Euphytica **109:** 131–140, 1999.

Breakdown of resistance to sorghum midge, *Stenodiplosis sorghicola*

H.C. Sharma[1], S.Z. Mukuru[2], Eric Manyasa[2] & J.W. Were[3]
[1]*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502 324, India;* [2]*East African Region Cereals and Legumes Program (EARCAL), ICRISAT, Nairobi, Kenya;* [3]*Kenya Agricultural Research Institute, Regional Research Station, Alupe, Busia, Kenya*

Received 24 February 1998; accepted 10 April 1999

Key words: diversity of resistance, plant resistance, resistance breakdown, sorghum, *Sorghum bicolor*, sorghum midge, *Stenodiplosis sorghicola*

Summary

Sorghum midge (*Stenodiplosis sorghicola* Coquillett) is an important pest of grain sorghum worldwide. Several sources of resistance to sorghum midge have been identified in the world sorghum germplasm collection, of which some lines show a susceptible reaction in Kenya. Therefore, we studied the insect density damage relationships for a diverse array of midge-resistant and midge-susceptible sorghum genotypes, and variation in association of glume and grain characteristics with expression of resistance to sorghum midge. AF 28 and IS 8891 showed resistance to sorghum midge both in India and Kenya; DJ 6514 and ICSV 197, which are highly resistant to sorghum midge in India, showed a susceptible reaction at Alupe, Kenya. Sorghum midge damage in general was greater in Kenya than that observed in India at the same level of midge density suggesting that the breakdown of resistance in Kenya is due to factors other than insect density. Glume length, glume breadth, and glume area were positively associated with susceptibility to sorghum midge at both locations. However, under natural infestation, the correlation coefficients were stronger in India than in Kenya. Grain mass at 3 and 6 days after anthesis was positively associated with susceptibility to midge in India, but did not show any association with midge damage in Kenya. Grain growth rate between 3 and 6 days after anthesis was more strongly correlated with susceptibility to midge in Kenya than in India. Variation in the reaction of sorghum genotypes across locations may be partly due to the influence of environment on association between glume and grain characteristics with susceptibility to sorghum midge, in addition to the possible differences in midge populations in different geographical regions.

Introduction

Sorghum, *Sorghum bicolor* (L.) Moench is one of the most important cereals in the semi-arid tropics (SAT). It provides food, feed and forage, but grain yields on peasant farms are generally low, partly due to insect pest damage. Nearly 150 species of insects have been recorded as pests of sorghum (Sharma, 1993), of which sorghum midge (*Stenodiplosis sorghicola* Coquillett) is the most important pest worldwide (Harris, 1976). Damage by the sorghum midge can be avoided through early and uniform planting of the same cultivar over a large area in a geographical region. However, it is difficult to plant at times when midge damage can be avoided because of uncertainties of rainfall, inability of the farmers to plant the entire sorghum crop in an area at the same time, and differences in flowering of the sorghum cultivars. Chemical control is costly, ineffective, and beyond the reach of most farmers in the SAT. Natural enemies exist, but their populations build up only after damage has been caused. Host plant resistance is an effective means of keeping midge populations below economic threshold levels (Sharma, 1993), and breeding for resistance to sorghum midge is an integral part of sorghum improvement programs.

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). Nearly 15,000 germplasm accessions were screened for resistance to sorghum midge between 1980 to 1990 at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, and 25 lines were found to be resistant to sorghum midge across seasons and locations (Sharma, 1985; Sharma et al., 1992, 1993a). Genotypes IS 2579C, TAM 2566, AF 28, DJ 6514, IS 10712, IS 7005, and IS 8891 showed high levels of resistance to sorghum midge across seasons under natural infestation and no-choice headcage screening in India. Most of the high yielding breeding lines developed at the ICRISAT Center were derived from DJ 6514 (Sharma et al., 1993a). However, DJ 6514 and the breeding lines derived from it showed susceptibility to sorghum midge at Alupe, Busia, Kenya, indicating the possibility of the occurrence of a new biotype of sorghum midge in this region or the environment-induced breakdown of resistance mechanisms (Sharma et al., 1999).

Oviposition nonpreference or difficulty in oviposition is one of the most important components of resistance to sorghum midge (Sharma, 1985; Franzmann, 1993; Rossetto et al., 1984; Sharma et al., 1990a; Waquil et al., 1986a). Antixenosis to visiting adults (Sharma & Vidyasagar, 1994) and antibiosis (survival and development of midge larvae) also contribute to midge resistance in sorghum (Sharma et al., 1993b; Waquil et al., 1986b). Short, tight, light-green and hard glumes, tannin content of grain, and rate of grain development in the initial stages are associated with resistance to sorghum midge (Sharma, 1985; Sharma et al., 1990a). In the present studies, we examined the expression of resistance to sorghum midge in a diverse array of midge-resistant and midge-susceptible genotypes, and variation in association of glume and grain characteristics with resistance to sorghum midge across locations.

Materials and methods

Ten sorghum genotypes were sown during the short rainy season (Sept to Dec) twice at fortnightly intervals during 1994 and 1995 at the Kenya Agriculture Research Institute (KARI), Regional Station, Alupe, Busia, Kenya. The tests were repeated during the 1994 and 1995 post-rainy season at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, and during the 1993 summer season at Tamil Nadu Agricultural University (TNAU), Regional Research Station, Kovilpatti, India. The genotypes tested included AF 28 – originating from Africa, and shown to be distinct from DJ 6514 (Sharma et al., 1990); IS 8891 – a midge-resistant line originating from Uganda; DJ 6514 – a midge-resistant line originating from Karnataka, India; ICSV 197 and ICSV 563 – improved midge-resistant lines developed from DJ 6514 as a resistant source; and Swarna, ICSV 112 (India), KAT 369, and Seredo (Kenya) – high yielding midge-susceptible commercial cultivars.

Crop. The test material was planted in a randomized complete block design, and there were three replications for each planting. Each entry was planted in a 4 row plot, 4 m long. The rows were 75 cm apart, and the plants were thinned to a spacing of 10 cm within the row 15 days after seedling emergence. Normal agronomic practices were followed for raising the crop. Carbofuran 3G (@ 1.2 kg ai per ha) was applied at the time of sowing to control the sorghum shoot fly, *Atherigona soccata* Rondani. No insecticide was applied during the reproductive stage of the crop. The test entries were exposed to the natural midge population at flowering; and to different midge densities (20, 40, and 80 midges per panicle for two consecutive days) under a no-choice headcage technique.

