

Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids

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ABSTRACT

Herbivore-induced plant volatiles have been suggested to function as indirect defence signals that attract natural enemies of herbivores. Several insect parasitoids are known to exploit such plant-provided cues to locate hosts. It is unclear if individual plants benefit from the action of parasitoids. We investigated this question in maize plants under attack by *Spodoptera littoralis* larvae and found that parasitization by the endoparasitoids *Cotesia marginiventris* and *Campoletis sonorensis* significantly reduced feeding and weight gain in the host larvae. As a result, young maize plants attacked by a single parasitized larva suffered much less feeding damage and, at maturity, produced about 30% more seed than plants that were attacked by an unparasitized larva. Such fitness benefits may have contributed to selection pressures that shaped the evolution of herbivore-induced indirect defence signals in plants.

Keywords: *Campoletis sonorensis*, *Cotesia marginiventris*, indirect defence, parasitoids, plant fitness, plant–insect interactions, *Spodoptera littoralis*, *Zea mays*.

INTRODUCTION

Herbivore-induced chemical defences in plants can be direct, resulting in antibiosis and antixenosis (as a result of toxic and deterrent chemicals, respectively), or indirect, for example in the form of volatiles that attract natural enemies of the herbivores. Surprisingly few studies have shown that herbivore-induced chemical changes in plants enhance plant fitness under field conditions (Karban and Baldwin, 1997; Agrawal and Karban, 1999; Baldwin, 1999). In one such study, Baldwin (1998) showed that tobacco plants benefit from the induced production of toxic compounds (direct defence) under intermediate rates of herbivore attack and produce more seeds if they are induced than when they are not induced. Agrawal (1998, 1999), in a field experiment with wild radish, found that early-season caterpillar feeding resulted in a decrease in subsequent herbivory and, consequently, in enhanced seed production.

Fitness benefits resulting from indirect defences have been well documented for plants

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that attract ants with domatia and/or food (e.g. Janzen, 1966; McKey, 1988; Oliveira, 1997). But, as pointed out by several authors (Sabelis and de Jong, 1988; Faeth, 1994; van der Meijden and Klinkhamer, 2000; Hare, in press), evidence has been lacking for potential fitness benefits for plants resulting from attracting natural enemies with herbivore-induced volatiles. Although it has been clearly demonstrated that natural enemies such as parasitoids make effective use of induced plant volatiles to locate the microhabitat of their hosts (e.g. Turlings *et al.*, 1990; McCall *et al.*, 1993; Steinberg *et al.*, 1993; Mattiacci *et al.*, 1994; Finidori-Logli *et al.*, 1996; Ngi-Song *et al.*, 1996; De Moraes *et al.*, 1998; Guerrieri *et al.*, 1998), it is not always evident that plants will benefit from attracting these parasitoids. Many parasitized Lepidoptera larvae continue to feed and, in some cases, they may even consume more than if they were not parasitized (Rahman, 1970; Hunter and Stoner, 1975; Slansky, 1978; Beach and Todd, 1986). On the other hand, numerous solitary parasitoids attack early instar larvae and seem to reduce significantly the development and feeding rate of their host (Rahman, 1970; Duodu and Antoh, 1984; Hegazi *et al.*, 1988; Grossniklaus-Bürgin *et al.*, 1994; Schopf and Steinberger, 1996; Kruse and Raffa, 1999). Evidence that parasitoids benefit plants comes from a study on seed feeding herbivores that showed increases in seed production by host plants due to parasitization of the herbivores (Gómez and Zamora, 1994). A notable recent study by Van Loon *et al.* (2000) showed that *Arabidopsis thaliana* plants produce considerably less seed after herbivory by healthy larvae of *Pieris rapae* (Lepidoptera: Pieridae) than after herbivory by larvae that were parasitized by the solitary endoparasitoid *Cotesia rubecula*. In such cases where a reduction in feeding by the larvae enhances the performance of a plant, it could be a selective advantage to the plant to assist such parasitoids in finding the caterpillars.

