

Interactions of spotted stem borer *Chilo partellus* with wild relatives of sorghum

VENKATESWARAN KAMALA^{1,6}, HARI C. SHARMA², DAGGU MANOHAR RAO³, KODEBOYINA S. VARAPRASAD¹, PAULA J. BRAMEL⁴ and SUBHASH CHANDRA⁵

¹National Bureau of Plant Genetic Resources, Regional Station, Rajendranagar, Hyderabad 500 030, Andhra Pradesh, India; ²International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India; ³Department of Genetics, Osmania University, Hyderabad 500007, Andhra Pradesh, India; ⁴International Institute for Tropical Agriculture, Ibadan, Nigeria; ⁵Department of Primary Industries, Tatura 3616, Vic., Australia; ⁶Corresponding author, E-mail: kgksvp@gmail.com

With 5 tables

Received August 10, 2011/Accepted February 22, 2012

Communicated by T. Lübberstedt

Abstract

The levels of resistance to spotted stem borer (*Chilo partellus*) in sorghum are low to moderate. We therefore evaluated wild relatives of sorghum to identify accessions with high levels of resistance to this pest and studied the mechanisms of resistance. *Heterosorghum* (*Sorghum laxiflorum*), *Para-sorghum* (*S. australiense*, *S. purpureo-sericeum*, *S. versicolor*, *S. matarankense*, *S. timorense*, *S. brevicallusum* and *S. nitidum*) and *Stiposorghum* (*S. angustum*, *S. ecarinatum*, *S. extans*, *S. intrans*, *S. interjectum* and *S. stipoidesum*) showed very high levels of resistance to stem borer. *Chaetosorghum* (*S. macrospermum*), four wild races of *S. bicolor* subsp. *verticilliflorum* and *S. halepense* were found to be susceptible. Under no-choice conditions, egg laying was observed on all accessions, which significantly differed among the species/accessions. Accessions belonging to *Stiposorghum* and *Para-sorghum* (*S. purpureo-sericeum*, *S. versicolor* and *S. timorense*) were significantly less preferred for oviposition than the resistant control, IS 2205. Accessions belonging to *Stiposorghum* showed slight leaf-feeding, but there was no deadheart formation. Although there was some damage in *Para-sorghum*, very few deadhearts were formed, and a few larvae that were recovered subsequently died. In *Heterosorghum*, the two accessions of *S. laxiflorum* were highly preferred for oviposition, and up to 82% deadhearts were recorded, but the six larvae that were recovered died within a month. Accessions belonging to *Eu-sorghum* showed maximum deadhearts, larval recovery and adult emergence. The results suggested that some of the wild relatives of sorghum possess high levels of resistance to *C. partellus* and both antixenosis and antibiosis are major components of resistance to this pest. Accessions showing high levels of resistance to stem borer can be utilized to increase the levels and diversify the bases of resistance to this pest in sorghum.

Key words: *Chilo partellus* — wild sorghums — host plant resistance — resistance mechanisms — spotted stem borer

Sorghum bicolor (L.) Moench is one of the major grain crops in the semi-arid tropics of Asia and Africa. It is known for its versatility and diversity; forage varieties are used widely for cut green fodder, silage and syrup production; stalks are used for stover, roughage, thatch and fuel. It is primarily a crop of resource-poor, small-scale farmers and is typically cultivated on marginal lands with low input use under adverse conditions. Pest problems pose a major challenge in achieving higher production. Nearly 150 species of insects have been recorded as pests on sorghum, and about 32% of the crop is lost because of insect pest infestation in India. In monetary terms, losses

owing to insect pests have been estimated to be over \$1000 million annually in the semi-arid tropics (ikisan.com 2000). Global sorghum crop losses owing to stem borer damage have been estimated at over US\$ 300 million annually (ICRISAT, 1992; Sharma 1997). In general, yield losses range between 5% and 10%, especially when the infestation occurs early. De Groote et al. (2003) found that all stem borer species caused average annual losses of 13.5% valued at US\$ 80 million in Kenya.

The spotted stem borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) is one of the economically most damaging pests in Asia and Africa, attacking all parts of the plant except the roots. Infestation starts approximately 2 weeks after seedling emergence. The first symptom of damage is the presence of shot-holes caused by early instar larval feeding, and the infested plants exhibit a ragged appearance. Feeding and stem tunnelling by the stem borer larvae on plants result in crop losses as a consequence of destruction of the growing point, early leaf senescence and interference with translocation of metabolites and nutrients that result in peduncle breakage and production of completely or partially chaffy panicles (Taneja and Leuschner 1985). Sorghum accessions with resistance to spotted stem borer, *C. partellus*, have been identified (Taneja and Leuschner 1985, Sharma et al. 1992, 2003, Jalaluddin et al. 1995, Patel et al. 1996). Improved genotypes such as ICSV 705, SPV 135, CSV 8R, SPV 104, SPV 238 and SPV 842 with moderate levels of resistance to stem borer have also been developed (Singh and Rana 1989, Sharma 1993). Wild relatives of crops have frequently been used as sources of resistance to insect pests, and genes from wild relatives have played a key role in developing crop cultivars with durable resistance to insect pests (Goodman et al. 1987). Wild relatives of sorghum, hitherto not systematically explored, may therefore offer additional opportunities to identify sources of resistance for developing sorghum cultivars with high and stable resistance to the spotted stem borer.

Sorghum is a highly variable genus. It has 24 species distributed in five sections: *Eu-sorghum*, *Chaetosorghum*, *Heterosorghum*, *Para-sorghum* and *Stiposorghum*. The most comprehensively studied section, *Eu-sorghum*, includes the cultivated grain and fodder sorghums (*Sorghum bicolor* subsp. *bicolor*), closely related wild annual sorghums (*S. bicolor* subsp. *verticilliflorum*) from Africa, weedy perennial sorghums

(*S. halepense*) from southern Europe and Asia and a perennial wild species (*S. propinquum*) from South and South-East Asia (Doggett 1988). The other four sections comprise wild species that are distributed in Africa, Australia and Asia. Earlier studies have identified wild relatives of sorghum with high levels of resistance to sorghum shoot fly, *Atherigona soccata* (Rondani) (Mote 1984, Kamala *et al.* 2009), sorghum midge, *Stenodiplosis sorghicola* (Coq.) (Sharma and Franzmann 2001), and greenbug, *Schizaphis graminum* (Rondani) (Duncan *et al.* 1991). This study investigated the potential of wild sorghums as sources of resistance to the spotted stem borer. To the authors' knowledge, this study is a maiden effort that systematically evaluated a diverse array of wild sorghums for resistance to spotted stem borer, *C. partellus*, and studied the underlying resistance mechanisms.

Materials and Methods

This investigation consisted of four experiments, one in the field and three in the greenhouse, all carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India. All accessions assessed were obtained from the ICRISAT Genebank. Fifty-five accessions representing 17 *Sorghum* species distributed in five sections, viz. *Eu-sorghum*, *Chaetosorghum*, *Heterosorghum*, *Para-sorghum* and *Stiposorghum*, were first evaluated in 1998 and 1999 for resistance to damage by the stem borer, *C. partellus*, under artificial infestation in the field. Based on field responses, 27 accessions were evaluated in 1999 under greenhouse conditions for antixenosis for oviposition under multi-choice conditions, and a subset comprising of 14 accessions was tested under no-choice conditions. Twenty-three accessions were assessed in 1999 for antibiosis component of resistance under no-choice conditions. Cultivated sorghum, *S. bicolor* cultivars, IS 2205 and ICSV 1 were used as resistant and susceptible control genotypes, respectively, along with two improved cultivars (ICSV 700 and ICSV 708) with moderate levels of resistance to this pest.

