Euphytica **130:** 365–375, 2003.

Environmental factors influence the expression of resistance to sorghum midge, *Stenodiplosis sorghicola*

H.C. Sharma*, G. Venkateswarulu & Anuj Sharma
*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502 324, India; (*author for correspondence; e-mail: H.Sharma@cgiar.org)*

Received 15 May 2002; accepted 14 November 2002

Key words: environmental factors, plant resistance, *Stenodiplosis sorghicola*, sorghum midge, *Sorghum bicolor*

Summary

Host plant resistance is an effective means of controlling sorghum midge (*Stenodiplosis sorghicola*). We studied the influence of environmental factors on expression of resistance to sorghum midge in three midge-resistant and two midge-susceptible genotypes. Midge-resistant lines AF 28, ICSV 197, and TAM 2566 suffered 8.8 to 17.3% damage across seven sowings compared to 25.6% damage in ICSV 112, and 69.4% damage in CSH 5. Susceptibility of the midge-resistant lines (AF 28, ICSV 197, and TAM 2566) decreased with an increase in open pan evaporation, maximum and minimum temperatures, and solar radiation; while the midge-susceptible lines (ICSV 112 and CSH 5) showed a poor interaction with these factors. Midge damage in ICSV 197 showed a negative correlation with minimum temperature and relative humidity and positive correlation with sunshine hours, while the reverse was true for CSH 5. Grain growth rate between 0 and 3 days after anthesis was lower in crops sown on 1st October, when AF 28 and ICSV 197 suffered maximum midge damage. Maximum and minimum temperatures and maximum relative humidity influenced the moisture content of the grain, grain growth rate, and sorghum midge damage. There was considerable variation in genotype $\times$ environment interaction for expression of resistance to sorghum midge, and the implications of these results have been discussed in relation to development of sorghum cultivars with resistance to this insect.

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, due partly to insect pest damage. Nearly 150 species of insects damage the sorghum crop, of which sorghum midge [(*Stenodiplosis sorghicola* (Coquillett)] (Diptera: Cecidomyiidae) is the most important pest worldwide (Harris, 1976). Several genotypes with resistance to sorghum midge have been identified (Johnson et al., 1973; Wiseman et al., 1973; Rossetto et al., 1975; Shyamsunder et al., 1975; Page, 1979; Peterson et al., 1985; Sharma et al., 1993a). However, some of the sources of resistance to sorghum midge have shown a susceptible reaction near the equator at Alupe, Kenya (Sharma et al., 1999a,b), and there are possibilities of environment-induced breakdown of resistance mechanisms or occurrence of different biotypes of sorghum midge in different geographical regions.

Oviposition nonpreference (Rossetto et al., 1984; Waquil et al., 1986a; Sharma et al., 1990b; Franzmann, 1993), antixenosis to visiting adults (Wiseman & McMillian, 1968; Sharma et al., 1990a; Sharma & Vidyasagar, 1994), and antibiosis (Waquil et al., 1986b; Sharma et al., 1993b) contribute to sorghum midge resistance in sorghum. Short, tight, and hard glumes, tannin content of grain, and faster rate of grain development are associated with resistance to sorghum midge (Sharma et al., 1990a, 1996). Tannin content of sorghum grain and rate of grain development vary across environments (Sharma et al., 1993b), and thus, may influence the expression of resistance to sorghum midge. Therefore, we studied the expression of resistance to sorghum midge involving three midge-resistant and two midge-susceptible genotypes for three years over seven sowings at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India.

Materials and methods

Crop

Three sorghum midge-resistant [AF 28 – a sorghum midge-resistant line originating from Africa (Rossetto et al., 1975), TAM 2566 – a midge-resistant line from the sorghum conversion program, Texas, USA (Johnson et al., 1973), and ICSV 197 – a midge-resistant variety developed at ICRISAT, India (Sharma et al., 1993a)], and two midge-susceptible cultivars (CSH 5 and ICSV 112) were evaluated for resistance to sorghum midge between 1991 and 1993. There were seven sowings at monthly intervals between 1st July (beginning of the rainy season) and 1st January. No sowings were undertaken between 1st February to 1st June because there is no sorghum midge during May to July, when the crop sown during this period reached the flowering stage. The five test genotypes were planted in a randomized complete block design (in each sowing), and there were three replications. Each entry was planted in a four-row plot, 4 m long. The rows were spaced 75 cm apart, and the plants were thinned to a spacing of 10 cm within the row at 15 days after seedling emergence. Recommended agronomic practices were followed for growing 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.

Screening for resistance to sorghum midge

A no-choice headcage screening technique (Sharma et al., 1988) was used to evaluate resistance to sorghum midge. Panicles were covered with muslin cloth bags at emergence from the flag leaf to avoid natural midge infestation. At 50% flowering, the muslin cloth bags were removed from the panicles. The top 25% portion of the panicle (where the spikelets had already flowered) and the bottom spikelets that would not reach the flowering stage in the next 2 days were removed with scissors. A wire-framed cage (20 cm in diameter, and 30 cm long) was tied around the sorghum panicle, and covered with a specially designed blue colored cloth bag (blue color is least attractive to midge females, and they settle readily on the sorghum panicles for oviposition) (Sharma et al., 1988). Sorghum midge females were collected from flowering sorghum panicles using plastic bottle aspirators (200 ml capacity) between 0800 and 1000 h. The midge females were then released inside the wire-framed cages. Each panicle was infested with 40 sorghum midges for two consecutive days (as most of the spikelets retained on the panicle completed flowering in two days). Three panicles were infested in each replication. The cages were removed 15 days after infestation (as most of the midge development is completed within this period), and the infested panicles were covered with muslin cloth bags.

