



Flowering events in sorghum in relation to expression of resistance to sorghum midge, *Stenodiplosis sorghicola*

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Summary

Sorghum midge (*Stenodiplosis sorghicola* Coquillett) is an important pest of grain sorghum, and host plant resistance is one of the most effective means of controlling this pest. Several studies have shown that resistance to sorghum midge is associated with short and tight glumes, faster rate of grain development, and tannins. However, some recent studies suggested that time of flowering is the principal component of resistance to sorghum midge. Therefore, we conducted a series of experiments under laboratory and field conditions on the flowering behaviour of a diverse array of midge-resistant and midge-susceptible genotypes to quantify the contribution of time of flowering in genotypic resistance to sorghum midge. Time of flowering under field and laboratory conditions did not show any differences between midge-resistant and midge-susceptible genotypes. Time to maximum flowering varied considerably between the rainy and the post-rainy seasons. Under field conditions, most of the spikelets in the midge-resistant lines opened between 0000 and 0400 h, while most of the spikelets in the susceptible check, CSH 1, opened at 0200 h. Under light and dark conditions in the laboratory, most of the spikelets opened at 0300 h in all genotypes, irrespective of their level of resistance to the sorghum midge. However, flowering events continued for a longer period under dark conditions outside the laboratory. There were no differences in oviposition in panicles on the midge-resistant genotype, ICSV 745, infested between 0200 and 0600 h, and significantly more eggs were laid in spikelets of the susceptible check, CSH 1, than in the midge-resistant, ICSV 745, at all infestation times. The peak oviposition was recorded at 0945 h irrespective of the level of resistance to sorghum midge, and significantly more eggs were laid in the spikelets of CSH 1 and Swarna than in ICSV 745 and ICSV 197. There was no evidence of change in the susceptibility of sorghum midge-resistant genotypes when infested at different times in relation to time of flowering. Therefore, flowering behaviour of sorghum genotypes seems to play little role in genotypic susceptibility to sorghum midge.

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important cereals in the semi-arid tropics (SAT). Nearly 150 species of insects have been recorded as pests of grain sorghum (Sharma, 1993), of which sorghum midge [*Stenodiplosis (Contarinia) sorghicola* Coquillett] (Diptera: Cecidomyiidae) is the most important pest worldwide (Harris, 1976). Host plant resistance is an effective means of keeping the sorghum 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; Sharma et al., 1993a).

Resistance to sorghum midge is associated with short, tight and hard glumes (Rossetto et al., 1984; Sharma et al., 1990), initial faster rate of grain development, and high tannin content of the grain (Sharma

et al., 1990, 1993b). In a recent study, Diarisso et al. (1998) reported that sorghum midge-resistant genotypes tend to flower at night, and their spikelets close by the time sorghum midge females emerge in the morning for oviposition, while flowering in the sorghum midge-susceptible genotypes occurs during the daytime, and hence are amenable for oviposition by the sorghum midge females. Therefore, we conducted a series of experiments to characterize the flowering pattern of known sources of resistance to sorghum midge, study the variation in flowering behaviour across seasons, and quantify the contribution of flowering behaviour to host plant resistance to sorghum midge.

Materials and methods

Crop

Experiments on the flowering pattern of sorghum midge-resistant genotypes and oviposition behaviour of the sorghum midge were conducted during the 1996 and 1997 rainy and post-rainy seasons at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, under laboratory and field conditions. Flowering pattern was studied in a diverse array of sorghum midge-resistant genotypes grown under field conditions during the 1997 rainy, and 1996/97 post-rainy seasons. Twenty-seven genotypes identified as being resistant to sorghum midge (Sharma et al., 1993a), and three susceptible commercial cultivars (Swarna, CSH 1, and CSH 14) were sown in a randomized complete block design. There were three replications. The experiment was sown 30 days later than the normal planting time to maximize infestation by the sorghum midge (i.e., 3rd week of July during the rainy season and 1st week of January during the post-rainy season). Each genotype was sown in a 4-row plot, 2 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 flowering and grain filling stages of the crop.

