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# *Trichogramma* egg parasitism of *Helicoverpa armigera* on pigeonpea and sorghum in southern India

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**Abstract**

*Trichogramma* spp. (Hymenoptera: Trichogrammatidae) only rarely parasitize eggs of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on pigeonpea (*Cajanus cajan* (L.) Millspaugh), while on other plants including sorghum (*Sorghum bicolor* (L.)) high parasitism levels of this host are found. In this study two strategies designed to increase the parasitoid activity on pigeonpea were tested in the field: intercropping pigeonpea with sorghum and mass-releasing *T. chilonis* Ishii. Neither strategy led to an increase in parasitism. On pigeonpea, *H. armigera* oviposited >74.8% of its eggs on calyxes and pods. Parasitism levels in host eggs collected from different plant structures varied significantly with 3.6, 0.3, and 40.7% of eggs on calyxes, pods, and leaves parasitized. Earlier studies have shown that calyxes and pods possess long glandular and non-glandular trichomes, and are covered by sticky trichome exudates which inhibit parasitoid searching behaviour. Parasitism levels between 27.9 and 100% were recorded from host eggs on the intercropped sorghum. *Trichogramma chilonis* was the dominant parasitoid species. The mean clutch size was 2.03, but up to six parasitoids emerged per egg. Progeny sex ratio (% females) decreased with clutch size, from 63.1% at a clutch size of one to 46.0% at a clutch size of five. Sticky trap catches showed that while the parasitoid population in sorghum increased when *H. armigera* started ovipositing, the population within pigeonpea did not benefit from either a high parasitoid population in sorghum or a high host egg density on pigeonpea. During one of five seasons studied, however, high parasitism levels (up to 73%) were recorded on pigeonpea. During this season, *H. armigera* oviposited on pigeonpea plants in the vegetative growth stage and a high proportion of eggs were collected from leaves. Parasitism levels were positively correlated with the percentage of eggs collected from leaves. This study shows that the parasitization efficiency of *Trichogramma* spp. on pigeonpea depends mainly on the location of the host eggs. This explains why parasitism levels of *H. armigera* eggs on pigeonpea did not increase when intercropped with sorghum or after mass-releasing *T. chilonis.*

## Introduction

*Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is one of the most serious insect pests in the Old World. The key pest status of *H. armigera* is due to several factors including its migratory ability, high fecundity, facultative diapause and polyphagy (Fitt, 1989). In India, more than 180 plants from 45 families are reported as hosts of *H. armigera* (Manjunath et al., 1989). The larvae cause major crop damage as they prefer feeding on plant parts rich in nitrogen such as reproductive structures and growing tips (Fitt, 1989). The management of *H. armigera* is difficult and in many crops, including cotton and pigeonpea, relies heavily on the use of insecticides (King, 1994; Shanower et al., 1997). This has led to high levels of resistance to major groups of insecticides (Armes et al., 1996). Thus, research now focuses on alterna-

tive control methods such as cultural and biological control, and host plant resistance as the major components of integrated pest management programmes (Shanower et al., 1997). The possibility for biological control of *Helicoverpa*/*Heliothis* spp. through conservation and augmentation of natural enemies, classical biological control, and the use of microbial insecticides has been reviewed by King & Coleman (1989). *Helicoverpa armigera* is a strong flier and the mobility and rapid colonization of new habitats is a major factor limiting the effectiveness of most natural enemies (Fitt, 1989). Promising biocontrol agents against *Helicoverpa/Heliothis* spp. are egg parasitoids belonging to the genus *Trichogramma* (Hymenoptera: Trichogrammatidae) as they have a short generation time and can be easily mass-produced. These parasitoids have been successfully released in biological control programmes against *Heliothis*/*Helicoverpa* spp. for example in cotton (King et al., 1986; Romeis & Shanower, 1996).

Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is an important pulse crop in the semi-arid tropics. Its uses are manifold; the seeds are used for human consumption, pod walls and leaves as fodder, and dried stems as fuel or thatch. In addition, it has a high nitrogen fixing ability and is therefore important in improving soil quality (Nene & Sheila, 1990). The pod boring *H. armigera* is the major biotic constraint to increasing production in pigeonpea (Shanower et al., 1999). One reason for its high pest status on pigeonpea is the lack of efficient natural enemies on this crop. For example in India, *Trichogramma* spp. cause high parasitism levels on *H. armigera* eggs on crops such as sorghum, cotton and tomato, but only rarely parasitize eggs on pigeonpea (Romeis & Shanower, 1996). Several pigeonpea plant characters have been identified which interfere with the searching behaviour of *Trichogramma* spp., resulting in low egg parasitism levels. These characters include: (1) volatiles produced by plants in the reproductive growth stage, the stage preferred for oviposition by *H. armigera*, are repellent to *T. chilonis* Ishii, (2) trichomes and trichome exudates on the surface of the reproductive plant structures inhibit the walking behaviour or trap the searching parasitoids, and (3) chemicals from the pod surface are deterrent to *T. chilonis* after contact (Romeis et al., 1997, 1998b).

Several authors reported that the activity of naturally occurring *Trichogramma* spp. can be increased by diversifying the agroecosystem (Kemp & Simmons, 1978; Altieri et al., 1981). For example, the parasitism levels of *H. zea* Boddie (Lepidoptera: Noctuidae) eggs on corn increased significantly when corn was intercropped with tomato and beans, two crops on which high egg parasitism levels are recorded (Nordlund et al., 1984). In India, intercropping medium-duration pigeonpea with sorghum is a common practice (Ali, 1990). In this system, sorghum is harvested more than one month before pigeonpea flowers and therefore the latter crop does not benefit from the buildup of *Trichogramma* spp. populations in sorghum (Manjunath et al., 1989). With the introduction of short-duration pigeonpea, sorghum and pigeonpea can be intercropped with a close synchronization of their flowering times, leading to simultaneous activity of *H. armigera* in the two crops. In this cropping system, *Trichogramma* spp. have been reported to parasitize up to 69% of *H. armigera* eggs collected from pigeonpea during one season (Duffield, 1994). The author suggested that parasitoids moved from sorghum into pigeonpea. Parasitism levels on pigeonpea declined once the influx from sorghum stopped, indicating that the parasitoid population was not sustained in the pigeonpea crop.

