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Mechanisms and diversity of resistance to sorghum midge, *Stenodiplosis sorghicola* in *Sorghum bicolor*

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Summary

Sorghum midge, *Stenodiplosis sorghicola* (Coquillett) is the most important pest of grain sorghum worldwide, and plant resistance is an important component for the control of this pest. To identify sorghum genotypes with diverse mechanisms of resistance to sorghum midge, we studied oviposition, larval survival, and midge damage in 27 sorghum midge-resistant genotypes, and a susceptible check under greenhouse conditions. Observations were also recorded on floral characteristics and compensation in grain mass. Of the 28 sorghum genotypes tested, 19 showed high levels of antixenosis to oviposition as a component of resistance, and had <20% spikelets with eggs when infested with 10 or 25 sorghum midge females per panicle under no-choice conditions in the headcage. Genotypes IS 8887, IS 10712, IS 21873, IS 21881, ICSV 745, and QL 39 showed antibiosis as one of the components of resistance. Lines IS 7005, IS 10712, IS 18563, IS 21873, IS 21881, PM 15936-2, ICSV 197, and ICSV 745 showed <20% spikelets with eggs, larvae, or, midge damaged chaffy spikelets across infestation levels, compared with >80% midge damaged spikelets in QL 12 – the susceptible check. Genotypes showing resistance to sorghum midge have smaller glumes than the susceptible check, QL 12. However, IS 7005, IS 18653, and ICSV 745 have relatively large sized glumes, but suffered <20% midge damage suggesting that factors other than glume size also contribute to midge resistance in sorghum. Fourteen genotypes showed >20% compensation in grain mass when the panicles were reduced to 250 spikelets and infested with 10 or 25 midges per panicle. There is considerable diversity in sorghum genotypes showing resistance to sorghum midge. Genotypes with diverse combination of characteristics associated with resistance to sorghum midge can be used in breeding programs to broaden the genetic base and increase the levels of resistance to this insect.

Introduction

Sorghum, *Sorghum bicolor* (L.) Moench is an important cereal crop in the semi-arid tropics (SAT). It provides food, feed and forage, but grain yields on peasant farms are generally low, due partly to insect pest damage. Nearly 150 species of insects have been recorded as pests of sorghum (Jotwani et al., 1980), of which sorghum midge, *Stenodiplosis* (*Contarinia*) *sorghicola* (Coquillett) is the most important pest worldwide (Harris, 1976). Sorghum midge females lay eggs inside the spikelets at flowering, and the larvae start feeding on the developing ovary immediately after pollination. As a result, the midge damaged spikelets become chaffy (without grain), and the panicles present a blasted appearance. Host plant resistance is an effective means of keeping midge populations below economic threshold levels (Sharma, 1993a), and breeding for resistance to midge is an integral part of sorghum improvement programs in Asia, Africa, Australia, and the Americas (Henzell et al., 1997).

Sources of resistance to sorghum midge have been identified by several workers (Johnson et al., 1973;

Wiseman et al., 1973; Rossetto et al., 1975; Shyamsunder et al., 1975; Jotwani, 1978; Page, 1979; Faris et al., 1979; Peterson et al., 1985; Sharma et al., 1993a, 1999; Henzell et al., 1997). Most of the high yielding genotypes developed at ICRISAT Center, India, have been derived from DJ 6514 (Sharma et al., 1993a). However, DJ 6514 and the breeding lines derived from it have shown a susceptible reaction to sorghum midge at Alupe, Kenya (Sharma et al., 1999). In Australia, sorghum hybrids with a range of resistance levels to sorghum midge are being grown by the farmers (Henzell et al., 1997; Franzmann, 1996). Most of these hybrids derive the midge resistance genes from a single source of resistance (Jordan et al., 1996). Resistance to insects often breaks down when a cultivar is planted continuously over large areas for several consecutive seasons. Large-scale cultivation of an insect-resistant cultivar exercises a selection pressure on insect populations, resulting in the evolution of new biotypes capable of feeding and development on the resistant genotypes. The evolution of new insect biotypes necessitates the development of cultivars with newer genes conferring resistance to the target insect or combine genes from diverse genotypes to broaden the genetic base and increase the levels of resistance to insects.

Antixenosis to visiting adults is a component of resistance to sorghum midge in some sorghum genotypes (Sharma & Vidyasagar, 1994; Waquil et al., 1986b). Difficulty in oviposition or oviposition nonpreference is the most important mechanism of resistance to sorghum midge (Sharma, 1985; Franzmann, 1993; Rossetto et al., 1984; Sharma et al., 1990; Waquil et al., 1986a). Fewer eggs are laid in the midge-resistant sorghums than in the susceptible ones. The survival and development of midge larvae is adversely influenced on some midge-resistant genotypes (Sharma et al., 1993b; Waquil et al., 1986b). Midge-resistant genotypes also show a better ability to compensate for midge damage (Sharma et al., 2001). However, Hallman et al. (1984), Franzmann & Butler (1993), and Waquil & Teetes (1990) did not observe any trend in compensation in grain mass between midge-resistant and midge-susceptible genotypes. Short, tight and hard glumes, faster grain development between 3rd and 7th day after anthesis, and tannin content of the grain are associated with resistance to sorghum midge (Rossetto et al., 1984; Sharma et al., 1990). Resistance to sorghum midge is also influenced by the chemical composition of the sorghum grain, which is influenced by the environment, and has been linked to variation in expression of resistance to sorghum midge (Sharma et al., 1993b). Diarisso et al. (1998) suggested that most of the spikelets of resistant sorghums flowered and closed early and thus evaded the midge damage. They suggested that resistance is caused by asynchrony between time of sorghum spikelet flowering and presence of sorghum midges in the field. However, observations in Australia and India have shown that there is no relationship between flowering time and expression of resistance to sorghum midge (Sharma, H.C., unpublished). In the present studies, we examined the interaction of sorghum midge with a diverse array of sorghum genotypes to identify sources with different mechanisms of resistance to this insect.