Infestation

The test material was exposed to natural infestation by the sorghum midge at the flowering stage. To overcome the staggered flowering of sorghum genotypes, and variation in sorghum midge density over time, the test entries were also infested with 40 sorghum midges panicle⁻¹ at flowering using the headcage technique during the 1996/97 post-rainy season (Sharma et al., 1988). The panicles at emergence from the boot-leaf were covered with muslin cloth bags to avoid natural infestation by the sorghum midge. Wire-framed cages were tied around the sorghum panicles at 50% flowering, and covered with blue cloth bags. Sorghum midge females collected in plastic bottle aspirators between 0800 and 1000 h in the field were released inside the cages. Each panicle was infested with 40 sorghum midge females for two consecutive days, and three panicles were infested in each plot. The cages were removed 15 days after infestation to evaluate the sorghum midge damage. The panicles were rated visually for sorghum midge damage on a 1 to 9 scale (1 = <10% spikelets with sorghum 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 sorghum midge damage) both under natural infestation and no-choice headcage screening.

For recording the flowering pattern of different genotypes, three primary rachis branches at 50% flowering were marked with thread at 1600 h. Spikelet opening in the marked rachis branches was observed at one-hour intervals between 0000 and 1100 h. Data were recorded on initiation of flowering (when the first spikelet was completely open), time when maximum numbers of spikelets were completely open, and time when the spikelets closed after flower opening (all the previously open spikelets closed).

Flowering pattern under field and laboratory conditions

Flowering patterns of five sorghum midge-resistant genotypes [AF 28 – a sorghum midge-resistant line from Africa (Rossetto et al., 1975), DJ 6514 – a sorghum midge-resistant genotype from India (Shyamsunder et al., 1975), TAM 2566 – a sorghum midge resistant genotype from the conversion program in the USA (Johnson et al., 1973), ICSV 197 and ICSV 745 – sorghum midge-resistant genotypes derived from DJ 6514 (Sharma et al., 1993a), and a susceptible hybrid (CSH 1) were observed under

field conditions, and under light and dark conditions in the laboratory. Five primary branches at the top-anthesis stage (with 2–3 spikelets at flowering) were retained on each panicle at 1600 h. The rest of the branches were removed with scissors. Observations were recorded on the number of spikelets at flowering at one-hour intervals between 0000 and 0900 h. Number of spikelets at flowering were expressed as a percentage of the total number of spikelets in five branches in each panicle. For studying the flowering behaviour under laboratory conditions, the panicles marked for these studies (as described before) were cut with a sharp knife at 2330 h, and placed in a 100-ml conical flask containing 75-ml water. Cotton wool was wrapped around the peduncles to keep the panicles in an upright position. The panicles were arranged in a randomized complete block design on a table under fluorescent tube lights in the laboratory, and there were three replications. Another set of panicles was kept outside the laboratory under dark conditions. Observations on flowering pattern of these genotypes were recorded at one hour intervals between 0000 and 1000 h, as described above.

Oviposition by sorghum midge females in sorghum panicles infested at different times

To test the hypothesis that resistance to sorghum midge is linked to flowering behaviour of sorghum genotypes, experiments were conducted on oviposition [which is the primary effect of resistance to this insect (Sharma et al., 1990)] by sorghum midge females on midge-resistant and midge-susceptible genotypes infested at different times. Five primary branches at the top-anthesis stage were retained on each panicle at 1600 h in the field [rachis branches at the top-anthesis stage flower completely by the next day – the stage at which the sorghum midge females lay eggs inside the spikelets (Harris, 1976)]. A headcage (Sharma et al., 1988) was placed around each panicle for releasing the sorghum midge females for oviposition. There were three replications for each infestation time for each genotype.

Sorghum midge females emerge in the morning (0600 to 0900 h), mate near the site of emergence, move to flowering sorghum panicles for egg laying between 0700 and 1400 h, and then die (Harris, 1976). However, if sorghum midge females do not find a suitable host for oviposition, they survive until the following day. Therefore, to collect sorghum midge females for infestation at different times at night,

sorghum panicles at the milk-stage (from which the sorghum midges were about to emerge) were brought to the laboratory, and placed in 1-L jars containing 500-ml water. Three jars, each containing 10 midge-infested sorghum panicles, were placed inside a cardboard box (60 × 30 × 45 cm). A two litre transparent plastic jar with wire-mesh ventilators (3-cm diameter), two on the sides and one the top, was placed on top of each cardboard box. Ten such boxes were used for obtaining the sorghum midge females for infestation in the field. The sorghum midges upon emergence, moved to the plastic jar because of attraction to light. The insects were allowed to mate inside the plastic jar. One hour before infestation, 10 sorghum midge females were collected in a 200-ml plastic bottle with the help of an aspirator. The bottles containing the sorghum midge females were taken to the field.