Observations

Data on sorghum midge damage was recorded in a sample of 250 spikelets drawn at random from the three panicles infested in each replication. For this purpose, five primary branches were taken at random from each panicle, and then split into smaller secondary branches, and mixed thoroughly. The secondary branches were picked at random to record sorghum midge damage in a sample of 250 spikelets. The numbers of midge-damaged spikelets were recorded as a percentage of the total number of spikelets examined.

Data were also recorded on fresh grain weight and moisture content (%) at 0, 3, 6, and 9 days after anthesis. For this purpose, three panicles were tagged at random in each replication, and the mid portion of the panicle at flowering was marked with a piece of twine at 50% flowering. One hundred spikelets were drawn at random from the marked portion of the panicles in each replication at 0, 3, 6, and 9 days after flowering. The grains were removed with forceps and immediately placed in glass vials. The fresh weight of the grain was recorded on a Mettler® balance, and the grains were then dried at 80 °C. The weight of the dried grain was recorded after 72 h. Percent moisture content was computed from the fresh and dry weights of the grain for each sample. The grain growth rate (GR) between 0 and 3, 3 and 6, and 6 and 9 days after flowering was calculated as a percentage increase in grain weight per day as a function of the mean grain weight during the observation period (Sharma et al., 1990a). Data on maximum and minimum temperatures (°C), maximum and minimum relative humidity (RH%), open pan evaporation (mm^{-1} day), sunshine hours, and solar radiation (Mj $M^{-2}D^{-1}$, mega joules per m^{-2} per day) for 15 days after flowering for each

Table 1. Mean temperature, relative humidity, open pan evaporation, sunshine hours, and solar radiation during flowering periods of sorghums sown at different dates (ICRISAT Centre, Patancheru, India 1991–93)

Date of planting	Date of flowering	Temperature (°C) Max	Min	Relative humidity (%) Max	Min	OPE[a] (mm)	Sunshine (h)	Solar radiation[b] (Mj/m^{-2}/D)
1 July	10–25 September	30.4	21.8	91.5	59.3	75.8	6.1	18.6
1 August	02–27 October	30.6	21.1	90.4	53.4	75.6	7.1	17.5
1 September	04–23 November	28.4	17.6	89.3	49.5	74.3	7.0	15.4
1 October	03–24 December	26.8	11.7	92.3	38.8	64.2	8.3	16.4
1 November	12–27 January	29.8	13.8	89.8	30.0	86.3	9.3	18.0
1 December	15 February–5 March	32.3	19.6	70.7	23.8	120.5	9.9	21.3
1 January	8 March–1 April	37.0	20.0	64.7	20.5	145.9	9.4	21.6

[a] = OPE = Open pan evaporation (mm per day).
[b] = Solar radiation = Mega joules m^{-2} per day.

sowing were recorded at the meteorological observatory at ICRISAT, Patancheru, Andhra Pradesh, India (Table 1).

Statistical analysis

The data were subjected to analysis of variance. The significance of differences between genotypes and sowing dates for midge damage, moisture content, fresh grain weight, and grain growth rates were determined by F-test, and the treatment means were compared by least significance difference (LSD) at p = 0.05. Data on midge damage, moisture content, fresh grain weight, and grain growth rates were subjected to correlation and regression analysis to determinate the association between these parameters. Data on sorghum midge damage and the grain parameters studied were also subjected to correlation and regression analysis in relation to maximum and minimum temperatures, relative humidity, open pan evaporation, sunshine hours, and solar radiation during flowering and grain development (mean of 15 days after flowering when midge oviposition and development occurs inside the spikelets) to understand the interaction of environmental factors with expression of resistance to sorghum midge. Multiple and stepwise regression of the environmental factors [maximum (Tmax) and minimum (Tmin) temperatures, maximum (RHmax) and minimum (RHmin) relative humidity, sunshine hours, and solar radiation (SR)] fresh grain weight, grain growth rates, moisture content of the grain, and midge damage was also carried out to determine the relationship between the environmental parameters and the expression of resistance to sorghum midge (SAS, 1995).

Results

Variation in environmental conditions and expression of resistance to sorghum midge across sowings

There was considerable variation in temperature, relative humidity, open pan evaporation, sunshine hours, and solar radiation during flowering periods of the sorghums sown at monthly intervals (Table 1). Maximum and minimum temperatures during the flowering period were lowest (26.8 and 11.7 °C, respectively) for the crop sown on 1st October. Maximum temperature (37 °C) and open pan evaporation during flowering and grain development were recorded for the crop sown on 1st January, whereas the reverse was true for maximum relative humidity. Minimum relative humidity ranged from 59.3% for the crop sown on 1st July to 20.5% for the crop sown on 1st January. Sunshine hours ranged from 6.1 to 9.9 hours, while solar radiation ranged from 15.4 to 21.6 Mj M^{-2}D^{-1}.

