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# Occurrence and direct control potential of parasitoids and predators of the fall armyworm (Lepidoptera: Noctuidae) on maize in the subtropical lowlands of Mexico

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## Abstract

1 Native natural enemies have the potential to control fall armyworm *Spodoptera frugiperda* (Smith) in tropical maize grown in Mexico, where this insect pest causes severe economic losses to farmers. It has been proposed that enhancing herbivore-induced volatile emissions in maize plants may help to increase the effectiveness of natural enemies, which use these volatiles to locate their prey. This will only be of immediate benefit to farmers if the activity of the natural enemies results in a direct reduction in herbivory. Here we report on field surveys for the most common natural enemies in a tropical maize-growing region in Mexico and the potential effects of these enemies on herbivory by fall armyworm.

2 Caterpillars were collected in maize fields near Poza Rica in the state of Veracruz during January and February 1999, 2000 and 2001. Plants were either naturally infested by *S. frugiperda*, or artificially infested with laboratory-reared larvae. Ten species of parasitoids emerged from the collected larvae and eight species of predators that are known to feed on larvae and eggs were observed on the plants. *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) was the dominant parasitoid species, in 1999 and 2001.

3 Of the nine larval parasitoids collected, six (all solitary) are known to reduce herbivory, whereas one causes the host to eat more (for two species this is not known). This implies that enhancing the effectiveness of solitary endoparasitoids may benefit subsistence farmers in developing countries by immediately reducing herbivory. The overall benefit for the plant resulting from parasitoid activity also has important implications for the evolutionary role of parasitoids in contributing to selection pressures that shape indirect defences in plants.

## Keywords

Biological control, fall armyworm, maize, Mexico, pest management, *Spodoptera frugiperda*, parasitoids, predators.

## Introduction

*Spodoptera frugiperda* (Smith) (Lepidopetra: Noctuidae) is one of the most destructive insect pests of maize in the Americas (Kranz *et al.*, 1977). First historical yield loss was registered in the United States in 1899 (Cruz, 1995). Since then various efforts have been undertaken to control this pest. Chemical control is still needed during times of outbreaks (Kranz *et al.*, 1977). Maize varieties resistant to fall armyworm have been selected and used in some countries (Mihm *et al.*, 1988). However, to achieve sustainable control an effective biological control that delays this pest's adaptation to resistant varieties would be desirable.

The combined use of resistant maize varieties and biological control may be improved further by enhancing the attractiveness of the varieties to natural enemies. Many

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plants release volatiles when under herbivore attack by herbivores and these volatiles serve as prey/host location cues for predators and parasitoids (Turlings & Benrey, 1998; Dicke & Vet, 1999). Indeed, several field assays show that parasitoids and predators are attracted to odours released by plants carrying the insects that these natural enemies attack (Drukker *et al.*, 1995; De Moraes *et al.*, 1998; Thaler, 1999; Kessler & Baldwin, 2001). Enhancing the release of these volatiles may improve the efficacy of these natural enemies. In maize, caterpillar feeding results in the release a blend of inducible volatiles that is attractive to various parasitoids (Turlings *et al.*, 2002). There is high variability among different maize varieties in the quality and quantity of the induced odour blends (Gouinǵuene *et al.*, 2001; Fritzsche Hoballah *et al.*, 2002), which should facilitate efforts to breed varieties that are highly attractive to parasitoids.

However, increased parasitism is no guarantee for reduced herbivory, as parasitoids not always cause their hosts to feed less. This has been a topic of discussion in the context of herbivore-induced volatiles functioning as indirect defence signals (Van der Meijden & Klinkhamer, 2000). Only if the action of parasitoids can benefit plant fitness directly are they expected to contribute to the selection pressures that shape the indirect defence traits (Hare, 2002; Janssen *et al.*, 2002). Few studies have demonstrated parasitoid-mediated plant fitness benefits (van Loon *et al.*, 2000; Fritzsche Hoballah & Turlings, 2001). For maize we found that a plant can produce on average 30% more seeds if a *Spodoptera* caterpillar attacking the plant is parasitized by *Cotesia marginiventris* (Hymenoptera: Braconidae) than if the plant is attacked by an unparasitized caterpillar (Fritzsche Hoballah & Turlings, 2001). Plants therefore may benefit from increasing the host-finding efficiency of this parasitoid and so may farmers as increased parasitism leads to increased yield. However, the effect of other native parasitoids on maize performance is still largely unknown. Teosinte, the wild ancestor of maize, originates from Mexico. Hence, studies into the natural defence traits of maize should be done with insects native to Mexico, which are most likely to have contributed to selection pressure that shaped these traits.