The main objective of this study was to further investigate the possibility of enhancing parasitism levels of *H. armigera* eggs on short-duration pigeonpea by intercropping with sorghum. A secondary objective was to understand the reasons for the variable parasitization efficiency of *Trichogramma* spp. on pigeonpea. A second strategy, the mass-release of *T. chilonis*, was also used to try to increase *H. armigera* egg parasitism levels on pigeonpea. With this strategy, the parasitoids were 'forced' into the field rather than attracted as the intercrop system attempted to do. In addition, the ovipositional preference of *H. armigera* for the different pigeonpea plant structures was evaluated as an earlier greenhouse study has shown that the parasitization efficiency of *Trichogramma* spp. varies with the plant structure on which the host eggs are located (Romeis et al., 1998b).

## Materials and methods

All field trials were conducted on black vertisols at ICRISAT Asia Center near Hyderabad, India.

*Pigeonpea-sorghum intercropping trials.* A total of five intercropping experiments were conducted between 1994 and 1997. The results from three trials are presented in this paper. Two trials are excluded

as the pigeonpea plant structures from which the *H. armigera* eggs were collected were not recorded (1994 rainy season) and the host density remained very low (1995/96 post-rainy season) (Romeis, 1997). In the two seasons not included in this paper, less than 2% of the *H. armigera* eggs collected from pigeonpea were parasitized.

Different genotypes of short-duration pigeonpea and sorghum (CSH 9) were used during different seasons (Table 1). Row spacing in all trials was 60 cm. Pigeonpea was planted in plots arranged in two parallel rows. The plots were separated by four to eight rows or 4 m of sorghum. The field was surrounded by eight rows or 4 m of sorghum. In two trials, sorghum was sown on two dates in alternate rows to extend the availability of flowering panicles in the field. During all trials, the growth stage of at least 10 pigeonpea and sorghum plants was noted on each sample date to identify the date on which 50% of the plants were flowering.

*1995 rainy season.* One pigeonpea genotype was planted on four sowing dates (Table 1). The different sowing dates were selected to ensure that some of the pigeonpea plants flowered before, at the same time, and shortly after sorghum.

*Helicoverpa armigera* eggs were collected from 10 plants of each pigeonpea sowing and 20 sorghum plants on each sample date (see sampling procedure below). With the exception of the first two and the last three samples, a minimum of 43 eggs were collected from sorghum per sample. A minimum of 43 eggs were collected from pigeonpea on each sample date with the exception of the first five samples.

A total of 550 pigeonpea pods were collected during the season and observed under a stereo microscope to see if *Trichogramma* spp. were trapped by the trichome exudates on the pigeonpea pod surface.

*1996 rainy season.* Twelve pigeonpea genotypes were sown on different dates, depending on the reported time to 50% flowering, ensuring that the plants flowered at about the same time that sorghum flowered (Table 1).

*Helicoverpa armigera* eggs were collected from 10 plants of each pigeonpea genotype (five in each plot) and 40 sorghum plants (20 from each of the two sowings) on each sample date. With the exception of the first two and the last four samples, a minimum of 40 eggs were collected from sorghum per sample. A minimum of 41 eggs were collected from pigeonpea (all genotypes) on all but the first three samples.

*1996/97 post-rainy season.* The field design was similar to the 1996 rainy season trial. Four pigeonpea genotypes were sown on one date (Table 1). *Helicoverpa armigera* eggs were collected from 20 plants of each pigeonpea genotype (10 per plot) and 40 sorghum plants (20 from each of the two sowings) on each sample date. A minimum of 40 eggs were collected from sorghum per sample with the exception of the first two and the last two samples. From each of the four pigeonpea genotypes a minimum of 30 eggs were collected on each sample date, with the exception of the last sample.

*Sampling procedures*

*Sampling* H. armigera *eggs.* All eggs collected during this study were oviposited by naturally occuring *H. armigera.* To evaluate host egg density, a fixed number (given above for each trial) of pigeonpea and sorghum plants were randomly sampled twice a week. Sorghum panicles were removed, dissected in the laboratory, and all eggs collected. Eggs on pigeonpea were counted and collected in the field. The plant structure (calyx = unopened flower-bud, flower-calyx; pod; leaf; stem; flower-petal) on which each egg was found was recorded. The plant growth stage was recorded based on the most advanced plant structure: vegetative, budding, flowering (open flowers, including small pods) and podding. *Helicoverpa armigera* eggs were kept individually in gelatine capsules or glass vials at room temperature. They were later examined to determine if a larva had emerged, if the egg failed to hatch, or was parasitized.

*Sampling egg parasitism levels.* There are several problems associated with the term 'percentage parasitism' (Van Driesche, 1983). In this study, the percentage of eggs parasitized has been estimated by simply dividing the number of eggs parasitized by *Trichogramma* spp. by the total number of eggs collected. All parasitism levels reported here are therefore likely to be an overestimate as parasitized *H. armigera* eggs stay longer in the field than unparasitized eggs. However, it is difficult to calculate the amount of overestimation for several reasons. First, because of the longer development time, parasitized eggs are more prone to predation and to being dislodged from the plant. Second, black (parasitized) eggs are more dif-

*Table 1.* Design of the pigeonpea-sorghum intercropping trials

| Season | Pigeonpea genotypes | Pigeonpea sowing dates | Number of pigeonpea plots | Pigeonpea plot size | Sorghum sowing dates |
|---|---|---|---|---|---|
| Rainy 1995 | ICPL 87 | 13 June 3, 18, 31 July | 28 (7 per sowing date) | 20 m × 8 rows | 3 July |
| Rainy 1996 | ICPL 87, ICPL 151, ICPL 269, ICPL 84052, ICPL 86012, ICPL 86015, ICPL 88034, ICPL 89030, ICPL 90028, ICPL 95028, ICPL 95045, MPG 537 | 18 July to 1 August | 24 (2 per genotype) | 30 m × 8 rows | 11, 24 July |
| Post-rainy 1995–1996 | ICPL 87, ICPL 151, ICPL 84052 ICPL 88034 | 17 October | 8 (2 per genotype) | 30 m × 8 rows | 16, 25 November |

ficult to find on a plant, and third, it is not known how long parasitized eggs, in which the parasitoid died, remain on the plant.