Sorghum midge damage (means across genotypes) ranged from 20.4% in the crop sown on 1st January to 31.9% in the crop planted on 1st August. Sorghum midge-resistant lines AF 28, ICSV 197, and TAM 2566 suffered 8.8–17.3% damage across sowing dates compared with 25.6% damage in ICSV 112 and 69.4% in CSH 5 – the susceptible checks (Table 2). Sorghum midge damage was generally lower in the crop planted on 1st July, 1st December, and 1st January than in the crop planted at other times. AF 28 and ICSV 197, and TAM 2566 suffered greater midge damage in the crop sown on 1st October and 1st November, respectively while ICSV 112 and CSH 5 suffered maximum midge damage in the crop planted on 1st August. Genotypes showing resistant reactions (AF 28, ICSV

Table 2. Percentage midge damage in five sorghum genotypes over seven sowings (ICRISAT Centre, Patancheru, India 1991–93)

Planting date	Genotypes and reaction					Mean
	AF 28 R	TAM 2566 R	ICSV 197 R	ICSV 112 S	CSH 5 S	
1 July	5.28	15.01	3.95	12.31	79.17	23.1
1 August	8.37	16.82	4.50	45.60	84.14	31.9
1 September	10.88	23.50	4.93	17.32	82.78	27.9
1 October	15.57	13.13	20.92	32.77	59.12	28.3
1 November	9.04	24.17	12.12	29.21	63.41	27.6
1 December	8.99	18.88	10.31	23.86	53.39	23.1
1 January	3.11	9.91	6.93	18.29	63.74	20.4
Mean	8.8	17.3	9.1	25.6	69.4	26.0
SE for comparing sowing dates (SD):			± 1.71*			
SE for comparing genotypes (G):			± 1.32**			
SE for comparing sowing SD × G:			± 3.56*			
Except when comparing G at the same SD:			± 3.49*			

*,** F-test significant at $p = 0.05$ and 0.01, respectively. R = Resistant, and S = Susceptible.

Table 3. Moisture content (%) of grain (means across seven sowings) in five sorghum genotypes at four growth stages after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Genotype	Days after anthesis			
	0 day	3 days	6 days	9 days
AF 28 – R	75.38	78.60	76.00	72.44
ICSV 197 – R	73.94	79.55	77.99	72.89
TAM 2566 – R	77.83	81.50	79.86	76.90
CSH 5 – S	79.87	81.44	80.16	75.27
ICSV 112 – S	78.04	79.53	78.38	73.33
Mean	77.01	80.12	78.48	74.17
SE	± 0.438*	± 0.314**	± 0.215**	± 0.308**

*, ** = F-test significant at $p = 0.05$ and 0.01, respectively. R = Resistant, and S = Susceptible.

Table 4. Moisture content (%) of grain (means for five sorghum genotypes) across seven sowings at four intervals after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Sowing date	Days after anthesis			
	0 day	3 days	6 days	9 days
1 July	77.48	79.42	77.08	70.79
1 August	77.91	80.56	78.32	72.96
1 September	78.30	80.42	79.35	76.65
1 October	78.52	81.35	80.58	80.55
1 November	74.07	80.50	80.04	76.84
1 December	76.63	80.11	78.67	73.79
1 January	76.17	78.51	75.32	67.59
Mean	77.01	80.12	78.48	74.17
SE	±0.576*	±0.387**	±0.171**	±0.293**

*, ** = F-test significant at $p = 0.05$ and 0.01, respectively.

197, and TAM 2566) suffered greater sorghum midge damage during periods of low maximum and minimum temperatures, low open pan evaporation, and high maximum relative humidity compared with the susceptible genotypes (CSH 5 and ICSV 112).

Variation in moisture content of grain in different genotypes at different intervals after anthesis

Differences in the moisture content of grain in different genotypes were statistically significant (df = 4, F-test significant at $p = 0.01$). Moisture contents of the grain at 0, 3, 6, and 9 days after anthesis were 77.01, 80.12, 78.48, and 74.17%, respectively. Moisture content of 0 day grain was numerically lower in the midge-resistant genotypes AF 28, TAM 2566, and ICSV 197 than in the midge-susceptible genotypes ICSV 112 and CSH 5 (Table 3). Moisture content of the 3 day grain ranged from 78.60% in AF 28 to 81.50% in TAM 2566, and that of the 9 day grain ranged from 72.44% in AF 28 to 76.90% in TAM 2566. Moisture content of the grain was generally greater in crops sown on 1st September and 1st October, and least in the crop sown on 1st December and 1st January, though the differences across sowing dates were not large (df = 6, F-test significant at

Table 5. Fresh grain weight (mg per 100 grains) (means across seven sowings) in five sorghum genotypes at four growth stages after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Genotype	Days after anthesis			
	0 day	3 days	6 days	9 days
AF 28 – R	30.7	385.4	760.5	1196
ICSV 197 – R	48.4	336.3	812.9	1423
TAM 2566 – R	45.4	339.0	786.6	1392
CSH 5 – S	40.1	380.2	813.9	1407
ICSV 112 – S	32.5	273.5	664.2	1141
Mean	39.4	342.9	767.9	1312
SE	±7.1	±10.1**	±13.5**	±2401**