Materials and methods

Plants

The experiments were conducted at the Queensland Department of Primary Industries, Toowoomba, Queensland, Australia. The plants were grown in plastic pots (20 cm diameter, 20 cm high) containing a mixture of soil (black Vertisols): sand: peat (3: 2: 1). The soil was thoroughly mixed in a rotary mixer, and 0.02 kg lime was added in each pot to adjust the pH of the potting mixture. Plants were watered regularly, as needed. A slow-release fertilizer (Osmocote Plus $^{(R)}$; N 15%, P 4.8%, K 10.8%, S 3.6%, Mg 1.2%, Mn 0.06%, Cu 0.05%, B 0.02%, Zn 0.015%, and Ca 3%) was applied to the pots 15 days after germination (10 g per pot). Two plants were retained in each pot 15 days after seedling emergence. The greenhouse was maintained at 30 $\pm$ 3 °C, and 70 $\pm$ 5% R.H. The plants were sprayed with endosulfan (0.07%) to control corn leaf aphid (*Rhopalosiphum maidis* Fitch.) infestation. No midge infestation was carried out up to 5 days after spraying. The test material included 21 midge-resistant sources (IS 2579C, IS 3461, IS 7005, IS 8100C, IS 8721, IS 8887, IS 9807, IS 10712, IS 15107, IS 18563, IS 18698 (AF 28) IS 18733, IS 19476, IS 19512, IS 21871, IS 21873, IS 21879, IS 21881, IS 21883-1, IS 22806, and IS 26789) and five midge-resistant genotypes (PM 7017, PM 8787-2, PM 15936-2; ICSV 197, and ICSV 745) developed at ICRISAT (Sharma et al., 1993a). Sorghum midge-resistant (QL 39) and susceptible (QL 12) genotypes developed at QDPI (Henzell et al. 1994) were included as experimental checks. The experiment was laid out in a randomised complete block design.

Insects

Insects were obtained from sorghum panicles collected from farmers' fields in the Darling Downs, Queensland. Nearly 25 panicles were kept in a 30 × 45 cm paper bag in the laboratory at 30 ± 3 °C, and 75 ± 5% R.H. A cylindrical transparent plastic jar with a handle (21.5 cm long, 10.5 cm diameter) having three wire-mesh screened windows (4 cm diameter), two on the sides and one at the top, was tied to the top of the paper bag with a strong (1 cm wide) elastic band. The elastic band was twisted at the rim of the jar, and pulled to the upper end of the handle of the jar. This kept the jar in upright position without any support. Upon emergence, the midges moved to the plastic jar because of their positive phototactic behavior. The insects were allowed to mate in the plastic jar until 10.00 h. The jars containing midges were brought to the laboratory, and covered with a black polyethylene sheet. Midges were collected through a 2.5 cm diameter outlet at the top of the jar in 20 ml glass vials. The glass vials were kept in an upright position on the outlet hole with a piece of clay. The midges moved to the glass vials as a result of attraction to light. Vials containing 40 to 50 midges were removed from the jars, and replaced with new ones. Midges in the glass vials were sexed, and females were collected in sets of 5 or 20 in fresh glass vials. Insects thus collected were used to infest the plants in the greenhouse.

Infestation

Wire-framed cylindrical cages (20 cm diameter, and 30 cm long) were placed around the panicles supported by a wooden stick. The height of the wooden stick was adjusted so that the panicles were placed in the center of the cage. Nine panicles were selected at random in each genotype, and 250 flowering spikelets were retained on each panicle. The panicles were caged with sorghum midge females in the morning hours. Three panicles were infested with 25 midges per panicle, and five panicles with 10 midges per panicle to observe the reaction of different genotypes to sorghum midge under two insect densities. The normal control panicles were covered with a cloth bag to avoid natural infestation by insects. Cages were removed 20 days after infestation (time required by the sorghum midge to complete the development from egg to adult emergence).

Observations

One day after infestation, 25 spikelets were taken at random from each infested panicle to record the oviposition preference. The spikelets were kept in the deep freeze till observation. The spikelets were dissected under a binocular microscope (50 X) to record the number of spikelets with eggs, and the number of eggs per 25 spikelets. On 10th day after infestation, another sample of 25 spikelets was taken at random from each panicle to record the number of spikelets with larvae, and the number of larvae per 25 spikelets under a binocular microscope as described above.

Length and breadth of the spikelets were recorded at the flowering stage. For this purpose, five spikelets were taken at random from the mid-portion of each panicle at anthesis, and three panicles were sampled in each genotype. The length of the upper glume (GL_1), lower glume (GL_2), breadth of upper glume at the middle (GB_1), exposed portion of the lower glume not covered by the upper glume due to glume coupling (EGB_2), and anther tube length (AL) were recorded under a binocular microscope (50 X) using an ocular micrometer (2.5 ocular units = 1 mm). From the linear measurements of floral parts, the extent of glume coupling was calculated as a ratio between GL1 /GL_2, and GB_1 /EGB_2. To measure the space available for oviposition, the glume area was obtained by $GL_1 \times GB_1$.

At maturity, the panicles were harvested, and kept in cloth bags. Data were recorded on percentage chaffy spikelets (spikelets without grain due to sorghum midge damage), and grain mass per 100 grains. For recording grain mass, 100 grains were taken at random from each panicle, and dried at 105 °C overnight to equilibrate the moisture content. In case of sorghum midge susceptible genotype QL 12, grain mass was recorded in 50 grains because of limited number of grains per panicle due to high midge damage. One normal panicle (without midge infestation and in which no spikelets were removed) was also harvested at maturity, threshed, and grain mass per 100 grains was recorded as described above. Grain mass was recorded on a Mettler® balance. Compensation in grain mass was recorded as a percentage increase in grain mass in the midge infested panicles in relation to grain mass of the normal uninfested panicles.

$$\text{Compensation in grain mass (\%)} = \frac{\text{100 grain mass of the infested panicle} - \text{100 grain mass of the normal panicle}}{\text{100 grain mass of normal panicle}} \times 100$$

Statistical analysis

Data were converted to N + 1 square root transformation because of zero values in some cases, and subjected to analysis of variance using a randomised complete block design. Significance of difference between treatments was judged by F-test, while the differences between the treatment means were compared by least significant difference (LSD) at $p < 0.05$. The data on sorghum midge damage, percentage spikelets with eggs and larvae, compensation in grain mass, and linear measurements of floral parts were subjected to principal component analysis to assess the diversity of resistance to sorghum midge.