Expression of resistance under field conditions: Field screening for resistance to spotted stem borer was conducted in 1998 rainy and 1999 post-rainy seasons. The experiments were laid out in a randomized complete block design with three replications. Recommended cultivation practices were followed to maintain a good crop stand. Accessions were planted in two row plots, 2 m long, with an inter-row distance of 75 cm. Plants were thinned to 20/row at 15 days after seedling emergence. A modified version of the Bazooka applicator (Sharma 1997) was used for infestation. Blackhead-stage egg masses (approximately 500) from the insect culture maintained in the laboratory (following Sharma *et al.* 1992), along with 85 g of poppy seeds (*Papaver* sp.), were kept overnight in a plastic jar with a tightly fitted lid. In the morning, the first-instar larvae were gently mixed with the carrier (poppy seeds) and transferred into the plastic bottle of the Bazooka applicator. The seedlings were infested with neonate larvae at 20 days after seedling emergence. The nozzle of the Bazooka applicator was placed close to the leaf whorl, and with a single stroke, each plant was infested with 5–7 larvae, sufficient to cause over 90% damage in the susceptible genotypes (Sharma 1997). The crop was infested in the morning between 08:00 and 11:00 h to avoid larval mortality because of high temperature. The Bazooka applicator was rotated after every 10 strokes to ensure uniformity in larval distribution. The whorl was gently tapped before infestation to avoid drowning of the larvae in water retained in the leaf whorl. A selective insecticide (cypermethrin) was used to control shoot fly infestation without causing any residual effect on stem borer establishment. One week after artificial infestation, stem borer damage was recorded as percentage of total number of plants showing leaf-feeding symptoms, and intensity of leaf-feeding as leaf damage score (LDS) on a 1–9 visual rating scale (1 = <10% leaf area damaged and 9 = >80% leaf area damaged). Plants showing deadhearts were recorded 20 days

after artificial infestation and expressed as a percentage of the total number of plants (Sharma *et al.* 1992).

Ovipositional non-preference (antixenosis) under greenhouse conditions: A subset of 22 accessions, representing 14 species belonging to *Hetero-*, *Para-* and *Stipo-sorghums*, which did not produce any deadhearts under artificial infestation in the field, was evaluated for ovipositional preferences (antixenosis) under multi-choice conditions in the greenhouse (23 ± 5°C and 65 ± 5% RH). In addition, five accessions of *Eu-sorghum*, including one of *S. halepense* and one each of the four wild races of *S. bicolor* ssp. *verticilliflorum* (*aethiopicum*, *arundinaceum*, *verticilliflorum* and *virgatum*), were also included in this test, although they showed high level of deadheart formation after artificial infestation in the field. Cultivars IS 2205 and ICSV 1 were used as resistant and susceptible control genotypes, respectively. The 27 accessions were randomly assigned to three sets with 8, 9 and 10 accessions in each, respectively, thus giving the moths a choice of 10, 11 and 12 accessions for oviposition (including the susceptible, ICSV 1, and resistant, IS 2205, controls in each set). The test entries were raised in pots (30 cm diameter and 30 cm high) in the greenhouse, and the seedlings were thinned to five seedlings/pot 10 days after emergence. The potting mixture consisted of black soil, sand and farm yard manure (2 : 1 : 1). Pots with 18-day-old plants were placed inside a wooden cage (80 × 70 × 60 cm) at random along with the resistant and susceptible controls. The wooden framed cages were covered with a wire-mesh screen on three sides and a glass door in the front. Fifty pairs of newly emerged adults were released inside each cage through a window in the front. The insects were raised on artificial diet in the insect-rearing laboratory following Sharma *et al.* (1992). Moths were provided with water in a cotton swab. Moths after release into the cage were allowed to oviposit on the plants for three nights. To avoid predation by ants, Tanglefoot[®] was smeared on all the four legs of the cages. The cages were placed on a table in a completely randomized design. Accessions in each experiment were replicated thrice, and their positions randomly changed everyday to minimize position effects.

Antixenosis for oviposition under no-choice conditions was studied by allowing the moths a choice of only one accession of 14 accessions (selected from 27 accessions based on low/nil oviposition in the multi-choice tests). Each accession along with the resistant and susceptible controls, IS 2205 and ICSV 1, respectively, was kept individually inside an oviposition cage. The plants were grown in pots in the greenhouse as described earlier, and there were five seedlings/pot. The oviposition cages were arranged on the table in a completely randomized design with three replications. Ten pairs of newly emerged adults were released inside each oviposition cage and allowed to oviposit on the test entries for three nights.

In both the multi- and no-choice experiments, the number of egg masses and the number of eggs in each egg mass were recorded on five plants and expressed as an average. The number of eggs/plant was based on total number of eggs in the egg masses recorded on five plants and expressed as average number of eggs per plant. The number of egg masses on lower (adaxial) and upper (abaxial) surfaces was recorded separately in the no-choice experiment.

Antibiosis under greenhouse conditions: Expression of antibiosis to *C. partellus* was studied in greenhouse in terms of survival and development of neonate larvae with 21 accessions representing 13 species (except *S. brevicallousum* as per Table 1). Also included for comparison were the two susceptible accessions, one each of race *virgatum* (*S. bicolor* ssp. *verticilliflorum*) and *S. halepense* along with the control resistant (IS 2205) and susceptible (ICSV 1) genotypes. The experiment was laid out in a completely randomized design with three replications. The plants were raised in trays (30 × 45 × 20 cm) in the greenhouse. Ten days after seedling emergence, 20 plants were retained in each tray. Urea (at 10 g per tray) was applied after thinning. The plants were infested artificially with 10 first-instar larvae/plant using a camel hairbrush at 20 days after seedling emergence. One week after infestation, the plant damage was recorded as percentage of total

Table 1: Resistance of *Sorghum* species to damage by the stem borer, *Chilo partellus*, after artificial infestation under multi-choice conditions in the field

Section/Species/Subsp/Race	Accession	Plant damage (%)			Leaf damage score (1–9 scale)			Deadhearts (%)		
		1998	1999	Pooled	1998	1999	Pooled	1998	1999	Pooled
<i>Chaetosorghum</i>										
<i>S. macrosperrum</i>	TRC-241162 (Australia)	100a	45.8j	72.9gh	2.7f	4.7defg	3.7hi	96.3ab	21.9hi	59.1hij
<i>Heterosorghum</i>										
<i>S. laxiflorum</i>	IS 18958 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. laxiflorum</i>	TRC-243486 (Australia)	14.1bcd	0k	7ij	lg	li	lj	3.9h	0i	2i
<i>S. laxiflorum</i>	TRC-243492 (Australia)	10.1bcd	3k	6.5ij	lg	li	lj	0h	0i	0i
<i>Para-sorghum</i>										
<i>S. australiense</i>	IS 18954 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. australiense</i>	IS 18955 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. australiense</i>	IS 18956 (Australia)	0d	3.9k	2ij	lg	li	lj	0h	0i	0i
<i>S. brevicallosum</i>	IS 18957 (Australia)	1.5cd	0k	0.7ij	lg	li	lj	0h	0i	0i
<i>S. brevicallosum</i>	TRC-243491 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. mator-ankense</i>	RN341 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. mator-ankense</i>	TRC-243576 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. nitidum</i>	TRC-243514 (Australia)	1.8cd	0k	0.9ij	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	IS 18943 (Africa)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	IS 18944 (Africa)	16.7bc	0k	8.4ij	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	IS 18945 (Africa)	21.7b	0k	10.9i	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	IS 18947 (India)	11.3bcd	4.4k	7.9ij	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	IS 18951 (India)	4.8cd	0k	2.4ij	lg	li	lj	0h	0i	0i
<i>S. purpureo-sericeum</i>	RN285 (India)	4.2cd	10.7k	7.4ij	lg	li	lj	0h	0i	0i
<i>S. timorensis</i>	TRC-243437 (Australia)	5.9bcd	7.7k	6.8ij	lg	li	lj	0h	0i	0i
<i>S. timorensis</i>	TRC-243498 (Australia)	3.9cd	9.1k	6.5ij	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 14262 (Africa)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 14275 (Africa)	6.1bcd	0k	3ij	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 18926 (Africa)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 18940 (Africa)	0d	1.9k	0.9ij	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 18941 (Africa)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. versicolor</i>	IS 23177 (Africa)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>Stiposorghum</i>										
<i>S. angustum</i>	TRC-243499 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. angustum</i>	TRC-243598 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. ecarinatum</i>	TRC-243574 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. extans</i>	TRC-243601 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. interjectum</i>	TRC-243461 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. intrans</i>	TRC-243571 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. intrans</i>	TRC-243602 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>S. stipoidesum</i>	TRC-243399 (Australia)	0d	0k	0j	lg	li	lj	0h	0i	0i
<i>Eu-Sorghum</i>										
<i>S. bicolor</i> ssp <i>verticilliflorum</i>										
<i>Race aethiopicum</i>	IS 14564 (Africa)	100a	81.1bcde	90.6abcde	5.3cd	5.3bcdef	5.3bcde	100a	80.5abcde	90.2abcd
<i>Race aethiopicum</i>	IS 18819 (Africa)	100a	75.4cdef	87.7bcdef	5.3cd	4.3efg	4.8defg	70.3cdef	97.3a	83.8abcde
<i>Race aethiopicum</i>	IS 27584 (Africa)	100a	73.3defgh	86.7cdef	7ab	5.7bcde	6.3ab	100a	90.6abcd	95.3ab
<i>Race aundinaceum</i>	IS 14571 (Africa)	100a	81.7bcde	90.9abcde	3f	4.7defg	3.8ghi	91.7abc	83.7abcde	87.7abcd
<i>Race aundinaceum</i>	IS 18826 (Africa)	100a	92.4ab	96.2abc	5cde	5.7bcde	5.3bcde	76.7bcde	92.4abc	84.6abcde
<i>Race aundinaceum</i>	IS 18830 (Africa)	100a	74.8defg	87.4cdef	3f	3.7gh	3.3i	100a	74.8bcdef	87.4abcd
<i>Race aundinaceum</i>	IS 18883 (Africa)	91.7a	52.4ij	72.1h	3.7ef	3.7gh	3.7hi	83.3abcd	81abcde	82.2bcdef