** = F-test significant at $p < 0.01$. R = Resistant, and S = Susceptible.

Table 6. Fresh grain weight (mg per 100 grains) (means for five sorghum genotypes) across seven sowings at four growth stages after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Sowing date	Days after anthesis			
	0 day	3 days	6 days	9 days
1 July	35.6	388.9	847.3	1421
1 August	36.3	391.5	849.2	1481
1 September	35.4	339.0	734.3	1271
1 October	38.7	228.2	516.3	967
1 November	44.0	265.3	676.0	1108
1 December	33.6	350.8	765.2	1287
1 January	52.3	436.5	985.0	1649
Mean	39.4	342.9	767.6	1312
SE	±7.3	±11.9**	±16.3*	28.4**

** = F-test significant at $p < 0.01$.

Table 7. Grain growth rates (%) on fresh weight basis of five sorghum genotypes (means across seven plantings) at three growth intervals after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Genotype	Days after anthesis		
	0–3	3–6	6–9
AF 28 – R	56.29	29.96	14.69
ICSV 197 – R	54.56	28.37	17.79
TAM 2566 – R	53.41	25.03	17.79
ICSV 112 – S	52.66	28.46	18.00
CSH 5 – S	51.63	26.55	18.93
Mean	53.71	26.08	17.44
SE	±0.004**	±0.007**	±0.006**

** = F-test significant at $p < 0.01$. R = Resistant, and S = Susceptible.

Table 8. Grain growth rates (%) on fresh weight basis (means for five sorghum genotypes) across seven sowings at three intervals after anthesis (ICRISAT Centre, Patancheru, India 1991–93)

Planting date	Days after anthesis		
	0–3	3–6	6–9
1 July	56.47	24.79	16.71
1 August	55.67	25.04	17.76
1 September	52.94	25.06	17.74
1 October	45.95	26.88	19.95
1 November	51.69	29.89	15.82
1 December	55.04	25.16	17.36
1 January	58.21	25.76	16.74
Mean	53.71	26.08	17.44
SE	±0.004**	±0.009**	±0.006**

** = F-test significant at $p = 0.01$.

$p = 0.01$) (Table 4). At 3 days after anthesis, moisture content of grain ranged from 78.51% in the sorghums sown on 1st January to 81.35% in the crop sown on 1st August. Moisture content of the 6 day grain ranged from 75.32% in the crop sown on 1st January to 80.58% in the crop sown on 1st October, and that of 9 day grain ranged from 67.59% in the crop sown on 1st January to 80.55% in the crop sown on 1st October.

Variation in fresh grain weight in different genotypes at different intervals after anthesis

There were significant differences in fresh grain weight amongst the genotypes tested (df = 4, *F*-test significant at $p = 0.01$) at 3, 6, and 9 days after anthesis (Table 5). Grain weight at the time of anthesis (0 day) was greater (45.4 to 48.4 mg per 100 grains) in ICSV 197 and TAM 2566 compared to ICSV 112 (32.5 mg per 100 grains). Fresh grain weights at 3, 6, and 9 days after anthesis were greater in ICSV 197, TAM 2566, AF 28, and CSH 5 compared to ICSV 112. There were significant differences in fresh grain weight across sowing dates (df = 6, *F*-test significant at $p = 0.01$) at 3, 6, and 9 days after anthesis (Table 6). At anthesis (0 day), fresh grain weight was greater in crops sown on 1st November and 1st January than those sown at other times. At 3, 6, and 9 days after anthesis, fresh weights were greater in crops sown on 1 July, 1 August, and 1 January than the crops sown on 1 October and 1 November.

Variation in grain growth rates (GR) in different genotypes at different intervals after anthesis

Grain GR between 0 and 3 days after anthesis in the midge-resistant genotypes AF 28, ICSV 197 and TAM 2566 was greater (53.41 to 56.29%) than in the midge-susceptible lines ICSV 112 and CSH 5 (51.63 to 52.66%), while the reverse was true for grain GR between 3 and 6, and 6 and 9 days after anthesis (except in ICSV 197 between 3 and 6 days after anthesis) (Table 7). Grain GR between 3 and 6 days after anthesis ranged from 21.96% in AF 28 to 28.46% in ICSV 112, while between 6 and 9 days after anthesis, the grain GR ranged from 14.69% in AF 28 to 18.93% in CSH 5. Sorghum midge-resistant genotypes showed a lower grain GR between 3 and 6 days after anthesis (21.96% to 25.03%) (except in ICSV 197) than the midge-susceptible genotypes (26.55 to 28.46%). There were significant differences in grain GR based on fresh grain weight across sowing dates (df = 6, F-test significant at $p = 0.01$) and genotypes (df = 4, F-test significant at $p = 0.01$). Mean grain GR between 0 and 3, 3 and 6, and 6 and 9 days after anthesis was 53.71, 26.08, and 17.44%, respectively (Table 8). The crop sown on 1st October showed the lowest grain GR between 0 and 3 days after anthesis (45.95%), while maximum grain GR was observed in the crop planted on 1st January (58.21%). The reverse was true for grain GR between 3 and 6 and 6 and 9 days after anthesis (except for the crop sown on 1st November for 3 and 6 days after anthesis). Between 3 and 6 days after anthesis, GR ranged from 24.79% in the crop planted in 1st July to 29.89% in the crop planted on 1st November. Between 6 and 9 days after anthesis, grain GR varied from 15.82% in the crop planted on 1st November to 19.95% in the crop planted on 1st October.

