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Tritrophic interactions in sorghum, midge (*Stenodiplosis sorghicola*) and its parasitoid (*Aprostocetus* spp.)

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Studies on tritrophic interactions involving sorghum genotypes, midge (*Stenodiplosis sorghicola*) and the predominant parasitoids (*Aprostocetus* spp.) at ICRISAT Asia Center were conducted using three midge resistant (ICSV 745, ICSV 89058 and IS 10712) and three susceptible (Swarna, CSH 9 and ICSV 112) genotypes during the post-rainy (1992/93) and rainy (1993) seasons. *A. coimbatorensis*, the predominant parasitoid during post-rainy season, preferred mid–late midge larvae for parasitization, while *A. gala*, which was predominant during the rainy season, preferred early–mid larval stages. Variations in the preference of *A. coimbatorensis* and *A. gala* for the developmental stage of their host larvae indicate good prospects for the biological control of sorghum midge populations. There were significant differences in parasitization level of midge by *Aprostocetus* spp. between resistant and susceptible sorghum genotypes, and season. Higher parasitization was observed on susceptible genotypes than on resistant ones during both post-rainy and rainy seasons. However, the level of parasitization was greater in post-rainy than in rainy seasons. There was also evidence of higher midge infestation in rainy than in post-rainy seasons. Susceptible genotypes attracted more parasitoids because of high levels of midge infestations. Low parasitoid density in midge resistant sorghum under glasshouse and field conditions was associated with low midge infestations in these genotypes. However, parasitoids were always associated with their host in spite of low midge densities in resistant genotypes. The present study revealed that the interaction between host plant resistance and parasitoids of sorghum midge would thus be synergistic and complementary and could result in successful integration of these two important pest management tactics. © 1998 Elsevier Science Ltd. All rights reserved

Sorghum midge, *Stenodiplosis* (*Contarinia*) *sorghicola* Coquillett (Diptera: Cecidomyiidae) is an economically important pest in Asia, Africa, Australia, Europe and the Americas (Harris, 1976; Sharma, 1985a,b). Control in India, Australia and the USA depends on host plant resistance and a range of crop management practices.

One crucial consequence of pest management involving more than one control method is that interactions between methods can occur (van Emden, 1981). Such interactions are fundamentally important to the concept of integrated pest management. For example, the secondary chemistry of plants used as a

resource by a herbivore not only affects the physiology and behaviour of the herbivore but can also affect the quality of the herbivore as a resource for a beneficial insect (Thomas and Waage, 1996). Natural enemies base their foraging decisions on information from these different trophic levels, and chemical information plays an important role in which plant volatiles mediate searching behaviour, especially at longer distances (Vet and Dicke, 1992). Plant resistance to insects can result from antagonism due to the presence of chemicals in various plant tissues. Campbell and Duffey (1979) showed that the antibiotic factor in tomato 'α Tomatine' which is absorbed by the endoparasitoid *Hyposoter exiguae* Viereck from its host *Heliothis zea* Boddie prolonged the larval period of the parasitoid, reduced pupal eclosion, reduced the adult size and shortened its longevity. Thorpe and Barbosa (1986) have shown

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that variation in dietary nicotine content influences parasitization of the tobacco hornworm, *Manduca sexta* (L.), by the braconid wasp *Cotesia congregata* Say. They found that the number of parasitoids surviving to adulthood was greater on *Manduca* reared on low-nicotine tobacco. Isenhour and Wiseman (1989) observed that feeding of fall army worm (*Spodoptera frugiperda* Smith) on the resistant corn genotypes did not affect its parasitoid *Campoletis sonorensis* Cameron. Hare (1992) presented a series of graphical models for a range of positive and negative interactions between host plant resistance and biological control in which variation in population density of herbivores was depicted as a function of host plant suitability in both the presence and absence of natural enemies.

With the identification and development of midge resistant sources, efforts are now underway at ICRISAT to develop midge resistant hybrids. The extent to which increased sorghum resistance could affect the complex of midge natural enemies and their biological activity is not known. This is crucial because the effects of resistance factor(s) in sorghum genotypes on the developing midge larvae are likely to be exhibited on the next trophic level of association, i.e. on midge parasitoids. Although there are reports indicating the efficacy of biocontrol agents in reducing midge infestation (Chundurwar, 1977; Garg and Taley, 1978), it is not known if plant resistance factors influence parasitoid activity, i.e. if host plant and biological agents have antagonistic, synergistic or/and complementary effects. Franzmann et al. (1989) reported that the parasitization of midge larvae was higher on resistant than on susceptible sorghum genotypes; however, no explanation was given for this observation. In other related studies at ICRISAT (Kausalya et al., 1997a), differences were observed in the levels of midge parasitization by *Aprostocetus* spp. in resistant and susceptible sorghum genotypes, indicating the possibility of tritrophic interaction in the system. These findings and Franzmann's preliminary observations formed the basis for further investigations into these interactions.