Results

Reaction of different genotypes infested with 10 midges per panicle

When the panicles were infested with 10 sorghum midge females per 250 spikelets, percentage of spikelets with eggs varied from 0.8% in IS 19476 to 49.6% in QL 12, the susceptible check (Table 1; Figure 1). Percentage of spikelets with larvae varied from 0.0% in IS 10712 and IS 22881 to 63.2% in QL 12. Genotypes IS 3461, IS 8887, IS 10712, IS 18698, IS 19512, IS 21881, IS 26789, PM 8787-2, PM 15936-2, ICSV 197, and QL 39 had less than 10% spikelets with eggs and larvae. Genotypes IS 10712, IS 18698, IS 19512, PM 8787-2, PM 15936-2, ICSV 197, and QL 39 had less than 2 eggs or larvae per 25 spikelets compared to 18.6 eggs and 16.6 larvae per 25 spikelets in QL 12. Percentage of midge damaged spikelets varied from 6.0% in PM 15936-2 to 63.8% in QL 12. Lines IS 7005, IS 8721, IS 8887, IS 10712, IS 15107, IS 18563, IS 19512, IS 21871, IS 21873, IS 21881, IS 26789, PM 8787-2, PM 15936-2, ICSV 197, and ICSV 745 had less than 20% midge damaged spikelets compared to 32.6% in QL 39, and 63.8% in QL 12.

Reaction of different genotypes infested with 25 midges per panicle

When the panicles were infested with 25 sorghum midge females per panicle, percentage of spikelets with eggs varied from 1.3% in IS 7005 to 88.3% spikelets with eggs in QL 12 (Table 2; Figure 1). Percentage of spikelets with larvae varied from 0.0% in IS 7005 to 88% in QL 12. Genotypes IS 3461, IS 7005, IS 10712, IS 18563, IS 21881, and PM 15936-2, had less than 10% spikelets with eggs and larvae compared with 88% spikelets with eggs and larvae in QL 12. Number of eggs and larvae were less than 5 per 25 spikelets in IS 3461, IS 9807, IS 7005, IS 10712, IS 18563, IS 18733, IS 21881, PM 15936-2, and ICSV 197 compared to 143 eggs and 29.3 larvae in QL 12 the susceptible check. Percentage of spikelets with midge damage varied from 7.0% in PM 15936-2 to 83.7% in QL 12. Genotypes IS 7005, IS 10712, IS 18563, IS

Table 1. Oviposition, larval numbers, and midge damaged spikelets in 28 sorghum genotypes (infested with 10 midges per 250 spikelets) under no-choice conditions in the headcage (QDPI, Toowoomba 1996)

Genotypes	% spikelets with eggs	% spikelets with larvae	Midge damage (%)
IS 2579c	15.2 (3.76)	19.2 (4.27)	49.6 (7.05)
IS 3461	7.2 (2.19)	9.6 (2.58)	26.0 (4.98)
IS 7005	16.0 (3.79)	16.8 (3.46)	13.6 (3.79)
IS 8100c	13.2 (3.69)	16.0 (4.02)	25.0 (4.97)
IS 8721	23.2 (4.80)	6.4 (2.69)	12.6 (3.60)
IS 8887	8.8 (2.77)	8.8 (3.04)	16.2 (3.95)
IS 9807	11.2 (3.27)	13.2 (3.54)	41.8 (6.27)
IS 10712	6.4 (2.42)	0.0 (1.00)	19.0 (4.46)
IS 15107	23.2 (4.80)	32.8 (5.37)	18.2 (4.36)
IS 18563	19.2 (4.39)	6.4 (1.95)	14.6 (3.83)
IS 18698	2.4 (1.74)	4.0 (2.05)	49.4 (6.89)
IS 18733	27.2 (4.64)	33 (5.59)	41.0 (6.35)
IS 19476	0.8 (1.25)	12.0 (3.08)	30.0 (5.45)
IS 19512	1.6 (1.49)	0.8 (1.25)	10.2 (3.33)
IS 21871	14.4 (3.89)	11.2 (3.16)	11.4 (3.49)
IS 21873	20.0 (4.39)	5.6 (2.32)	7.8 (2.93)
IS 21879	6.4 (2.66)	14.4 (3.79)	28.2 (5.31)
IS 21881	8.8 (2.74)	0.0 (1.00)	7.6 (2.90)
IS 21883-1	9.6 (3.07)	14.4 (3.56)	37.2 (6.16)
IS 22806	19.2 (4.11)	11.0 (3.09)	37.8 (6.13)
IS 26789	4.0 (2.02)	8.8 (2.96)	13.4 (3.71)
PM 7017	45.2 (6.78)	12.8 (3.61)	25.0 (4.98)
PM 8787-2	4.8 (2.17)	4.0 (1.92)	19.4 (4.28)
PM 15936-2	4.4 (2.13)	2.4 (1.52)	6.0 (2.62)
ICSV 197	2.4 (1.65)	2.4 (1.52)	12.2 (3.42)
ICSV 745	15.2 (3.88)	4.0 (1.87)	19.4 (4.41)
QL 39	8.0 (2.57)	4.0 (1.71)	32.6 (5.68)
QL 12	49.6 (7.07)	63.2 (8.00)	63.8 (8.05)
Mean	13.8 (3.36)	12.0 (3.00)	24.6 (4.76)
SE±	(0.60)	(0.64)	(0.51)
LSD at 5%	(1.68)	(1.78)	(1.42)

Figures in parentheses are N + 1 square root transformed values.