The responses to herbivore-induced plant volatiles have been extensively studied for the New World endoparasitoids *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae). These solitary parasitoids attack mostly young lepidopteran larvae (Jalali *et al.*, 1987; Rajapakse *et al.*, 1992) on various plants, including crops such as maize, soybean and cotton. For *C. marginiventris*, it has been shown that females are highly attracted by the odours emitted by caterpillar-damaged maize seedlings (Turlings *et al.*, 1990) and that they spend more time on such plants than on artificially damaged or unattacked plants (Loke *et al.*, 1983). *C. sonorensis* is also attracted to the odours of plants attacked by its hosts (Elzen *et al.*, 1984; McAuslane *et al.*, 1991) and was found to remain longer on host-damaged cotton plants than on undamaged plants (Baehrecke *et al.*, 1990). The exploitation of plant-provided chemical cues by parasitoids can be expected to enhance parasitism rates, but it is not yet clear if the plants benefit from this interaction. If increased parasitism yields fitness benefits for herbivore-attacked plants, parasitoids may have contributed to selection pressures that shaped the evolution of herbivore-induced indirect defence signals in plants.

In the current study, we tested if parasitism by *C. marginiventris* increased the fitness of maize plants attacked by larvae of *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae). In a first experiment, we confirmed a dramatic difference in weight gain during development between larvae that were unparasitized or parasitized by either *C. marginiventris* or *C. sonorensis*. In a series of subsequent experiments, we demonstrated that parasitism reduced feeding damage on individual plants and that such a reduction in damage increased seed production.

MATERIALS AND METHODS

Origin of insects and plants

Zea mays plants (var. Delprim) were grown from seed in pots (360 ml, 10 cm diameter, 8 cm high) with regular potting soil (COOP, Switzerland) and kept in a climate chamber (23°C, 60% relative humidity, 16D:8L, 50,000 $\text{lm}\cdot\text{m}^{-2}$). Maize seedlings were used for experiments 2 weeks after planting when the plants had four fully developed leaves.

Spodoptera littoralis larvae were used as hosts for the parasitoids and reared under ambient laboratory conditions. Host-eggs were supplied by Novartis (Switzerland) weekly and were incubated in a Petri dish (9 cm diameter, 1.5 cm high) on humidified filter paper. Eclosed larvae were supplied daily with fresh pieces of maize leaves and kept in plastic boxes (15 × 9 × 5 cm).

The New World endoparasitoids *Cotesia marginiventris* and *Campoletis sonorensis* originated from the USDA-ARS, Biological Control and Mass Rearing Research Unit (Mississippi, USA) and from our own field collections in Poza Rica (Veracruz, Mexico), respectively. For practical reasons, parasitoids were reared on the Old World host *S. littoralis*. Both parasitoid species are generalists and their development and survival on this foreign host was the same as on their natural host *S. frugiperda* (M.E. Fritzsche Hoballah, unpublished data). For the rearing of the parasitoid, 25 caterpillars (3–4 days old) were offered to a single mated female parasitoid (3–7 days old) in a plastic box (9.5 cm diameter, 5 cm high). After 2 h, the female was removed and caterpillars were reared on fresh maize leaves until cocoon formation. Cocoons were kept in Petri dishes until adult emergence. Emerging adults were sexed and kept in cages (30 × 30 × 30 cm) at a sex ratio of 0.5:1 (male:female), with drops of honey and distilled water on cotton wool. Parasitoids were kept in the laboratory under ambient light and temperature conditions.