Experiments were designed to determine the effects of sorghum genotypes and age of midge larvae on development and emergence of *Aprostocetus coimbatorensis* Rohwer and *A. gala* Walker as well as to determine the level of midge parasitization. Initial experiments were carried out during the 1992/93 post-rainy season under glasshouse conditions. Based on the results obtained, the experiments were further modified and a detailed study was conducted during the 1993 rainy season under field conditions.

Materials and methods

Parasitoid culture

Midge infested sorghum panicles were collected from sorghum fields in the experimental farm at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, and put into plastic tubs partially filled with moist sand. These were placed in a wooden cage, fitted with a collection jar at its top. Prior to adult emergence, the entire

cage except the collection jar was covered with a black cloth, thus leaving the collection jar as the only source of light. Emerging insects migrated into the jar and were collected the following morning. The midge flies died during the day of emergence and *Aprostocetus* spp. were collected using an aspirator and transferred into a rearing cage containing 10% sucrose solution. They were held in the cage for two days for mating and preoviposition period (Taley et al., 1978) and thereafter gravid females were collected for use in the interaction studies. Kausalya et al. (1997a) reported that the predominance of different *Aprostocetus* spp. varied with season, i.e. *A. coimbatorensis* being predominant during the post-rainy and *A. gala* during the rainy season. Accordingly, the predominant parasitoid was used in the interaction studies.

Host stage preference of *Aprostocetus* spp. in relation to sorghum genotypes

Glasshouse and field studies were conducted at ICRISAT in the 1992/93 post-rainy and 1993 rainy seasons. Three resistant (ICSV 745, ICSV 89058, IS 10712) and three susceptible (Swarna, CSH 9, ICSV 112) sorghum genotypes were used in these studies. The procedure was similar in each cropping season, except that *A. coimbatorensis* was used in the post-rainy and *A. gala* was used in the rainy season. Eighteen panicles of each of the six sorghum genotypes at 50% anthesis were randomly selected and caged in each replication. Forty female midges collected between 0830 and 1100 hours from surrounding flowering sorghum fields were artificially released into the cages (Kausalya et al., 1997b) for two successive days. Forty midge flies were used to obtain maximum midge damage in the cage (Sharma et al., 1988). Parasitoids were released into midge infested panicles at 3-day intervals on five occasions: 3, 6, 9, 12 and 15 days after midge infestation (DAI). This procedure ensured that each larval stage of midge was exposed to parasitization by *Aprostocetus* spp., since each midge larval instar lasts 2–3 days and there is a total of four instars (Taley et al., 1971). In each treatment there were three panicles of each genotype and 15 gravid *Aprostocetus* females (obtained from culture) were released into each midge infested panicle usually between 1730 and 1800 hours. The released parasitoids were removed after 48 h and the panicles left intact in the head cage for the development and emergence of adult parasitoids. Daily observations on emerging midge flies and parasitoids were recorded on a total of 90 panicles (18 panicles of each genotype × 5 treatments) for several weeks to ensure that all emerging flies and parasitoids were collected.

Statistical analysis

Data were statistically analysed by analysis of variance (ANOVA) (SAS Institute, 1985). Significant differences between sorghum genotypes and age of midge larvae on emergence of *Aprostocetus* spp. were compared by the Student Neuman–Keuls (SNK) multiple range test at 5% probability level. The level of parasitization was calculated on the basis of total

emerging parasitoids (*p*) and midge flies (*m*) from caged panicles (Kausalya *et al.*, 1995) as follows:

$$\% \text{ parasitism} = \frac{p}{m+p} \times 100$$

Results

Host stage preference of *Aprostocetus* spp. in relation to sorghum genotypes

Studies on age of midge larvae for parasitization by *Aprostocetus* spp. revealed that preference varied greatly with season and genotype. During the 1992/93 post-rainy season, there was no significant difference in *A. coimbatorensis*'s preference for 3- and 6-day-old midge larvae in either susceptible or resistant genotypes (*Table 1*). However, significant differences ($P < 0.05$) were observed with 9-, 12- and 15-day-old midge larvae in all genotypes, indicating that *A. coimbatorensis* preferred mid–late larval stages for parasitization. There was consistently more emergence of *A. coimbatorensis* in susceptible genotypes (CSH 9 > Swarna > ICSV 112) than in resistant ones (ICSV 89058 > ICSV 745 > IS 10712). The host stage preference varied during the 1993 rainy season. *A. gala* exhibited higher parasitization for 3-, 6- and 9-day-old midge larvae than for later larval stages (*Table 1*). Evidence of maximum emergence of *A. gala* upon parasitization of early–