A minimum number of *H. armigera* eggs were collected from pigeonpea and sorghum plants at each sample date to calculate the level of parasitism (given above for each trial). If a sample contained less than the minimum number of eggs, because of low host density, the parasitism level for that sample was not calculated.

After the parasitoids from each egg had died, the clutch size and progeny sex ratio were recorded. In total 624 male *Trichogramma* spp. were identified by Dr. J. C. Monje (Institute of Phytomedicine, University of Hohenheim, Germany, where voucher specimens are deposited) (see Monje et al., 1998).

*Monitoring* Trichogramma *spp. adults.* Adult *Trichogramma* spp. populations were monitored in the field using white cylindrical sticky traps (Romeis et al., 1998c). Traps were placed within sorghum at panicle height and within pigeonpea at crop canopy and sorghum panicle height. During rainy season trials, sorghum panicle height and pigeonpea crop canopy height were approximately 1.5 m and 0.7 m, respectively. Because of the smaller size of the plants during the post-rainy season, traps were placed at approximately 1.0 m and 0.3 m. Five traps were placed in each crop and at each height and replaced with fresh traps after 2 or 3 days. *Trichogramma* spp. on each trap were counted and sexed under a stereo microscope in the laboratory. The number of parasitoids caught is expressed as parasitoids per trap per day. Correlation and linear regression analysis was used to evaluate the relationship between trap catches in sorghum and pigeonpea (SYSTAT, 1996).

*Mass-release trial.* The *T. chilonis* egg-cards (trichocards) used for the mass-releases were obtained from the Central Integrated Pest Management Centre (CIPMC) in Hyderabad. A rectangular 1.1 ha pigeonpea (ICPL 87) field was sown on 27 June 1996. The field was divided into two halves. In one half, a plot of 42 × 60 m (0.25 ha) was marked and used for the parasitoid releases, while the other half of the field was used as a control. A total of seven parasitoid releases were made at a weekly interval between 13 September and 26 October. At each release, fourteen to sixteen trichocards were liberated from 14 equally distributed release points. The cards were attached to a rod at crop canopy height (0.7 m) and covered with a black plastic cup. Honey agar was provided on the inner wall of the cup to increase the longevity of the parasitoids. A ring of glue (Bird-Tanglefoot®) around the rod prevented predators from reaching the egg-cards. The trichocards were placed in the field in the late afternoon of the day when the first parasitoids began emerging to minimize the detrimental effect of high temperatures. The approximate number of healthy females (i.e., not deformed) liberated was estimated for each release based on the quality of three trichocards as described in Romeis et al. (1998a). Parts of the three cards were kept in the laboratory and after the emerged parasitoids had died, progeny sex ratio and the percentage of deformed females was counted. The following parameters were assessed on the same

cards after field exposure: number of eggs per card, percentage parasitism, percentage emergence.

On each sample date *H. armigera* eggs were collected from 20 randomly selected plants in both the release and the control field. Additional eggs were collected in both fields from different plant structures between the releases. The plant structure on which each egg was found was recorded.

Five sticky traps were placed at crop canopy height in both the release and the control field to monitor the population of adult *Trichogramma* spp. The minimum distance between a sticky trap and a parasitoid release point was 4 m.

## Results

### *Pigeonpea – sorghum intercropping trials*

Helicoverpa armigera *egg density.* *Helicoverpa armigera* eggs were found on sorghum as soon as the first panicles emerged, but most eggs were found on flowering panicles. The crop lost its attractiveness to ovipositing *H. armigera* females when grains started to develop. The maximum egg density was reached when about 50% of the plants were flowering (Figures 1–3). The highest egg density, 13.6 eggs/plant, was recorded during the 1995 rainy season (Figure 1). During the 1996 rainy season the activity of *H. armigera* in sorghum could not be extended even though sorghum was sown at two dates with a two week interval (Figure 2). The plants of the second sowing remained small, up to half the size of the plants from the first sowing, and were heavily infected with sorghum ergot (*Sphacelia sorghi* McRae). Infected panicles were covered with a honey-like secretion and no *H. armigera* eggs were found. Sowing sorghum at two dates at an interval of one week during the 1996–1997 post-rainy season extended the activity of *H. armigera* in the crop to about five weeks (Figure 3).

In all intercropping trials, pigeonpea flowering coincided with the *H. armigera* oviposition on sorghum (Figures 1–3). With the exception of the 1996–1997 post-rainy season where up to 23.6 *H. armigera* eggs were found per plant (Figure 3), peak egg densities on pigeonpea were much lower than on sorghum (Figures 1 and 2).

The egg density curves from the four pigeonpea sowings during the 1995 rainy season and the 12 pigeonpea genotypes during the 1996 rainy season followed a similar pattern even though the plants reached 50% flowering at different dates within a two week interval (Romeis, 1997). They were therefore combined and the mean value plotted (Figures 1 and 2). During the 1996–1997 post-rainy season the maximum *H. armigera* egg density recorded was much higher on the two pigeonpea genotypes with determinate growth habit (ICPL 87, ICPL 151) than on the genotypes with indeterminate growth habit (ICPL 88034, ICPL 84052) (Figure 3).

*Egg parasitism levels and egg mortality.* From a total of 4680 *H. armigera* eggs collected from sorghum during all seasons, 3040 (65%) were parasitized by *Trichogramma* spp. or, rarely, *Trichogrammatoidea* spp. ($n = 50$). During all field trials, egg parasitism levels on sorghum were high throughout the period eggs were available, varying from a minimum of 27.9% to a maximum of 100% (Figures 1–3).