Panicles of ICSV 745 and CSH 1 were infested with 10 sorghum midge females at 0200, 0400, 0600, 0800, and 1000 h. There were five replications. Panicles exposed to the sorghum midge females for oviposition at different times were harvested the following day, and stored in a deep freeze. For recording the number of eggs laid on each panicle, the spikelets were dissected under a microscope (40X). Data were recorded on the number of spikelets with eggs, and number of eggs laid; and expressed as a percentage of the total number of spikelets examined on each panicle.

In another experiment, oviposition behaviour of sorghum midge females was observed on two midge-resistant (ICSV 745 and ICSV 197) and two midge-susceptible (Swarna and CSH 1) genotypes. The panicles were infested at 0730, 0845, and 1045 h with 10 sorghum midge females collected from the flowering sorghum panicles with the help of aspirators (Sharma et al., 1988). The other experimental details were similar to those described above. Data were recorded on the number of spikelets with eggs and number of eggs laid per 100 spikelets.

Effect of stage of flowering on oviposition by sorghum midge females

Since oviposition by sorghum midge females is linked to stage of flowering (Sharma et al., 1988), panicles of ICSV 197 (resistant) and CSH 1 (susceptible) were infested with sorghum midge females at the pre-anthesis, half-anthesis, and post-anthesis stages. Five primary branches were retained on each panicle (enclosed in a headcage) at the appropriate stage of

flowering, and each panicle was infested with 10 field-collected sorghum midge females during the morning hours (0830 to 0930 h). The midge infested panicles were harvested the following day, and numbers of spikelets with eggs and the number of eggs per 100 spikelets were recorded as described before.

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 the least significant difference (LSD) at $p = 0.05$. Data on midge damage under natural and headcage conditions were correlated with initiation of flowering, maximum flowering, and flower closing during the rainy and post-rainy seasons to determine the association between flowering events and expression of resistance to sorghum midge.

Results

Flowering pattern of sorghum genotypes in relation to response to sorghum midge

Under natural infestation, 23 sorghum genotypes suffered a damage rating (DR) of <3.0 (20 to 30% midge-damaged spikelets), while four genotypes had a DR of 3.0 to 4.5 as compared to a DR of 6.5 to 8.5 in susceptible checks (Swarna, CSH 1, and CSH 14). Under no-choice headcage screening, 11 genotypes suffered a DR of <3.0 (resistant), and 15 genotypes had a DR of 3.0 to 5.0 (moderately resistant), compared to a DR of 6.1 in Swarna, 7.0 in CSH 1, and 5.0 in CSH 14. Genotypes IS 7005, IS 8721, IS 8887, IS 8891, IS 10712, IS 18563, IS 18698, IS 19512, IS 21881, DJ 6514, and PM 7068B showed high levels of resistance to sorghum midge, both under natural infestation and no-choice headcage screening.

Flowering started between 0000 and 0300 h during the rainy season, and between 0100 and 0600 h during the post-rainy season (Table 1). In 17 genotypes (including the susceptible checks, CSH 1 and Swarna), flowering began between 0000 and 0100 h during the rainy season. In five genotypes, the flowering began between 0100 to 0200 h (including the susceptible check, CSH 14). In eight sorghum midge-resistant genotypes, flowering started between 0200 and 0340 h. During the post-rainy season, flowering started before 0200 h in eight genotypes, including the susceptible check, CSH 14, while in another 16 genotypes,

flowering started between 0300 and 0600 h (including the susceptible checks, CSH 1 and Swarna). Flowering events in midge-resistant and midge-susceptible genotypes differed across seasons. Initiation of flowering was significantly correlated with maximum flowering during the rainy ($r = 0.71^{**}$, correlation coefficient significant at $p = 0.01$) and the post-rainy seasons ($r = 0.42^*$; correlation coefficient significant at $p = 0.05$). However, initiation of flowering was correlated with flower closing during the rainy season ($r = 0.63^{**}$), but not during the post-rainy season ($r = -0.14$). Similarly, maximum flowering was significantly correlated with flower closing during the rainy season ($r = 0.68^{**}$), but not during the post-rainy season ($r = 0.21$).