Infestation. To overcome the variation in midge density under natural infestation, the test entries were infested with 20, 40, or 80 midges panicle^{-1} at flowering using the headcage technique (Sharma et al., 1988). One panicle was infested in each replication at each infestation level. The panicles were covered with muslin cloth bags at panicle emergence from the flag leaf to avoid natural midge infestation. The sorghum midge females were collected in plastic bottle aspirators between 0800 to 1000 h from flowering sorghum panicles. The midges were immediately released inside the wire-framed cages tied around the sorghum panicles, and covered with blue colored cloth bags. Each panicle was infested with midges for two consecutive days at each level of infestation. The cages were removed 15 days after infestation to evaluate sorghum midge damage. The panicles were first rated visually on a 1 to 9 scale, and then samples were drawn from the sorghum midge infested portion to record the number of midge damaged spikelets from a sample of 250 spikelets in each panicle.

Observations. Sorghum midge damage was evaluated visually on a 1 to 9 scale (1 = $<$10% spikelets with midge damage, 2 = 11–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, 6 = 51–60%. 7 = 61–70%, 8 = 71–80%, and 9 = >80% spikelets with midge damage) both under natural infestation and no-choice headcage screening. Data were also recorded on the percentage spikelets with midge damage. For this purpose, samples were drawn from three panicles at random in each plot. Three branches were drawn from each panicle, and the primary branches were split into smaller secondary branches. The secondary branches were picked up at random and the number of midge damaged spikelets were recorded in a sample of 250 spikelets. The midge damaged spikelets were expressed as a percentage of the total number of spikelets examined.

Data on temperature and relative humidity for six weeks during flowering and grain development recorded at the meteorological stations at these locations was used to examine the effect of these factors on expression of resistance to sorghum midge. Data were also recorded on the linear measurements of the glumes (length and breadth) on a metric scale (in mm) at flowering. Grain mass was recorded at 3 and 6 days after anthesis. For this, the primary branches were marked at flowering with a twine in three panicles in each replication. One hundred spikelets with grain were picked up at random from the marked panicles in each replication, and the grain were removed gently with forceps and placed in 20 mL stoppered glass vials, and then dried in an oven at 80°C, and the weight of the dried grain was recorded after 72 h on a Mettler balance. The rate of grain development per day on dry weight basis was calculated as follows:

Rate of grain development (%) =

$$\frac{\text{Grain wt on 6th day after anthesis} - \text{Grain wt on 3rd day after anthesis}}{3[\text{Grain wt on 3rd day after anthesis} + \text{Grain wt on 6th day after anthesis}]/2} \times 100$$

Statistical analysis. The data were subjected to analysis of variance. The significance of differences between the genotypes was determined by F-test, while the treatment means were compared using least significant difference (LSD) at $p = 0.05$. The grain mass, rate of grain development, and linear measurements of the glumes were correlated with sorghum midge damage to determine the variation in association of these factors with resistance to sorghum midge.

Table 1. Relative responses of 10 sorghum genotypes to sorghum midge, *S. sorghicola*, across locations (1993–95)[a]

Genotype	Headcage screening					
	DR-C			MD (%)		
	20[b]	40	80	20	40	80
ICRISAT, Patancheru, India (1994 – 95)[a]						
AF 28	1.4	1.9	1.3	7.0	7.0	6.5
IS 8891	1.2	1.2	1.7	7.0	13.5	14.5
DJ 6514	2.2	2.7	2.1	8.0	11.0	11.0
ICSV 197	1.3	2.2	3.5	12.0	14.0	18.0
ICSV 563	1.3	2.2	1.3	11.0	14.0	15.0
ICSV 112	6.0	9.0	9.0	47.0	26.5	52.5
SEREDO	7.7	8.2	8.4	41.5	38.0	57.5
KAT 369	7.0	8.2	8.2	89.5	69.0	84.0
SERENA	7.5	9.0	8.5	45.0	39.0	59.5
SWARNA	7.5	9.0	8.9	68.0	73.0	82.5
Mean	4.4	5.2	5.4	33.6	30.0	39.8
SE±	0.73	0.48	0.57	11.2	4.58	7.48
TNAU, Regional Research Station, Kovilpatti, Tamil Nadu, India (1993)						
AF 28	6.0	5.3	5.7	30	40	40
DJ 6514	2.7	2.7	2.7	15	13	12
ICSV 197	2.0	2.3	2.3	9	10	12
ICSV 112	9.0	9.0	9.0	85	77	86
Swarna	8.0	7.7	8.7	71	56	85
Mean	5.5	5.4	5.7	42	39	47
SE±	0.24	0.83	0.51	4.0	8.7	5.4
KARI, Regional Research Station, Alupe, Kenya (1994–95)[a]						
AF 28	2.4	2.5	3.0	26	26	30
IS 8891	1.5	1.6	2.3	19	18	18
DJ 6514	3.8	5.2	6.4	40	44	55
ICSV 197	4.0	6.0	6.9	48	60	60
ICSV 743	6.9	7.7	8.4	60	72	77
ICSV 112	4.8	6.3	8.5	55	69	75
Seredo	5.0	7.3	8.7	51	67	77
KAT 369	5.9	8.5	8.8	64	81	79
Swarna	6.3	8.1	8.6	57	79	75
Mean	4.5	5.9	6.8	47	57	61
SE±	0.51	0.60	0.53	4.04	2.8	4.99

[a] Mean over two sowing dates and two seasons.
[b] Number of sorghum midge females released per panicle for two consecutive days.
DR-C = Damage rating (1 = <10% midge damage, and 9 = >80% midge damage) under headcage screening, and MD (%) = Percentage spikelets with midge damage.