Despite the high levels of egg parasitism on sorghum, parasitism on pigeonpea was low during the first two seasons (Figures 1 and 2). During the 1995 rainy season, 0.4% (total number of eggs collected $n = 1301$) of the *H. armigera* eggs collected on pigeonpea were parasitized. The overall parasitism level in the 1996 rainy season was 3.0% ($n = 811$), though up to 11.5% parasitism was recorded in some samples (Figure 2). A high percentage of parasitized eggs were collected from pigeonpea only during the 1996–1997 post-rainy season (Figure 3). During this trial, 14.1% of the eggs collected ($n = 2985$) from the four pigeonpea genotypes were parasitized. Early in this season, a majority of *H. armigera* eggs, between 51.6 and 100%, were found on leaves even before *H. armigera* eggs were present on sorghum. This was the case in the samples 1, 1–2, 1–5 and 1–3 from ICPL 87, ICPL 151, ICPL 88034 and ICPL 84052, respectively. Parasitism levels up to 73.0% were recorded in these early samples.

The percentage of parasitized eggs collected from pigeonpea varied with the plant structure on which the eggs were found. The highest parasitism level, 40.7%, was recorded on eggs collected from leaves (number of eggs collected, $n = 808$), followed by stems (17.5%, $n = 63$), calyxes (3.6%, $n = 4383$), flower-petals (1.5%, $n = 403$) and pods (0.3%, $n = 716$). There is a significant positive relationship between parasitism levels recorded on pigeonpea during the 1996–1997 post-rainy season (Figure 3) and the proportion of eggs found on leaves (Figure 4).

Parasitoids died, during the pupal stage, in 509 (16.7%) of 3040 parasitized *H. armigera* eggs col-

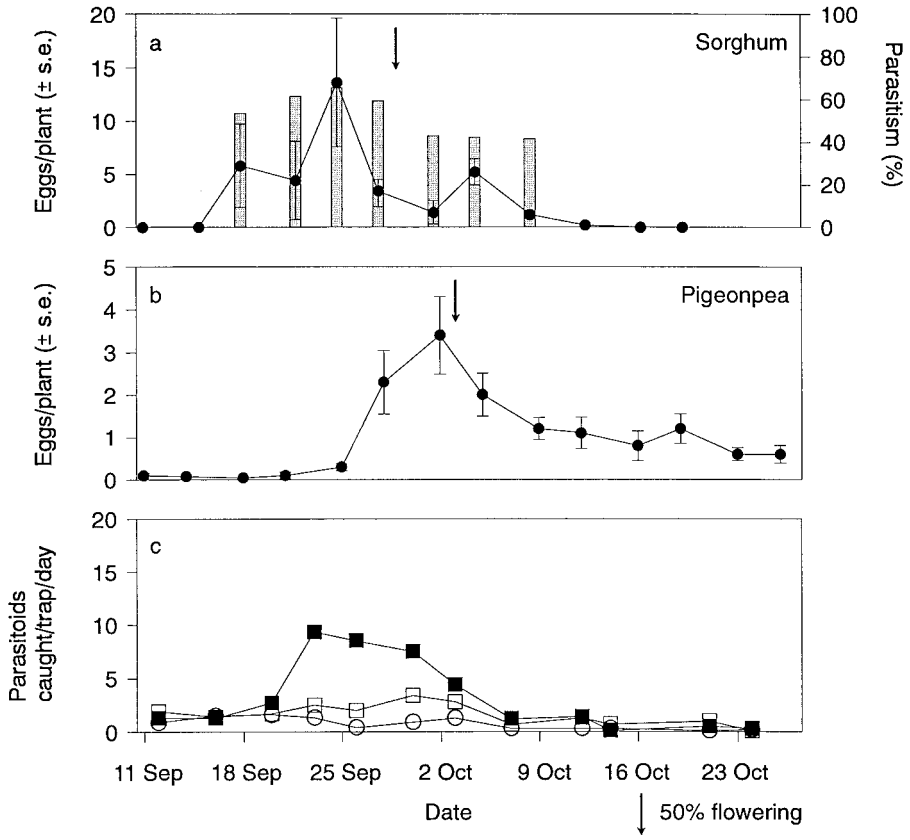


*Figure 1. Helicoverpa armigera* and *Trichogramma* spp. in a pigeonpea-sorghum intercrop during the 1995 rainy season, (a) *H. armigera* egg density (line) on sorghum and level of parasitism (bars) by *Trichogramma* spp., (b) *H. armigera* egg density on pigeonpea (four different sowings combined), (c) *Trichogramma* spp. population recorded on sticky traps in sorghum (■ 1.5 m) and pigeonpea (first sowing; □ 1.5 m, ○ 0.7 m). Note the different scales on the y-axes.

lected from sorghum. More than 99% of the emerged parasitoids belonged to *T. chilonis*. The mean (± s.e.) clutch size of *T. chilonis* was 2.03 ± 0.015 and the overall sex ratio was 51.7% females. Two parasitoids emerged from most (58.3%) *H. armigera* eggs, but one egg produced six wasps (Figure 5). The progeny sex ratio (% females) decreased with clutch size, from 63.1% at a clutch size of one to 46.0% at a clutch size of five. Out of a total of 420 parasitized eggs collected from pigeonpea during the 1996–1997 post-rainy season, parasitoids died in 55 (13.1%). About 83% of the emerged parasitoids belonged to *T. chilonis*. In addition to the mortality caused by egg parasitoids, 18.2% of the eggs collected from sorghum and 10.2% of the eggs collected from pigeonpea failed to hatch for unknown reasons.

*Monitoring* Trichogramma *spp. adults.* The sticky trap catches show that *Trichogramma* spp. were present in the field in low numbers before the first *H. armigera* eggs were found on the plants. The parasitoid population recorded on sticky traps in sorghum at panicle height increased when *H. armigera* began ovipositing (Figures 1–3). The parasitoid density above the pigeonpea plants, at sorghum panicle height, increased significantly with the parasitoid density in sorghum ($y = 0.67 + 0.15x$; $R^2 = 0.44$; $P < 0.001$; $n = 40$) (Figures 1–3) but remained much lower than in sorghum. The number of parasitoids caught in pigeonpea at canopy height did not increase when *H. armigera* started ovipositing and was not correlated with a high parasitoid population in sorghum ($r = 0.15$; $P = 0.369$; $n = 40$).

