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Factors influencing oviposition behaviour of the sorghum midge, *Contarinia sorghicola* Coq.

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Summary

Visual stimuli influence the orientation behaviour of the sorghum midge, *Contarinia sorghicola* Coq. (Diptera: Cecidomyiidae). Yellow, red and white colours are attractive to the midge while blue and black are least attractive. Sorghum panicles covered with blue- or black-coloured bags in a headcage showed maximum midge damage, while the reverse was true for panicles covered with yellow, red, and white coloured bags.

Panicles at half-anthesis with viable pollen and receptive stigmata suffered higher damage than those at the pre- and post-anthesis. Physical removal of anthers and stigmata significantly reduced the oviposition by the sorghum midge. Reduced oviposition/adult emergence was also recorded in male sterile sorghum lines (2219A and 296A) or through chemically- (Ethrel®) (2-Chloro ethyl-phosphonic acid) induced male sterility in panicles of the sorghum cultivar, Swarna. Chemical stimuli from viable pollen and receptive stigmata and to a limited extent physical stimuli, govern the oviposition behaviour of the sorghum midge.

Sorghum cultivars IS 12573C, S-GIRL-MR1 and IS 2816C showed antixenosis to adult midges. However, these cultivars became susceptible under no-choice conditions in the headcage. DJ 6514 and IS 12666C were attractive to the adult midges, but showed antixenosis to oviposition under natural and no-choice conditions. Genotypes with short florets showed antixenosis for oviposition. Ovary and anther breadth and tannin content of grain showed negative associations with oviposition. Cultivar antixenosis to adult midges and oviposition is an important component of resistance to the sorghum midge.

Key words: Sorghum, *Contarinia sorghicola*, ethrel, oviposition, plant resistance

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is one of the most important cereal crops in Asia and Africa. The grain yields on farmers' fields in the semi-arid tropics are generally low, and insect pests are one of the main factors limiting production. Sorghum midge, *Contarinia sorghicola* Coq. (Diptera: Cecidomyiidae), is the most destructive pest of grain sorghum on a world-wide basis (Harris, 1976). The females mate soon after emergence and eggs are laid in sorghum florets at anthesis with the help of a long ovipositor. The eggs hatch in 2-3 days and the larvae suck the sap of the developing ovary. The ovary remains undeveloped which results in the production of chaffy spikelets.

The female midge has a life span of almost 24 h. During this period it has to locate sorghum panicles at the optimum stage of development (i.e. anthesis) for oviposition. It can be assumed

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that a number of visual stimuli and chemicals emitted by the sorghum plant guide the insect to its host. Oviposition is a biological response which to a large extent is influenced by the genotype of the host-plant (Budford, Jenkins & Maxwell, 1968; Sharma & Agarwal, 1983). Antixenosis (non-preference) for adult midges and/or oviposition has been considered to be one of the factors resulting in lower susceptibility in some sorghum genotypes (Wiseman & McMillian, 1968; Sharma, 1985; Sharma & Leuschner, 1986). The present studies were undertaken to study the factors influencing oviposition behaviour of the sorghum midge, *Contarinia sorghicola*.

Materials and Methods

Visual stimuli. The effect of different colours on midge behaviour was studied using coloured sticky traps and muslin cloth bags. Preliminary observations indicated that green was not particularly attractive to the midge. Traps made of plastic jars (11 cm in diameter × 25 cm long) were painted deep red (2.5R 3.5/12), yellow (5Y 8.5/14), white (N 9.4), deep blue (2.5 PB 3.5/10), and black (N 1.5). The traps were mounted on bamboo poles 1.5 m above the ground and placed 50 m apart at random in the field. There were five replicates. The outer trap surface was smeared with Tanglefoot® (sticky material). The number of midges trapped were counted twice a week, and the Tanglefoot® smear was renewed each week.

The effect of different colours on midge behaviour was also studied using different coloured (same colours as described above) muslin cloth bags in a cage technique developed to screen sorghums for resistance to sorghum midge (Sharma, Vidyasagar & Leuschner, 1988). Preliminary observations had indicated that the colour of the muslin cloth bag influenced the egg laying behaviour of females inside the headcage. A test was set up to observe the effect of deep red, yellow, white, deep blue or black coloured muslin cloth bags on midge behaviour in the headcage as measured by the percentage of midge-damaged florets. Forty midges were released into the headcage covering the sorghum panicle at anthesis. The procedure was repeated the following day. There were five replicates in a randomised block design. Percentage of midge-damaged chaffy florets was recorded 15 days after infestation.