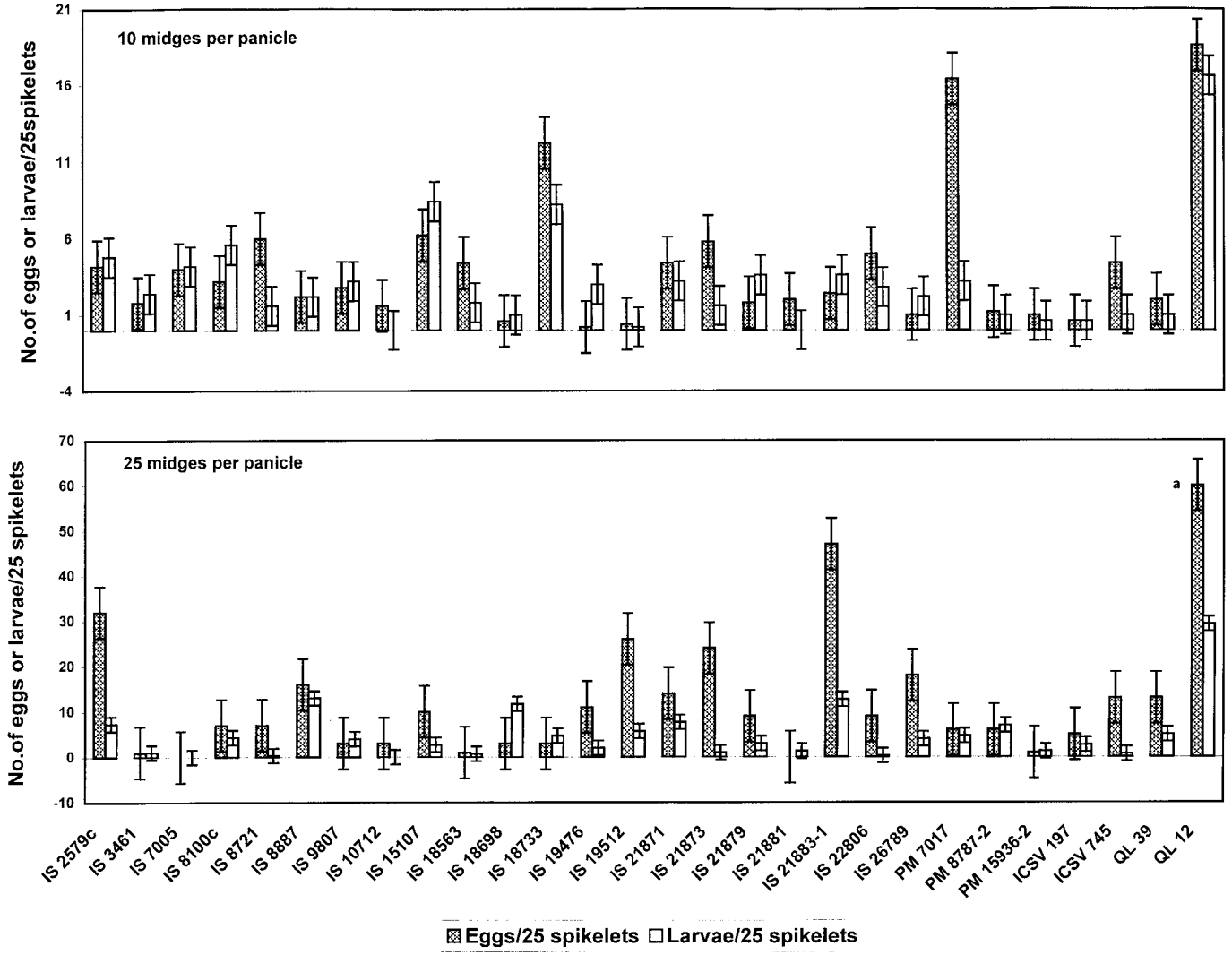

Figure 1. Numbers of eggs and larvae per 25 spikelets in 28 sorghum genotypes infested with 10 and 25 sorghum midge females under no-choice headcage conditions. Line bars on the histograms are standard error of mean (SE) values (QDPI, Toowoomba, 1996).

Table 2. Oviposition, larval numbers, and midge damaged spikelets in 28 sorghum genotypes (infested with 25 midges per 250 spikelets) under no-choice headcage screening (QDPI, Toowoomba, 1996)

Genotypes	% spikelets with eggs	% spikelets with larvae	Midge damage (%)
IS 2579c	61.3 (7.86)	28 (5.48)	63.7 (8.03)
IS 3461	8.0 (2.86)	0 (2.08)	27.0 (5.11)
IS 7005	1.3 (1.41)	0 (1.00)	12.0 (3.60)
IS 8100c	13.3 (3.67)	36 (3.74)	28.7 (5.19)
IS 8721	28.0 (5.35)	4 (1.41)	45.0 (6.74)
IS 8887	44.0 (6.41)	60 (7.23)	59.7 (7.72)
IS 9807	14.7 (3.95)	12 (3.95)	57.7 (7.66)
IS 10712	9.3 (3.20)	0 (1.00)	14.3 (3.72)
IS 15107	18.7 (3.84)	28 (2.87)	30.3 (5.53)
IS 18563	8.0 (2.87)	0 (1.82)	8.7 (3.09)
IS 18698	20.0 (4.49)	56 (6.57)	63.0 (7.97)
IS 18733	13.3 (3.78)	8 (4.32)	28.0 (5.26)
IS 19476	13.3 (3.25)	16 (2.71)	37.3 (6.04)
IS 19512	49.3 (6.95)	32 (4.82)	59.7 (7.63)
IS 21871	28.0 (5.38)	32 (5.61)	38.0 (6.24)
IS 21873	13.3 (3.25)	0 (2.08)	15.0 (3.89)
IS 21879	32.0 (5.70)	8 (3.57)	38.7 (6.22)
IS 21881	8.0 (2.71)	8 (2.33)	11.0 (3.46)
IS 21883-1	54.7 (7.37)	64 (7.16)	54.0 (7.34)
IS 22806	12.0 (2.99)	0 (1.41)	18.7 (4.43)
IS 26789	32.0 (5.72)	12 (4.07)	33.0 (5.54)
PM 7017	20.0 (4.52)	18 (4.32)	27.3 (5.32)
PM 8787-2	30.7 (5.53)	40 (5.16)	38.3 (6.22)
PM 15936-2	4.0 (2.08)	4 (2.28)	7.0 (2.79)
ICSV 197	18.7 (4.37)	12 (3.20)	8.7 (3.05)
ICSV 745	34.7 (5.96)	4 (1.82)	8.0 (2.95)
QL 39	40.0 (6.36)	12 (4.34)	42.7 (6.60)
QL 12	88.3 (9.45)	88 (9.22)	83.7 (9.20)
Mean	25.7 (4.69)	18.4 (3.77)	34.3 (5.59)
SE±	(0.77)	(0.70)	(0.65)
LSD at 5%	(2.17)	(1.97)	(1.85)