The majority of parasitoids, 93 to 98% during the different seasons, caught on the sticky traps were female. The proportion of females caught was much higher than the progeny sex ratio recorded from par-

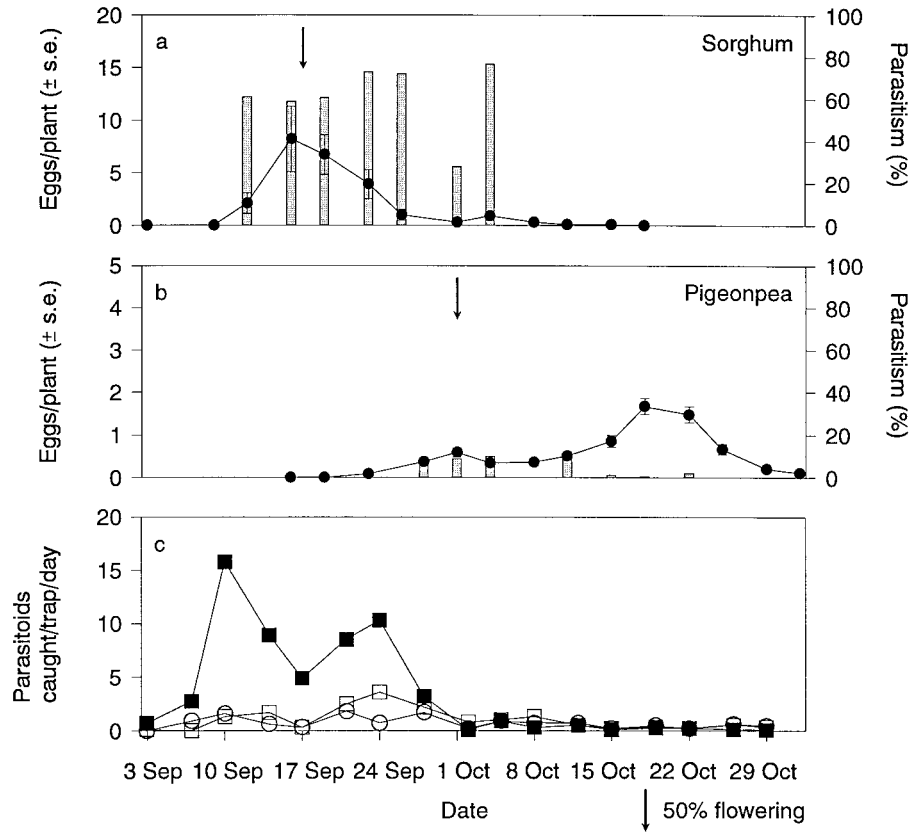


*Figure 2. Helicoverpa armigera* and *Trichogramma* spp. in a pigeonpea-sorghum intercrop during the 1996 rainy season, (a) *H. armigera* egg density (line) on sorghum and level of parasitism (bars) by *Trichogramma* spp., (b) *H. armigera* egg density on pigeonpea (12 genotypes combined) and level of parasitism by *Trichogramma* spp., (c) *Trichogramma* spp. population recorded on sticky traps in sorghum (■ 1.5 m) and pigeonpea (ICPL 87; □ 1.5 m, ○ 0.7 m). Note the different scales on the y-axes.

asitized *H. armigera* eggs collected from sorghum (49–55%).

*Mass-release trial*

The density of *H. armigera* eggs reached a maximum of 4.1 eggs/plant about three weeks after 50% of the pigeonpea plants were flowering. Throughout the season, 1383 eggs were collected in the release field and 1339 in the control field. Even though between 132 000 and 186 000 healthy *T. chilonis* females were liberated per ha in the release field at each release, the parasitism level remained low (2.2%). In the control field, 1.5% of the collected eggs were parasitized. In both fields, eggs collected from leaves ($n = 150$) were most frequently parasitized (15.3%), while parasitism levels of eggs collected from flower-petals ($n = 192$), calyxes ($n = 1775$), and pods ($n = 605$) were 3.1%, 1.0%, and 0.3%, respectively.

The parasitoid population in the field remained low. In 17 samples taken with the sticky traps, a total of 271 *Trichogramma* spp. were caught in the release field as compared to 228 in the control field.

Temperatures during the mass-release period were between 16 °C and 32.5 °C. Total rainfall in the month of September and October was 200 mm.

Helicoverpa armigera *egg distribution on pigeonpea*

Most *H. armigera* eggs were found on the green parts of the reproductive structures, i.e., calyxes and pods (Figure 6). Out of a total of 6479 eggs collected during all trials from pigeonpea plants at different growth stages, 80.7% were found on calyxes or pods, 11.9% on leaves, 6.4% on flower-petals, and 1.0% on stems. There was some variation in the distribution of eggs between the different plant growth stages (Figure 6), but a minimum of 74.8% of the eggs were collected from calyxes or pods. The proportion of eggs on leaves