Effect of stage of panicle development. The oviposition by the sorghum midge was studied on sorghum hybrid CSH 1 panicles at pre-, half- and complete-anthesis. Sets of 40 midge females were introduced into the headcage for 2 consecutive days at each developmental stage. Five panicles were infested at each stage of development. The midge damage (which gives a measure of the extent of oviposition) was recorded 15-days after infestation.

Role of stimuli from anthers and stigmata in oviposition. The role of chemo-stimuli from anthers and stigmata in influencing oviposition by the sorghum midge was also studied by removing them at anthesis individually or jointly in the sorghum hybrid CSH 1. The effect of physical re-arrangement of the florets on oviposition was studied by physically disturbing the florets with forceps. In another treatment, florets were cut in half with scissors, which also disturbed the florets physically and also removed anthers and stigmata. Ten primary branches with or without anthers and stigmata were exposed to 20 midge females in a headcage (Sharma, 1985). There were five replicates of each treatment. The number of eggs laid were recorded in 100 randomly selected florets on the third day after confinement. Florets were dissected under a 10X microscope, and the number of eggs laid were recorded.

Effect of male sterility on oviposition. The role of possible chemo-stimuli from anthers with viable pollen on oviposition was also investigated by using fertile (B line, with viable pollen)

and sterile (A line, non-viable pollen) sorghum lines. In the first experiment, panicles of 2219A and 2219B were exposed to 40 midges for 1 day in headcages. There were five replications in a randomised block design. Florets were dissected under a 10X microscope and the number of eggs laid were recorded in 100 randomly-selected florets. In another experiment, panicles of 296A were exposed to 40 midges under headcages for one day. Five panicles were dusted with viable pollen from another sorghum cultivar (Swarna), while the other five were left unpollinated. The number of midges emerging from pollinated and unpollinated panicles was recorded between 15 to 20 days after infestation to get a measure of oviposition through adult emergence.

The effect of male sterility (non-viable pollen) on oviposition by the sorghum midge was also studied by inducing male sterility through Ethrel® (2-chloroethyl phosphonic acid) spray before anthesis on a sorghum variety Swarna. Concentrations of 200 to 4000 ppm of ethrel in water were sprayed with a compression sprayer at pre-anthesis stage. When the treated panicles reached top-anthesis stage, they were exposed to 40 midges for one day in headcages. Untreated panicles were used as a control. There were three replicates in a randomised block design. The egg-laying was recorded in 100 randomly-selected florets as described above.

Cultivar antixenosis and its role in oviposition and damage. The number of midges attracted to the panicles of 10 genotypes were recorded by counting the flies hovering around the panicles at half-anthesis. The midges were counted between 0900 h and 1000 h on five panicles chosen at random from each replication on 3 successive days under free choice conditions in the field. Data were also recorded on the midge damage 15 days after flowering to differentiate between cultivar antixenosis to adults and/or oviposition and antibiosis. The extent of damage was also recorded under no-choice conditions using the headcage technique (Sharma *et al.*, 1988). Each panicle was infested with 40 midges for two consecutive days at top-anthesis. There were five replications. Midge damage was recorded 15 days after releasing the midges into the headcage.

To differentiate between antixenosis to adults and oviposition, egg laying, larval numbers and adult emergence were recorded in 11 cultivars under no-choice conditions in the headcage. Panicles at top-anthesis were exposed to 60 midges for one day. Six panicles were infested in each genotype, of which three were used for recording egg and larval numbers while the other three were kept for recording adult emergence. The numbers of eggs laid were counted on the second day after confinement. Eggs were recorded from a sample of 250 randomly selected florets in each panicle. Adult emergence in infested panicles was recorded between 15 to 25 days after infestation. Ten fresh florets from each genotype were dissected under the microscope, and the length and breadth of glume, lemma, palea, lodicule, ovary, stigma, style and anther were measured with the help of an ocular micrometer. Tannin content of mature grain was determined by the method of Mertin, Scoyoc & Butler (1978).

The data were subjected to analysis of variance after appropriate transformations as indicated in each table. Significance of difference between treatment means was determined by using least significant difference (L.S.D.). Correlation and regression coefficients for each floral parameter in relation to oviposition were computed, as appropriate.