Surveys of parasitoids of *S. frugiperda* are still few (Ashley, 1986), as are studies on predators of fall armyworm (Van Huis, 1981; Andrews, 1988; Cruz, 1995). In the current study, we recorded and identified parasitoids that we obtained from *S. frugiperda* larvae collected from maize plants and predators that were observed feeding on caterpillars, near Poza Rica (Veracruz, Mexico). Using our own results and those reported by others on the effects of parasitoids on host development and feeding, we compared the potential of the recorded parasitoids to reduce herbivory directly.

## Materials and methods

### Infestation of maize plants with *S. frugiperda* larvae

The maize variety used in 1999 and 2000 was Insect Tolerant Synthetic (ITS) G1 (white), which was selected for its relatively high emission of induced volatiles (unpublished data). Three and four field plots (5 m × 10 m), consisting of 400–500 maize plants each (4–5 leaf stage), were used in 1999 and 2000, respectively. Plant spacing was 20 cm within and 50 cm between rows with 10 rows per plot. We artificially infested maize plants with first-instar larvae of *S. frugiperda*. The experiments were carried out at the International Maize and Wheat Improvement Centre (CIMMYT) station in Lindero near Poza Rica (20.492° N; 97.547° W; state of Veracruz, Mexico). One week prior to infestation, insecticide methomyl (Lannate 90, DuPont) was applied in all plots at a rate of 125 g a.i./ha to eliminate *S. frugiperda* larvae and other herbivorous insects on the plants. Groups of three neighbouring plants were chosen randomly and infested with fall armyworm larvae, two groups per row per plot. *Spodoptera frugiperda* larvae were obtained from a colony reared on artificial diet at CIMMYT (Texcoco, state of Mexico) and were 4 days old (first instar) when they were used for infestation. Each plant was infested with 20 larvae. In 1999, 20 groups of three plants were infested starting on 21 January at weekly intervals, for 3 weeks. In 2000, 20 groups of three plants were infested starting on 31 January, four times at weekly intervals. Larvae were placed onto plants in the morning. Predators that were observed feeding on *S. frugiperda* larvae between 09.00 and 10.00 hours, 12.00 and 13.00 hours and 17.00 and 18.00 hours in January and February 1999 and 2000 in the maize field were recorded. The third day after infestation, infested plants were placed in a paper bag. In the laboratory, plants were individually removed from their bag and carefully examined for fall armyworm larvae and egg masses of *S. frugiperda*. *Spodoptera frugiperda* larvae were placed singly in plastic cups (4 cm top diameter, 2 cm bottom diameter, 4 cm high) because of their cannibalistic behaviour, and reared on artificial diet until formation of the pupa. Parasitoid emergence was recorded. Emerged parasitoids were kept and later identified. Identification was done with the use of a manual (Cave, 1995) and the identity of selected samples was confirmed by R. Cave (Zamorano Escuelá Agrıcola Panamericana, Honduras).

### Collection of naturally occurring *S. frugiperda* larvae

In January and February 2000 and 2001, *S. frugiperda* larvae of different stages were collected from maize fields in two locations, Lindero and Agua Fria, near Poza Rica. Larvae collected from maize plants were brought to the laboratory and placed singly in cups with artificial diet until pupa formation. Parasitoid cocoon formation was checked regularly and emerged parasitoids were identified as above.

## Results

### Parasitoids of *S. frugiperda*

In 1999, more than half of the larvae were recovered 3 days after their release (Table 1), whereas in 2000, less than 25% of the caterpillars were recovered after 3 days (Table 2). Only the parasitoid *Campoletis sonorensis* was reared

**Table 1** Number of insects found on maize plants artificially infested with *Spodoptera frugiperda* larvae, Poza Rica, Veracruz, Mexico, 1999

| On maize plants | 21 January 1999 | 28 January 1999 | 5 February 1999 |
|---|---|---|---|
| *S. frugiperda* larvae | 573/1420* | 1024/1420* | 833/1260* |
| Aphids | 159 | 298 | 277 |
| Thrips | 48 | 121 | 70 |
| Spiders | 20 | 21 | 6 |
| *Orius* sp. | 17 | 4 | 2 |
| *Chrysopa* sp. eggs | 0 | 39 | 26 |
| *C. sonorensis* | 12 (2.1%) | 103 (10.05%) | 0 |

*Total number of larvae released on plants, (%) percent parasitism.

from the larvae collected in 1999 and the highest parasitism rate among the three replications was 10% (Table 1). In contrast, in 2000, several parasitoid species were found, but parasitism rates were low, between 0.7% and 4.1% (Table 2).