Table 1: (Continued)

Section/Species/Subsp/Race	Accession	Plant damage (%)			Leaf damage score (1-9 scale)			Deadhearts (%)		
		1998	1999	Pooled	1998	1999	Pooled	1998	1999	Pooled
<i>Race verticilliflorum</i>	IS 14278 (Africa)	96.3a	73.6defgh	85def	4.7de	4.3efg	4.5efgh	85.2abcd	56.8fg	71efgh
<i>Race verticilliflorum</i>	IS 14717 (Africa)	100a	92.1ab	96.1abc	2.7f	5cdefg	3.8ghi	78.2abcde	86.8abcde	82.5bcde
<i>Race verticilliflorum</i>	IS 18865 (Africa)	100a	88.3abcd	94.2abcd	3f	5cdefg	4fghi	86.1abcd	88.3abcd	87.2abcd
<i>Race verticilliflorum</i>	IS 20995 (Africa)	100a	93ab	96.5abc	5.7bcd	4.7defg	5.2cde	86abcd	91.7abcd	88.8abcd
<i>Race virgatum</i>	IS 18803 (USA)	100a	96.1ab	98.1ab	5cde	6.7ab	5.8abcd	100a	96.1ab	98.1a
<i>Race virgatum</i>	IS 18808 (Africa)	100a	89abcd	94.5abcd	7.3a	6.3abc	6.8a	97.3ab	72.9cdef	85.1abcde
<i>Race virgatum</i>	IS 18813 (Africa)	100a	100a	100a	4.7de	6.3abc	5.5bcde	98.3ab	91.3abcd	94.8ab
<i>Race virgatum</i>	IS 18817 (Africa)	96.7a	100a	98.3a	6.3abc	6abcd	6.2abc	93ab	91.4abcd	92.2abc
<i>S. halepense</i>	IS 14212 (Africa)	100a	84abcd	92abcde	5.3cd	4.7defg	5def	68.8def	42.4gh	55.6ijk
<i>S. halepense</i>	IS 14299 (Africa)	100a	58.5ghij	79.2fgh	3.7ef	3.7gh	3.7hi	76.7bcde	66.1ef	71.4efgh
<i>S. halepense</i>	IS 18845 (India)	100a	72.8defg	86.4cdef	2.3fg	4.7defg	3.5hi	59.3efg	70.3def	64.8ghi
<i>S. halepense</i>	IS 18849 (India)	94.4a	94.4ab	94.4abcd	3.7ef	6abcd	4.8defg	53.1fg	81.2abcde	67.2fghi
<i>S. halepense</i>	IS 18891 (USA)	100a	81bcde	90.5abcde	5cde	4fgh	4.5efgh	77.8bcde	79.1abcde	78.4cdefg
<i>S. halepense</i>	IS 33712 (India)	100a	100a	100a	3.7ef	3h	3.3i	65.3def	76.7abcdef	71efgh
<i>S. bicolor</i> (IC)	ICSV 700	100a	64.4fghi	82.2efgh	7ab	5.3bcdef	6.2abc	66.1def	23.4h	44.8jk
<i>S. bicolor</i> (IC)	ICSV 708	100a	66.4efghi	83.2efg	6.3abc	4.3efg	5.3bcde	67.3def	30.3h	48.8jk
<i>S. bicolor</i> (IR)	ICSV 743	100a	98.6a	99.3a	6.3abc	7.3a	6.8a	83.3abcd	70.3def	76.8defg
<i>S. bicolor</i> (RC)	IS 2205	100a	58.1hij	79fgh	5.3cd	4.3efg	4.8defg	44.4g	37.2gh	40.8k
<i>S. bicolor</i> (SC)	ICSV 1	100a	91.7abc	95.9abc	6.3abc	7.3a	6.8a	100a	87.2abcde	93.6abc
Fp (Acc)		<0.001	<0.001	<0.001	<0.001	<0.001	<0.017	<0.001	<0.001	<0.001
LSD (Acc) 5%		7.12	20.18	10.56	1.26	1.60	0.51	22.93	20.95	5.21
Fp (Acc × year)				<0.001			<0.017			<0.001
LSD (Acc × year) 5%				16.65			1.51			21.99

IR, improved resistant cultivar; IC, improved cultivar; RC, resistant check; SC, susceptible check; LSD, least significant difference.

number of plants showing leaf-feeding symptoms, and the intensity of leaf-feeding was recorded as LDS on a 1–9 visual scale (1 = <10% leaf area damage and 9 = >80% leaf area damage). Plants showing deadhearts were recorded 20 days after artificial infestation and expressed as a percentage of the total number of plants (Sharma et al. 1992). Observations on larval survival were recorded by cutting open the stems with deadhearts 20 days after infestation. Live larvae were provided with fresh stems of respective genotypes on alternate days till pupation. Data were recorded on percentage pupation and adult emergence.

Statistical analysis: Count and binomial percentage data, as required to meet the ANOVA assumptions, were transformed to $\log(x + 1)$ and angular scales, respectively, and subjected to analysis of variance (ANOVA) in accordance with the experimental design used. The results from transformed and original scales were similar, with ANOVA assumptions reasonably met in both cases. Therefore, results from original scales only are presented. Significance of differences in accessions was tested using least significant difference (LSD) at 5% level of significance. All analyses were conducted using GenStat 10.2 statistical software (Payne et al. 2007).

Results

Resistance under field conditions

There were significant differences among the wild relatives of sorghum in their response to artificial infestation with first-instar larvae of *C. partellus* in the field. The results of individual seasons' and across-season analyses are presented in Table 1. The accessions exhibited significant differences ($P < 0.001$) for plants damaged, LDS and percentage deadhearts. The resistant (IS 2205) and susceptible (ICSV 1) control genotypes differed significantly in the two seasons, except for leaf damage in the 1998 rainy season. Stem borer damage was greater in the 1998 rainy season than in the 1999 post-rainy season. The relative ranking of accessions in the two seasons was consistent. This allowed identification of accessions with stable resistance across seasons. Thirty-three accessions belonging to *Para-sorghum* (*S. australiense*, *S. purpureo-sericeum*, *S. brevicallousum*, *S. timorensis*, *S. versicolor*, *S. matarankense* and *S. nitidum*), *Stiposorghum* (*S. angustum*, *S. ecarinatum*, *S. extans*, *S. intrans*, *S. interjectum* and *S. stipodeum*) and *Heterosorghum* (*S. laxiflorum*) were highly resistant to stem borer damage and did not suffer any damage under multi-choice conditions in the field over the two seasons. One accession of *S. laxiflorum* (TRC 243486) showed negligible stem borer damage. *S. macrospermum* of *Chaetosorghum* along with the 21 accessions of *Eu-sorghum* representing *S. bicolor* ssp *verticilliflorum* and *S. halepense* were highly susceptible to the stem borer although some of the *Eu-sorghums* were significantly less damaged than the susceptible ICSV 1.