Figures in parentheses are /N + 1 square root transformed values.

21873, IS 21881, IS 22806, PM 15936-2, ICSV 197, and ICSV 745 suffered less than 20% midge damage compared to 83.7% midge damage in QL 12.

Linear measurements of floral parts

Glume length G_1 varied from 2.42 mm in IS 8887 to 3.90 mm in QL 12, and glume length G_2 from 2.54 mm in IS 8887 to 4.04 mm in QL 12 (Table 3). Glume length G_1 in IS 2579C, IS 8887, IS 21881, IS 21883-1, IS 22806, PM 7017, PM 15936-2, ICSV 197, and QL 39 was less than 2.8 mm compared to 3.74 mm in QL 12. Glume G_1 breadth ranged from 1.72 mm in IS 8887 to 2.36 mm in PM 15936, and the exposed portion of glume G_2 (not covered by glume G_1) ranged from 1.30 mm in IS 8887 to 1.75 mm in IS 21879. Anther length varied from 1.65 mm in IS 3461 to 2.73 mm units in QL 12. Genotypes IS 3461, IS 8721, IS 8887, IS 10712, IS 18698, IS 19512, IS 21871, IS 21873, IS 21881, IS 22806, IS 26789, PM 7017, PM 8787-2, PM 15936-2, and ICSV 197 had anther length of <2.0 mm compared to 2.73 mm in QL 12.

Percentage spikelets with eggs were significantly and positively associated with glume length GL_1(r = 0.29–0.33) and glume length GL_2 (r = 0.24–0.39). Anther length (AL) was also positively associated with percentage spikelets with eggs and larvae (r = 0.30–0.51). Glume breadth ($GB_{1)}$ showed a negative association (r = –0.22 – –0.35) with percentage spikelets with midge larvae. Correlation coefficients above 0.32 were statistically significant at $p = 0.05$. Stepwise multiple linear regression analysis showed that in panicles infested with 10 midges per panicle, glume breadth GB_1 (X_1), glume length GL_1 × glume breadth $GB_1(X_2)$, and glume length GL_1 divided by glume length GL_2 (X_3) explained 28.0% variation in percentage spikelets with eggs (Y) [Y = 183.1–18.8 X_1^* + 1.8 X_2^* – 149.4 X_3^*]. Glume breadth $GB_1(X_1)$, and anther length (X_2) explained 39.4% of the variation in percentage spikelets with larvae (Y = –1.1 – 2.5 X_1^* + 3.3 X_2^*). Glume breadth GB_1 (X_1) and anther length (X_2) explained 17.9% of the variation in sorghum midge damage (Y = 17.1 – 8.9 X_1 + 10.6 X_2^*) [* = regression coefficient statistically significant at $p = 0.05$]

In panicles infested with 25 midges per panicle, glume breadth GB_1 (X_1), glume breadth GB_1 divided by exposed area of glume $EGB_2(X_2)$, and anther length (X_3) accounted for 24.4% of the variation in percentage spikelets with eggs [Y = –76.0 – 17.4 X_1^* + 81.7 X_2 + 16.3 X_3^*]. These floral parameters also accounted for 26.0% of the variation in percentage spikelets with larvae [Y = –52.5 – 27.8 X_1^* + 113.7 X_2^* + 12.5 X_3]. Exposed area of glume $EGB_2(X_1)$, glume breadth $GB_1(X_2)$, glume breadth GB_1 divided by exposed area of glume EGB_2 (X_3), glume length GL_1 (X_4), glume length GL_1 divided by glume length $GL_2(X_5)$ explained 19.4% of the total variation in midge damage [Y = 369.0 + 289.0 X1 – 236.0 X2* + 892.0x3* + 217.6 X4 – 1514.0 X5].

Table 3. Linear measurements* of floral parts of 28 sorghum genotypes (QDPI, Toowoomba, 1996)