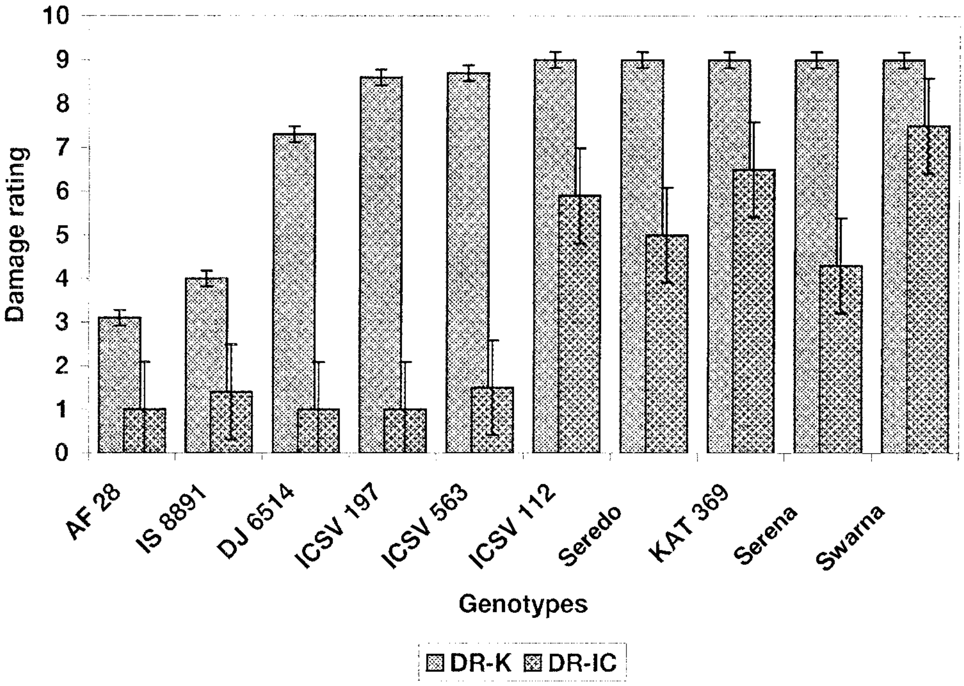

Figure 1. Sorghum midge, *Stenodiplosis sorghicola* damage in 10 sorghum genotypes at Patancheru, India (DR-IC) and at Alupe, Kenya (DR-K) under natural infestation. (Damage rating, 1 = <10% midge-damaged spikelets, and 9 = >80% midge-damaged spikelets).

Results

Reaction of sorghum genotypes to midge infestation across locations

Natural infestation. At ICRISAT Center, India; AF 28, IS 8891, DJ 6514, ICSV 197, and ICSV 563 suffered a damage rating (DR) of <1.5 under natural infestation compared to a DR of 4.3 to 7.5 in ICSV 112, KAT 369, Serena, Seredo, and Swarna (Figure 1). Across infestation levels under no-choice headcage conditions, AF 28, IS 8891, DJ 6514, ICSV 197, and ICSV 563 suffered a DR of 1.2 to 3.5 compared to 7.0 to 9.0 in the susceptible checks ICSV 112, KAT 369, Serena, Seredo, and Swarna (Table 1). Percentage spikelets with midge damage were <18% in the midge-resistant lines, 26.5 to 59.5% in ICSV 112, Serena, and Seredo, and 69.0 to 89.5% in KAT 369 and Swarna. With increase in midge infestation from 20 to 80 midges per panicle, midge DR increased by 1.0, and percentage midge damage by 9.8%. Midge DR increased by 0.5 to 2.2 in the midge-resistant lines and 0.7 to 1.5 in the susceptible checks. Increase in percentage midge damage was <7.5% in the midge-resistant lines compared to 14.5 to 26.0% increase in the susceptible controls. These results indicated that AF 28, IS 8891, DJ 6514, ICSV 197, and ICSV 563 were fairly stable in their response to sorghum midge across infestation levels in India.

At TNAU, Kovilpatti, India, DJ 6514 and ICSV 197 suffered a DR of 2.0 to 2.7, and had 9 to 15% spikelets with sorghum midge damage, whereas AF 28 suffered a DR of 5.3 to 6.0, and had 30 to 40% sorghum midge damage across infestation levels (Table 1). The susceptible checks, ICSV 112 and Swarna had a DR of 7.7 to 9.0, and 56 to 86% spikelets with sorghum midge infestation across infestation levels, Visual damage ratings at Kovilpatti were slightly greater than those recorded at Patancheru, possibly because of head bug (*Calocoris angustatus* Lethiery) damage, which is similar to the sorghum midge damage under heavy infestation. However, sorghum midge damage in AF 28 was greater at Kovilpatti than that observed at Patancheru in India and at Alupe, Kenya.

In Kenya, AF 28 and IS 8891 suffered a DR of 3.1 and 4.0, respectively, compared with 7.3 in DJ 6514, 8.6 in ICSV 197, and 9.0 in the susceptible checks, ICSV 112, KAT 369, Seredo and Swarna under natural infestation (Fig. 1). AF 28 and IS 8891 suffered a DR

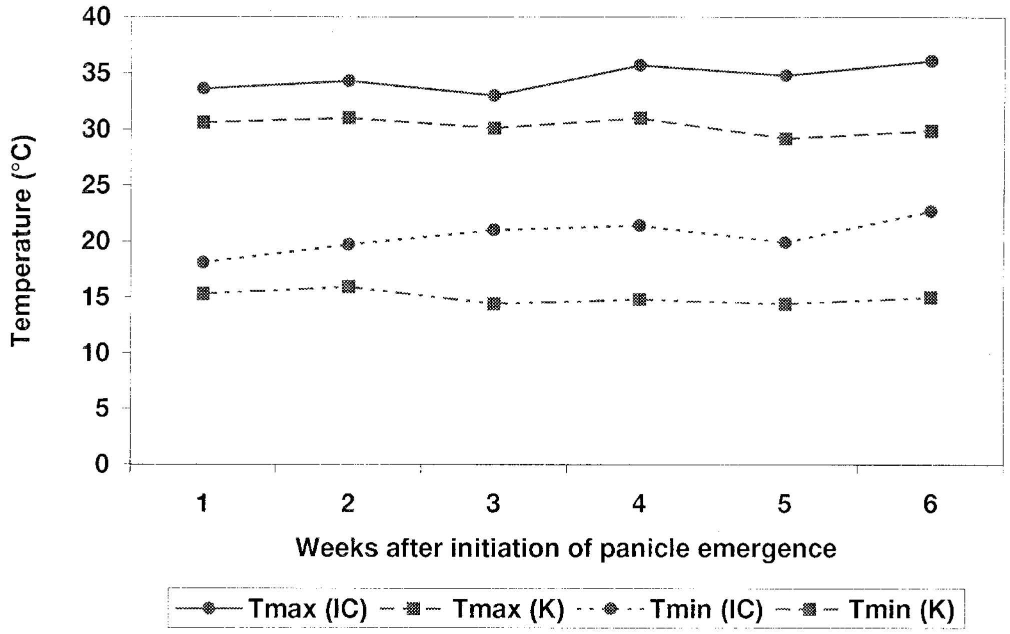

Figure 2. Maximum and minimum temperatures (°C) at Patancheru, India (IC) (20 Feb–30 March 1995) and at Alupe, Kenya (K) (20 Nov–30 Dec 1995) for six weeks during flowering and grain development.