Association between moisture content of grain, fresh grain weight, grain growth rates, and sorghum midge damage

Moisture contents of the grain at 6 and 9 days after anthesis were negatively associated with fresh (r = –0.30 to –0.69**) weight of the grain at 6 and 9 days after anthesis (*, ** correlation coefficients significant at $p = 0.05$ and 0.01, respectively) (Table 9). Grain GR between 0 to 3 days after anthesis was also negatively associated with the moisture content of the grain (r = –0.37* to –0.82**), but positively associated with grain GR between 6 to 9 days after anthesis (r = 0.32* to 0.46**). Grain GR between 0 to 3 days after anthesis was negatively associated with the grain GR between 3 to 6 and 6 to 9 days after anthesis (r = –0.38* to –0.40*). Fresh grain weights at 3, 6, and 9 days after anthesis were positively associated with the grain GR between 0 and 3 days after anthesis (r = 0.59** to 0.76**), while grain GR between 3 to 6 days was negatively associated with grain weight at 3 days after anthesis (r = –0.65**).

Moisture content of grain at 0, 3, 6, and 9 days after flowering was positively associated with sorghum midge damage (r = 0.23 to 0.57**), indicating that genotypes with succulent grain were more susceptible to damage by the sorghum midge. Grain GR on fresh weight basis between 0 and 3 days after anthesis was negatively associated with sorghum midge damage (r = –0.32*), whereas fresh weight of the 0 day grain was positively associated with midge damage (r = 0.25 to 0.58**). However, there was no association between sorghum midge damage and grain weights at 3, 6, and 9 days after anthesis.

Influence of environmental factors on moisture content of grain, grain weight, and grain growth rates

Moisture contents of the grain at 3, 6, and 9 days after anthesis were negatively associated with maximum and minimum temperatures (r = –0.35* to –0.78**), open pan evaporation (r = –0.36* to –0.60**), and solar radiation (r = –0.36* to –0.64**), while maximum relative humidity showed a positive association (r = 0.32* to 0.54**) (Table 10). Grain GR between 0 to 3 days after anthesis was positively associated with maximum and minimum temperatures (r = 0.71** to 0.76**), maximum relative humidity (r = 0.48**), open pan evaporation (r = 0.54**), and solar radiation (r = 0.56**). However, there was no association between grain GR between 0 and 3 days after anthesis with minimum relative humidity and sunshine hours. Grain GR between 3 to 6, and 6 to 9 days after anthesis showed poor association with the weather parameters. Fresh weight of the grain at 3, 6, and 9 days after anthesis was positively associated with maximum and minimum temperatures (r = 0.60** to 0.76**), open pan evaporation (r = 0.44** to 0.568**), and solar radiation (0.43** to 0.54**). Maximum relative humidity was negatively associated (r = –0.42** to –0.50**) with the grain weights at 3, 6, and 9 days after flowering.

Maximum and minimum temperatures, maximum relative humidity, and solar radiation accounted for 34.5% of the variation in moisture content of the grain at 6 days after anthesis. However, stepwise regres-

Table 9. Correlation coefficients between grain moisture content, grain growth rates and weight, and midge damage (ICRISAT Centre, Patancheru, India 1991–93)

	Moisture content (%)				GRF			FWT			
	M 0	M 3	M 6	M 9	0–3	3–6	6–9	0	3	6	9
M 0	1.00										
M 3	0.40*	1.00									
M 6	0.43**	0.75**	1.00								
M 9	0.28	0.70**	0.81**	1.00							
GR 0–3	–0.37*	–0.55**	–0.71**	–0.82**	1.00						
GR 3–6	–0.15	0.05	0.18	0.20	–0.38*	1.00					
GR 6–9	0.45**	0.41*	0.46**	0.32*	–0.40*	–0.07	1.00				
FWT 0	0.25	–0.02	0.08	0.01	–0.03	0.30	0.04	1.00			
FWT 3	0.16	–0.25	–0.46**	–0.63**	0.76**	–0.65**	–0.19	0.06	1.00		
FWT 6	0.12	–0.27	–0.50**	–0.69**	0.73**	–0.18	–0.30	0.35*	0.85**	1.00	
FWT 9	0.30	–0.10	–0.30	–0.57**	0.59**	–0.22	0.13	0.35*	0.81**	0.90**	1.00
MD (%)	0.57**	0.46**	0.48**	0.23	–0.32	0.14	0.29	0.25	–0.03	0.09	0.20

M 0, M 3, M 6, and M 9 = Moisture content of grain at 0, 3, 6, and 9 days after anthesis. GRF = Grain growth rate based on fresh grain weight basis between 0–3, 3–6, and 6–9 days after anthesis. MD (%) = Percentage midge damage. FWT = Fresh weight of grain at 0, 3, 6, and 9 days after anthesis. ** = Correlation coefficients significant at $p = 0.05$ and 0.01, respectively.

sion showed that maximum temperature and sunshine hours exercised the maximum influence (44.2%) on moisture content of the grain at 6 days after anthesis. At 9 days after anthesis, maximum and minimum temperature, maximum relative humidity, and solar radiation accounted for 73.5% of the variation in moisture content of the grain, of which maximum temperature and minimum relative humidity showed maximum influence (76.1%) on the moisture content of the grain at 9 days after anthesis.