Ovipositional non-preference under greenhouse conditions

The accessions showed considerable variation in oviposition non-preference by the *C. partellus* females under multi-choice conditions in the greenhouse (Table 2). Ten accessions were significantly less preferred for oviposition as compared to the resistant control, IS 2205, particularly with respect to egg masses per plant and eggs per plant. No eggs were laid on four accessions belonging to *Stiposorghum* (*S. extans* – TRC-243601) and *Para-sorghum* (*S. versicolor* – IS 14262 and IS 14275; and *S. purpureo-sericeum* – IS 18944). Six accessions

[*Para-sorghum* – *S. purpureo-sericeum* (RN 285, IS 18947, IS 18943 and IS 18945), *S. australiense* (IS 18956) and *Stiposorghum* – *S. interjectum* (TRC 243461)] were significantly less preferred for oviposition relative to the resistant control, IS 2205, in terms of the number of egg masses/plant. Other *Para-sorghum* accessions including those of *S. timorensis*, *S. nitidum*, *S. brevicallousum*, *S. purpureo-sericeum* (RN 285, IS 18947, IS 18943, IS 18945) and *S. australiense* (IS 18956) had significantly less number of egg masses/plant as compared to the susceptible control, ICSV 1, but were comparable to the resistant control, IS 2205. The two accessions of *S. laxiflorum* (*Heterosorghum*) were highly preferred for egg laying as compared to ICSV 1, both in terms of egg masses and number of eggs/plant. In *Eu-sorghum*, all accessions of wild races of *Sorghum* ssp *verticilliflorum* were highly preferred for oviposition, except for IS 14564 (race *aethiopicum*), which was comparable with the resistant control, IS 2205, for eggs/plant. Oviposition on *S. halepense* (IS 14212) did not differ significantly from the resistant control, IS 2205. Responses of the controls, resistant (IS 2205) and susceptible (ICSV 1), in terms of number of egg masses/plant were significantly different from each other in sets 2 and 3. They, however, did not differ with respect to the number of eggs/egg mass. In set 1, responses of both IS 2205 and ICSV 1 were similar for all three variables.

Accessions belonging to *Para-* and *Stiposorghums* that exhibited antixenosis for oviposition under multi-choice tests were significantly different for number of egg masses (0.1–4.3), number of eggs/egg mass (2.7–64.8) and number of eggs/plant (0.5–141.9) under no-choice conditions (Table 3). All four accessions of *Stiposorghum* (*S. ecarinatum*, *S. extans*, *S. intrans* and *S. interjectum*) and nine accessions of *Para-sorghum* showed significantly less number of egg masses (0.3–2.5), while TRC 243601 (*S. extans*) and IS 23177 and IS 14262 (*S. versicolor*) had significantly less number of eggs/egg mass as compared to the resistant control, IS 2205. A few eggs were laid on the three accessions, namely TRC 243601 (*S. extans*) and IS 14262 and IS 14275 (*S. versicolor*), that showed no oviposition under multi-choice conditions, but were significantly less preferred than the resistant control, IS 2205. Responses of the resistant and susceptible controls differed significantly. There were also significant differences among the accessions in terms of distribution of egg masses on the adaxial and abaxial surfaces of the leaves (Table 4). Overall, there were more egg masses and eggs on the adaxial surface of the leaves, except for *S. timorensis* (*Para-sorghum*) and *S. interjectum* (*Stiposorghum*). The resistant and susceptible control genotypes differed significantly for total number of eggs/plant, but not for egg masses or eggs/egg mass on both adaxial and abaxial surfaces of the leaves.

Antibiosis under greenhouse conditions

Under no-choice conditions, when plants were infested with first-instar larvae in greenhouse (10 larvae per plant), there was no plant damage (Table 5) in terms of leaf-feeding on any of the *Stiposorghums* and one *Para-sorghum* (IS 18944). These accessions also did not show any deadheart formation. However, there was considerable variation in leaf damage among other accessions of *Para-sorghum*. *Sorghum australiense* (IS 18956), *S. matarankense*, *S. purpureo-sericeum* (IS 18943, IS 18944, IS 18945), *S. timorensis* and *S. versicolor* showed very low levels of leaf damage (LDS 1), while accessions of *S. nitidum* (TRC 243514) and *S. purpureo-*

Table 2: Oviposition by spotted stem borer on *Sorghum* species under multi-choice conditions in greenhouse

Section/Species/Subsp/Race	Accession	Number of egg masses per plant	Number of eggs per egg mass	Number of eggs per plant
Set 1				
<i>Heterosorghum</i>				
<i>S. laxiflorum</i>	TRC-243492	3.3a	39.9ab	132.9a
	IS 18958	2.9a	52.9a	158.9a
<i>Para-sorghum</i>				
<i>S. australiense</i>	IS 18955	3.1a	38.6ab	123.5ab
<i>S. matarakense</i>	TRC-243576	2.4ab	45.9ab	106.3ab
<i>S. purpureo-sericeum</i>	RN 285	0.3bc	19b	7.6b
	IS 18947	0.4bc	19.3b	7.7b
<i>S. versicolor</i>	IS 23177	1.1abc	37.9ab	48.5ab
<i>Eu-sorghum</i>				
<i>S. bicolor</i> ssp. <i>verticilliflorum</i>				
Race <i>virgatum</i>	IS 18808	2.9a	49.9a	152.0a
<i>S. bicolor</i> (RC)	IS 2205	1.7abc	59.3a	95.0ab
<i>S. bicolor</i> (SC)	ICSV-1	2.2abc	53.3a	122.2ab
Fp		0.134	0.081	0.136
LSD (5%)		2.44	27.77	122.07
Set 2				
<i>Para-sorghum</i>				
<i>S. versicolor</i>	IS 14262	0d	0d	0e
	IS 14275	0d	0d	0e
<i>S. purpureo-sericeum</i>	IS 18944	0d	0d	0e
	IS 18943	0.5cd	30.5abcd	24.4cde
	IS 18945	0.1d	7.7cd	71.5bc
<i>S. australiense</i>	IS 18956	0.5cd	21.4abcd	18.2cde
<i>Stiposorghum</i>				
<i>S. angustum</i>	TRC-243499	1.9bc	37abc	62.1bcd
<i>S. interjectum</i>	TRC-243461	0.3d	12.8bcd	10.2de
<i>Eu-sorghum</i>				
<i>S. halepense</i>	IS 14212	3.3b	39.6ab	113.5b
<i>S. bicolor</i> (RC)	IS 2205	2.8b	40.8ab	91.1b
<i>S. bicolor</i> (SC)	ICSV 1	5.5a	46.3a	249.3a
Fp		<0.001	0.017	<0.001
LSD (5%)		1.56	30.94	56.44
Set 3				
<i>Para-sorghum</i>				
<i>S. brevicallousum</i>	IS 18957	3.1abc	66.4ab	215.4ab
<i>S. nitidum</i>	TRC-243514	2.2bcde	41.9bcd	104.6bcd
<i>S. timorensis</i>	TRC-243498	0.4ef	38.7bcd	14.9cd
<i>Stiposorghum</i>				
<i>S. extans</i>	TRC-243601	0f	0d	0d
<i>S. ecarinatum</i>	TRC-243574	0.2f	24cd	7.5cd
<i>S. stipoides</i>	TRC-243399	1.6cdef	22.2cd	36.6bcd
<i>S. intrans</i>	TRC-243571	0.8def	46.3bcd	62.1bcd
<i>Eu-sorghum</i>				
<i>S. bicolor</i> ssp. <i>verticilliflorum</i>				
Race <i>aethiopicum</i>	IS 14564	2.4bcd	93.4a	204.4ab
Race <i>arundinaceum</i>	IS 18826	3.7ab	51.8bc	192.5abc
Race <i>verticilliflorum</i>	IS 18865	4.1ab	71.7ab	317.6a
<i>S. bicolor</i> (RC)	IS 2205	1.7cdef	51.7bc	86.5bcd
<i>S. bicolor</i> (SC)	ICSV 1	4.6a	42.3bcd	196abc
Fp		<0.001	0.007	0.036
LSD (5%)		1.97	38.6	188.86

RC, resistant control; SC, susceptible control; LSD, least significant difference.

sericeum (RN 285 and IS 18947) suffered moderate leaf damage (2.7–6.0 LDS). All these accessions, however, produced very few deadhearts (0.0–14.8% deadhearts). In the two accessions of *Heterosorghum* (TRC-243492 and IS 18958), leaf damage was low (LDS 1.3 and 1.7, respectively). However, TRC-243492 had only 15.3% deadhearts, while IS 18958 showed 82.5% deadhearts. Compared to the *Stipo*-, *Para*- and *Heterosorghums*, accessions of *Eu-sorghum* were highly susceptible. *Sorghum halepense* (IS 14212) and race *virgatum* of *S. ssp. verticilliflorum* (IS 18808) were highly susceptible (98.4% and 98.2% deadhearts, respectively, and LDS 6.0 for both) and were on par with the susceptible control, ICSV 1.