Results and Discussion

Visual stimuli. Maximum numbers of midges were attracted to yellow traps (34 midges/trap). However, the differences in midge numbers trapped on yellow, red and white traps were not significant (Table 1). Blue and black traps were least attractive to the sorghum midge (< 10

Table 1. *Attractiveness of colour in sticky traps to the sorghum midge*

Trap colour	Munsell colour notation	No. of flies trapped/ trap in 20 days
Black	N 1.5	1 (1.4)*[a]
Blue	2.5 PB 3.5/10	7 (2.8)[a]
White	N 9.4	22 (4.8)[b]
Yellow	5 Y 8.5/14	34 (5,9)[b]
Red	2.5 R 3.5/12	27 (5.3)[b]
L.S.D.		(1.4)
D.F.		16

* Figures in parenthesis are $\sqrt{N}$ transformed values.

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

Table 2. *Effect of muslin bag colour on midge damage under headcage test in CSH 1*

Bag colour	Midge damage (%)
Black	77 (61.4)*[c]
Blue	76 (60.1)[bc]
White	66 (54.7)[ab]
Red	61 (51.6)[a]
Yellow	63 (52.7)[a]
L.S.D.	(6.3)
D.F.	16

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

midges/trap). Wiseman, Widstrom & McMillian (1972) have also reported yellow to be the most attractive to sorghum midge. The influence of different colours on midge behaviour was also confirmed using the muslin cloth bags used to cover the headcages. Higher levels of midge damage in panicles covered with blue and black bags suggested that the females are not attracted to these colours which resulted in higher egg-laying and damage, while the reverse was true for yellow, red and white (Table 2). These observations suggest that visual stimuli play a role in the orientation behaviour and oviposition by the sorghum midge. These observations have been very useful in developing a no-choice headcage technique to screen for resistance to sorghum midge in which blue bags are used to cover a wire-framed cage attached to the sorghum panicle (Sharma *et al.*, 1988).

Effect of stage of panicle development. The exposure of CSH 1 sorghum panicles to the midge at different developmental stages under the headcage indicated maximum susceptibility/oviposition at half-anthesis followed by panicles infested at top-anthesis. The CSH 1 is highly susceptible to the sorghum midge (Sharma, 1985), and midge damage was taken as an indirect measure of the extent of oviposition at different stages of panicle development (Table 3). Maximum damage/oviposition in panicles at half-anthesis was because of a maximum number of florets at anthesis in these panicles compared with others. Chemical and/or physical stimuli emanating from florets at anthesis with viable pollen and receptive

Table 3. *Effect of panicle development on midge damage under headcage test in CSH 1*

Stage of development	Midge damage (%) Rainy season	After rainy season
Pre-anthesis	33[ab]	14*[a]
Top-anthesis	40[b]	25[b]
Half-anthesis	51[c]	27[b]
Post-anthesis	27[a]	14[a]
L.S.D.	9.9	6.8
D.F.	12	12

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

Table 4. *Effect of removing anthers and stigma on oviposition by the sorghum midge*

Part(s) removed	No. of eggs laid/100 florets Post rainy season 1982–83	Rainy season 1983	1984
Anther	18 (3.7)**[ab]	25 (4.6)*[ab]	41 (6.2)*[b]
Stigma	—	29 (5.3)[ab]	33 (5.6)[b]
Half cut flowers	31 (5.6)[b]	—	4 (1.9)[a]
Anther + Stigma	7 (2.6)[a]	20 (4.0)[a]	11 (2.8)[ab]
Physically disturbed florets	80 (8.8)[c]	62 (7.9)[b]	140 (11.6)[2]
L.S.D.	(2.2)	(3.6)	(3.5)
D.F.	12	16	16

**, * are $\sqrt{N} + 1$ and $\sqrt{N}$ transformed values.

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

stigmata possibly elicit an oviposition response by the sorghum midge. Panicles exposed to the midges at pre- and post-anthesis were less damaged.

Role of stimuli from anthers and stigmata in oviposition. The role of possible chemical/physical stimuli from the florets at anthesis was further investigated by removing pollen tubes or stigmata or both (Table 4). There were 7 – 20 eggs per 100 florets when both anthers and stigmata were removed compared with 62 – 140 eggs per 100 florets in normal flowers. Cutting the florets in half, which removed both anthers and stigmata, also resulted in less oviposition by the sorghum midge. Physical disturbance also resulted in some reduction in egg laying (41 eggs/100 florets), although its effect was much less than the removal of anthers and stigmata (20 eggs/100 florets). Chemostimuli from anthers and stigmata, and to some extent physical stimuli from the flowers, seem to govern the oviposition by the sorghum midge.