Maximum and minimum temperatures, maximum relative humidity, and solar radiation accounted for 54.7% of the variation in fresh grain weight at 3 days after anthesis (Table 10). Amongst the environmental factors, minimum temperature and maximum relative humidity accounted for most of the variation (61.2%) in grain weight at 3 days after anthesis. Maximum and minimum temperatures, maximum relative humidity, and solar radiation accounted for 71.8% of the variation in fresh grain weight at 6 days after anthesis, of which minimum temperature and minimum relative humidity exercised the maximum influence (75.8%). Maximum and minimum temperatures, maximum relative humidity, and solar radiation accounted for 58.1% of the variation in fresh grain weight at 9 days after anthesis. Stepwise regression analysis showed that minimum temperature and minimum relative humidity had the maximum influence (63.6%) on grain weight at 9 days after anthesis. Maximum and minimum temperatures, maximum relative humidity, and solar radiation accounted for 69.5% of the variation in grain GR between 0 to 3 days after anthesis, of which minimum temperature and sunshine hours showed the maximum influence (74.6%) on grain GR between 0 and 3 days after anthesis.

Influence of environmental factors on expression of resistance to sorghum midge

Mean sorghum midge damage across genotypes did not show any association with environmental factors. However, different genotypes showed diverse interactions with environmental factors (Table 11). There was a negative association between sorghum midge damage and minimum temperature in AF 28 (r = –0.43**) and ICSV 197 (r = –0.70**). Midge damage in ICSV 197 was also negatively associated with minimum relative humidity (r = –0.43**), while a positive correlation (r = 0.41*) was observed between midge damage and minimum relative humidity in CSH 5. Sorghum midge damage in ICSV 197 showed a positive correlation with sunshine hours (r = 0.53**), while the reverse was true in case of CSH 5 (r = –0.56**). Only in the case of CSH 5, sorghum midge damage was significantly and negatively correlated with solar radiation.

Moisture content of the grain at 0, 3, and 6 days after anthesis, and grain GR between 0 and 3 days after anthesis explained 32.0% of the total variation in sorghum midge damage (Table 11). Maximum and minimum temperatures, and solar radiation accounted

Table 10. Association of grain weight, moisture content of the grain, and rate of grain development with temperature, relative humidity, open pan evaporation, sunshine hours, and solar radiation (ICRISAT Centre, Patancheru, India 1991–93)

Trait	Temperature (°C)		RH (%)		OPE	Sun-shine	Solar radiation
	Max	Min	Max	Min	(mm)	(h)	(Mj m^{-2}D^{-1})
M 0	–0.22	0.04	0.16	0.27	–0.23	–0.28	–0.25
M 3	–0.43**	–0.35*	0.32*	0.10	–0.36*	–0.03	–0.36*
M 6	–0.59**	–0.53**	0.43**	0.08	–0.46**	0.01	–0.47**
M 9	–0.78**	–0.72**	0.54**	0.10	–0.60**	–0.01	–0.64**
FWT 0	0.23	0.01	–0.17	–0.21	0.21	0.17	0.16
FWT 3	0.60**	0.71**	–0.42**	0.06	0.44**	–0.13	0.43**
FWT 6	0.74**	0.76**	–0.50**	–0.04	0.56**	–0.04	0.54**
FWT 9	0.65**	0.72**	–0.44*	0.01	0.48**	–0.09	0.46**
GR 0–3	0.71**	0.76**	0.48**	–0.02	0.54**	–0.05	0.56**
GR 3–6	–0.08	–0.27	0.09	–0.17	–0.04	0.19	–0.05
GR 6–9	–0.22	–0.16	0.11	0.08	–0.18	–0.07	–0.19

Multiple linear regression analysis
M 6 (Y) = 92.5 **+ 0.31Tmax – 0.24Tmin + 0.004RHmax – 0.05SR (R^2 = 34.5%)
M 9 (Y) = 118.9** + 0.64Tmax – 0.59Tmin* + 0.06RHmax – 0.53SR (R^2 = 73.5%)
GR 0–3 (Y) = 0.318 + 0.002Tmax + 0.008 Tmin** – 0.002Rhmax + 0.004SR (R^2 = 69.5%)
FWT3 (Y) = 0.54 – 0.01Tmax + 0.02Tmin + 0.003RHmax* – 0.001RHmin + 0.002SR (R^2 = 54.7%)
FWT6 (Y) = 0.39 + 0.009Tmax + 0.054Tmin + 0.001RHmax – 0.009RHmin – 0.003SR* (R^2 = 71.8%)
FWT9 (Y) = 0.27 + 0.039Tmax + 0.039Tmin – 0.005RHmax + 0.001RHmin – 0.025SR (R^2 = 58.1%)
Stepwise regression analysis
M6 (Y) = 91.95** – 0.61Tmax** + 0.66SH* (R^2 = 44.2%)
M9 (Y) = 128.0** – 1.55Tmax** – 0.15RHmin** (R^2= 76.1%)
GR 0–3 (Y)=0.19** + 0.012 Tmin** + 0.016SH** (R^2 = 74.6%)
FWT3 (Y) 0.28** + 0.016Tmin** – 0.0027RHmax** (R^2 = 61.2%)
FWT6 (Y) = 0.23** + 0.043Tmin** – 0.0054RHmin** (R^2 = 75.8%)
FWT9 (Y) = 0.45** + 0.066Tmin** – 0.0074RHmin** (R^2 = 63.6%)