Peak flowering in eight genotypes was observed between 0140 and 0300 h during the rainy season (including the susceptible checks, Swarna and CSH 1). In 11 genotypes, peak flowering occurred between 0300 and 0600 h, while in the other nine genotypes, the maximum flowering was observed between 0700 and 0800 h (including the susceptible check, CSH 14). During the post-rainy season, the peak flowering occurred by 0300 h in three genotypes, whereas in 10 genotypes, maximum flowering was observed between 0300 and 0600 h. In the remaining 11 genotypes, peak flowering occurred at 0700 h. Spikelets of most of the genotypes had closed by 0800 h (Table 1). Some genotypes behaved differently during the rainy and post-rainy seasons. There was no trend in flowering behaviour of midge-resistant and midge-susceptible genotypes. Midge damage under natural and headcage conditions did not show any association with initiation of flowering ($r = -0.02$ to 0.11), maximum flowering ($r = -0.08$ to 0.12), or flower closing ($r = -0.19$ to 0.24).

During the rainy season, the mean maximum temperature during the flowering period in October was 30.6 °C, and the mean minimum temperature was 19.5 °C, while during the post-rainy season, the maximum temperature during the flowering period in March was 35.2 °C, and the minimum temperature was 18.4 °C. Relative humidity was greater during the flowering period in the rainy season (89.6% maximum, and 53.6% minimum) than in the post-rainy season (77.4% maximum, and 23.8% minimum relative humidity). The mean maximum temperature was lower, and the relative humidity higher during the rainy season compared to the post-rainy season. Initiation of flowering and peak flowering in some genotypes were delayed by a few hours during the post-rainy season, possibly because of the influence

Table 1. Flowering pattern of 30 sorghum genotypes during the rainy and post-rainy seasons (ICRISAT Center, Patancheru, 1996/1997)