The resistant control IS 2205 suffered moderate levels of leaf damage (LDS 6) and deadheart formation (43.4%).

When plants with deadhearts were cut open to check for the presence of larvae 20 days after infestation, no larvae were observed in 11 accessions of *Para-sorghum*, while one larva each was recovered in two accessions IS 18945 (*S. purpureo-sericeum*) and IS 18956 (*S. australiense*) (Table 5). These larvae stopped feeding by the 24th day and died. In *S. laxiflorum* (*Heterosorghum*), no larvae were observed in the deadhearts of TRC-243492, but six larvae were recorded from 20 deadhearts in IS 18958, which subsequently stopped feeding and died in 28–30 days. There was no larval survival

beyond 30 days in the *Para*- and *Heterosorghums*, and consequently no adult emergence. Among the *Eu-sorghums*, 65% and 55% larvae were obtained from *S. halepense* and race *virgatum*, in comparison with 40% and 95% larvae recovered from IS 2205 and ICSV 1, respectively. Larval period varied from 37 to 43 days in race *virgatum* and 37–45 days in *S. halepense* as compared to 30–36 days in the susceptible ICSV 1. Pupation ranged from 66% in *S. halepense* to 100% in race *virgatum* and ICSV 1. Pupal period varied from 8 to 12 days in *S. halepense*, 9–13 days in race *virgatum* and

7–8 days in ICSV 1. Adult emergence was 27% and 37.5% in race *virgatum* and *S. halepense*, respectively, in comparison with 63.2% in the susceptible ICSV 1.

Discussion

Thirty-three accessions representing 14 species of sorghum showed high levels of resistance to the spotted stem borer, *C. partellus*, under artificial infestation in the field, with some accessions showing very high levels of resistance that were close to immunity. Species/accessions belonging to *Heterosorghum*, *Para-sorghum* and *Stiposorghum* suffered very low stem borer damage, except for one accession of *Heterosorghum*, which had 2% plants with deadhearts. In contrast, accessions belonging to *Chaetosorghum* and *Eu-sorghum* were highly susceptible to stem borer damage, suffering very high levels of leaf damage and plant deadhearts. Overall, more damage was observed in the 1998 rainy season than in the 1999 postrainy season, although levels of infestation were similar. As reproduction in sorghum is photothermal responsive, panicle initiation is usually earlier during the postrainy season than in the rainy season because of cooler temperatures and a shorter photoperiod. The early panicle initiation probably accounted for low deadheart formation in the postrainy season because of inability of the larvae to reach the growing point, which would already have pushed up above larval entry point, thus hampering the ability of the larvae to reach it. Thus, although larvae may feed in the sorghum stem and cause tunnelling, this activity alone may not cause deadhearts, the critical damage factor associated with yield loss. This has been shown to be one of the mechanisms of resistance to stem borer in sorghum (Sharma and Nawanze 1997). In contrast, delayed panicle initiation in the rainy season probably resulted in greater deadheart formation. The absence of significant differences in LDS and percentage plants with deadhearts over the two seasons in accessions belonging to *Hetero*-, *Para*- and *Stipo-sorghums* indicate stability in their response to

Table 3: Oviposition by spotted stem borer on *Sorghum* species under no-choice conditions in greenhouse

Section/species	Accession	Egg masses per plant	Eggs per egg mass	Eggs per plant
<i>Para-sorghum</i>				
<i>S. australiense</i>	IS 18956	4.3a	22.5cdef	94.9cd
<i>S. purpureo-sericeum</i>	IS 18947	0.3e	53.3abc	14.2e
	IS 18943	0.5e	18.5def	10.9e
	RN285	0.9e	54.0ab	51.5de
	IS 18945	2.5d	44.3abcd	108.0bc
	IS 18944	2.6cd	47.0abcd	120.5bc
<i>S. timorensis</i>	TRC-243498	2.5d	57.7ab	141.9bc
<i>S. versicolor</i>	IS 23177	0.1e	2.7f	0.5e
	IS 14262	0.1e	3.7f	0.7e
	IS 14275	0.1e	32.0cdef	6.4e
<i>Stiposorghum</i>				
<i>S. ecarinatum</i>	TRC-243574	0.7e	53.4abc	37.1de
<i>S. intrans</i>	TRC-243571	2.1d	41.1abcde	86cd
<i>S. extans</i>	TRC-243601	0.3e	11.6ef	5.9e
<i>S. interjectum</i>	TRC-243461	0.7e	64.8ab	42.2de
<i>Sorghum</i>				
<i>S. bicolor</i> (SC)	ICSV 1	4.1ab	71.6a	287.7a
<i>S. bicolor</i> (RC)	IS 2205	3.4bc	49.6abcd	163.7b
F Prob		<0.001	<0.036	0.007
LSD (5%)		0.84	31.41	58.47

RC, resistant control; SC, susceptible control; LSD, least significant difference.

Table 4: Ovipositional preferences for adaxial and abaxial leaf surfaces of *Sorghum* species under no-choice conditions in greenhouse

Section/species	Accession ID	Egg masses per plant		Eggs per egg mass		Eggs per plant	
		Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
<i>Para-sorghum</i>							
<i>S. australiense</i>	IS 18956	2.3a	1.9ab	19.3cdef	27.2def	44.1cd	50.8bcd
<i>S. purpureo-sericeum</i>	IS 18944	1.2bcd	1.4abc	62.8ab	24.9def	79.9ab	40.5bcd
	IS 18945	1.3bc	1.1bc	36.9abcde	41.1bcde	54.9bc	53.1bcd
	IS 18943	0.5cde	0d	18.5def	0f	10.9de	0d
	IS 18947	0.3de	0d	35.5bcdef	0f	14.2de	0d
	RN285	0.5cde	0.5cd	48.4abcd	60.3abc	22.9cde	28.6cd
<i>S. versicolor</i>	IS 23177	0.1e	0d	2.7f	0f	0.5e	0d
	IS 14262	0.1e	0d	3.7f	0f	0.7e	0d
	IS 14275	0.1e	0d	32bcdef	0f	6.4e	0d
<i>S. timorensis</i>	TRC-243498	0.7cde	1.9ab	68.7a	55.9abcd	45.3c	96.7b
<i>Stiposorghum</i>							
<i>S. ecarinatum</i>	TRC-243574	0.6cde	0.1d	53.1ab	21ef	32.9cde	4.2d
<i>S. intrans</i>	TRC-243571	1.3bc	0.7cd	44.6abcde	30.9cdef	53.5bc	32.5cd
<i>S. extans</i>	TRC-243601	0.3de	0.1d	13.3ef	2.7f	5.3e	0.5d
<i>S. interjectum</i>	TRC-243461	0.1e	0.5cd	40abcde	68.8ab	8e	34.2cd
<i>Eu-sorghum</i>							
<i>S. bicolor</i> (SC)	ICSV 1	1.9ab	2.1a	56.5ab	81.5a	102.7a	185.1a
<i>S. bicolor</i> (RC)	IS 2205	1.9ab	1.7ab	51.6abc	46.6bcde	96.3a	67.3bc
F Prob		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
LSD (5%)		0.78	0.94	32.99	32.31	33.47	60.58

RC, resistant control; SC, susceptible control; LSD, least significant difference.