Effect of sorghum male sterility on oviposition. There were only 26 eggs/100 florets in 2219A compared with 59 eggs/100 florets in 2219B (L.S.D. 7.4), indicating the presence of chemical stimuli from viable pollen that elicit the oviposition response by the female midge flies. Similar results were also obtained with pollinated and un-pollinated panicles of 296A. 316

Table 5. *Effect of Ethrel spray at pre-anthesis to suppress male gametogensis in sorghum on oviposition by sorghum midge (1984-85, after rainy season)*

Ethrel conc. (ppm)	No. of eggs/100 florets
200	56*[c]
300	54[c]
2000	32[b]
4000	5[a]
Untreated control	87[d]
L.S.D.	3.8
D.F.	1.6

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

midges/panicle were recorded in un-pollinated panicles compared with 607 midges/panicle in those pollinated with viable pollen (L.S.D. 6.0). The inhibition of oviposition as a result of induction of male sterility through ethrel is given in Table 5. There was a progressive reduction in oviposition with increasing concentration of ethrel. Concentrations of 2000 and 4000 ppm inhibited the oviposition substantially. However, some florets dried up in panicles sprayed with 4000 ppm of ethrel. Ethrel has earlier been reported to induce sterility in cereals (Powell & Miller, 1971; Stoskopf & Law, 1972; Verma & Kumar, 1978; Thakur & Rao, 1988). The reduced oviposition by the sorghum midge as a result of the induction of male sterility also confirms the role of chemical stimuli from pollen in the oviposition behaviour of sorghum midge.

Cultivar antixenosis and its influence on oviposition and damage. Under multi-choice conditions in the field, lines IS 12573C, TAM 2566, S-GIRL-MR1 and IS 2816C were relatively less preferred (< 25 midges/five panicles) compared with CSH 1, DJ 6514, IS 12666C, IS 2579C and ENTM 1 (31 to 78 midges/five panicles) (Table 6). Cultivars that were non-preferred by adult midges also suffered lower levels of midge damage. DJ 6514 and IS 12666C were relatively attractive to the midges, but suffered lower midge damage under multi-choice conditions in the field. Under no-choice conditions in the headcage, DJ 6514 and IS 12666C and TAM 2566 were significantly less damaged (< 35% damage) than other cultivars. IS 12573C, S-GIRL-MR1 and IS 2816C (non-preferred by the adult midges) suffered higher midge damage (63.3% to 79.0%) under no-choice conditions in the headcage, indicating non-preference for adults to be the major component of resistance to midge in these cultivars. Thus, antixenosis for adults is an important component of resistance in some genotypes, while other mechanisms/factors may result in less oviposition/damage in others.

To differentiate between antixenosis to adults and oviposition, midge eggs, larvae and adult emergence were recorded in 11 cultivars under uniform insect pressure (60 midges/panicle) under no-choice conditions in the headcage (Table 7). Oviposition was less in DJ 6514, AF 28, IS 15107 and TAM 2566 (< 42 eggs/100 florets) compared to IS 8544, IS 12664C, CSH 1 and Swarna (142 to 185 eggs/100 florets). Cultivars that showed antixenosis to oviposition also had significantly lower numbers of larvae than the susceptible (preferred) checks, CSH 1 and Swarna. Less than 85.5 midges/panicle emerged from these cultivars compared with 320 to 341 midges/panicle recorded in CSH 1 and Swarna. Lower larval/adult counts in DJ 6514, AF 28, IS 15107 and TAM 2566 suggest oviposition non-preference/antibiosis to be the mechanisms of resistance in these cultivars. Antixenosis to adults (Rossetto, 1985; Sharma, 1985) or oviposition (Rossetto, Nagai & Overman, 1984; Rossetto, 1985; Sharma, 1985; Sharma

Table 6. *Cultivar antixenosis to adult midges and midge damage in 10 cultivars under multi and no-choice conditions*

Cultivar	No. of midge flies/5 panicles (Multi-choice field conditions	Midge damage (%) Multi-choice field conditions	No-choice head-cage conditions
DJ 6514	37.0 (6.1)*ae	8.3 (16.5)**abc	19.0[a]
TAM 2566	19.0 (4.3)[bc]	12.3 (20.5)[cd]	27.0[a]
IS 12666C	31.0 (5.5)[d]	13.0 (21.0)[cd]	35.0[a]
IS 12573C	8.0 (2.8)[a]	6.0 (14.1)[ab]	63.7[b]
S-GIRL-MR 1	18.0 (4.1)[b]	5.0 (12.8)[a]	64.3[b]
IS 12579C	41.0 (6.2)[de]	15.0 (22.3)[de]	64.7[b]
IS 12664C	30.0 (5.4)[cd]	14.8 (22.5)[de]	72.7[b]
ENTM 1	46.0 (6.7)[e]	22.0 (27.8)[e]	72.7[b]
IS 2816C	25.0 (4.9)[c]	11.3 (19.2)[bcd]	79.0[b]
CSH 1	78.0 (8.8)[f]	34.3 (35.8)[f]	84.7[b]
L.S.D.	(1.1)	(5.6)	22.9
D.F.	36	36	36

*, ** Figures in parenthesis are $\sqrt{N}$ and Arcsin $\sqrt{\%}$ transformed values.