Genotypes	Linear measurements (mm)					GL_1/	GB_1/	$GL_1 \times$
	GL_1	GL_2	GB_1	EGB_2	AL	GL_2	EGB_2	GB_1
IS 2579c	2.49	2.82	1.98	1.58	2.34	0.89	1.26	30.77
IS 3461	2.96	3.05	1.76	1.32	1.65	0.97	1.34	32.57
IS 7005	3.26	3.46	2.01	1.60	2.49	0.94	1.26	40.96
IS 8100c	3.01	3.20	1.98	1.46	1.83	0.94	1.37	37.18
IS 8721	2.88	3.11	2.07	1.56	1.82	0.93	1.35	37.28
IS 8887	2.43	2.54	1.72	1.30	1.70	0.96	1.34	26.15
IS 9807	3.37	3.42	2.25	1.68	2.31	0.98	1.34	47.28
IS 10712	2.78	3.06	1.94	1.63	1.78	0.91	1.20	33.79
IS 15107	3.00	3.61	2.09	1.82	3.34	0.83	1.15	39.15
IS 18563	2.92	3.22	2.28	1.79	2.33	0.91	1.28	41.62
IS 18698	2.98	2.97	2.12	1.66	2.21	1.01	1.27	39.54
IS 18733	2.90	3.21	2.35	1.86	2.17	0.91	1.27	42.70
IS 19476	2.97	3.10	1.99	1.55	2.18	0.96	1.29	36.92
IS 19512	3.14	3.22	2.05	1.63	1.89	0.98	1.26	40.13
IS 21871	2.77	2.96	2.06	1.54	1.74	0.94	1.34	35.59
IS 21873	2.85	2.87	1.96	1.49	1.75	0.99	1.32	34.90
IS 21879	2.98	2.95	1.96	1.75	2.30	1.01	1.12	36.54
IS 21881	2.58	2.73	2.20	1.64	1.82	0.95	1.34	35.38
IS 21883-1	2.54	2.71	2.07	1.45	2.09	0.94	1.44	32.86
IS 22806	2.70	2.85	1.81	1.49	1.78	0.95	1.22	30.58
IS 26789	2.82	2.79	1.74	1.45	1.78	1.01	1.21	30.79
PM 7017	2.67	2.95	1.79	1.55	1.74	0.91	1.16	29.96
PM 8787-2	2.69	2.85	2.03	1.48	1.87	0.94	1.40	34.14
PM 15936-2	2.50	2.97	2.37	1.65	1.81	0.84	1.44	36.94
ICSV 197	2.77	2.99	1.78	1.38	1.97	0.93	1.30	30.89
ICSV 745	3.07	3.32	2.26	1.53	2.37	0.93	1.48	43.51
QL 39	2.71	2.81	2.22	1.43	2.05	0.97	1.56	37.54
QL 12	3.90	4.04	1.98	1.50	2.73	0.97	1.33	48.38
Mean	2.78	2.96	1.96	1.52	1.98	0.94	1.30	34.66
SE±	0.06	0.04	0.04	0.06	0.06	0.02	0.06	1.08
LSD at 5%	0.16	0.12	0.12	0.16	0.16	0.07	0.16	3.03

* Mean of 15 spikelets in each genotype.
GL_1 = Glume G_1 length. GL_2 = Glume G_2 length. GB_1 = Glume G_1 breadth. EGB_2 = Exposed portion of glume G_2 width. AL = Anther length.

Compensation in grain mass

Compensation in grain mass in panicles having 250 spikelets and infested with 10 midges per panicle varied from 56.3% in IS 26789 to –41.3% in QL 12 (Table 4). Compensation in grain mass was 55.2% in IS 26789 to –17.8% in QL 12 panicles infested with 25 midges per panicle. IS 7005, IS 9807, IS 15107, IS 26789, and ICSV 745 showed >20% compensation in grain mass compared to a reduction of –29.5% in QL 12. Lines IS 2579C, IS 21883-1, PM 7017, and QL 12 showed a reduction in grain mass in panicle having 250 spikelets and infested with 10 or 25 sorghum midge females.

Diversity of resistance

Of the 28 genotypes tested, IS 8721, IS 10712, IS 21873, IS 21881, ICSV 745, and QL 39 showed evidence for antibiosis when infested with 10 or 25 midges

Table 4. Compensation in grain mass in 23 sorghum genotypes having 250 spikelets per panicle and infested with 10 and 25 midges under no-choice headcage conditions (QDPI, Toowoomba, (1996)

Genotypes	Compensation in grain mass (%)	
	10 midges per panicle	25 midges per panicle
IS 2579c	–1.3	–4.1
IS 7005	29.8	31.4
IS 8721	4.8	21.4
IS 8887	3.8	6.5
IS 9807	21.4	31.0
IS 15107	25.7	49.8
IS 18563	2.1	10.9
IS 18698	8.1	3.9
IS 19476	6.6	10.5
IS 19512	15.4	15.3
IS 21871	14.8	9.4
IS 21879	17.6	9.6
IS 21881	19.2	10.7
IS 21883-1	–7.6	–6.7
IS 22806	–2.7	15.2
IS 26789	56.3	55.2
PM 7017	–11.2	–3.3
PM 8787-2	4.1	3.7
PM 15936-2	6.3	9.8
ICSV 197	3.4	3.7
ICSV 745	26.7	26.4
QL 39	0.8	2.3
QL 12	–41.3	–17.8
Mean	8.8	12.8
SE±	6.0	3.9
LSD at 5%	16.6	11.3

– = Negative sign means reduction in 100-grain mass of the infested panicles in relation to the 100 grain mass of the normal uninfested panicle.

per panicle, as these genotypes had correspondingly fewer number of larvae than the number of eggs laid (Figure 1). Genotypes IS 19512, IS 21879, IS 26789, and ICSV 197 showed lower larval numbers than the eggs laid in one out of two infestation levels. QL 12 also had proportionately fewer larvae than the eggs laid when infested with 25 sorghum midge females. The lower numbers of larvae in this genotype is because more than one egg was laid in each spikelet, but only one larva is able to complete development in each spikelet.