of 1.5 to 3.0 compared with a DR of 3.8 to 6.4 in DJ 6514, 4.0 to 6.9 in ICSV 197, and 4.8 to 8.8 in ICSV 112, Seredo, KAT 369 and Swarna (Table 1). Average midge DR was 4.5, 5.9, and 6.8 when the panicles were infested with 20, 40, and 80 midges panicle^{-1}, respectively. Percentage midge damage was 26 to 30% in AF 28, 16 to 18% in IS 8891, 40 to 55% in DJ 6514, 48 to 60% in ICSV 197 and 51 to 81% in the susceptible checks, ICSV 112, Seredo, KAT 369 and Swarna. At infestation levels of 20, 40, and 80 midges panicle^{-1}, the sorghum midge damage was 47, 57 and 61%, respectively. With increase in midge density from 20 to 80 midges per panicle, the increase in midge DR was 2.3, and the percentage midge damage increased by 15%. There was a progressive increase in midge damage with increase in midge density, and such an increase was greater in DJ 6514, ICSV 197, ICSV 112, Seredo, KAT 369 and Swarna than in AF 28 and IS 8891. The results indicated that AF 28 and IS 8891 were resistant to sorghum midge both in India and Kenya, whereas DJ 6514 and ICSV 197 showed susceptible reactions in Kenya. Midge damage levels were greater in Kenya than in India. The breakdown of resistance to sorghum midge in Kenya thus appeared to be due to factors other than midge density.

The maximum temperatures during flowering and grain development ranged from 29.2–31.0 °C and 33.0–35.7 °C, and the minimum temperatures from 14.4–15.9 °C and 18.1–22.7°C at Alupe, Kenya, and Patancheru, India, respectively (Figure 2). The mean maximum and minimum temperatures at Alupe, Kenya were 30.3 and 15.0 °C, respectively; and 34.6 and 20.5 °C, respectively, at Patancheru, India. Maximum and minimum temperatures were higher by 4.5 and 5.5 °C at Patancheru, India than at Alupe, Kenya during flowering and grain development. Maximum relative humidity was 67.3% (range 57.4–79.7%) at Alupe, Kenya and 71.9% (range 59.6–77.6%) at Patancheru, India (Figure 3). The minimum relative humidity was 47.7% (range 39.9–56.4%) at Alupe, Kenya; and 26.7% (range 23.1–29.0%) at Patancheru, India. The minimum relative humidity, which influences both adult emergence and oviposition, was much lower at Patancheru, India than at Alupe, Kenya. Maximum sunshine hours at Alupe, Kenya (at the equator) are 12 throughout the year, and 10.3 (actual 9.4) during Feb and 7.3 (actual 7.3) during Oct at Patancheru, India. These differences in temperature, relative humidity, and solar radiation may affect the genotypic susceptibility to sorghum midge.

Linear measurements of glumes. There was a considerable variation in glume and grain characteristics among the sorghum genotypes. At ICRISAT Centre,

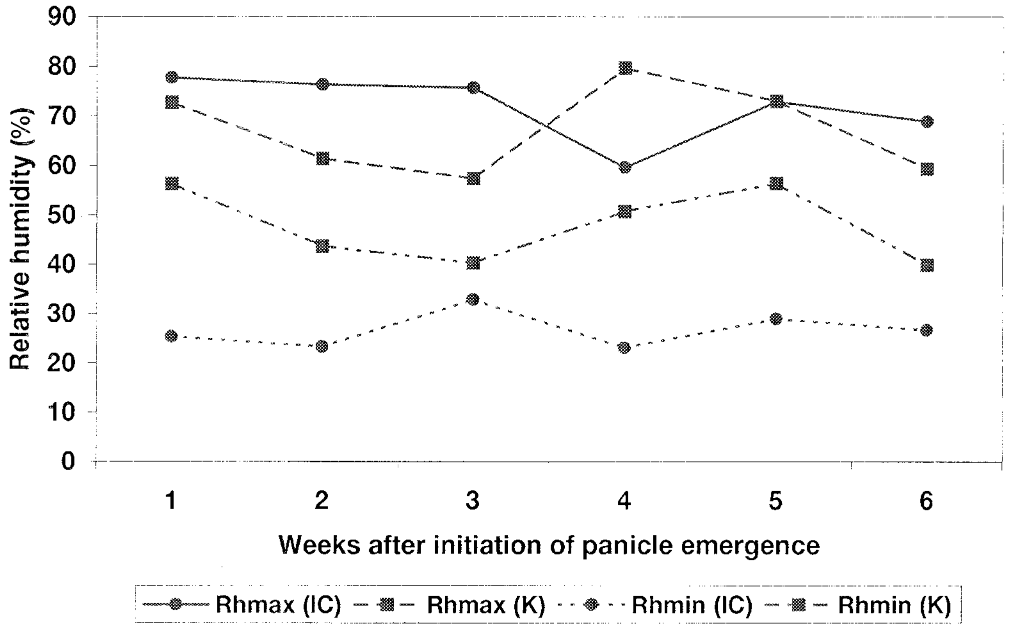

Figure 3. Maximum and minimum relative humidities (%) at Patancheru, India (IC) (20 Feb–30 March 1995) and at Alupe, Kenya (K) (20 Nov–30 Dec 1995) for six weeks during flowering and grain development.