The four braconid, four ichneumonid, one eulophid and one trichogrammatid parasitoid species found in 2000 are listed in Table 3. All are solitary endoparasitoids with the exception of *Euplectrus plathypenae*, which is gregarious. Larvae parasitized by this latter parasitoid increase their feeding by 30–50% compared to non-parasitized larvae (Coudron *et al.*, 1997). All other parasitoid species for which this information is available cause the caterpillars to eat less (Table 4). *Ophion flavidus*, *Pristomerus spinator* and *E. plathypenae* attack third- and fourth-instar larvae, whereas the majority of the other parasitoid species parasitize earlier instars of the caterpillars (Table 4).

In 2001, a 34.8% parasitism rate was found, with *Campoletis sonorensis* emerging from 23.1% of the recovered caterpillars (Table 5). The second most abundant parasitoid was *Cotesia marginiventris* (6.2%), followed by *Meteorus laphygmae* (1.9%), *P. spinator* and *Chelonus insularis* (1.7% each), *E. plathypenae* (0.2%), and finally *Aleiodes laphygmae* (0.1%). *Trichogramma atopovirilia* emerged from some of the *S. frugiperda* egg batches that we had collected.

### Predators of *S. frugiperda*

We observed several predators preying on *S. frugiperda* in the field (Table 3). The most common predators were the true bugs *Castolus* sp., *Podisus sagitta*, *Zelus longipes* and an unidentified Reduviidae, which all predominantly attack larger *S. frugiperda* larvae, and the coccinellid *Coleomegilla* sp., an unidentified Chrysopidae, a forficulid *Doru* sp. and the bug *Orius* sp., which attack newly emerged larvae (Tables 1 and 2).

## Discussion

### Natural enemies of *S. frugiperda* on maize plants

Parasitism levels varied considerably among the surveys. Lower parasitism rates in 2000 may have been due to higher competition of parasitoids with predators, whereas diversity and size of the habitat surrounding the plots could explain the higher diversity of parasitoids at that time. The 2000 location was near the 1999 site, but due to major floods 4 months earlier, only a few hectares surrounded by natural vegetation were planted in 2000, as opposed to the 43 ha in 1999. This caused the presence of a much higher number of weedy plants, which is often associated with higher numbers and diversity of natural enemies (Altieri & Whitcomb, 1980; Van Huis, 1981). High densities of egg-predators such as *Orius* sp. and an unidentified Chrysopidae in 2000 could also explain the low recovery of released caterpillars. These predators also feed on aphids and thrips, which were found in high numbers when predator abundance was also high (Table 2). Several other potential predators of *S. frugiperda* were frequently observed in 2000. The *Doru* sp. (Dermaptera) attacks eggs and first-instar larvae. The heteropteran bugs *Zelus longipes*, *Castolus* sp., *Podisus sagitta* and the

**Table 2** Number of insects found on maize plants artificially infested with *Spodoptera frugiperda* larvae, Poza Rica, Veracruz, Mexico, 2000

| On maize plants | 31 January 2000 | 7 February 2000 | 14 February 2000 | 21 February 2000 |
|---|---|---|---|---|
| *S. frugiperda* larvae | 459/1200* | 269/1200* | 242/1200* | 245/1200* |
| Aphids | 6/60† | 3/60† | 4/39† | 4/35† |
| Thrips | 558 | 598 | 497 | 407 |
| Spiders | 15 | 6 | 10 | 33 |
| *Orius* sp. | 55 | 46 | 38 | 52 |
| *Chrysopa* sp. eggs | 36 | 59 | 76 | 70 |
| Parasitoid cocoons | 8 (1.7%) | 2 (0.7%) | 10 (4.1%) | 3 (1.2%) |
| Parasitoid species | 5 | 2 | 5 | 2 |

*Total number larvae released on plants, (%) percent parasitism,
†number of adults/number of nymphs.