Using principal component analysis, the test genotypes were placed in seven groups when the panicles were infested with 10 and 25 sorghum midge females per panicle in relation to the linear measurements of the floral parts (Figure 2). In both cases, the resistant check, AF 28, and the susceptible check, QL 12 were placed distantly from the other genotypes tested, and thus were placed individually in separate groups. ICSV 745 was also placed singly when the panicles were infested with 25 midges per panicle. When the panicles were infested with 10 midges per panicle, the seven groups comprised of: A = IS 8100c, IS 21879, IS 3461, IS 22806, IS 9807, IS 21883-1, QL 39 and IS 19476; B = IS 18733, PM 7017 and IS 15107; C = IS 7005, IS 8721, IS 21873, IS 18563 and IS 21871; D = ICSV 745, IS 8887, IS 21881, PM 15936-2, IS 26789, IS 19512, ICSV 197, IS 10712 and PM 8787-2; E = IS 2579c; F = IS 18698; and G = QL 12. In panicles infested with 25 midges per panicles, the seven groups consisted of: A = IS 2579c, IS 19512, IS 21883-1 and IS 8887; B = QL 39, IS 26789, IS 21879 and IS 8721; C = IS 9807, IS 21871, PM 8787-2, PM 7017, IS 19476, IS 15107 and IS 8100c; D = IS 21873, IS 18733, IS 22806, IS 10712, IS 18563, IS 7005, PM 15936-2, IS 21881, IS 3461 and ICSV 197; E = QL 12; F = ICSV 745; and G = IS 18698. Thus, there is a considerable diversity in genotypes showing resistance to sorghum midge.

Discussion

Antixenosis to visiting adults (Sharma & Vidyasagar, 1994; Waquil et al., 1986b), oviposition nonpreference (Sharma, 1985; Franzmann, 1993; Rossetto et al., 1984; Sharma et al., 1990), and poor survival and development of midge larvae (Sharma et al., 1993b; Waquil et al., 1986b) are the principle components of resistance to sorghum midge. Of the 28 sorghum genotypes tested, 19 genotypes showed antixenosis for egg laying as the principal component of resistance, and had <20% spikelets with eggs and larvae. Of these, IS 8721, IS 10712, IS 21873, IS 21881, ICSV 745, and QL 39 showed evidence for antibiosis when infested with 10 or 25 midges per panicle, as these genotypes had correspondingly fewer larvae than the number of eggs laid. Genotypes IS 19512, IS 21879, IS 26789, and ICSV 197 showed lower larval numbers than the eggs laid in one out of two infestation levels. These genotypes should be studied in detail to quantify the antibiosis component of resistance. Of the nineteen

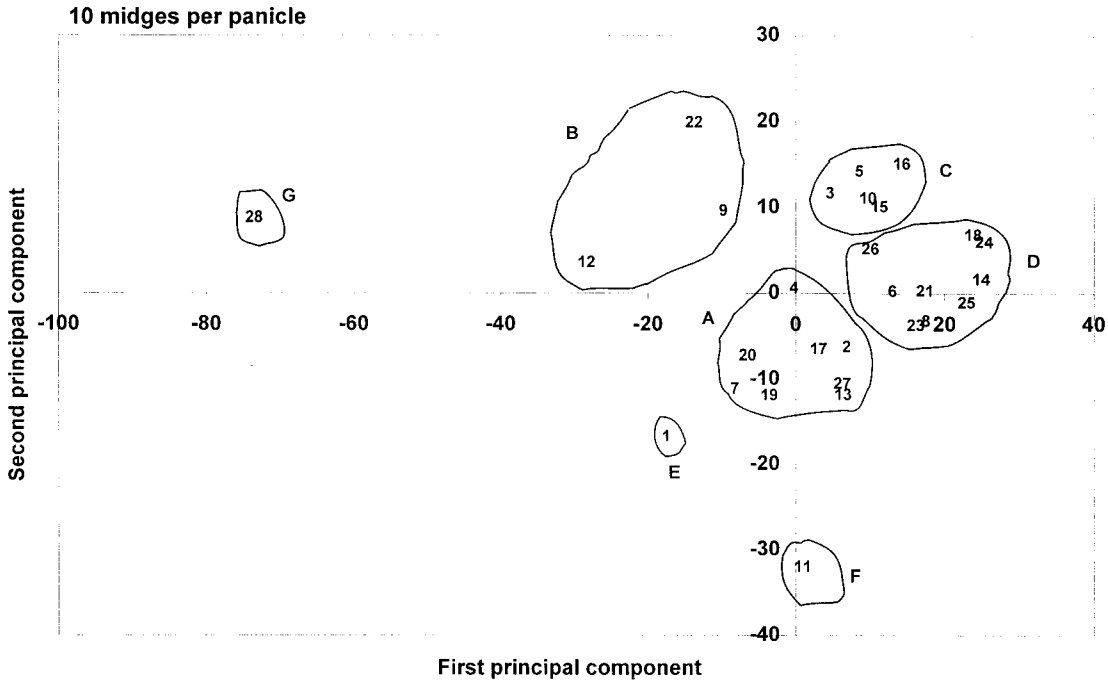

Figure 2. Principal component analysis of 28 sorghum genotypes based on midge damage, numbers of eggs and larvae, and linear measurements of the floral parts (panicles having 250 spikelets infested with 10 and 25 sorghum midges under no-choice headcage conditions) (QDPI, Toowoomba, 1996). 1 = IS 2579c; 2 = IS 3461; 3 = IS 7005; 4 = IS 8100c; 5 = IS 8721; 6 = IS 8887; 7 = IS 9807; 8 = IS 10712; 9 = IS 15107; 10 = IS 18563; 11 = IS 18698; 12 = IS 18733; 13 = IS 19476; 14 = IS 19512; 15 = IS 21871; 16 = IS 21873; 17 = IS 21879; 18 = IS 21881; 19 = IS 21883-1; 20 = IS 22806; 21 = IS 26789; 22 = PM 7017; 23 = PM 8787-2; 24 = PM 15936-2; 25 = ICSV 197; 26 = ICSV 745; 27 = QL 39; and 28 = QL 12.

genotypes showing less than 20% spikelets with eggs or larvae, only eight genotypes (IS 7005, IS 10712, IS 18563, IS 21873, IS 21881, PM 15936-2, ICSV 197, and ICSV 745) had <20% midge damaged spikelets under both the infestation levels, indicating that factors other than midge damage also contributed to chaffiness (spikelets without grain).