Weight gain during development of parasitized and unparasitized *S. littoralis* larvae

In a first experiment, we compared weight gain during development of parasitized and unparasitized *S. littoralis* larvae. One mated female (3–5 days old) of either *C. marginiventris* or *C. sonorensis* was introduced into a plastic box (9.5 cm diameter, 5 cm high) with 25 *S. littoralis* larvae (3 days old). Larvae were assumed to be parasitized when they were observed to be stung by a parasitoid. From approximately 70% of these larvae, a parasitoid emerged. The first 5 larvae stung by a single parasitoid were used for the experiment; the other 20 larvae were discarded. With both parasitoid species, 60 larvae were parasitized. An additional 30 control larvae were left unparasitized. Unparasitized larvae originated from the same egg batches as parasitized larvae. The larvae were kept singly in small Petri dishes (5 cm diameter, 2 cm high) in an incubator (25°C, 85% relative humidity, 11L:13D). Food (fresh pieces of maize leaves) was replaced daily. The weight of larvae was assessed starting from the sixth day after eclosion until the unparasitized *S. littoralis* larvae pupated or the emergence of parasitoid larvae from parasitized *S. littoralis*. Only data of parasitized larvae that yielded a cocoon and unparasitized larvae that yielded a pupa were used for analysis. Larval weights were ln-transformed to obtain homogeneity of variance. Then, the following statistical model was fitted to each treatment group:

$$\ln(\text{weight}) = a(\text{day})^2 + b(\text{day}) + c$$

A 95% confidence interval was computed for each day. A *t*-test was performed to compare development time between larvae parasitized by *C. marginiventris* and *C. sonorensis*.

Dry weight of young maize plants after an attack by a parasitized or unparasitized *S. littoralis* larva

During a second experiment, the dry weight of stems and leaves of maize seedlings attacked by a parasitized or an unparasitized larva was measured. Three-day-old larvae were parasitized by *C. marginiventris* and left for 3 days on fresh maize leaves. Unparasitized larvae of the same egg batch were placed in a separate box on the same diet. After 3 days, each larva, whether parasitized or unparasitized, was placed on an individual 13-day-old maize plant. A cellophane bag allowing gas exchange (30 × 15.5 cm; quality 400P, Celloclair AG, Liestal, Switzerland) was placed over each plant to prevent the larvae from escaping. Plants were kept in a climate chamber (23°C, 60% relative humidity, 16L:8D, 50,000 $\text{lm} \cdot \text{m}^{-2}$) until the last pupae were formed (in the unparasitized treatment). Only data of parasitized larvae that yielded a cocoon and unparasitized larvae that yielded a pupa were used for analysis. At this time, the plants were dried for 4 days at 80°C and the weight of leaves and stems was determined. Analysis of variance and Fisher's PLSD *post-hoc* test were used to compare dry weights among treatments.

Seed production by maize plants after an attack by a parasitized or unparasitized *S. littoralis* larva

In a third experiment, we assessed the yield of maize plants after an attack by a single parasitized or unparasitized larva. The initial part of the experiment was the same as in the previous experiment until the larvae stopped feeding on their respective plants. After formation of host pupae (in the unparasitized treatment), the plants were taken from the climate chamber and transplanted in an open plot (5 × 10 m) in a farmer's maize field (Marin, Switzerland), early during the local maize growing season. The plants were planted randomly, 50 cm apart, and left to grow until maturity. One month before maturity, the height of each plant was measured ($n = 13$ for control plants, $n = 16$ for plants attacked by *C. marginiventris*-parasitized larvae, $n = 24$ for plants attacked by unparasitized larvae). At maturity, the plants were removed and the number of ears and seeds and the dry weight of seeds of individual maize plants were determined. The number of replicates was different for each treatment because several plants were destroyed by vandals: $n = 8$ for control plants, $n = 14$ for plants attacked by parasitized larvae, $n = 17$ for plants attacked by unparasitized larvae. Analysis of variance and Fisher's PLSD *post-hoc* test were used to compare height, dry weight of seeds and number of seeds and ears among treatments.