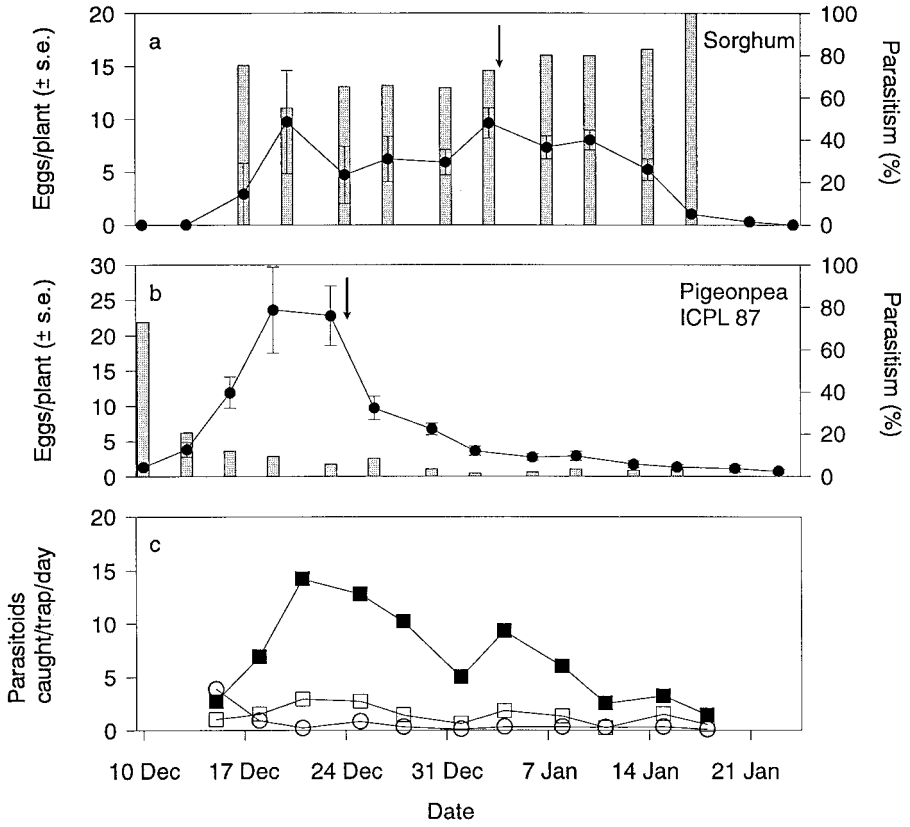


*Figure 3. Helicoverpa armigera* and *Trichogramma* spp. in a pigeonpea-sorghum intercrop during the 1996–1997 post-rainy season, (a) *H. armigera* egg density (line) on sorghum and level of parasitism (bars) by *Trichogramma* spp., (b, d, e, f) *H. armigera* egg density on four different pigeonpea genotypes and level of parasitism by *Trichogramma* spp., (c) *Trichogramma* spp. population recorded on sticky traps in sorghum (■ 1.0 m) and pigeonpea (ICPL 87; □ 1.0 m, ○ 0.3 m). Note the different scales on the y-axes.

decreased with plant development from 22.8% on budding plants to 2.5% on podding plants. In general, eggs were only rarely found on vegetative plants. But during the 1996–1997 post-rainy season, *H. armigera* started ovipositing on pigeonpea while the plants were still in the vegetative growth stage. Thus, during the early samples, up to 100% of the eggs were collected from leaves (see above).

## Discussion

*Helicoverpa armigera* was attracted to sorghum throughout anthesis with the peak egg density coinciding with the 50% flowering stage, as has been reported earlier (Parsons, 1940; Duffield, 1994). The sticky trap catches show that *Trichogramma* spp. occurred in the field in low numbers before *H. armigera* began ovipositing on sorghum and caused high parasitism levels as soon as host eggs were present. The parasitoid population increased when *H. armigera* started ovipositing and remained high as long as hosts were available. There was no asynchrony in colonization of sorghum by *H. armigera* and *Trichogramma* spp. This asynchrony is generally regarded as one of the major factors limiting the effectiveness of natural enemies of *Helicoverpa*/*Heliothis* spp. (Fitt, 1989).

The high parasitoid population in sorghum during anthesis may be partly due to volatiles emitted from panicles in the flowering and soft dough stage. Olfactometer studies have shown that volatiles emitted during these stages arrest *T. chilonis*, the predominate egg parasitoid of *H. armigera* in India (Romeis et al., 1997). However, it seems that host kairomones and/or host eggs must also be present to sustain a high parasitoid population. The *Trichogramma* spp. population remained low until *H. armigera* eggs were available, even though the parasitoids are also arrested by volatiles from sorghum leaves (Romeis et al., 1997).

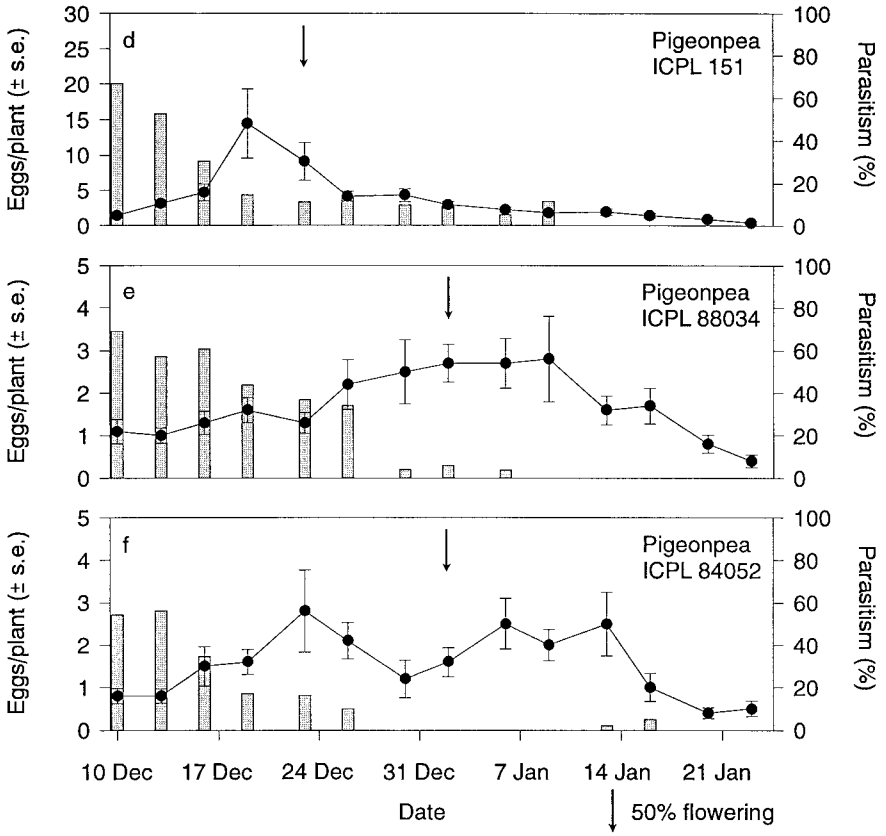


*Figure 3.* Continued.