Short, tight and hard glumes (which possibly make it difficult to lay eggs inside the spikelets), faster grain development, and tannin content of the grain are associated with resistance to sorghum midge (Rossetto et al., 1984; Sharma et al., 1990). Most of the genotypes tested had smaller glumes than the susceptible check, QL 12. Eighteen genotypes had smaller floral parts (glume and anther length, and glume area), and better glume coupling (ratio of GB_1/EGB_2 >1.3) (except IS 18698, IS 19512, and ICSV 197). Of these, IS 2579 C, IS 8887, IS 19512, and IS 21883-1 showed >50% midge damage, while IS 7005, 18563, and ICSV 745 had relatively larger glumes, but suffered <20% midge damage. Percentage spikelets with eggs were significantly and positively associated with glume length and anther length. Stepwise multiple linear analysis showed that the proportion of the total variation explained by the floral parameters was low, and factors other than the linear measurements of the spikelets also played an important role in genotypic resistance to sorghum midge. Diarisso et al. (1998) suggested that resistance is caused by asynchrony between time of sorghum spikelet flowering and presence of sorghum midges in the field. However, observations in Australia and India have shown that there is no relationship between flowering time and expression of resistance to sorghum midge (Sharma, H.C., unpublished).

Fourteen genotypes showed >20% compensation in grain mass when the panicles size was reduced to 250 spikelets per panicle, and infested with 10 or 25 midges per panicle. However, there was considerable variation in compensation in grain mass in panicles infested with 10 and 25 midges per panicle, which may be because of inherent genotypic variation in grain mass, and the influence of environmental factors on grain development because of variation in days to 50% flowering. Eleven genotypes did not show appreciable gain in grain mass and some even showed a reduction in grain mass. This indicates variability in genotypic ability to compensate for loss in grain mass as a result of midge damage or physical removal of spikelets from the panicle. It has been observed that there is some compensation in grain mass in sorghum genotypes following midge damage (Franzmann & Butler, 1993; Waquil & Teetes, 1990), and that such an increase in grain mass is greater in midge-resistant genotypes than in the susceptible ones (Sharma et al., 2002). However, compensation in grain mass is not apparent at damage levels below 40% (Hallman et al., 1984). Thus, compensation in grain mass is influenced by panicle size, midge damage, and genotypic resistance to sorghum midge. Some of the observed variations in compensation in grain mass may be due to differences in environmental factors during grain development. Further studies are required across a range of midge-infestations in a diverse array of sorghum genotypes flowering at the same time to study the influence of panicle size, infestation levels, and genotypic resistance to midge on compensation in grain mass in sorghum.

Lines IS 3461, IS 9807, IS 10712, IS 18563, IS 19476, IS 21873, IS 21881, IS 22806, PM 15936-2, and ICSV 197 showed low oviposition and/or suffered low midge damage (< 20%) across infestation levels, and these lines have high levels of resistance to sorghum midge (Table 5). Genotypes IS 8721, IS 10712, IS 21873, ICSV 745, and QL 39 had proportionally lower number of larvae than the eggs laid, and thus may possess some level of antibiosis to sorghum midge larvae. IS 7005, IS 18563, IS 19476, IS 19512, IS 21873, IS 21881, ICSV 745, and QL 39 showed high levels of resistance, but had medium sized glumes, and these genotypes possibly have a different combination of characteristics imparting resistance to sorghum midge. Of the genotypes showing high levels of resistance to sorghum midge, IS 7005, IS 9807, IS 18563, IS 19476, IS 21881, IS 22806, PM 15936-2 and ICSV 745 also showed >20 compensation in grain mass. Using principal component analysis, the test genotypes were placed in seven groups when the panicles were infested with 10 and 25 sorghum midge females per panicle in relation to the linear measurements of the floral parts. The resistant check, IS 18698, and the susceptible check, QL 12 were placed distantly from the other genotypes tested. ICSV 745 was also placed singly when the panicles were infested with 25 midges per panicle. The results suggested that there is a considerable diversity in sorghum genotypes showing resistance to sorghum midge, and these genotypes have different combinations of characteristics associated with midge resistance. Therefore, there are good possibilities for increasing the resistance levels and diversifying the genetic base for resistance to sorghum midge.

Table 5. Components of resistance to sorghum midge in 28 sorghum genotypes (QDPI, Toowoomba, 1996)

Genotype	10 midges per panicle				25 midges per panicle				Glume traits		
	Eggs	LV	MD	ANTB	Eggs	LV	MD	ANTB	GL_1	GA	CG
IS 2579c	+	+						+	+	+	
IS 3461	+	+			+	+				+	
IS 7005	+	+	+		+	+	+				+
IS 8100c	+	+			+						
IS 8721		+	+	+		+		+			+
IS 8887	+	+	+						+	+	
IS 9807	+	+			+	+					+
IS 10712	+	+	+	+	+	+	+	+	+	+	
IS 15107			+		+						+
IS 18563	+	+	+	+	+	+	+				+
IS 18698	+	+			+				+	+	
IS 18733					+	+					
IS 19476	+	+			+	+					+
IS 19512	+	+	+					+			+
IS 21871	+	+	+						+	+	+
IS 21873	+	+	+	+	+	+	+		+		+
IS 21879	+	+				+					+
IS 21881	+	+	+	+	+	+	+		+		+
IS 21883-1	+	+							+	+	
IS 22806	+	+			+	+	+	+	+	+	+
IS 26789	+	+	+			+		+	+	+	+
PM 7017		+			+	+			+	+	
PM 8787-2	+	+	+						+	+	
PM 15936-2	+	+	+	+	+	+	+		+	+	+
ICSV 197	+	+	+		+	+	+	+	+	+	
ICSV 745	+	+	+	+		+	+	+			+
QL 39	+	+		+		+		+	+		
QL 12											

LV = Larvae, ANTB = Antibiosis, MD = Midge damage, GL_1 = Glume length G_1, GA = Glume area, and CG = Compensation in grain mass.

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