RESULTS

Weight gain during development of parasitized and unparasitized *S. littoralis* larvae

Weight gain in parasitized larvae was considerably less than that in unparasitized larvae (Fig. 1A). Fitted functions (program S-Plus) for the three treatment groups were:

- $\ln(\text{weight}) = -0.0370(\text{day})^2 + 1.3971(\text{day}) - 12.9651$ (non-parasitized larvae, $n = 29$)
- $\ln(\text{weight}) = -0.0442(\text{day})^2 + 1.1615(\text{day}) - 11.4221$ (*C. sonorensis*-parasitized, $n = 40$)
- $\ln(\text{weight}) = -0.0525(\text{day})^2 + 1.2991(\text{day}) - 11.9859$ (*C. marginiventris*-parasitized, $n = 37$)

Estimated values of the non-parasitized treatment group were significantly higher than those of the parasitized groups starting from day 7 after parasitization (Fig. 1B). There was no difference in weight gain between larvae parasitized by the two parasitoid species *C. marginiventris* and *C. sonorensis* (Fig. 1B).

Furthermore, the period of growth was shorter for parasitized larvae (approximately 11 days) than for the unparasitized larvae (approximately 15 days) (Fig. 1). The parasitoid larvae emerged from 4th instar hosts, which died soon after, while unparasitized larvae pupated at the 6th instar. The final weight of parasitized larvae was 13.8% and 14.5% for *C. marginiventris* and *C. sonorensis* parasitized larvae, respectively, of the weight of unparasitized larvae at the same age and 2.61% and 2.75% of the final weight of unparasitized larvae.

Development time until cocoon formation was shorter for the parasitoid *C. marginiventris* than for *C. sonorensis* (mean \pm standard error: 13.16 ± 0.1 vs 14.15 ± 0.1 days, $P < 0.0001$, $t = -7.07$, d.f. = 75). This was also reflected in an earlier emergence of the adults after initial parasitization (18.11 ± 0.1 vs 20.57 ± 0.1 days, $P < 0.0001$, $t = -15.75$, d.f. = 75).

Dry weight of young maize plants after an attack by a parasitized or unparasitized *S. littoralis* larva

No difference in dry weight of stems was found between plants attacked by parasitized or unparasitized caterpillars and control plants (Fig. 2A: $P = 0.7217$, $F = 0.329$, d.f. = 2). However, the dry weight of leaves of plants attacked by an unparasitized larva was about a third of that of control plants and plants attacked by a parasitized larva (Fig. 2B: $P < 0.0001$, $F = 34.921$, d.f. = 2; Fisher's PLSD *post-hoc* test: parasitized–unparasitized $P < 0.0001$, control–parasitized $P = 0.0379$, control–unparasitized $P < 0.0001$).

Seed production by maize plants after an attack by a parasitized or unparasitized *S. littoralis* larva

One month after transferring the plants into the field (i.e. 1 month before assessing yield), a significant difference in plant height was noted. Plants that had been attacked by an unparasitized larva were significantly shorter than control plants, while the height of plants that were attacked by a parasitized larva was not significantly different from that of control plants (Fig. 3: $P = 0.0097$, $F = 5.093$, d.f. = 2; Fisher's PLSD *post-hoc* test: parasitized–unparasitized $P = 0.0578$, control–parasitized $P = 0.2520$, control–unparasitized $P = 0.0034$). At the end of the season, maize seedlings attacked by parasitized *S. littoralis* larvae had the same yield (expressed in number of ears and seeds and dry weight of seeds) as control plants, which was significantly higher than the yield of plants that had been attacked by unparasitized larvae (Fig. 4A: $P = 0.0008$, $F = 8.803$, d.f. = 2; Fisher's PLSD *post-hoc* test: parasitized–unparasitized $P = 0.0038$, control–parasitized $P = 0.2558$, control–unparasitized $P = 0.0005$. Fig. 4B: $P = 0.0008$, $F = 8.702$, d.f. = 2;

