were unable to complete the life cycle on these species. Among the *Parasorghum*s, there was no adult emergence on *S. matarankense* (TRC 243576), *S. nitidum* (TRC 243514), *S. purpureosericeum* (IS 18945) and *S. versicolor* (IS 14262). Larval mortality was observed in accessions belonging to *S. versicolor*, *S. purpureosericeum*, *S. timorense* and *S. nitidum*. Low adult emergence was also observed in accessions belonging to section *Sorghum*, including the four wild races (*aethiopicum*, *arundinaceum*, *verticilliflorum* and *virgatum*) and *S. halepense*, although the duration of postembryonic development was similar to that on the susceptible check, CSH 1. Physical barriers such as hairs, trichomes and tight leafsheath may result in poor establishment of the larvae

and low deadheart formation. Secondary metabolites or poor nutritional quality of the host may also result in poor survival and growth of *A. soccata*.

The present study indicated that wild relatives of sorghum are valuable source of resistance to sorghum shoot fly, *A. soccata* in sorghum. While the accessions belonging to primary genepool may be amenable for use in sorghum improvement (*aethiopicum*, *arundinaceum*, *verticilliflorum* and *virgatum* that have shown antibiosis to shoot fly), the accessions belonging to *Stiposorghum*, *Parasorghum*, *Heterosorghum* and *Chaetosorghum* (tertiary genepool), constitute the extreme outer limit of potential genetic resource for crop improvement. Some of these accessions can be exploited for sorghum improvement through embryo rescue and gene cloning. While oviposition non-preference is the primary mechanism of resistance to shoot fly, *A. soccata* in cultigen, there was strong evidence that antibiosis is an important mechanism of resistance in wild relatives of sorghum. Therefore, there is a possibility of increasing the levels and diversifying the basis of resistance to *A. soccata* by introgressing the resistance genes from the wild relatives into the cultigen.

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