| Entry | Initiation of flowering | | Maximum flowering | | Flower closing | | Damage rating ¹ | |
|------------|-------------------------|-------------------|-------------------|-------------------|----------------|-------------------|----------------------------|--------------------|
| | Rainy season | Post-rainy season | Rainy season | Post-rainy season | Rainy season | Post-rainy season | Natural infestation | Headcage screening |
| IS 2579C | 0240 | – | 0800 | – | 0940 | – | 4.50 | 8.30 |
| IS 3461 | 0020 | 0400 | 0140 | 0600 | 0800 | 0800 | 2.00 | 3.15 |
| IS 7005 | 0000 | 0300 | 0200 | 0500 | 0800 | 0800 | 2.15 | 2.55 |
| IS 8100C | 0340 | 0400 | 0700 | 0700 | 0940 | 0800 | 4.35 | 4.70 |
| IS 8721 | 0300 | 0100 | 0700 | 0600 | 1000 | 0700 | 2.00 | 2.50 |
| IS 8887 | 0140 | 0300 | 0500 | 0500 | 0800 | 0800 | 2.35 | 2.35 |
| IS 8891 | 0240 | – | 0530 | – | 0800 | – | 2.85 | 2.25 |
| IS 9807 | 0020 | 0200 | 0140 | 0300 | 0800 | 0800 | 2.35 | 3.30 |
| IS 10712 | 0140 | 0400 | 0440 | 0600 | 0800 | 0800 | 2.15 | 2.15 |
| IS 15107 | 0040 | – | 0340 | – | 0920 | – | 2.35 | 3.85 |
| IS 18563 | 0100 | 0300 | 0340 | 0700 | 0800 | 0800 | 2.00 | 1.65 |
| IS 18698 | 0000 | 0200 | 0140 | 0300 | 0800 | 0800 | 2.15 | 2.80 |
| IS 18733 | 0100 | 0300 | 0700 | 0600 | 0900 | 0800 | 2.00 | 3.85 |
| IS 19476 | 0040 | 0200 | 0240 | 0700 | 0800 | 0800 | 2.00 | 3.10 |
| IS 19512 | 0100 | 0100 | 0220 | 0700 | 0800 | 0800 | 2.35 | 2.75 |
| IS 21871 | 0300 | 0400 | 0700 | 0700 | 1000 | 0800 | 3.00 | 4.65 |
| IS 21879 | 0220 | – | 0540 | – | 0840 | – | 3.80 | 4.65 |
| IS 21881 | 0300 | 0600 | 0800 | 0700 | 1020 | 0800 | 3.00 | 3.00 |
| IS 21883 | 0040 | 0100 | 0220 | 0500 | 0840 | 0800 | 3.80 | 3.55 |
| IS 22806 | 0040 | 0200 | 0220 | 0600 | 0820 | 0800 | 2.00 | 3.15 |
| IS 26789 | 0000 | 0500 | 0700 | 0700 | 0930 | 0800 | 2.15 | 3.35 |
| DJ 6514 | 0020 | 0400 | 0720 | 0500 | 0900 | 0700 | 2.00 | 1.90 |
| TAM 2566 | 0300 | 0400 | 0600 | 0700 | 1100 | 0800 | 2.15 | 3.75 |
| ICSV 197 | 0100 | 0400 | 0500 | 0700 | 0820 | 0800 | 2.00 | 3.20 |
| ICSV 745 | 0120 | 0300 | 0500 | 0700 | 0840 | 0800 | 2.85 | 3.10 |
| PM 7061 B | 0100 | – | 0430 | – | 0800 | – | 2.50 | 4.50 |
| PM 7068 B | 0200 | – | 0600 | – | 0800 | – | 2.35 | 1.75 |
| Swarna (S) | 0000 | 0330 | 0140 | 0700 | 0800 | 0800 | 8.50 | 6.05 |
| CSH 1 (S) | 0030 | 0330 | 0220 | 0300 | 0820 | 0700 | 8.00 | 6.95 |
| CSH 14 (S) | 0200 | 0200 | 0800 | 0500 | 0900 | 0700 | 6.50 | 5.00 |
| Mean | 0126 | 0307 | 0461 | 0588 | 0864 | 0783 | 3.07 | 3.59 |
| SE ± | 0.20 | 0.26 | 0042 | 0028 | 0015 | 0008 | 0.62 | 0.71 |
| LSD at 5% | 0.56 | 0.73 | 0118 | 0079 | 0042 | 0023 | 1.75 | 2.00 |

S = Susceptible check.

1 = Damage rating (1 = <10% spikelets damaged by sorghum midge, and 9 = > 80% spikelets damaged by sorghum midge).

of temperature and relative humidity on flowering behaviour.

Flowering pattern under light and dark conditions in the field/laboratory

Under field conditions, maximum spikelet opening occurred at 0200 h in AF 28, TAM 2566, and CSH 1, and at 0300 h in ICSV 745, and 0400 h in ICSV 197

and DJ 6514 (Figure 1a). Under light conditions in the laboratory, maximum flowering occurred at 0300 h in all genotypes, irrespective of levels of resistance (Figure 1b). Under dark conditions outside the laboratory, maximum flowering was recorded at 0300 h, as was the case with flowering patterns inside the laboratory. However, in DJ 6514 and CSH 1, more spikelets opened between 0300 and 0500 h than in other genotypes (Figure 1c). Flowering continued for a longer