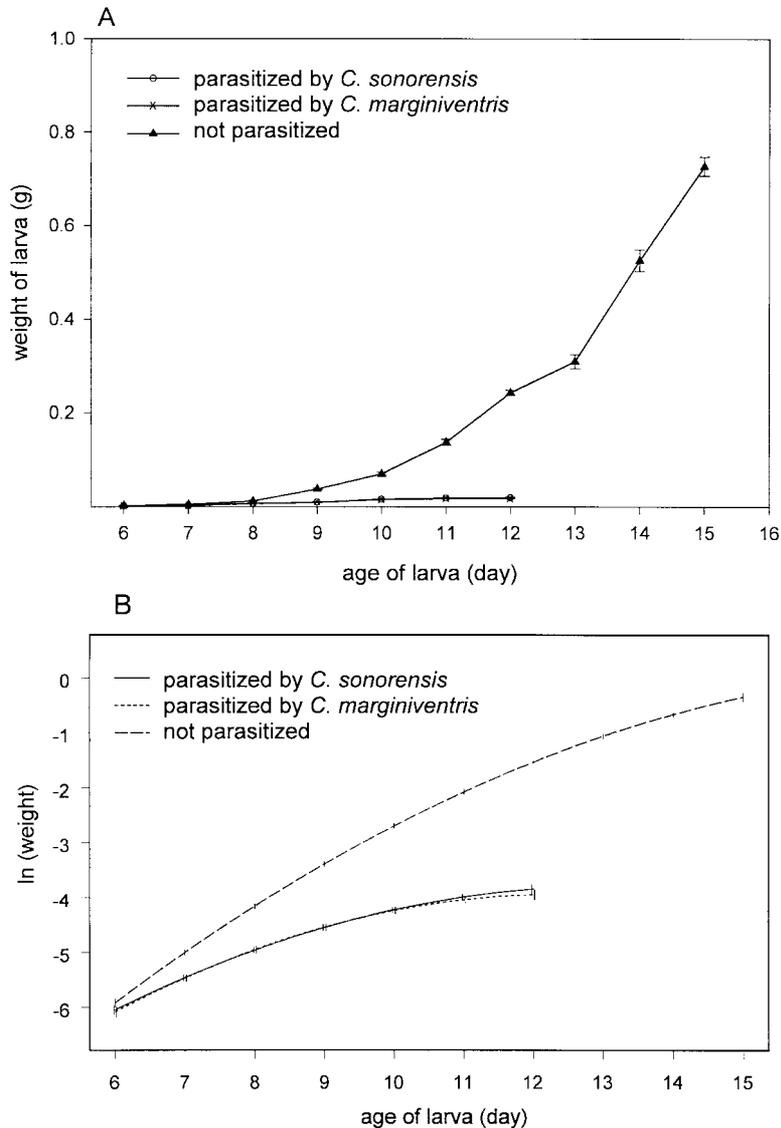


Fig. 1. (A) Weight during development of *Spodoptera littoralis* larvae, parasitized by *Campoletis sonorensis* (x, $n = 40$) and by *Cotesia marginiventris* (O, $n = 37$) or left unharmed (▲, $n = 29$). Values are the mean \pm standard error. (B) Fitted functions for the three treatment groups with predicted values of the model with 95% confidence intervals of logarithmic transformed data.

Fisher's PLSD *post-hoc* test: parasitized–unparasitized $P = 0.0028$, control–parasitized $P = 0.3515$, control–unparasitized $P = 0.0008$. Fig. 4C: $P = 0.0010$, $F = 8.432$, d.f. = 2; Fisher's PLSD *post-hoc* test: parasitized–unparasitized $P = 0.0054$, control–parasitized $P = 0.2305$, control–unparasitized $P = 0.0006$.