OPE = Open pan evaporation. M O, M 3, M 6, M 9 = Moisture content (%) at 0, 3, 6, and 9 days after anthesis. GR = Grain growth rate on fresh weight basis between 0–3, 3–6, and 6–9 days after anthesis. FWT = Fresh grain weight at 0, 3, 6, and 9 days after anthesis. Tmax = Maximum temperature, Tmin = Minimum temperature, RHmax = Maximum relative humidity, RHmin = Minimum relative humidity, SR – Solar radiation, SH = Sunshine hours, and OPE = Open pan evaporation. R^2 = Coefficient of determination. *, ** = Correlation / regression coefficients significant at $p = 0.05$ and 0.01, respectively.

for 2.5, 37.7, and 36.8% of the variation in sorghum midge damage in AF 28, ICSV 197, and CSH 5, respectively. Stepwise regression analysis showed that minimum temperature exercised maximum influence on sorghum midge damage in AF 28 and ICSV 197, while sunshine hours had the maximum influence on midge damage in CSH 5. The reaction of AF 28 was stable across environments, while the reaction of ICSV 197 (resistant) and CSH 5 (susceptible) was unstable across environments.

Discussion

Sorghum genotype, AF 28 was found to be stable in its expression of resistance to sorghum midge, while the reactions of ICSV 197 and TAM 2566 were unstable across sowing dates. Earlier studies have shown that there are significant differences in the expression of resistance to sorghum midge across seasons and locations (Sharma et al., 1999a). TAM 2566, DJ 6514, and IS 12666C (Sharma et al., 1988) and AF 28 have been reported to be stable across sowing dates (Faris et al., 1979). Genotypes with succulent grain were more susceptible to sorghum midge, and moisture content of the grain was negatively associated with grain growth rates. Sorghum midge-resistant genotypes AF 28, ICSV 197, and TAM 2566 showed a higher grain GR than the midge-susceptible genotypes ICSV 112 and CSH 5 between 0 and 3 days after anthesis, and this has earlier been reported to be one of the components of resistance to sorghum midge (Sharma et

Table 11. Association of climatic factors with percentage midge damage (MD) in five sorghum genotypes (ICRISAT Centre, Patancheru India 1991–93)

Genotype	OPE (mm)	Temperature (°C) Max	Temperature (°C) Min	Relative humidity (%) Max	Relative humidity (%) Min	Sunshine (h)	Solar radiation ($Mj/m^{-2}/D$)
AF 28	–0.24	–0.39*	–0.43*	0.19	–0.06	0.08	–0.31
TAM 2566	–0.13	–0.23	–0.19	0.02	0.06	0.00	–0.32*
ICSV 197	0.03	–0.19	–0.70**	–0.02	–0.43*	0.53**	0.08
ICSV 112	–0.09	–0.06	–0.10	0.10	–0.07	0.25	0.02
CSH 5	–0.27	–0.10	0.38*	0.29	0.41*	–0.56**	–0.45*
Mean (across genotypes)	–0.07	–0.03	0.07	0.03	–0.07	–0.02	–0.09

Multiple linear regression equations
MD mean (Y) = 592.0* +3.4M0** +2.27M3 + 2.04M6 + 23.9 GRD (R^2= 32.0%)
MD AF 28 (Y) = 22.0* + 0.11Tmax + 0.42Tmin – 0.51SR (R^2 = 2.5%)
MD ICSV 197 (Y) = 18.2 + 0.10Tmax – 0.91Tmin* + 0.47SR (R^2 = 37.7%)
MD CSH 5 (Y) = 67.7 + 4.05Tmax + 0.55Tmin + 7.26SR* (R^2 = 36.8%)].
Stepwise regression analysis
MD AF 28 (Y) = 15.97** – 0.43Tmin (R^2 = 18.5%)
MD ICSV 197 (Y) = 23.77** – 0.91Tmin** (R^2 = 48.9%)
MD CSH 5 (Y) = 111.0** – 5.34SH* (R^2 = 31.2%)].

OPE = Open pan evaporation. MD = Midge damage (%), M = Moisture content of grain, GRD = Grain growth rate, Tmax = Maximum temperature, Tmin = Minimum temperature, SR = Solar radiation. R^2 = Coefficient of determination. *, ** = Correlation / regression coefficients significant at p = 0.05 and 0.01, respectively.

al., 1990a). Grain GR between 0 and 3 days after anthesis was lowest in the crop sown on 1st October (the sowing in which the midge-resistant lines suffered maximum midge damage) than in the crop sown at other times. However, the reverse was true for grain GR between 3 and 6 and 6 and 9 days after anthesis (except in ICSV 197).