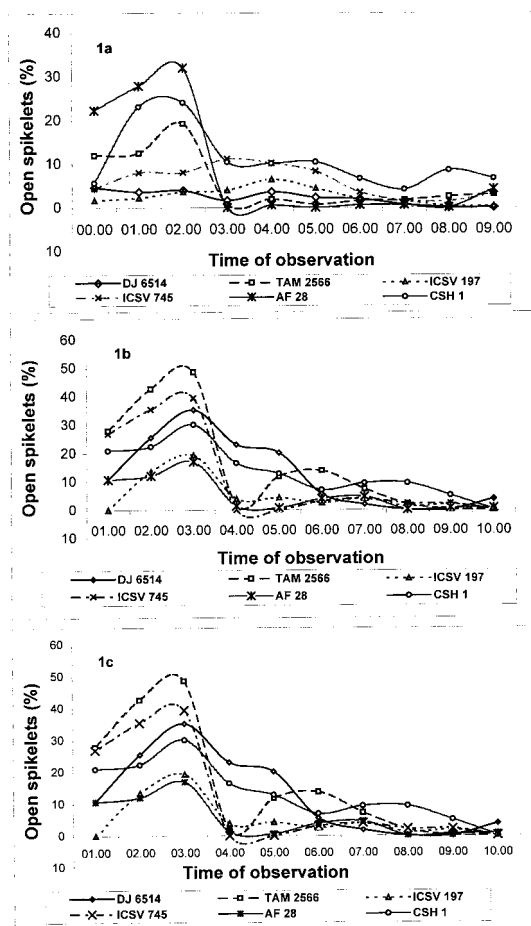


Figure 1. Flowering patterns (percentage of open spikelets) of (a) six sorghum genotypes under field, (b) under tube lights in the laboratory, and (c) under dark conditions outside the laboratory (ICRISAT, 1996/97 post-rainy season).

period under dark conditions outside the laboratory. Flowering continued up to 0500 h in AF 28, 0800 h in DJ 6514, and 0900 h in TAM 2566, ICSV 197, ICSV 745, and CSH 1. As observed under field conditions, there was no trend in the flowering pattern of midge-resistant and the midge-susceptible genotypes under light and dark conditions in the laboratory.

Oviposition by sorghum midge females in panicles infested at different times

Significantly more eggs were laid in spikelets of CSH 1 than those of ICSV 745 at all infestation times (Figures 2a and b). Maximum oviposition was recorded in panicles of CSH 1 infested at 1000 h and at 0800 h in panicles of ICSV 745. Low (CSH 1) or

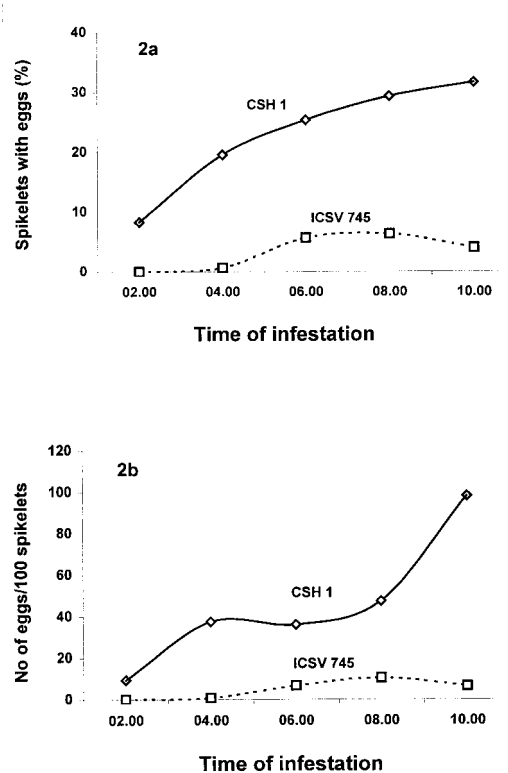


Figure 2. Percentage spikelets with (a) eggs and (b) number of eggs per 100 spikelets in panicles of sorghum midge-resistant (ICSV 745) and midge-susceptible (CSH 1) genotypes infested at different times between 0200 and 1000 h under field conditions (ICRISAT, Patancheru 1996/97 post-rainy season).

no (ICSV 745) oviposition was recorded in the panicles infested between 0200 and 0400 h. There was no evidence of greater oviposition in the panicles of sorghum midge-resistant genotype infested during the early hours.

In experiments conducted with field collected sorghum midge flies, a few eggs were recorded in panicles infested at 0730 h (possibly because of the unmated status of females or low temperatures), and at 1045 h [because of high temperatures and low humidity, which affect the activity and oviposition of sorghum midge (Harris, 1976)] (Figures 3a and b). Maximum oviposition was recorded in panicles of all genotypes infested at 0845 h, and significantly more eggs were laid in spikelets of Swarna and CSH 1 than those of ICSV 745 and ICSV 197. There was no evidence of change in the relative susceptibility of sorghum midge-resistant genotypes at different infestation times. Maximum oviposition was recorded at different times in the two experiments, possibly