Table 2. Linear measurements of glumes and rate of grain development of 10 sorghum lines at ICRISAT Centre (IC), Patancheru, India, and KARI, Alupe, Kenya (K) (1994 and 1995)

Genotype	Glume length (mm)		Glume breadth (mm)		Area (mm^2		Grain mass (g) 100^{-1} grains 3D		6D		Growth rate (%)		Area/ 3D		Area/ 6D	
	IC	K	IC	K	IC	K	IC	K	IC	K	IC	K	IC	K	IC	K
AF 28	3.35	3.40	2.22	1.87	7.44	6.35	0.101	0.152	0.240	0.269	26.5	18.33	75	42	33	24
IS 8891	2.87	2.80	2.02	1.92	5.77	5.44	0.075	0.130	0.127	0.209	17.0	15.27	77	71	46	40
DJ 6514	2.92	2.84	2.28	2.04	6.67	5.77	0.060	0.132	0.135	0.218	25.5	16.31	111	45	50	27
ICSV 197	3.05	2.86	2.42	2.12	7.37	6.06	0.057	0.116	0.152	0.238	30.5	21.40	131	53	48	26
ICSV 563	3.62	3.69	2.54	2.22	9.16	8.16	0.051	0.105	0.119	0.195	26.5	19.87	179	79	77	42
ICSV 112	4.28	4.21	3.40	2.82	14.58	10.53	0.071	0.122	0.183	0.232	29.3	20.67	204	86	79	46
Seredo	4.75	4.40	3.04	2.92	14.41	11.83	0.106	0.206	0.279	0.278	30.0	21.27	136	58	58	43
KAT 369	4.75	4.54	3.50	3.12	16.63	14.16	0.130	0.188	0.315	0.356	27.7	20.38	129	75	53	40
Serena	4.42	–	2.74	–	12.08	–	0.096	–	0.250	–	29.7	–	127	–	48	–
Swarna	4.95	5.16	2.96	2.84	14.68	14.70	0.059	0.114	0.151	0.204	29.1	19.44	248	131	97	72
Mean	3.89	3.76	2.71	2.43	10.88	9.22	0.081	0.141	0.195	0.244	27.2	19.21	141.7	71	58.2	40.0
SE±	0.086	0.143	0.164	0.078	0.799	0.796	0.006	0.0089	0.017	0.0089	3.47	2.202	13.90	9.2	4.68	4.4

D = Days after anthesis.

India; glume length varied from 2.87 mm in IS 8891 to 4.95 in Swarna (Table 2). Glume breadth ranged from 2.02 mm in IS 8891 to 3.50 mm in KAT 369. Glume area varied from 5.77 mm^2 in IS 8891 to 16.63 mm^2 in KAT 369. Glume length was $<$3.62 mm and glume breadth $<$2.54 mm in lines showing resistant reactions to sorghum midge; while the glume length and breadth were 4.28 to 4.95 mm and 2.74 to 3.50 mm, respectively, in the susceptible lines. Glume area was $<$9.16 mm^2 in resistant lines compared to 12.08 to 16.63 mm^2 in susceptible lines. Mass per 100 grains ranged from 0.051 g in ICSV 563 to 0.130 g in KAT 369 at 3 days after anthesis. At 6 days after anthesis, grain mass ranged from 0.119 g in ICSV 563

Table 3. Association of linear measurements of glumes and rate of grain development with resistance to sorghum midge, *S. sorghicola*

Trait	DR-N		MD-C						DR-C					
			20[a]		40		80		20		40		80	
	IC	K	IC	K	IC	K	IC	K	IC	K	IC	K	IC	K
Glume length	0.94**	0.55*	0.89**	0.70**	0.88**	0.71**	0.94**	0.69**	0.64**	0.68**	0.63*	0.75**	0.67*	0.70*
Glume breadth	0.88**	0.74**	0.89**	0.68**	0.74**	0.79**	0.85**	0.80**	0.47*	0.77**	0.46*	0.82**	0.51*	0.79**
Area	0.95**	0.63**	0.94**	0.71**	0.86**	0.77**	0.94**	0.73**	0.58*	0.73**	0.56*	0.79**	0.61*	0.73**
Grain mass 3D	0.36	0.03	0.52*	–0.03	0.41*	0.13	0.45*	0.12	0.34	0.05	0.33	0.08	0.25	0.13
Grain mass 6D	0.47*	0.10	0.60*	0.08	0.45*	0.25	0.55*	0.19	0.51*	0.24	0.50*	0.24	0.43*	0.22
Growth rate	0.45*	0.71**	0.44*	0.63**	0.33	0.72**	0.46*	0.74**	0.63*	0.76**	0.65*	0.77**	0.65*	0.76**
Area/3D	0.67**	0.43	0.51*	0.56**	0.56*	0.49*	0.57*	0.46*	0.27	0.49*	0.26	0.56**	0.38	0.43*
Area/6D	0.59**	0.44*	0.42*	0.56**	0.51*	0.50**	0.48*	0.49*	0.10	0.46*	0.89**	0.55*	0.23	0.46*

*, ** = Correlation coefficients significant at P 0.05 and 0.01, respectively.
D = Days after anthesis, [a] Number of midges released per panicle.
DR-N = Damage rating under natural infestation.
DR-C = Damage rating under headcage screening.
MD-C = Percentage spikelets with midge damage under headcage screening.
IC = ICRISAT Centre, Patancheru, India, and K = KARI, Alupe, Kenya.

to 0.315 g in KAT 369. Rate of grain development on a dry weight basis varied from 17.0% in IS 8891 to 30.0% in Seredo.

In Kenya, glume length ranged from 2.80 mm in IS 8891 to 5.16 mm in Swarna, and the glume breadth from 1.87 mm in AF 28 to 3.12 mm in KAT 369 (Table 2). Glume area varied from 5.44 mm^2 in IS 8891 to 14.70 mm^2 in Swarna. Grain mass per 100 grains ranged from 0.105 g in ICSV 743 to 0.206 g in Seredo at 3 days after anthesis. At 6 days after anthesis, grain mass varied from 0.195 g in ICSV 743 to 0.356 g in KAT 369. Grain growth rate varied from 15.27% in IS 8891 to 21.40% in ICSV 197.