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

Table 7. *Oviposition, larval numbers and adult emergence in 11 cultivars under no-choice conditions*

Cultivar	No. of eggs laid/ 100 florets	No. of larvae/ 100 florets	No. of adults emerged/ panicle
DJ 6514	39.0 (6.1)*a	8.5 (2.6)*a	28.5 (5.1)*a
AF 28	36.0 (5.9)[a]	49.0 (7.0)[b]	37.0 (5.9)[a]
IS 12666C	66.5 (6.9)[ab]	65.5 (7.7)[bc]	142.0 (11.3)[b]
IS 12664C	142.0 (11.7)[abc]	94.0 (9.6)[bcd]	133.0 (10.8)[b]
IS 8544	221.5 (14.7)[c]	100.0 (10.0)[cd]	149.5 (12.1)[bc]
IS 7034	86.0 (9.2)[abc]	98.5 (9.8)[bcd]	265.0 (16.2)[cd]
IS 15107	41.0 (5.9)[a]	72.0 (8.4)[bc]	86.5 (9.2)[ab]
IS 8721	109.5 (10.1)[abc]	103.5 (10.1)[cd]	164.5 (12.4)[bc]
TAM 2566	41.5 (6.0)[a]	72.0 (8.4)[bc]	86.5 (9.2)[a]
CSH 1	145.5 (12.0)[abc]	130.5 (11.4)[d]	319.5 (17.8)[d]
SWARNA	184.5 (13.2)[bc]	131.5 (11.4)[d]	340.5 (18.4)[d]
L.S.D.	(6.4)	(2.9)	(4.5)
D.F.	20	20	20

Figures followed by the same letter in a column were not significantly different at $P < 0.05$.

& Leuschner, 1986) are important components of resistance to sorghum midge. Cultivar resistance based on antixenosis to adults breaks down under no-choice conditions. However, this trait can be combined with other mechanisms to diversify the basis of resistance to sorghum midge.

Of the various floral parts (Table 8), glume length (G1 and G2), lemma length (L2) and

Table 8. *Correlation and regression coefficients between oviposition and floral parameters under no-choice conditions*

Parameter	Correlation coefficient (r)	Intercept (a)	Regression coefficient (b)	Coefficient of determination (%) (R^2)
Glume length (G1)	0.66*	−237.7	2.2 ± 0.9*	37[a]
Glume length (G2)	0.64*	−244.8	2.3 ± 0.9*	35
Lema length (L1)	0.51	−262.8	2.7 ± 1.5	18
Lema length (L2)	0.70*	−152.6	2.3 ± 0.8*	44
Palea length	0.26	−148.9	2.7 ± 3.2	3
Lodicule length	0.60*	−325.8	7.1 ± 3.2*	28
Lodicule breadth	0.38	−155.8	9.2 ± 7.5	5
Ovary length	0.15	− 46.1	2.9 ± 6.3	8
Ovary breadth	−0.19	270.1	− 4.7 ± 8.0	7
Style length	0.09	− 40.6	3.1 ± 2.1	11
Stigmata length	0.51	−119.3	4.2 ± 2.4	17
Anther length	0.48	−117.9	2.9 ± 1.7	15
Anther breadth	−0.39	373.6	− 8.4 ± 6.6*	6
Tannins in mature grain	−0.56	124.8	−19.7 ± 9.7	24

* Significant at $P < 0.05$

a R^2 adjusted for degrees of freedom (n = 9)

lodicule length were significantly and positively correlated with the number of eggs laid. Their regression coefficients were also significant. Other floral parts which showed positive but non-significant correlation with oviposition included lemma length (L1), lodicule breadth, anther length and stigma length. Anther and ovary breadth showed a negative, but non-significant correlation with oviposition. Tannin content of mature grain showed a negative association with oviposition. Santos & Carmo (1974) suggested a positive correlation between tannin content and midge resistance. However, in a number of situations, it is not possible to establish a clear relationship between midge damage and tannin content because of a number of other factors which also contribute to midge resistance.

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