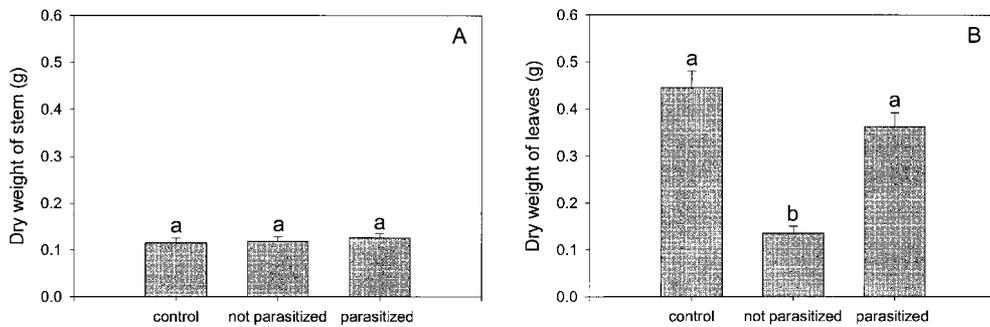


Fig. 2. Dry weight of stem (A) and leaves (B) of maize seedlings left unharmed ($n = 13$), infested with one unparasitized larva ($n = 17$), or infested with one *S. littoralis* larva parasitized by *C. marginiventris* ($n = 19$). Values are the mean \pm standard error. Different letters above bars indicate significant differences among treatments.

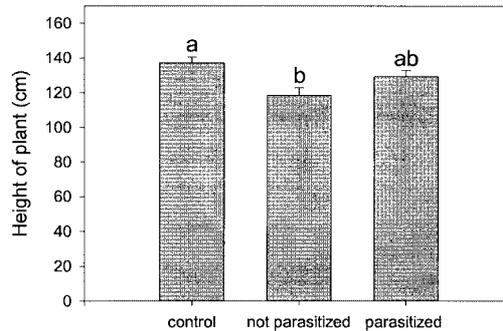


Fig. 3. Height of plants measured 1 month before plant maturity. The plants were left unharmed ($n = 13$), infested with one unparasitized larva ($n = 24$), or infested with one *S. littoralis* larva parasitized by *C. marginiventris* ($n = 16$). Values are the mean \pm standard error. Different letters above bars indicate significant differences among treatments.

DISCUSSION

Our results show that herbivore-infested plants may benefit from the activity of parasitoids even if these do not instantaneously kill their herbivorous hosts. Seed production by maize plants that, at an early stage of development, were subjected to an attack by a single healthy *S. littoralis* larva was about 30% lower than that of plants that had been attacked by a parasitized larva. In fact, the plants that had carried a parasitized larva produced as many seeds as unattacked control plants (Fig. 4). This simple experiment shows that the fitness of a plant can increase due to parasitization of herbivores that feed on it. Van Loon *et al.* (2000) obtained comparable results with *Arabidopsis thaliana*, which produces more seeds when it is eaten by *Pieris rapae* larvae parasitized by *Cotesia rubecula* than when it is eaten by unparasitized larvae. These findings may have important implications for understanding the evolution of plant traits that promote the presence of the third trophic level.

Previous studies had already shown that the solitary endoparasitoid *Cotesia marginiventris* significantly reduces weight gain of its hosts. Ashley (1983) found an average