Table 5: Adult emergence after artificial infestation with first-instar larvae under no-choice conditions in the greenhouse

Section/species	Accession	Plants damaged (%)	Deadhearts (%)	Leaf damage rating ¹	Larvae recovered (no.)	Remarks
<i>Heterosorghum</i>						
<i>S. laxiflorum</i>	TRC-243492	29g	15d	1f	0	
	IS 18958	100a	83b	2e	6	Larvae died in 28–30 days
<i>Para-sorghum</i>						
<i>S. australiense</i>	IS 18955	23h	11de	1f	0	
	IS 18956	73c	11de	1f	1	Larva died on 24th day
<i>S. matarakense</i>	TRC-243576	33fg	5f	1f	0	
<i>S. nitidum</i>	TRC-243514	94b	0j	3d	0	
<i>S. purpureo-sericeum</i>	RN 285	100a	11de	6b	0	
	IS 18943	38ef	0j	1f	0	
	IS 18944	0j	0j	0f	0	
	IS 18945	29g	13de	1f	1	Larva died on 24th day
	IS 18947	61d	8ef	4c	0	
<i>S. timorese</i>	TRC-243498	22h	0j	1f	0	
<i>S. versicolor</i>	IS 23177	42e	0j	1f	0	
	IS 14262	8i	0j	1f	0	
	IS 14275	71c	15d	1f	0	
<i>Stiposorghum</i>						
<i>S. angustum</i>	TRC-243499	0j	0g	0g	0	
<i>S. ecarinatum</i>	TRC-243574	0j	0g	0g	0	
<i>S. extans</i>	TRC-243601	0j	0g	0g	0	
<i>S. intrans</i>	TRC-243571	0j	0g	0g	0	
<i>S. interjectum</i>	TRC-243461	0j	0g	0g	0	
<i>S. stipoides</i>	TRC-243399	0j	0g	0g	0	
<i>Eu-sorghum</i>						
<i>S. bicolor</i> subsp. <i>verticilliflorum</i> race <i>virgatum</i>	IS 18808	98ab	98a	6b	11	Larval period: 37–43 days. Pupal period: 9–13 days. Adults emerged: 2 normal males; 1 male with malformed wings; 1 moth half emerged from pupa; 7 pupae with no emergence
<i>S. halepense</i>	IS 14212	98ab	98a	6b	13	Larval period: 37–45 days. Pupal period: 8–12 days. Adult emergence: 3 males; 5 pupae with no emergence; 3 escaped; 2 died
<i>S. bicolor</i> (SC)	ICSV-1	98ab	98a	7a	19	Larval period: 30–36 days. Pupal period: 7–8 days. Adult emergence: 6 males; 5 females; 3 egg masses; larvae hatched
<i>S. bicolor</i> (RC)	IS 2205	97ab	43c	6b	8	Larvae died by 30th day
F Prob		<0.001	<0.001	<0.001		
LSD (5%)		5.9	4.4	0.4		

SC, susceptible control; RC, resistant control; LSD, least significant difference.

¹Leaf damage score (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged).

artificial infestation of stem borer larvae. As larval dispersal occurs through silken threads by the first and second instars, it is likely that the larvae started feeding in the whorl, but when they found the host plant to be unsuitable, they migrated to neighbouring plants in search of suitable hosts (Taneja and Woodhead 1989). This mechanism probably accounted for the low plant damage and absence of deadhearts in accessions with high levels of resistance to stem borer damage. Field experiments by Woodhead *et al.* (1980) showed that damage by first-instar larvae placed directly into the whorl was inversely correlated with the amount of HCN produced in the leaves. Accessions of *Eu-sorghum* showed a wide variation in their responses across the two seasons. Wild races/species in *Eu-sorghum* have earlier been reported to be common hosts of stem borers under natural conditions (Reddy 1985) and probably serve as alternate hosts/reservoirs of this insect. ICSV

700, an improved variety bred for resistance to stem borer, which showed significant differences in deadhearts in the two seasons, exemplified the absence of durable resistance among the cultivated sorghums in the present study.

Under greenhouse conditions, accessions of *Heterosorghum*, *Para-sorghum* and *Stiposorghum* that suffered little plant damage under field conditions exhibited wide variation in plant damage, deadheart formation, larval survival and adult emergence. These observations suggest a high level of antibiosis and/or antixenosis at the feeding site in most of the accessions belonging to *Stiposorghums* (traces of leaf-feeding, and no deadhearts), *Para-sorghums* (some plant damage, very few deadhearts, two larvae recovered and no adult emergence) and *Heterosorghums* (considerable plant damage, 82% plants with deadhearts, six larvae recovered, no adult emergence). As all plants were artificially infested directly in the whorl, the

larvae were not exposed to factors that otherwise could have influenced their movement outside the plant. Wherever there were traces of leaf damage in the form of pinholes (LDS 1), it is possible that the larvae fed for a short time on the leaf tissue. However, the absence of deadhearts and low larval recovery in the *Para-sorghums* and *Stiposorghums* could be attributed to either larval mortality because of antibiotic effect of chemicals in the plant tissues or larval escape owing to their inability to feed on the leaves/shoots because of anatomical features of the stems. Similar observations have been made earlier on mechanisms of resistance in the cultivated sorghums (Lal and Pant 1980, Singh and Verma 1988, Taneja and Woodhead 1989).

Eu-sorghum accessions showed maximum plant damage and deadhearts. There was 95% recovery of larvae and pupae from susceptible control, ICSV 1, most of which survived to adulthood. In resistant control, IS 2205, larval recovery was low, and they did not survive. In accessions of *S. halepense* and race *virgatum*, larval period was prolonged, and all pupae did not develop into normal adult moths. Antibiosis in terms of reduced larval survival and prolongation of larval development has earlier been reported to be a component of resistance to stem borer in sorghum (Dayal 1989, Taneja and Woodhead 1989, Saxena 1990, 1992, Verma et al. 1992).

The use of multi-choice and no-choice tests is useful to confirm resistance to insects in a wide variety of plants (Smith et al. 1994). Significant differences were observed among the wild species/accessions of sorghum in terms of egg masses/plant, eggs/egg mass and eggs/plant under no-choice conditions. This clearly indicated the presence of antixenosis for oviposition as one of the mechanisms of resistance to *C. partellus*. Overall, more eggs were laid under no-choice conditions than under multi-choice conditions. Further, under no-choice conditions, egg laying was observed on all genotypes, even on those which were not preferred for oviposition under multi-choice conditions. Least egg laying was observed on *Stiposorghums*, and in varying levels on *Para-sorghums*, while wild accessions of *Eu-sorghum* were highly preferred for egg laying. There was a poor correlation between number of egg masses/plant, eggs/egg mass and eggs/plant. Van den Berg and van den Westhuizen (1997) also did not observe any correlation between the three variables for egg laying. The gravid females of *C. partellus* prefer to lay eggs on susceptible varieties of maize and sorghum than on the resistant ones (Lal and Pant 1980, Dabrowski and Kidiavai 1983, Singh and Rana 1984, Saxena 1987, Taneja and Woodhead 1989, Van den Berg and van den Westhuizen 1997, Rebe et al. 2004).

Differences in oviposition on different species/accessions could be attributed to non-suitability of the given host for oviposition. Leaf surface waxes are known to contribute significantly to host specificity in which the presence of certain compounds on the leaf may elicit oviposition and influence the establishment of first-instar larvae in sorghum (Bernays and Chapman 1994). Larval movement is influenced by trichomes, while ligular hairs act as traps for young larvae (Sharma 1993, Sharma and Nawanze 1997); the rate of establishment in a plant is thus reduced (Bernays et al. 1983). Most of the accessions of *Para-sorghum*, *Stiposorghum* and *Heterosorghum* had a medium to high density mat of hairs on the abaxial and the adaxial surfaces of the leaves. Kumar and Saxena (1985) also observed differential distribution of egg masses on the adaxial and abaxial leaf surfaces because of differences in trichome density/hairiness. More eggs were observed on the adaxial surface in the present study. However, Dabrowski and

Kidiavai (1983) observed an even distribution of eggs on adaxial and abaxial leaf surfaces of some genotypes, while Alghali (1985) reported that the females showed a preference for egg laying on the adaxial leaf surface. Species/accessions, which showed significantly reduced oviposition relative to the resistant control, IS 2205, may be used to investigate physicochemical stimuli involved in oviposition preference by the *C. partellus* females. Moore (1928) demonstrated that volatile chemicals emanating from corn foliage play an important role in orientation of moths of the European corn borer, *O. nubilalis*.

The present studies suggested that some of the accessions of wild relatives of sorghum exhibited both oviposition non-preference and antibiosis to *C. partellus*, suggesting that the suitability of plants for feeding of the neonate larvae is not a major factor in determining the choice of oviposition site by the *C. partellus* females (Ampofo and Nyangiri 1986). While the wild races/species within *Eu-sorghum* were highly preferred for oviposition, it is possible that those accessions in which there was prolonged larval development and reduced survival contain some antibiotic compounds that are inimical to larval growth and development. Reduction in feeding by first-instar larvae of *C. partellus* on resistant sorghum cultivars has been ascribed to high concentration of HCN in the plants (Woodhead et al. 1980).