mid larval stages was more in susceptible genotypes (CSH 9 > ICSV 112 > Swarna) than in resistant ones (IS 10712 > ICSV 89058 > ICSV 745). Though the parasitoid preferred the early–mid larval stages, few individuals emerged upon parasitization of late larval stages.

There were significant differences in midge infestation and parasitoid numbers between resistant and susceptible genotypes and seasons (*Table 2*). There was evidence of higher midge infestation during the rainy than during the post-rainy season. Higher parasitization was also observed on susceptible genotypes than on resistant ones during post-rainy and rainy seasons. However, parasitization was much higher during the post-rainy season than during the rainy season (*Table 2*). Combined ANOVA over seasons showed highly significant differences ($P < 0.001$) in midge parasitization between season, genotype, and the interactions of season × genotype (*Table 3*).

Discussion

Host stage preference of the parasitoid species varied with age of midge larvae and season. *A. coimbatorensis* preferred host larvae (midge) in the mid–late stages for parastization, whereas *A. gala* preferred early–mid larval stages (*Table 1*). Seasonal preferences between both parasitoid species reduce interference or competitive exclusion in the presence or absence of host. In our study, we did not observe

Table 1. Effect of sorghum genotypes and age of midge larvae on emergence of *Aprostocetus* spp. during 1992/93 post-rainy and 1993 rainy seasons at ICRISAT Asia Center

	Age of midge larva					RG				
	No. of *A. coimbatorensis* (1992/93 post-rainy) emerging					No. of *A. gala* (1993 rainy) emerging				
Genotype	3 DAI*	6 DAI	9 DAI	12 DAI	15 DAI	3 DAI	6 DAI	9 DAI	12 DAI	15 DAI
Swarna (*n* = 3)	1.0a	5.0a	14.3b	11.7ab	24.3a	40.0b	12.7ab	3.0b	0.0b	0.0a
CSH 9 (*n* = 3)	1.0a	9.3a	47.0a	20.3ab	22.3a	116.0a	37.3ab	0.7b	0.7b	0.3a
ICSV 112 (*n* = 3)	0.0a	0.0a	11.0b	23.7a	17.3a	0.0c	82.7a	22.7a	17.3a	0.7a
ICSV 745 (*n* = 3)	0.0a	0.3a	1.0c	2.0b	1.3b	2.0c	0.3b	0.3b	0.0b	0.3a
ICSV 89058 (*n* = 3)	0.0a	12.7a	1.7c	0.0b	2.7b	3.3c	0.7b	1.7b	1.7b	0.0a
IS 10712 (*n* = 3)	0.0a	0.0a	0.3c	0.0b	0.0b	7.7c	12.7ab	2.0b	0.0b	0.0a

Means within columns not followed by the same letter differ significantly ($P < 0.05$); Student Neuman–Keuls (SNK) test
*Release of *Aprostocetus* sp. 3 days after midge infestation (DAI)

Table 2. Level of parasitization of midge on sorghum genotypes during 1992/93 post-rainy and 1993 rainy seasons

	Post-rainy 1992/93 season			Rainy 1993 season		
Genotype	No. of midge collected	No. of *A. coimbatorensis* collected	% Parasitism	No. of midge collected	No. of *A. gala* collected	% Parasitism
Swarna (*n* = 3)	173.7a	56.3ab	23.9b	384.7a	28.7ab	7.0b
CSH 9 (*n* = 3)	61.3bc	100.0a	58.8a	352.7a	17.7bc	4.9b
ICSV 112 (*n* = 3)	103.7b	52.0ab	31.6b	267.0b	42.7a	13.5a
ICSV 745 (*n* = 3)	17.7c	8.7b	29.8b	11.3c	0.0c	0.0b
ICSV 89058 (*n* = 3)	0.0c	17.0b	0.0b	19.7c	0.3c	1.4b
IS 10712 (*n* = 3)	6.3c	0.3b	1.7b	62.7c	3.7c	5.8b

Means within columns not followed by the same letter differ significantly ($P < 0.05$); Student Neuman–Keuls (SNK) test