Association of glume and grain characteristics with susceptibility to sorghum midge

Natural infestation. Under natural infestation, glume length, glume breadth, and glume area were more strongly correlated with sorghum midge damage in India (r = 0.88–0.94) than in Kenya (r = 0.55–0.74) (Table 3). Grain mass at 3 and 6 days after anthesis was positively associated with midge damage in India (r = 0.45–0.47), while there was no association between these parameters in Kenya (r = 0.03–0.10). However, the reverse was true in the case of rate of grain development (r = 0.45 at Patancheru, India, and 0.71 in Kenya). Glume size: grain mass ratios at 3 and 6 days after anthesis showed moderate levels of association with susceptibility to sorghum midge both in India (r = 0.59–0.67), and in Kenya (r = 0.43–0.44).

No-choice headcage screening. Under no-choice headcage testing across infestation levels, glume length (r = 0.63–0.94 in India, and 0.68–0.71 in Kenya), glume breadth (r = 0.46–0.89 in India, and 0.68–0.82 in Kenya), and glume area (r = 0.56–0.94 in India, and 0.71–0.79 in Kenya) showed positive association with susceptibility to sorghum midge (Table 3). There was little or no change in the correlation coefficients as the midge density increased from 20 to 80 midges per panicle. Grain mass at 3 and 6 days after anthesis was positively associated with susceptibility to midge in India (r = 0.25–0.60), but did not show any association with midge damage in Kenya (r = –0.03–0.25). Grain growth rate between 3 and 6 days after anthesis was more strongly correlated with susceptibility to sorghum midge in Kenya (0.63–0.77) than in India (0.33–0.65). Glume size: grain mass ratios at 3rd and 6th day after anthesis showed a moderate degree of association with sorghum midge damage across infestation levels in Kenya (r = 0.43–0.56), while such an association between these parameters in India was quite variable (0.10–0.89). The variation in association between glume and grain characteristics with midge damage across locations may partly account for the differences in reaction of sorghum genotypes across locations.

Glume length, glume breadth, and glume area were highly correlated both in India (r = 0.91–0.98), and in Kenya (r = 0.88–0.97). Grain mass at 3 and 6 days after anthesis was more strongly correlated with glume length, glume breadth, and glume area in India

Table 4. Association between glume and grain growth parameters in ten sorghum genotypes at ICRISAT Centre, India (above the diagonal), and at KARI, Alupe, Kenya (below the diagonal) (1994 and 1995)

	Glume length	Glume breadth	Area mass 3D	Grain mass 6D	Grain rate	Growth 3D	Area/ 6D	Area/
Glume length	–	0.91**	0.98**	0.45	0.58*	0.54*	0.73**	0.64**
Glume breadth	0.88**	–	0.95**	0.52*	0.65**	0.56*	0.58*	0.48*
Area	0.97**	0.94**	–	0.50*	0.61**	0.52*	0.70**	0.61*
Grain mass 3D	0.29	0.47*	0.37	–	0.95**	0.10	–0.26	–0.33
Grain mass 6D	0.31	0.51*	0.43	0.82**	–	0.41	–0.10	–0.24
Growth rate	0.53*	0.63**	0.53*	0.22	0.37	–	0.47	0.24
Area/3D	0.73**	0.54*	0.70**	–0.33	–0.26	0.17	–	0.97**
Area/6D	0.80**	0.62**	0.76**	–0.14	–0.22	0.18	0.96**	–

*, ** = Correlation coefficients significant at $p = 0.05$, and 0.01, respectively.

(r = 0.45–0.63) than in Kenya (r = 0.29–0.51). Rate of grain growth between 3 and 6 days after anthesis showed a moderate association with glume characteristics at both locations (r = 0.52–0.56 in India, and 0.53–0.63 in Kenya). Glume area: grain mass ratios also showed a similar association with the glume characteristics at these locations (r = 0.58–0.70 in India, and 0.54–0.80 in Kenya). There was no association between grain mass and glume size: grain mass ratios at 3 and 6 days after anthesis (r = –0.10–0.33 in India, and –0.14– –0.33 in Kenya), and rate of grain development (r = 0.24–0.47 in India, and 0.17–0.18 in Kenya). These results suggested that grain mass is not influenced by glume size, and rate of grain development is independent of the grain mass.

Discussion

Using principle component analysis, TAM 2566, DJ 6514, and IS 12666C were found to be stable for resistance to sorghum midge under no-choice headcage screening over four seasons (Sharma et al., 1988). Faris et al. (1979) reported that AF 28 was the most stable line for resistance to sorghum midge across several planting dates. In another study, using Canonical variate and D^2 cluster analysis, AF 28 was found to be distinct from other genotypes, while DJ 6514 and TAM 2566 were grouped together (Sharma et al., 1990b). These studies have shown that there is a considerable diversity in sorghum genotypes for resistance to midge.

Among the midge-resistant lines tested in Kenya, AF 28 and IS 8891 showed resistance to midge across planting dates and infestation levels. However, midge damage in these lines was generally 1.5 to 2 times greater in Kenya than that observed in India. DJ 6414 and ICSV 197 showed moderate levels of susceptibility to sorghum midge (DR 6.7–7.5, 49–55% midge damage) in Kenya, and suffered 4 to 5 times more damage in Kenya than at ICRISAT Centre, India. AF 28 suffered greater damage at Kovilpatti, Tamil Nadu, India than at Patancheru, India or in Kenya. All the commercial and susceptible checks suffered high midge damage at all locations. Serena and Seredo (which have a colored grain) suffered slightly less damage at ICRISAT Centre, India than in Kenya.

There was a 4 to 5% increase in midge damage with an increase in midge density from 20 to 80 insects per panicle in AF 28 and IS 8891 compared to a 11 to 15% increase in DJ 6514 and ICSV 197. At ICRISAT Centre, India, the increase in midge damage with increased midge density was 1 to 7%. Also, there was a progressive increase in midge damage both in Kenya and India with increased midge density in ICSV 112, Seredo, KAT 369, and Swarna. At ICRISAT Centre, India, ICSV 112 and Seredo suffered relatively less damage than KAT 369 and Swarna across infestation levels. However, the differences in midge damage between KAT 369, Seredo, ICSV 112, and Swarna were not apparent. DJ 6514 and ICSV 197 not only showed greater susceptibility to midge in Kenya, but also showed a greater increase in damage with an increase in density from 20 to 80 midges per panicle, compared to AF 28 and IS 8891.