Studies by Van den Berg (2006), Rebe et al. (2004) and Muyekho et al. (2005) have reported that indigenous wild grasses in Africa are major hosts for the spotted stem borer, with higher levels of oviposition on napier grass, blue thatching grass and vetiver grass as compared to that on cultivated maize or sorghum. *Chilo partellus* has also been shown to develop on Sudan grass (Khan et al. 2000) and *S. arundinaceum*, indicating their suitability as hosts. *Sorghum versicolor* showed highest number of *C. partellus* larvae under natural conditions (Muyekho et al. 2005). However, in our greenhouse study, no larvae were recovered from the few deadhearts obtained after artificial infestation on the accessions of this species. While environmental conditions and accessional differences could have contributed to this, it is likely that population differences in larval behaviour could be a major factor (Verma and Jotwani 1985). Therefore, these wild species that are preferred for oviposition, but unsuitable for larval development, have a considerable potential for use in management of stem borers in cultivated sorghum by acting as a barrier crop.

Sorghum improvement has hitherto relied on exploitation of variability within the primary gene pool as gene transfer from one background to another can be made quite readily. A few accessions of wild/weedy races (IS 18808 and IS 14212) expressing antibiosis could therefore be exploited for transferring resistance from wild relatives into the cultigen. However, in the present studies, several accessions of wild sorghum species with high levels of resistance to stem borer have been identified, which could be exploited as a valuable source of germplasm for sorghum improvement for insect resistance. Thirty-three accessions of 14 species belonging to sections *Stiposorghum*, *Para-sorghum* and *Heterosorghum* have been identified as immune/highly resistant to the spotted stem borer. Several of these species/accessions have also been reported to possess resistance/immunity to the sorghum shoot fly (Kamala et al. 2009). Further, various factors, traits and mechanisms appear to contribute to insect resistance in wild relatives of sorghum. These species belong to the tertiary gene pool and

constitute the extreme outer limit of the potential genetic resource for crop improvement. While their benefit to sorghum improvement through conventional breeding may be limited, recent breakthroughs in cellular and molecular biology have now provided new tools to utilize these species for crop improvement.

A wide range of insecticidal genes from *Bt* strains have been used to control insect pests. Maize plants transformed with *Bt* genes expressing Cry1Ab protein initially developed for control of *Ostrinia nubilalis* (Hubner) and *Diatrea grandiosella* (Dyar) have been found to provide effective control of stem borers (Van Rensburg 1999, 2007, Van den Berg and Van Wyk 2007). Although insect-resistant transgenic sorghums are yet to hit the market, Girijashankar *et al.* (2005) as a start reported partial tolerance against first instars of *C. partellus* in transgenic sorghum plants developed by particle bombardment of shoot apices expressing a synthetic *Cry1Ac* gene under a wound-inducible promoter *mpiC1*.

Besides *Bt* genes, other biotechnological mediations for insect control include the exploitation of enzymes including protease inhibitors, alpha amylase inhibitors, plant lectins, vegetative insecticidal proteins, toxins from predators, secondary metabolites and gene pyramiding (Sharma *et al.* 2000). In addition, down-regulation of the expression of specific genes through RNA interference (RNAi), where double-stranded RNA (dsRNA) produced *in planta* can lead to targeted gene silencing in Lepidoptera and Coleoptera (Baum *et al.* 2007, Mao *et al.* 2007), is also a possible way forward for controlling insect pests. Recent findings that the recessive *iap* allele circumvents pollen-pistil incompatibilities in the genus *Sorghum*, and hybrids can be used to make crosses between sorghum and members of the tertiary gene pool (Kuhlman *et al.* 2006, Price *et al.* 2005, 2006) auger well for utilizing the enormous potential that exists within the wild *Sorghum* gene pool to increase the levels of and diversify the bases of resistance to *C. partellus* in sorghum.

Acknowledgements

The first author thanks the Director, NBPGR (ICAR), New Delhi, for the financial support during the course of this research. The technical assistance provided by Mr. N. Chandra, Mr Y. V. R. Reddy and Mr K. V. Hariprasad is gratefully acknowledged. We thank Dr K. Anitha, Principal Scientist, NBPGR, Regional Station, Hyderabad, Andhra Pradesh, for reviewing the manuscript. We also gratefully thank the reviewers for many good suggestions for improvement of the manuscript.

References

- Alghali, A. M., 1985: Insect–host plant relationships. The spotted stalk-borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) and its principal host, sorghum. *Insect Sci. Appl.* **6**, 315–322.
- Ampofo, J. K. O., and E. O. Nyangiri, 1986: Maize resistance to *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae): behaviour of newly hatched larvae and movement from oviposition sites to feeding sites. *Appl. Ent. Zool.* **21**, 269–276.
- Baum, J. A., T. Bogaert, W. Clinton, G. R. Heck, P. Feldmann, O. Ilagan, S. Johnson, G. Plaetinck, T. Munyikwa, M. Pleau, T. Vaughn, and J. Roberts, 2007: Control of coleopteran insect pests through RNA interference. *Nat. Biotechnol.* **25**, 1322–1326.
- Bernays, E. A., and R. F. Chapman, 1994: Host Plant Selection by Phytophagous Insects. Chapman & Hall, New York.
- Bernays, E. A., R. F. Chapman, and S. Woodhead, 1983: Behaviour of newly hatched larvae of *Chilo partellus* associated with their establishment in the host plant sorghum. *Bull. Entomol. Res.* **73**, 75–83.
- Dabrowski, Z. T., and E. L. Kidiavai, 1983: Resistance of some sorghum lines to spotted stalk-borer *Chilo partellus* under western Kenya conditions. *Insect Sci. Appl.* **4**, 119–126.
- Dayal, T. K. S. 1989: Host plant preferences of the spotted stem borer, *Chilo partellus* Swinhoe in different sorghum genotypes. MSc Thesis. Andhra Pradesh Agricultural University, Hyderabad, India.
- De Groote, H., W. Overholt, J. O. Ouma, and S. Mugo, 2003: Assessing the impact of Bt maize in Kenya using a GIS model. Paper presented at the International Agricultural Economics Conference, Durban, 17th–23rd, August, pp. 78–79.
- Doggett, H. 1988: Sorghum. Longmans, London, UK, 512 pp.
- Duncan, R. R., P. J. Bramel-Cox, and F. R. Miller, 1991: Contributions of introduced sorghum germplasm to hybrids development in the USA. In: H. L. Shands, and L. E. Wiesner (eds), Use of Plant Introductions in the Cultivar Development, Part 1, 69–101. CSSA Special Publication 17. Crop Sci. Soc. Amer. Madison, WI.
- Girijashankar, V., H. C. Sharma, K. K. Sharma, V. Swathisree, L. S. Prasad, B. V. Bhat, M. Royer, B. San Secundo, M. L. Narasu, I. Altosaar, and N. Seetharama, 2005: Development of transgenic sorghum for insect resistance against the spotted stem borer (*Chilo partellus*). *Plant Cell Rep.* **24**, 513–522.
- Goodman, R. M., H. Hauptli, A. Crossway, and V. C. Knauf, 1987: Gene transfer in crop improvement. *Science* **236**, 48–54.
- International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), 1992: The Medium Term Plan, Volume II. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.
- Jalaluddin, S. M., S. Thirumurthy, and V. S. Shanmugasundaram, 1995: Multiple resistance in sorghum to shoot fly and stem borer. *Mad. Agric. J.* **82**, 611–612.
- Kamala, V., H. C. Sharma, D. Manohar Rao, K. S. Varaprasad, and P. J. Bramel, 2009: Wild relatives of sorghum as sources of resistance to sorghum shoot fly *Atherigona soccata*. *Plant Breeding* **28**, 137–142.
- Khan, Z. R., J. A. Picket, J. van den Berg, L. J. Wadhams, and C. M. Woodcock, 2000: Exploiting chemical ecology and species diversity: stem borer and striga control for maize and sorghum in Africa. *Pest Manag. Sci.* **56**, 957–962.
- Kuhlman, L. C., B. L. Burson, P. E. Klein, D. M. Stelly, and W. L. Rooney, 2006: Interspecific sorghum breeding using *S. macrosperrum*. Proceedings of the ASA-CSSA-SSA. International Meetings; Indianapolis, pp. 12–16.
- Kumar, H., and K. N. Saxena, 1985: Ovipositional response of *Chilo partellus* (Swinhoe) to certain susceptible and resistant maize genotypes. *Insect Sci. Appl.* **6**, 331–335.
- Lal, G., and J. C. Pant, 1980: Laboratory and field testing for resistance in maize and sorghum varieties to *Chilo partellus* (Swinhoe). *Indian J. Entomol.* **42**, 606–610.
- Mao, Y.-B., W.-J. Cai, J.-W. Wang, G.-J. Hong, X.-Y. Tao, L.-J. Wang, Y.-P. Huang, and X.-Y. Chen, 2007: Silencing a cotton bollworm P450 monooxygenase gene by plant-mediated RNAi impairs larval tolerance of gossypol. *Nat. Biotechnol.* **25**, 1307–1313.
- Moore, R. H., 1928: Odorous constituents of the corn plant in their relation to the European corn borer. *Prod. Okh. Acad. Sci.* **8**, 16–18.
- Mote, U. N., 1984: Sorghum species resistant to shoot fly. *Indian J. Entomol.* **46**, 241–243.
- Muyekho, F. N., A. T. Barrion, and Z. R. Khan, 2005: Host range for stemborers and associated natural enemies in different farming systems of Kenya. *Afr. Crop Sci. J.* **13**, 173–183.
- Patel, G. M., T. R. Sukhani, M. B. Patel, and S. P. Singh, 1996: Relative susceptibility of promising sorghum genotypes to stem borer in Delhi and Hisar conditions. *Indian J. Entomol.* **57**, 279–284.