Table 3. Pooled ANOVA (mean square) showing effect of genotype, seasonal variation, and their interactions on level of parasitization of midge

Source of variation	df	No. of midge collected	No. of parasitoids collected	% Parasitism
Genotype	5	81277.0***	3769.8**	805.3**
Season	1	135178.8***	4993.8**	3203.6***
Genotype × season	5	20866.5***	1399.8*	687.8**
Error	22	820.8	494.2	103.7
r^2		0.9	0.8	0.8
CV (%)		23.5	81.5	68.5

*$P<0.05$, **$P<0.01$, ***$P<0.001$

coexistence of *Aprostocetus* spp. on sorghum genotypes at a given season. But where it does occur, it would not constitute a problem because there is a trade-off in host stage preference. Chesson (1986) suggests that spatial and temporal heterogeneity allows coexistence of nearly identical species. Since these two closely related species parasitize the same host, variations in their preferences for host stages would greatly contribute towards suppressing midge populations.

Parasitization was significantly higher during the post-rainy season under glasshouse conditions than during the rainy season under field conditions due to prevailing environmental conditions for the parasitoids. Variations in midge infestation and parasitoid numbers could be another reason for differences in parasitization levels between both seasons (*Table 2*). There was consistently more midge infestations during the rainy than during the post-rainy season. Mote and Ghule (1986) reported a positive correlation between rainfall and sorghum midge populations when temperatures and relative humidity ranged from 25–27°C and 75–90%, respectively. However, *Aprostocetus* adults were collected at slightly higher temperatures of 29–36°C and lower relative humidity levels of 60–75% (Garg and Taley, 1978). Perhaps this difference in environmental requirements between parasitoid and sorghum midge may account for the delay in parasitoid build-up until later in October and March in the rainy and post-rainy seasons, respectively. Susceptible genotypes attracted high parasitoid numbers because of high levels of midge infestations. Such advantages that plants may enjoy from attracting parasitoids when under attack by herbivores make them likely sources of synomones. Vet and Dicke (1992) pointed out that the value of plant information depends on the degree of herbivore infestation. That is, if infestation is high, plant information is reliable. Studies by Dicke *et al.* (1990) have shown that, upon damage by herbivores, host plants produce volatile allelochemicals which attract natural enemies and may be the key elements in host finding. These volatiles are different from those emitted in response to mechanical damage and are produced at the site of herbivore damage as well as systematically throughout the plant (Dicke, 1994). Recent studies with maize (Potting *et al.*, 1995) have shown that the major source of the attractive volatiles to the parasitoid *Cotesia flavipes* Cameron was not only the borer-injured stem, but also kairomones in frass produced by the feeding larvae of *Chilo partellus* Swinhoe. Low parasitoid density in midge resistant sorghum under glasshouse and field conditions was

associated with low midge infestations in these genotypes (*Table 2*). Low numbers of midge in resistant genotypes was due to antibiosis (Sharma *et al.*, 1990), and is known to affect midge fecundity, larval development and adult emergence. However, parasitoids were always associated with their host in spite of low midge densities in resistant genotypes; an observation which confirms an earlier report by Franzmann *et al.* (1989). This indicates that varietal resistance did not adversely affect parasitoid development and activity.

The findings from our present study lead us to hypothesize that different sorghum genotypes emit different blends and/or quantities of volatiles and that susceptible sorghum produce more semiochemicals attractive to parasitoids of midge, but host-induced volatiles associated with this reaction have not been identified. An identification of the specific chemicals can establish whether there are qualitative and/or quantitative differences in the volatile blends emanating from the stem or leaves of an infested plant and may also reveal whether the same terpenoids are involved as is shown for the maize–*Spodoptera exigua* Hübner–*Cotesia marginiventris* Cresson system (Turlings *et al.*, 1990, 1991) and the maize–*Pseudaletia separata* Walker–*Cotesia kariyai* Watanabe system (Takabayashi *et al.*, 1995). The present study revealed that the interaction between host plant resistance and parasitoids of sorghum midge would thus be synergistic and complementary and could result in successful integration of these two important pest management tactics because they are environmentally compatible and can effectively contribute to keep pest populations below economic threshold levels especially under low input subsistence farming. This is an area that calls for further studies and increased understanding of such tritrophic interactions. Furthermore, knowledge of such interactions should be explored and intensified by plant breeders and chemical ecologists with the hope of developing plant materials with adequate levels of resistance to sorghum midge but which would encourage higher natural enemy abundance and activity under cereal-based ecosystems.

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