Resistance to sorghum midge is influenced by visual and chemical stimuli from the host plant (Sharma et al., 1990b). Short, tight and hard glumes, faster rate of initial grain development, and higher tannin content of the grain (Rossetto et al., 1975;

Sharma, 1985; Sharma et al., 1990a) are associated with resistance to sorghum midge. Nutritional quality of the grain (in terms of sugars, proteins, and tannins) also influences genotypic resistance to sorghum midge (Sharma et al., 1993b), and chemical composition of the sorghum grain is influenced by the environment (Butler, 1982; Price et al., 1979; Sharma et al., 1993b). Variations in the chemical composition of the grain over seasons have been linked to the expression of resistance to midge (Sharma et al., 1993b). AF 28 and IS 8891 have red/chalky grain with high tannin content (Sharma et al., 1993b), while DJ 6514 and ICSV 197 have white grain with very little or low tannin content, and this may be partly responsible for diffferences in genotypic susceptibility to sorghum midge across locations.

Several climatic and edaphic factors influence the nature and level of resistance to insects (Kogan, 1975). Inherited characters, especially physico-chemical factors, are influenced by the environment. Moisture stress (McMurtry, 1962), plant nutrition (Chand et al., 1979; Schwiessing & Wilde, 1979), temperature (Benedict & Hatfield, 1988; Tingey & Singh, 1980; Kogan, 1975; Schwiessing & Wilde, 1978), photoperiod (Khan et al., 1986), and insect biotypes (Kogan, 1975; Pathak, 1980; Bentur et al., 1988) influence the expression of resistance to insects in crop plants. Sorghum midge damage across genotypes and sowing dates did not show any association with the climatic factors. However, the reactions of different genotypes across sowing dates have shown diverse interactions with the environment (Sharma & Venkateswarulu, 1999).

Susceptibility to sorghum midge decreases with increase in maximum and minimum temperatures in sorghum midge-resistant genotypes (Sharma & Venkateswarulu, 1999). Maximum and minimum temperatures were lower by 4.5 and 5.5 °C at Alupe, Kenya, than at Patancheru, India during flowering and grain development. Therefore, lower temperatures at Alupe, Kenya may be one of the factors leading to greater sorghum midge damage. Sorghum midge damage in ICSV 197 is also associated positively with sunshine hours (Sharma & Venkateswarulu, 1999). Continuous high intensity light increases susceptibility to cabbage looper, *Trichoplusia ni* (Walker) in soybean (Khan et al., 1986). The sorghum crop at Alupe in Kenya is exposed to a constant photoperiod of 12 h, whereas the sorghum crop at Patancheru, India is exposed to 7.3 sunshine hours during the rainy season and 9.4 sunshine hours in the post-rainy period. Longer daylength at Alupe, Kenya may contribute to greater susceptibility to sorghum midge by inducing some physico-chemical changes in glume and grain characteristics. Grain mass at the 3rd and 6th day after anthesis, which is associated positively with temperature and solar radiation (Sharma & Venkateswarulu, 1999), was positively correlated with sorghum midge damage at Patancheru, India; but not at Alupe, Kenya. These differences in association of grain mass with damage by sorghum midge may contribute to variations in genotypic susceptibility to this insect. Grain growth rate between 3 to 6 days after anthesis, which is positively associated with susceptibility to sorghum midge, showed a negative association with temperature and solar radiation, and hence may contribute to greater susceptibility to sorghum midge at Alupe, Kenya. There were only slight differences in maximum relative humidity between Patancheru, India (71.9%) and Alupe, Kenya (67.3%). Minimum relative humidity, which is negatively associated with sorghum midge damage in ICSV 197, is much lower at Patancheru, India (26.7%) than at Alupe, Kenya (47.7%), and hence may contribute to greater susceptibility to sorghum midge in Kenya. Sorghum midge emergence and oviposition are also influenced by relative humidity (Fisher & Teetes, 1982; Sharma et al., 1988). Minimum relative humidity at Alupe, Kenya is higher than at Patancheru, India, and may contribute to greater midge activity and infestation at Alupe, Kenya, than at Patancheru, India at the same level of midge infestation. Temperature, relative humidity, and possibly solar radiation partly account for greater susceptibility of DJ 6514 and ICSV 197 in Kenya. However, AF 28 and IS 8891 showed the same level of resistance to sorghum midge across locations, and hence factors other than the climate may be responsible for breakdown of resistance to sorghum midge. Genetic differences in sorghum midge populations from different geographical regions may be one of the factors responsible for variation in genotypic susceptibility to this insect across locations.

Acknowledgments

We are thankful to Dr J.M. Lenne for her comments on the manuscript. Approved as JA no. 2041 by ICRISAT.

References

Benedict, J.H. & J.L. Hatfield, 1988. Influence of temperature induced stress on host plant suitability to insects. In: E.A. Hienrichs (Ed), Plant-Stress Insect Interactions, pp. 139–165. John Wiley and Sons, New York, USA.

Bentur, J.S., T.E. Srinivasan & M.B. Kalode, 1987. Occurrence of a virulent rice gall midge (GM) *Orseolia oryzae* Wood-Mason biotype (?) in Andhra Pradesh, India. Int Rice Res Newsl 12: 33–34.

Butler, L.G., 1982. The degree of polymerization of sorghum tannin during seed development and maturation. J Agric Fd Chem 30: 1090–1094.

Chand, P., M.P. Sinha & A. Kumar, 1979. Nitrogen fertilizer reduces shoot fly incidence in sorghum. Sci Cult 45: 61–62.

Faris, M.A., M. de A. Lira & A.F. de S.L. Viega, 1979. Stability of sorghum midge resistance. Crop Sci 19: 557–560.

Fisher, R.W. & G.L. Teetes, 1982. Effect of moisture on sorghum midge (Diptera: Cecidomyiidae) emergence. Environ Entomol 11: 946–948.

Franzmann, B.A., 1993. Ovipositional antixenosis to *Contarinia sorghicola* (Coquillett) (Diptera: Cecidomyiidae) in grain sorghum. J Aust Ent Soc 32: 59–64.