**Table 3** Parasitoid species that emerged from collected *Spodoptera frugiperda* eggs and larvae and predators observed feeding on *S. frugiperda* eggs or larvae found on maize plants near Poza Rica (Veracruz, Mexico, 1999–2001)

| | | |
|---|---|---|
| Parasitoids | | |
| 1 | *Aleiodes laphygmae* (Viereck) | (Hymenoptera: Braconidae) |
| 2 | *Campoletis sonorensis* (Cameron) | (Hymenoptera: Ichneumonidae) |
| 3 | *Cotesia marginiventris* (Cresson) | (Hymenopetra: Braconidae) |
| 4 | *Chelonus insularis* Cresson | (Hymenopetra: Braconidae) |
| 5 | *Euplectrus plathypenae* Howard | (Hymenoptera: Eulophidae) |
| 6 | *Homolobus truncator* (Say) | (Hymenopetra: Braconidae) |
| 7 | *Meteorus laphygmae* Viereck | (Hymenoptera: Ichneumonidae) |
| 8 | *Ophion flavidus* Brullé | (Hymenoptera: Ichneumonidae) |
| 9 | *Pristomerus spinator* (Fabricius) | (Hymenopetra: Ichneumonidae) |
| 10 | *Trichogramma atopovirilia* Oatman & Platner | (Hymenoptera: Trichogrammatidae) |
| Predators | | |
| 1 | *Castolus* sp. | (Heteroptera: Reduviidae) |
| 2 | *Coleomegilla* sp. | (Coleoptera: Coccinellidae) |
| 3 | Unknown Chrysopidae | (Neuroptera: Chrysopidae) |
| 4 | *Doru* sp. | (Dermaptera: Forficulidae) |
| 5 | *Orius* sp. | (Heteropetra: Anthocoridae) |
| 6 | *Podisus sagitta* (Fabricius) | (Heteroptera: Pentatomidae) |
| 7 | Unknown Reduviidae | (Heteroptera: Reduviidae) |
| 8 | *Zelus longipes* Linnaeus | (Heteroptera: Reduviidae) |

unknown Reduviidae were observed to feed on larger *S. frugiperda* larvae (fourth and fifth instar), whereas *Coleomegilla* sp. was observed to feed on younger larvae.

As in 1999, *Campoletis sonorensis* was the dominant parasitoid on the naturally occurring *S. frugiperda* larvae collected in 2001. This was also reported for the Cascavel region in Brazil with 47% parasitism by *Campoletis* sp. (Valicente & Barreto, 1999). Molina-Ochoa *et al*. (2001) recovered 11 parasitoid species during collections carried out in four Mexican states. We found the same six parasitoid genera in the state of Veracruz. We collected one *Chelonus* and one *Meteorus* species, whereas they listed three species of *Chelonus* and two species of *Meteorus*. Furthermore, the *Campoletis* found by Molina-Ochoa *et al*. (2001) was identified as *C. flavicincta* Ashmead, whereas the specimens that we collected were identified as *C. sonorensis*. Confusion in the determination of the parasitoids may explain these discrepancies (R. Cave, personal communication). Collections from Honduran maize fields yielded five species of parasitoids (Canas & O'Neil, 1998) also found among the 10 in our study, suggesting that these parasitoids are common to a large part of North and Central America. Parasitism of *S. frugiperda* by *C. marginiventris* on maize was low compared to that by other parasitoids in Florida (Ashley *et al*., 1980, 1982) as found in our study.

## Impact on herbivory

With the exception of the gregarious parasitoid *Euplectrus plathypenae*, all parasitoids can be expected to reduce herbivory by their victims. This is in agreement with the view of van Loon *et al*. (2000) that most parasitoids will directly benefit plant fitness. Predators, of course, immediately kill their victims and their impact on herbivory solely depends on what stage in the herbivores' development they attack. Maize and its wild ancestor teosinte originate from Mexico.