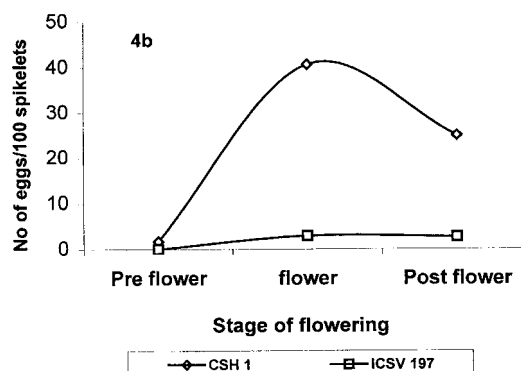
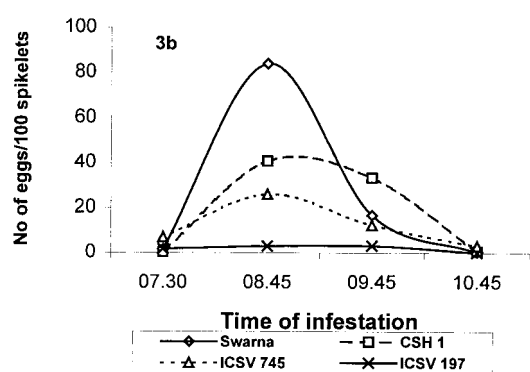
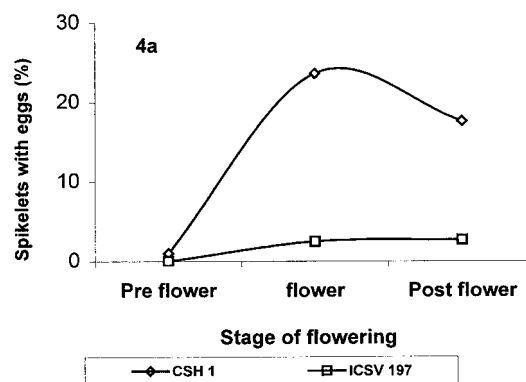
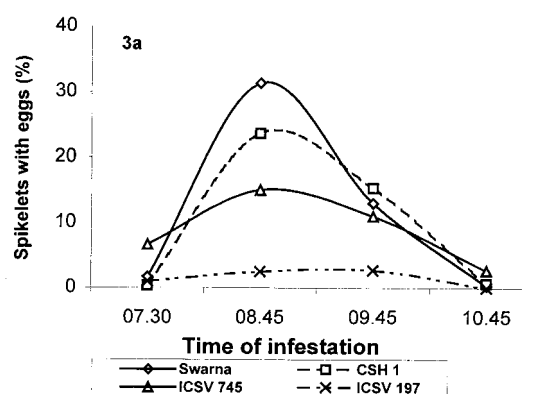


Figure 3. Percentage spikelets with (a) eggs and (b) number of eggs per 100 spikelets in panicles of two sorghum midge-resistant (ICSV 745 and ICSV 197) and two midge-susceptible (CSH 1 and Swarna) sorghum genotypes infested with field collected sorghum midge females at different times (0730 to 1045 h) under field conditions (ICRISAT, Patancheru 1996/97 post-rainy season).

Figure 4. Percentage spikelets with (a) eggs and (b) number of eggs per 100 spikelets in panicles of a sorghum midge-resistant (ICSV 197) and a midge-susceptible (CSH 1) genotype infested with sorghum midge at different stages of flowering under field conditions (ICRISAT, Patancheru 1996/97 post-rainy season).

influenced by the weather conditions during the experimental period.

Effect of stage of panicle flowering on susceptibility to sorghum midge

There was little or no oviposition in panicles of sorghum midge-resistant (ICSV 197) and midge-susceptible (CSH 1) genotypes infested at the pre-anthesis stage (Figures 4a and b). Maximum numbers of eggs were laid in panicles infested at 50% anthesis. Oviposition declined significantly in panicles infested at the post-anthesis stage, suggesting that sorghum midge females lay their eggs in spikelets at the anthesis stage.

Discussion

Flowering patterns of sorghum genotypes under field conditions did not differ between sorghum midge-resistant and midge-susceptible genotypes. Time to maximum flowering varied considerably between the rainy and the post-rainy seasons. Differences in temperature and relative humidity may be responsible for such variation in flowering behaviour of sorghum genotypes over seasons. Flowering in sorghum is triggered by the swelling of the lodicules, which is influenced by the plant water potential and relative humidity, and these factors may be one of the reasons for the variation in flowering behaviour of sorghum genotypes across seasons.