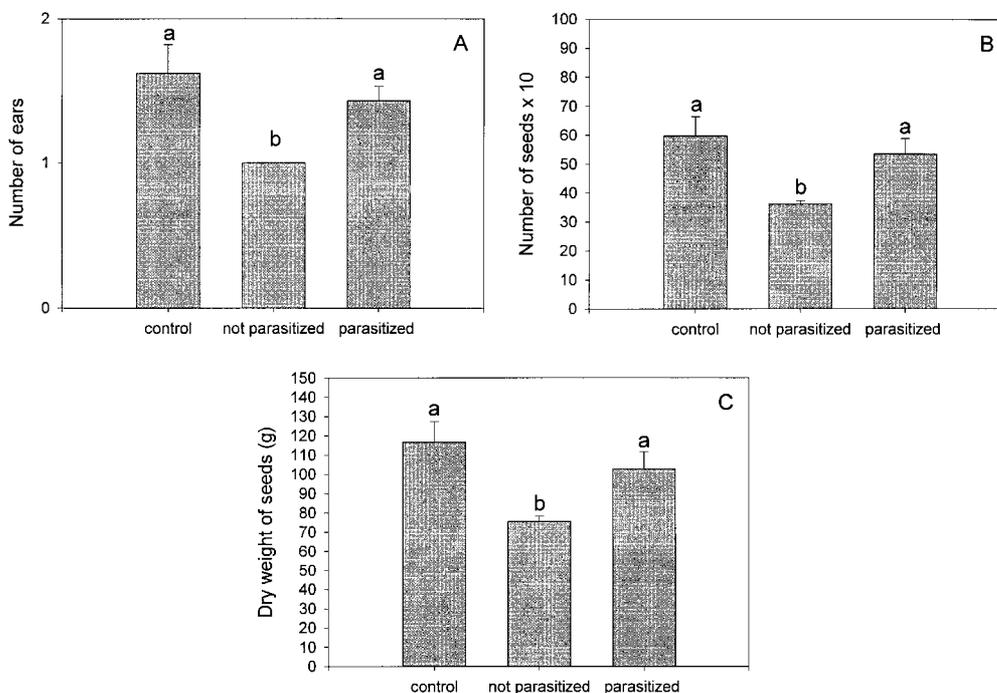


Fig. 4. Number of ears (A), number of seeds (B) and mean dry weight of seeds (C) of maize seedlings left unharmed ($n = 8$), infested with one unparasitized larva ($n = 17$), or infested with one *S. littoralis* larva parasitized by *C. marginiventris* ($n = 14$). Values are the mean \pm standard error. Different letters on bars indicate significant differences among treatments.

reduction in final weight of 93% in the host *S. frugiperda* and Jalali *et al.* (1988) reported that the host *S. litura* consumes significantly less food starting 72 h after being parasitized. Similar results were obtained by McCutcheon *et al.* (1991) for *Pseudophusia includens* (Lepidoptera: Noctuidae) after parasitization by *C. marginiventris*. No such studies had been conducted with *C. sonorensis*, but a related species *C. flavicincta* caused reduced foliar consumption in the host *S. frugiperda* (Van-Cruz-Maria *et al.*, 1997). The current study confirms these results. The average maximum weight of *S. littoralis* larvae parasitized by either *C. marginiventris* or *C. sonorensis* was less than 3% of the final weight of healthy larvae. This considerable effect on host development was shown to significantly reduce the amount of leaf tissue that the larvae consumed (Fig. 2). Despite ample evidence for reduced feeding by parasitized herbivorous hosts, there appear to have been no previous studies on the fitness consequences for plants on which these herbivores feed.

The frequently demonstrated emissions of herbivore-induced volatiles have been suggested to have a defence function, in which they serve as signals to attract natural enemies of herbivores (Vet and Dicke, 1992; Turlings and Benrey, 1998; Dicke, 1999). Such a function would require that the attraction of natural enemies enhances plant fitness. It is obvious that this is the case when predators are attracted, as they can immediately kill a herbivore and instantaneously stop their damaging effects (Sabelis and de Jong, 1988). Experimental evidence for selective pressures favouring such a signalling function had been

missing. This is especially critical for the attraction of parasitoids (Sabelis and de Jong, 1988; Karban *et al.*, 1997; Baldwin, 1998; Turlings and Benrey, 1998; Van der Meijden and Klinkhamer, 2000), which commonly allow their hosts to develop further and in some cases cause their hosts to eat more than if they are not parasitized (Rahman, 1970; Hunter and Stoner, 1975; Slansky, 1978; Beach and Todd, 1986). Van der Meijden and Klinkhamer (2000) and Hare (in press) list several criteria or research objectives that they feel are required to demonstrate that natural enemies are agents of natural selection on plants. The most important criterion to be satisfied seems to be that, 'in the presence of both herbivores and natural enemies, plant fitness should be greater for plants expressing the natural enemy-enhancing trait than for those that do not' (Hare, in press). The current study was conducted to determine whether or not parasitoids can increase plant fitness.