- Payne, R. W., D. A. Murray, S. A. Harding, D. B. Baird, and D. M. Soutar, 2007: GenStat for Windows, 10th edn. Introduction. VSN International, Hemel Hempstead, UK.
- Price, H. J., G. L. Hodnett, B. L. Burson, S. L. Dillon, and W. L. Rooney, 2005: A *Sorghum bicolor* × *S. macrospermum* hybrid recovered by embryo rescue and culture. *Aust. J. Bot.* **53**, 579–582.
- Price, H. J., G. L. Hodnett, B. L. Burson, S. L. Dillon, D. M. Stelly, and W. L. Rooney, 2006: Genotype dependent interspecific hybridization of *Sorghum bicolor*. *Crop Sci.* **46**, 2617–2622.
- Rebe, M., J. van den Berg, and M. A. McGeoch, 2004: Colonization of cultivated and indigenous graminaceous host plants by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) under field conditions. *Afr. Entomol.* **12**, 187–199.
- Reddy, K. V. S., 1985: Integrated approach to the control of Sorghum stem borers. In: K. Leuschner, and G. L. Teetes (eds), Proceedings of the International Sorghum Entomology Workshop, 205–215. 15–21 July 1984, Texas A&M University, College Station, TX. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India.
- Saxena, K. N., 1987: Ovipositional responses of the stem borer *Chilo partellus* (Swinhoe) to certain sorghum cultivars in relation to their resistance or susceptibility. In: V. Labeyrie, G. Fabres, and D. Lachaise (eds), *Insects – Plants*, 313–318. Junk Publishers, Dordrecht, The Netherlands.
- Saxena, K. N., 1990: Mechanisms of resistance susceptibility of certain sorghum cultivars to the stem borer *Chilo partellus*: role of behaviour and development. *Entomol. Exp. Appl.* **55**, 91–99.
- Saxena, K. N., 1992: Larval development of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) on artificial diet incorporating leaf tissues of sorghum lines in relation to their resistance or susceptibility. *Appl. Entomol. Zool.* **27**, 325–330.
- Sharma, H. C., 1993: Host plant resistance to insects in sorghum and its role in integrated pest management. *Crop Protection* **12**, 11–34.
- Sharma, H. C., 1997: Screening for resistance to spotted stem borer. In: H. C. Sharma, F. Singh, and K. F. Nwanze (eds), *Plant Resistance to Insects in Sorghum*, 38–45. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India.
- Sharma, H. C., and B. A. Franzmann, 2001: Host plant preference and oviposition responses of the sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Diptera: Cecidomyiidae) towards wild relatives of sorghum. *J. Appl. Ent.* **125**, 109–114.
- Sharma, H. C., and K. F. Nwanze, 1997: Mechanisms of Resistance to Insects in Sorghum, 51pp. Information Bulletin No 45. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India.
- Sharma, H. C., S. L. Taneja, K. Leuschner, and K. F. Nwanze, 1992: Techniques to screen sorghums for resistance to insects, 48pp. Information Bulletin no. 32. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India.
- Sharma, H. C., K. K. Sharma, N. Seetharama, and R. Ortiz, 2000: Prospects for using transgenic resistance to insects in crop improvement. *Elec. J. Biotechnol.* **3**, 1–26.
- Sharma, H. C., S. L. Taneja, N. Kameswara Rao, and K. E. Prasada Rao, 2003: Evaluation of Sorghum Germplasm for Resistance to Insect Pests. 177 pp. Information Bulletin No. 63. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.
- Singh, B. U., and B. S. Rana, 1984: Influence of varietal resistance on oviposition and larval development of stalk borer, *Chilo partellus* Swin. and its relationship to field resistance in sorghum. *Insect Sci. Appl.* **5**, 287–296.
- Singh, B. U., and B. S. Rana, 1989: Varietal resistance in sorghum to spotted stem borer, *Chilo partellus* (Swinhoe). *Insect Sci. Appl.* **10**, 3–27.
- Singh, S. P., and A. N. Verma, 1988: Antibiosis mechanism of resistance to stem borer, *Chilo partellus* (Swinhoe) in sorghum. *Insect Sci. Appl.* **9**, 579–582.
- Smith, M. S., Z. R. Khan, and M. D. Pathak, 1994: Techniques for Evaluating Insect Resistance in Crop Plants. CRC Press, Boca Raton, FL.
- Taneja, S. L., and K. Leuschner, 1985: Methods of rearing, infestation, and evaluation for *Chilo partellus* resistance in sorghum. In: K. Leuschner, and G. L. Teetes (eds), Proceedings of the International Sorghum Entomology Workshop, 178–185. 15–21 July 1984, Texas A&M University, College Station, TX. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India.
- Taneja, S. L., and S. Woodhead, 1989: Mechanisms of stem borer resistance in sorghum. In: Proceedings of the International Workshop on Sorghum Stem Borers, 137–144. 17–20 Nov. 1987. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India.
- Van den Berg, J., 2006: Oviposition preference and larval survival of *Chilo partellus* (Lepidoptera: Pyralidae) on Napier grass (*Pennisetum purpureum*) trap crops. *Int. J. Pest Manag.* **52**, 39–44.
- Van den Berg, J., and M. C. van den Westhuizen, 1997: *Chilo partellus* (Lepidoptera: Pyralidae) moth and larval response to levels of antixenosis and antibiosis in sorghum inbred lines under laboratory conditions. *Bull. Ent. Res.* **87**, 541–545.
- Van den Berg, J., and A. Van Wyk, 2007: The effect of Bt maize on *Sesamia calamistis* in South Africa. *Ent. Exp. Appl.* **122**, 45–51.
- Van Rensburg, J. B. J., 1999: Evaluation of Bt-transgenic maize for resistance to the stem borers *Busseola fusca* (Fuller) and *Chilo partellus* (Swinhoe) in South Africa. *S. Afr. J. Plant Soil* **16**, 38–43.
- Van Rensburg, J. B. J., 2007: First report of field resistance by the stem borer, *Busseola fusca* (Fuller) to Bt-transgenic maize. *S. Afr. J. Plant Soil.* **24**, 147–151.
- Verma, K. K., and M. G. Jotwani, 1985: Life process of the sorghum stem borer *Chilo partellus* (Swinhoe) of different agroclimatic areas. *Indian J Entomol.* **45**, 477–478.
- Verma, O. P., J. P. Bhanot, and A. N. Verma, 1992: Development of *Chilo partellus* (Swin.) on pest resistant and susceptible sorghum cultivars. *J. Insect Sci.* **5**, 181–182.
- Woodhead, S., D. E. Padgham, and E. A. Bernays, 1980: Insect feeding on different sorghum cultivars in relation to cyanide and phenolic acid content. *Ann. Appl. Biol.* **95**, 151–157.