Harris, K.M., 1976. The sorghum midge. Ann Appl Biol 64: 114–118.

Johnson, J.W., D.T. Rosenow & G.L. Teetes, 1973. Resistance to the sorghum midge in converted sorghum cultivars. Crop Sci 13: 754–755.

Jotwani, M.G., 1978. Investigations on insect pests of sorghum and millets with special reference to host plant resistance. Final Technical Report. Bulletin of Research. Indian Agricultural Research Institute, New Delhi, India. 114 pp.

Khan, Z.R., D.M. Norris, H.S. Chaing & A.S. Oosterwyk, 1986. Light induced susceptibility in soybean to cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae). Environ Entomol 15: 803–808.

Kogan, M., 1975. Plant resistance in pest management. In: R.L. Metcalf & W.H. Luckmann (Eds), Introduction to Insect Pest Management, pp. 103–146. John Wiley and Sons, New York, USA.

McMurtry, J.A., 1962. Resistance of alfalfa to spotted alfalfa aphid in relation to environmental factors. Hilgardia 32: 501–539.

Page, F.D., 1979. Resistance to sorghum midge (*Contarinia sorghicola* Coquillett) in grain sorghum. Aus J Exp Agric Anim Husb 19: 97–101.

Pathak, M.D., 1970. Genetics of plants in pest management. In: R.L. Rabb & F.E. Guthrie (Eds), Concepts of Pest Management, pp. 138–157. North Carolina State University, Raleigh, USA.

Peterson, G.C., J.W. Johnson, G.L. Teetes & D.T. Rosenow, 1985. Registration of midge resistant sorghum germplasm. Crop Sci 25: 372.

Price, M.L., A.M. Stremberg & L.G. Butler, 1979. Tannin content as a function of grain maturity and drying conditions, in several varieties of *Sorghum bicolor* (L.) Moench. J Agric Fd Chem 27: 1270–1274.

Rossetto, C.J., N.V. Banzatto, J.F.M. Lara & J.L. Overman, 1975. AF 28, a *Sorghum bicolor* variety resistant to sorghum midge, *Contarinia sorghicola*. Sorghum Newsl 18: 5.

Rossetto, C.J., G. Nagai & J.L. Overman, 1984. Mechanisms of resistance in sorghum variety AF 28 to *Contarinia sorghicola* (Diptera: Cecidomyiidae). J Econ Entomol 77: 1439–1440.

Schwiessing, F.C. & G. Wilde, 1978. Temperature influence on greenbug resistance of crops in the seedling stage. Environ Entomol 7: 831–834.

Schwiessing, F.C. & G. Wilde, 1979. Temperature and plant nutrient effects on resistance of seedling sorghum to the greenbug. J Econ Entomol 72: 20–23.

Sharma, H.C., 1985. Screening for sorghum midge resistance and resistance mechanisms. In: Proceedings, International Sorghum Entomology Workshop, 15–21 July 1984, pp. 275–292. College Station, Texas, USA. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India.

Sharma, H.C., 1993. Host-plant resistance to insects in sorghum and its role in integrated pest management. Crop Prot 12: 11–34.

Sharma, H.C., B.L. Agrawal, P. Vidyasagar, C.V. Abraham & K.F. Nwanze, 1993a. Identification and utilization of resistance to sorghum midge, *Contarinia sorghicola* (Coquillett), in India. Crop Prot 12: 343–351.

Sharma, H.C., S.Z. Mukuru, K.V. Hari Prasad, E. Manyasa & S. Pande, 1999. Identification of stable sources of resistance in sorghum to midge and their reaction to leaf diseases. Crop Prot 18: 29–37.

Sharma, H.C., S.L. Taneja, K. Leuschner & K.F. Nwanze, 1992. Techniques to screen sorghums for resistance to insects. Information Bulletin No. 32. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India. 48 pp.

Sharma, H.C. & G. Venkateswarulu, 1999. Effect of environmental factors on expression of resistance to sorghum midge, *Stenodiplosis sorghicola*. Ann Appl Biol (submitted).

Sharma, H.C. & P. Vidyasagar, 1994. Antixenosis component of resistance to sorghum midge, *Contarinia sorghicola* Coq. in *Sorghum bicolor* (L.) Moench. Ann Appl Biol 124: 495–507.

Sharma, H.C., P. Vidyasagar & K. Leuschner, 1990a. Components of resistance to the sorghum midge, *Contarinia sorghicola* Coq. Ann Appl Biol 116: 327–333.

Sharma, H.C., P. Vidyasagar & V. Subramanian, 1993b. Antibiosis component of resistance in sorghum to midge, *Contarinia sorghicola*. Ann Appl Biol 123: 469–483.

Sharma, H.C., P. Vidyasagar & K. Leuschner, 1988. No-choice cage technique to screen for resistance to sorghum midge (Cecidomyiidae: Diptera). J Econ Entomol 81: 415–422.

Sharma, H.C., P. Vidyasagar & K. Leuschner, 1990b. Componential analysis of the factors associated with resistance to sorghum midge, *Contarinia sorghicola* Coq. Insect Sci Appl 11: 889–898.

Shyamsunder, J., R. Parameshwarappa, H.K. Nagaraja & N.B. Kajjari, 1975. A new genotype in sorghum resistant to midge (*Contarinia sorghicola*). Sorghum Newsl 18: 33.

Tingey, W.M. & S.R. Singh, 1980. Environmental factors affecting the magnitude and expression of resistance. In: F.G. Maxwell & P.R. Jenkins (Eds), Breeding Plants Resistant to Insects, pp. 87–113. John Wiley and Sons, New York, USA.

Waquil, J.M., G.L. Teetes & G.C. Peterson, 1986a. Sorghum midge (Diptera: Cecidomyiidae) adult ovipositional behavior on resistant and susceptible sorghum hybrids. J Econ Entomol 79: 530–532.

Waquil, J.M., G.L. Teetes & G.C. Peterson, 1986b. Comparison of immature sorghum midge (Diptera: Cecidomyiidae) development on resistant and susceptible sorghums. J Econ Entomol 79: 833–837.

Wiseman, B.R., W.W. McMillian & N.W. Widstrom, 1973. Registration of S-GIRL-MR-1 sorghum germplasm. Crop Sci 13: 398.