**Table 4** Parasitoids that emerged from *Spodoptera frugiperda* caterpillars, the instar of the host they are known to attack, the host instar they emerge from and the effect they have on their host in terms of host feeding rate and final weight (fw)

| Parasitoid | Host instarattacked | Instar emerged from | % less feeding or % less final weight (fw) |
|---|---|---|---|
| *Aleiodes laphygmae* (Viereck) | First, second[a] | Fourth[a] | Similar to *C. sonorensis*[h] |
| *Campoletis sonorensis* | 2–6 days old[a] | Before fourth[a] | 85.5% (fw) (*C. flavicincta*, 93% less[e]) |
| *Cotesia marginiventris* (Cresson) | First[a] | Fourth[a] | 86.2% (fw) |
| *Chelonus insularis* Cresson | Egg | Fifth[b] | 84% less[b] |
| *Euplectrus plathypenae* Howard* | Third, fourth[d] | – | 30–50% more (for host *Heliothis virescens*)[f] |
| *Homolobus truncator* (Say) | Small[a] | – | – |
| *Meteorus laphygmae* Viereck | Small[a] | – | Similar to *C. sonorensis* [i] |
| *Ophion flavidus* Brullé | Third, fourth, fifth[a] | – | 28–48% less[a]; 17, 20% less (2 size groups)[c] |
| *Pristomerus spinator* (Fabricius) | Third, fourth[a] | – | – |

*Is the only gregarious parasitoid, the other listed parasitoids are solitary.
[a](Cave, 1995); [b](Cruz, 1995), [c](Rohlfs & Mack, 1983); [d](Parkman & Shepard, 1982), [e](Vvan Cruz Figueiredo *et al*., 1997);
[f](Coudron *et al*., 1997), [g](Fritzsche Hoballah & Turlings, 2001), [h](Isenhour, 1988), [i](personal observation, Thomas Degen and Maria Elena Fritzsche Hoballah).

**Table 5** Location, date, number of corn plants checked for *Spodoptera frugiperda* larvae and number of larvae collected, that died during rearing in the laboratory, that formed a pupa (sex female, male, malformation), that gave a parasitoid cocoon and number of adult parasitoid species (for which species, see Table 3).

| Location | Date | Plants | Larvae | Dead | Pupae (f/m/malformation) | Cocoons | Species |
|---|---|---|---|---|---|---|---|
| Lindero | 31 Jan. 2000 | 396 | 135 | 42 | 88 (41/45/2) | 7 | 4 (2,3,6,10) |
| Lindero | 07 Feb. 2000 | 357 | 50 | 19 | 27 (9/16/2) | 1 | 1 (3) |
| Lindero | 14 Feb. 2000 | 438 | 69 | 21 | 47 (19/28/0) | 6 | 3 (3,4,10) |
| Lindero | 21 Feb. 2000 | 418 | 70 | 20 | 47 (20/27/0) | 9 | 5 (1,3,7,8,10) |
| Agua Fria | 09 Mar. 2000 | random | 15 | 5 | 3 (1/2/0) | 7 | 1 (4) |
| Agua Fria | 19 Mar. 2000 | random | 41 | 14 | 19 (8/10/1) | 3 | 1 (4) |
| Agua Ffria | 03 April 2000 | random | 56 | 3 | – | 3 | 1 (5) |
| Agua Fria | 15 Feb. 2001 | random | 1072 | 159 | – | 373 | 9 (1–9) |

Therefore, the insects studied here are likely to have contributed to the evolution of defence traits in this plant. The results imply that most natural enemies of *S. frugiperda* can have a positive impact on the plant's fitness, and therefore emitting signals that attract these natural enemies is advantageous to the plant.

*Campoletis sonorensis* and *C. marginiventris* accounted for at least 85% of the observed parasitism. These solitary parasitoids have very similar biologies and a precise estimate has been obtained for the maize fitness benefit posed by *C. marginiventris* (Fritzsche Hoballah & Turlings, 2001). The current study does not provide information on the impact of genuine pupal parasitoids, which have no direct impact on feeding rate by immature stages. However, in the context of the evolution of plant-produced signals as attractants for natural enemies, only larval and egg (Hilker *et al*., 2002) parasitoids are likely to use such signals. We may have missed some of the parasitism of the later larval stages, but because the density of these stages is very low, their impact is considered less important. Here we show that the great majority of larval parasitoids that attack early stages of *S. frugiperda* in Mexico are likely to have a positive impact on seed production, suggesting that both plant (in an evolutionary sense) and farmer (in terms of crop yield) will benefit from increasing the search efficiency of these wasps.

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