Our results demonstrate that parasitoids have the potential to reduce herbivory to an extent that it can increase a plant's fitness. We used a system for which the role of induced volatiles in parasitoid host location is well studied and the induced odour emissions in cultivated maize are very similar to those of its wild ancestors (Gouinguéné *et al.*, 2001). The conditions under which the plants were subjected to larval attack were realistic. Although *S. frugiperda* lays clusters of eggs, as a result of rapid dispersal and cannibalism only one larva is commonly found on small plants in maize fields in the sub-tropical lowlands of Mexico (M.E. Fritzsche Hoballah, personal observation). Moreover, of eight species of parasitoids that we reared from *S. frugiperda* larvae collected in maize fields near Poza Rica (Mexico), four always emerged from larvae with a size similar to that of unparasitized 2nd or 3rd instar *S. frugiperda* larvae (M.E. Fritzsche Hoballah, unpublished data). As pointed out by Van Loon *et al.* (2000), it appears that all species of solitary parasitoids of Lepidoptera reduce food consumption in their host. How the herbivore-parasitoid interactions affect plant fitness under natural conditions will depend on many factors, but in cases where parasitoids reduce herbivory by as much as shown here, they are likely to have a significant positive effect. It can therefore be expected that, under certain circumstances, plants that are able to lure more parasitoids with volatiles will increase their fitness by doing so. However, we have to consider other interactions that will be affected by the volatiles and associated chemical compounds, which can have either positive or negative consequences for the performance of a plant (Turlings and Benrey, 1998; Dicke and Vet, 1999).

Herbivore-induced volatiles emitted by plants can also play a role in direct defence. In some cases, particularly those involving beetles, induced changes can attract herbivores (Dicke and Vet, 1999). However, in many cases, the changes render the plants less appealing to herbivores. For example, mites and aphids are repelled by plant volatiles induced by conspecifics (Dicke and Dijkman, 1992; Bernasconi *et al.*, 1998). Induced plant changes also have been shown to negatively affect consumption by *Spodoptera* species. Edwards *et al.* (1985) found a nine-fold reduction in the area consumed by *S. littoralis* if tomato leaves are artificially damaged. Induced maize plants are less palatable to *S. exigua* larvae (Turlings and Tumlinson, 1991). *S. littoralis* larvae take fewer and shorter meals on leaves from previously wounded plants than on control leaves (Barker *et al.*, 1995). Both *S. exigua* and *S. littoralis* prefer leaves of undamaged over leaves of damaged cotton plants and *S. littoralis* larvae perform very poorly on previously damaged cotton plants and may eventually die (Alborn *et al.*, 1996). These and various other consequences of induced changes in plant defence chemistry suggest that the outcome of their combined effects can be expected to vary tremendously.

Conclusive evidence that, under natural conditions, plant-released volatiles increase the likelihood that natural enemies will attack herbivores on the signalling plants is still lacking, but indirect evidence is accumulating. For instance, field studies by Drukker *et al.* (1995) and Shimoda *et al.* (1997) showed that predators (anthocorid bugs and the predatory thrips *Scolothrips takahashii*) are more attracted to attacked plants than to control plants. Most convincing are the direct field observations of De Moraes *et al.* (1998), who found that females of the braconid parasitoid *Cardiochiles nigriceps* visited plants that were damaged by its specific host *Heliothis virescens* much more frequently than plants attacked by a non-host or plants that were undamaged. This distinct attractiveness was even observed when the larvae and damaged leaves had been removed. Moreover, Thaler (1999) found that parasitism of *Spodoptera exigua* larvae by the ichneumonid *Hyposoter exiguae* was higher on field-grown tomato plants sprayed with jasmonic acid to induce volatile emissions than on controls. These field studies and many preceding laboratory studies strongly suggest that the induced plant odours increase the chances that herbivores are attacked by their natural enemies. The study by Van Loon *et al.* (2000) and the study presented here show that increases in attack rates by parasitoids may benefit plants. Therefore, these members of the third trophic level may contribute to the selective pressures shaping plant traits that promote the effectiveness of natural enemies.

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