Influence of environmental conditions on expression of resistance to sorghum midge was least in case of AF 28, while ICSV 197 (midge-resistant) and CSH 5 (midge-susceptible) were similar in their interaction with environmental factors. Greater interaction of ICSV 197 with environmental conditions may be one of the factors for the breakdown of resistance to sorghum midge in this genotype in Kenya (Sharma et al., 1999a,b). Minimum temperature and maximum relative humidity accounted for maximum variation in grain weights at 3, 6 and 9 days after anthesis. Minimum temperature and sunshine hours influenced the grain GR between 0 to 3 days after anthesis (which is associated negatively with sorghum midge damage), which in turn possibly influenced the expression of resistance to sorghum midge across sowing dates.

Temperature and photoperiod influence the growth (Sharma et al., 1999b) and chemical composition of sorghum grain (Butler, 1982; Price et al., 1978, 1979) (in addition to genetic and edaphic factors), which in turn may affect the expression of resistance to sorghum midge (Sharma et al., 1999b). Variations in temperature can induce changes in physico-chemical defenses of the plant, and affect the level of genotypic resistance to insects (Kogan, 1975) through a change in the nutritional quality of the grain (Sharma et al., 1993b). Temperature not only affects plant growth and the extent of insect damage, but also influences the growth and development of insects (Tingey & Singh, 1980), which in turn can influence the insect behaviour and their ability to cause damage. In general, temperature has a significant effect on the expression of resistance to insects. Differences in susceptibility to greenbug, *Schizaphis graminum* Rondani in sorghum genotypes increase with an increase in temperature (Schweissing & Wilde, 1978). In alfalfa, the resistance levels are greater at higher temperatures (Kogan, 1975). In the present studies, sorghum midge-resistant genotypes suffered greater damage at lower temperatures (except TAM 2566). Photoperiod, which varies across seasons and locations, influences both plant growth and insect behaviour. Intensity and quality of light influences the biosynthesis of phenyl-propanoids

(Hahlbrock & Grisebach, 1979), and anthocyanins (Carew & Krueger, 1976). Continuous high intensity light decreases levels of resistance to cabbage looper, *Trichoplusia ni* (Walker), by influencing the flavonoid composition of soybean leaves (Khan et al., 1986). Interaction of sorghum genotypes with sunshine hours and solar radiation may be one of the factors influencing the expression of resistance to sorghum midge.

Sorghum midge-resistant lines suffered maximum damage in the crop planted on 1 October (when grain GR was lowest due to low temperatures), while the reverse was true for the midge-susceptible lines. Genotypes with succulent grain were more susceptible to sorghum midge, and moisture content of the grain was negatively associated with grain growth, which is one of the factors associated with resistance to sorghum midge. Grain mass, moisture content of the grain, and grain GR were influenced by temperature, relative humidity, solar radiation, and sunshine hours; and these interactions in turn influenced the expression of resistance to sorghum midge. The interactions of the midge-resistant genotypes (AF 28, ICSV 197, and TAM 2566) with the environmental factors were quite diverse, and hence, there is a distinct possibility of increasing the levels, and diversifying the basis, of resistance to midge in sorghum improvement programs.

Acknowledgements

We thank D. Krishna and V.V. Rao for their help in carrying out these experiments. Approved as JA no. 2319 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India.

References

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

Carew, D.P. & J. Krueger, 1976. Anthocyanidins of *Catharanthus* callus cultures. Phytochem 15: 442.

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

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

Hahlbrock, K. & H. Grisebach, 1979. Enzymatic controls in the biosynthesis of lignins and flavonoids. Ann Rev Pl Physiol 30: 105–130.

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.

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.

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

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.

Price, M.L., L. van Scoyoc & L.G. Butler, 1978. A critical evaluation of vanillin reaction as an assay in sorghum grain. J Agric Fd Chem 26: 1214–1218.

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*. Sor Newslett 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.

SAS, 1995. The SAS System for Windows, Release 6.12. SAS Institute, Cary, North Carolina, USA.

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

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., K. Leuschner & P. Vidyasagar, 1990a. Factors influencing the oviposition behaviour of the sorghum midge, *Contarinia sorghicola* Coq. Ann Appl Biol 116: 431–439.

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

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., 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, 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., C.V. Abraham, P. Vidyasagar & J.W. Stenhouse, 1996. Gene action for resistance in sorghum to midge, *Contarinia sorghicola*. Crop Sci 36: 259–265.

Sharma, H.C., S.Z. Mukuru, K.V. Hari Prasad, E. Manyasa & S. Pande, 1999a. 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.Z. Mukuru, E. Manyasa & J. Were, 1999b. Breakdown of resistance to sorghum midge, *Stenodiplosis sorghicola*. Euphytica 109: 131–140.

Shyamsunder, J., R. Parameshwarappa, H.K. Nagaraja & N.B. Kajjari, 1975. A new genotype in sorghum resistant to midge (*Contarinia sorghicola*). Sor Newslett 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. 87–103. 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, 1968. Resistance in sorghum to sorghum midge, *Contarinia sorghicola* (Coquillett) (Diptera: Cecidomyiidae). J Ent Soc Ga 3: 147.

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