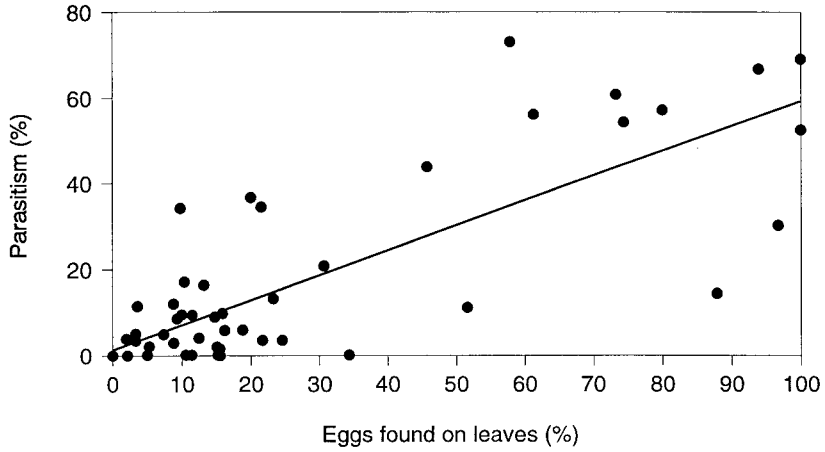


*Figure 4.* Relationship between the percentage of *Helicoverpa armigera* eggs collected from leaves of four pigeonpea genotypes during the 1996–1997 post-rainy season and the percentage of eggs parasitized per sample ($n = 56$). The linear regression equation is: $y = 1.32 + 0.58x$, $R^2 = 0.66$, $P < 0.001$.

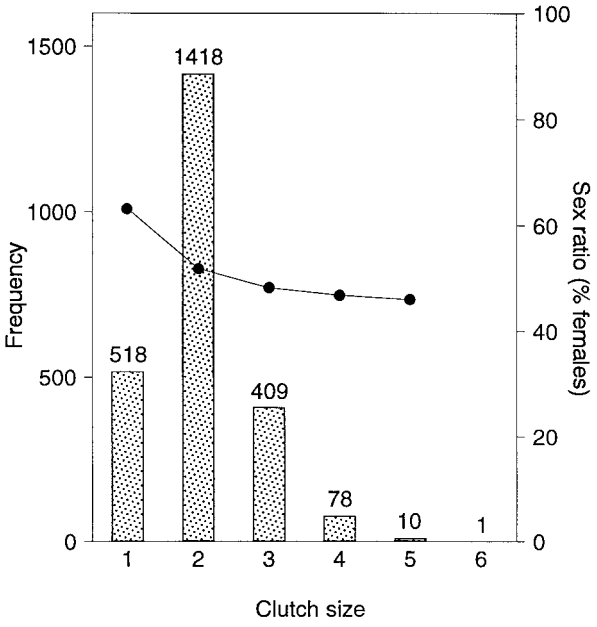


*Figure 5.* Clutch size (bars) and sex ratio (line) of *Trichogramma chilonis* emerging from *Helicoverpa armigera* eggs collected from sorghum ($n = 2434$).

*Trichogramma* spp. are effective parasitoids of *H. armigera* on sorghum even at low host densities. During an intercropping experiment in the 1995–1996 post-rainy season, parasitism levels on sorghum were greater than 42% despite a maximum host density of only 1.5 eggs/plant (Romeis, 1997). This, together with the fact that parasitism levels increase with host egg density (King, 1988) and the synchrony in colonization of the field, makes *Trichogramma* spp. promising biological control agents for *H. armigera* on sorghum. However, the impact of egg parasitoids on the dynamics of *H. armigera* populations on sorghum has not been investigated.

We believe that superparasitism was common on *H. armigera* eggs collected from sorghum. *Trichogramma* spp. allocate male eggs preferably at the second oviposition and then later in an oviposition bout, after a series of females (Suzuki et al., 1984; Waage, 1986). This sex allocation sequence should lead to an increase in the proportion of female progeny with increasing clutch size, what has been documented in several field and laboratory studies (Suzuki et al., 1984; Calvin et al., 1984; Waage, 1986). The decrease in sex ratio with increasing clutch size observed in our study is interesting and could be due to superparasitism, which has been found to increase the proportion of male progeny (Salt, 1936; Chacko, 1969; Suzuki et al., 1984).

Pigeonpea gained no benefit from the high *Trichogramma* spp. population in the sorghum intercrop. The number of parasitoids caught on the sticky traps within pigeonpea was much lower than on the traps within sorghum, even though the distance between traps was only about 4 m. The parasitoid population in pigeonpea remained low even when *H. armigera* eggs were found on the plants. This may be partly caused by volatiles emitted by pigeonpea plants in the reproductive growth stage which repel the parasitoids (Romeis et al., 1997, 1998b). Once sorghum became unattractive to *H. armigera* the parasitoids also left the field. There was no detectable movement of *Trichogramma* spp. from sorghum into pigeonpea as has been suggested by Duffield (1994). In a single season trial, Duffield reported high parasitism levels of eggs collected from pigeonpea when *H. armigera* was ovipositing simultaneously in both crops. In the present study, pigeonpea did not sustain a high *Trichogramma* spp. population even when parasitoids were mass-released into the field. Few *Trichogramma* spp. were caught on the sticky traps within the release field, indicating that the parasitoids did not move around in the field but left shortly after the release.

In addition to parasitism by trichogrammatids, eggs collected from sorghum suffered a higher mortality due to unknown causes than eggs collected from pigeonpea. This difference may have been caused by sucking egg predators such as *Orius* spp. (Hemiptera:Anthocoridae), which are more abundant in sorghum than in pigeonpea (Duffield & Reddy, 1997). But heavy superparasitism by *Trichogramma* spp. can also lead to the death of both the developing parasitoids and the host (Salt, 1936).