Under field conditions, maximum flowering in midge-resistant genotypes was recorded between 0100 to 0400 h, and at 0200 h in the sorghum midge-susceptible check, CSH 1. Under light conditions in the laboratory, maximum flowering occurred at 0300 h in all genotypes, irrespective of levels of resistance to sorghum midge. Flowering events continued for a longer period of time under dark conditions outside the laboratory, which may be due to lower temperatures outside as well as the absence of light. However, there were no differences in trends in the flowering patterns of midge-resistant and midge-susceptible genotypes under light or dark conditions in the laboratory.

There were no differences in percentage of spikelets with eggs and number of eggs per 100 spikelets in panicles (either of sorghum midge-resistant or of midge-susceptible genotypes) infested between 0200 to 0600 h. Significantly more eggs were laid in CSH 1 than ICSV 745 at all the infestation times. Maximum oviposition was recorded in panicles infested at 1000 h in CSH 1 and at 0800 h in ICSV 745. A few (CSH 1) or no (ICSV 745) eggs were laid in panicles infested at 0200 h. These results did not show any indication of more oviposition in panicles of sorghum midge-resistant genotypes infested during the early hours. In experiments conducted with field-collected sorghum midge females, maximum oviposition was recorded in panicles infested at 0845 h. Significantly lower oviposition was recorded in panicles of TAM 2566 and ICSV 197 than in those of the susceptible check, Swarna. There was no evidence of change in the response of sorghum genotypes across infestation times. Maximum numbers of eggs were laid in panicles infested at 50% anthesis, as observed in the past (Sharma et al., 1988), and at no stage was the oviposition in sorghum midge-resistant genotypes equivalent to that of the susceptible genotypes.

There was considerable variation in flowering times of midge-resistant genotypes within and across seasons. Environmental factors, particularly temperature, relative humidity, and photoperiod, influence the response to sorghum midge (Sharma et al., 1999). Flowering of sorghum genotypes varied across seasons and under light and dark conditions in the laboratory. Flower opening in sorghum is linked to swelling of the lodicules, which is influenced by temperature, water potential of the plant, and relative humidity. Similar observations on the flowering behaviour of sorghum genotypes were recorded under greenhouse conditions at Toowoomba, Queensland, Australia (H.C. Sharma, unpublished). The conclu-

sions of Diarisso et al. (1998) were based on five lines and two hybrids, which were different from the 30 genotypes (involving all the known sources of resistance to sorghum midge) used in the present study. Therefore, in addition to genotypic differences, the sample size (number of genotypes used in the study) may also account for the different conclusions.

There is considerable diversity in sorghum genotypes with resistance to sorghum midge (Faris et al., 1979; Sharma et al., 1990). Oviposition nonpreference (Rossetto et al., 1984; Waquil et al., 1986a; Sharma et al., 1990), antixenosis to visiting adults (Wiseman & McMillian, 1968; Sharma & Vidyasagar, 1994), and antibiosis (Waquil et al., 1986b; Sharma et al., 1993b) contribute to midge resistance in sorghum. Resistance to sorghum midge is strongly associated with short and tight glumes, tannin content of grain, and faster rate of grain development (Rossetto et al., 1984; Sharma et al., 1990). Amounts of tannins and phenols (Santos & Carmo, 1974; Sharma et al., 1993b; Naik et al., 1996), hydrocyanic acid (Hanna et al., 1999), proteins and soluble sugars (Sharma et al., 1993b) are associated with resistance to sorghum midge. Diarisso et al. (1998) observed that midge-resistant sorghums had shorter filaments, stigmas, and anthers, but wider and longer ovaries than susceptible sorghums. However, the authors concluded that size of floral parts was not an important mechanism of resistance. They suggested that most of the flowers of midge-resistant sorghums opened in early hours, and thus evaded the oviposition by sorghum midge females. However, observations on flowering times and expression of resistance to sorghum midge in the present studies have shown that there is no relationship between flowering time and expression of response to sorghum midge.

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