Most *H. armigera* eggs on pigeonpea were found on calyxes and pods. In general, only a small proportion of eggs were collected from leaves even though leaves constitute the largest part of the total plant surface area. However, the number of eggs oviposited on leaves is likely to be underestimated as dislodgement from leaves is higher than from reproductive structures (Romeis et al., 1998b). There was also some variation in the distribution of eggs within each plant growth stage among the different seasons (Romeis, 1997). Pigeonpea possesses a distinct set of five different types of glandular and non-glandular trichomes and their distribution, density and length varies among the green parts of the reproductive structures and other parts of the plant (Romeis et al., 1999). Compared to

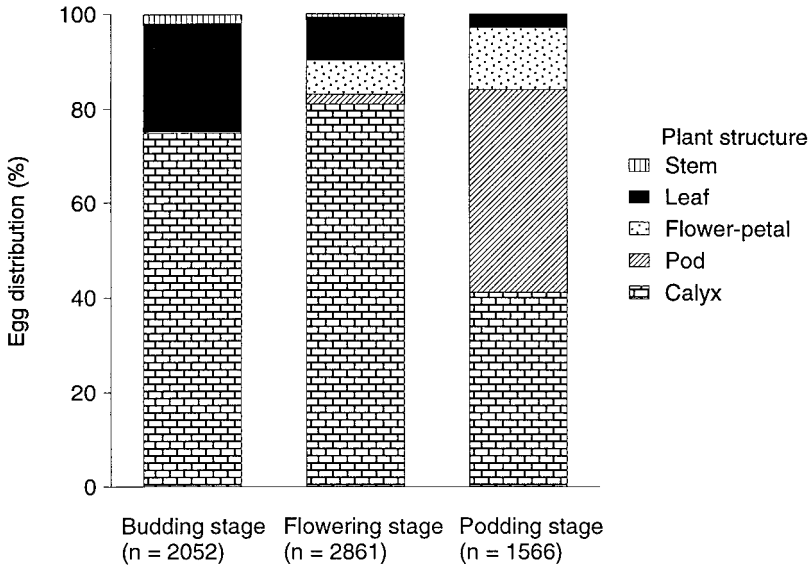


*Figure 6.* Distribution of *Helicoverpa armigera* eggs among different plant structures of pigeonpea (ICPL 87) plants at different growth stages.

leaves, trichomes on calyxes and pods are longer and the exudate-secreting trichomes are more common. These differences between plant structures may contribute to the oviposition preference of *H. armigera*. It is reported that *Helicoverpa*/*Heliothis* spp. generally prefer hairy over glabrous surfaces for oviposition (Zalucki et al., 1986; King, 1994). The long trichomes and exudates on pigeonpea reproductive structures also inhibit the movements of *Trichogramma* spp. (Romeis et al., 1998b). In the laboratory, wasps are often trapped by the sticky trichome exudates on the pod surface. This was not confirmed in the field as during the 1995 rainy season trial, only a single trichogrammatid was found stuck on 550 pigeonpea pods collected. This difference might be partly due to the low parasitoid population in the field, but it is also likely that the adhesive effect of the trichome exudates is negated by environmental factors such as dust, wind and rain (Obrycki & Tauber, 1984). The majority of *H. armigera* eggs oviposited on pigeonpea were therefore inaccessible to *Trichogramma* spp. Much higher parasitism levels were recorded on eggs collected from leaves as compared to eggs collected from reproductive structures, confirming earlier greenhouse studies (Romeis et al., 1998b). Few of the eggs on flower-petals were parasitized. Although these structures do not possess any trichomes, searching *Trichogramma* spp. would have to either land directly on the flower-petals or cross the hairy calyx to reach them. The relatively high parasitism level of eggs collected from stems may be due to the fact that the exudate secreting glandular trichomes are absent from this plant structure (Romeis, 1997).

High egg parasitism levels on pigeonpea were observed early in the 1996–1997 post-rainy season, before 50% of the plants reached the flowering stage. This is similar to results published by Duffield (1994). The high parasitoid efficiency was due to the large proportion of host eggs which were collected from leaves. The reasons why *H. armigera* oviposited on vegetative plants during this season are not known. One possibility is that a large *H. armigera* population had built up in adjacent chickpea fields, and the moths, looking for an alternate oviposition site, entered the pigeonpea-sorghum field before the plants had reached the reproductive growth stage. This could also explain the high egg densities on pigeonpea observed during this season. Pigeonpea leaves are not an optimal food source for *H. armigera* larvae when compared to reproductive structures, though the larvae can succesfully develop on leaves (Sison & Shanower, 1994). The high parasitism levels reported by Duffield (1994) may have also been a result of an exceptionally high proportion of *H. armigera* eggs oviposited on leaves.

Three evolutionary pressures may influence *H. armigera*'s ovipositional preference for pigeonpea calyxes and pods versus leaves. First, these structures provide an 'enemy-free space' (Price et al., 1980) as they are unsuitable for *Trichogramma* spp. and most likely for other small natural enemies. Second, calyxes

and pods are the plant structures most preferred and best suited for larvae to feed on (Fitt, 1989; Sison & Shanower, 1994), and third, eggs adhere better to the reproductive than vegetative structures due to the sticky glandular exudates (Romeis et al., 1998b). The latter is important as dislodgement from plants, probably caused by wind or rain, is an important mortality factor for *H. armigera* eggs (Kyi et al., 1991).

Our study has shown that the low parasitization efficiency of *Trichogramma* spp. on pigeonpea is the result of the ovipositional preference of *H. armigera*. Eggs laid on the plants' reproductive structures are almost out of reach of the parasitoids. Therefore, parasitism of *H. armigera* eggs on pigeonpea can not be increased through intercropping with sorghum or mass-releases of *T. chilonis*. Intercropping short-duration pigeonpea with sorghum may, however, benefit other groups of natural enemies of *H. armigera* (Duffield & Reddy, 1997) and could still be an important component to a successful integrated pest management programme.

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