Biological Control 66 (2013) 21–26

Contents lists available at SciVerse ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Effect of fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) strain and diet on oviposition and development of the parasitoid *Euplectrus platyhypenae* (Hymenoptera: Eulophidae)

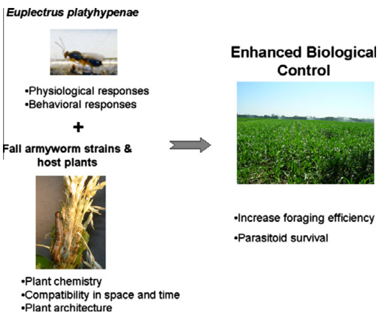
Mirian M. Hay-Roe *, Robert L. Meagher, Rodney N. Nagoshi

Behavior and Biocontrol Unit, USDA, ARS, CMAVE, 1700 SW 23rd Dr., Gainesville, FL 32608, United States

HIGHLIGHTS

- *Euplectrus* wasps preferred to oviposit on corn strain larvae fed corn plants.
- No oviposition preference was observed for corn or rice strain larvae fed grass.
- Larger parasitoid offspring resulted from the largest host fed corn plants.
- Wasp larval mortality occurred in hosts of both strains fed stargrass.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 24 August 2012
Accepted 3 March 2013
Available online 13 March 2013

Keywords:
Allelochemical
Biological control
Ectoparasitoid
Fall armyworm
Spodoptera frugiperda
Euplectrus platyhypenae

ABSTRACT

Oviposition tendency and subsequent development of the parasitoid wasp *Euplectrus platyhypenae* Howard was compared using the corn and rice host strains of *Spodoptera frugiperda* (J. E. Smith) fed corn (*Zea mays*, 'Truckers Favorite') or stargrass (*Cynodon nlemfuensis* Vanderyst var. *nlemfuensis*, 'Florona'). In no-choice and two-choice experiments using newly molted fourth instar hosts, female wasps preferred to oviposit on corn strain larvae fed corn plants. Rice strain larvae were parasitized when fed corn plants, but only after the host had reached an optimal size. This preference might be due to differences in size between host strains at a given stage. No oviposition preference for corn or rice strain larvae fed grass was observed. When female wasps were given a choice between corn and rice strain larvae, they always produced more female offspring on the corn strain than the rice strain larvae, irrespective of the host plant the larvae fed upon. Among rice strain hosts, those fed corn hosted more female offspring than those fed grass. The data also show that host quality had a direct effect on parasitoid size, since larger parasitoid offspring resulted from the largest host fed corn plants, and smaller offspring resulted from the smallest hosts, rice strain larvae fed stargrass. Furthermore, *E. platyhypenae* larval mortality occurred in hosts of both strains fed stargrass, which may indicate that stargrass allelochemicals are not appropriate for this parasitoid. Implications of these results for biological control methods are discussed.

Published by Elsevier Inc.

1. Introduction

Parasitoid wasps have long been known to inflict substantial mortality on immature Lepidoptera and are therefore likely to have an important role in the evolution of caterpillar behavior (Fatouros et al. 2005; Poelman et al., 2011). It has been suggested that parasitoid-caterpillar associations can be influenced by host plant factors, including nutritional quality, phenology, and the presence of allelochemicals that, when ingested by the host, could inhibit parasitoid development and survival (Barbosa et al., 1991; Campbell and Duffy, 1979; Reitz and Trumble, 1997). Also, in the last two

---

* Corresponding author. Fax: +1 352 374 5804.
E-mail address: mmhr@ufl.edu (M.M. Hay-Roe).

1049-9644/$ - see front matter Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.biocontrol.2013.03.003

decades many studies of these factors indicate it could be a significant contributor to the diversification of Lepidoptera with respect to host plant usage (Lill et al., 2002).

Fall armyworm *S. frugiperda* is a potentially useful system for studies in this area. The species is highly polyphagous, with over 60 different host plants identified to date (Casmuz et al., 2010; Pashley, 1988). This diverse host range is due in part to the presence of two genetically distinct subpopulations, previously identified as host strains (Pashley, 1988; Pashley et al., 1987). The strains are morphologically indistinguishable, requiring the use of genetic markers to distinguish them (Lu and Adang, 1996; Nagoshi and Meagher, 2003; Nagoshi et al., 2006; Pashley, 1988; Pashley et al., 1987). Their defining behavioral phenotype is host preference, with the rice-strain preferentially found in turf and pasture habitats, while the corn-strain predominates in agricultural settings containing corn, sorghum, or cotton (Lu and Adang, 1996; Nagoshi and Meagher, 2003; Nagoshi et al., 2007; Pashley, 1988). This suggests that if these are populations undergoing incipient speciation, as previously hypothesized (Drès and Mallet, 2002; Prowell, 1998), then there must be disruptive selection pressure for diverging host ranges. In addition, while there have been reports that the developmental performance and mortality of the strains can vary on different hosts, the results have been inconsistent (often contradictory) and typically not of sufficient magnitude to easily explain the often strong compartmental distribution of the two strains into different habitats (Meagher et al., 2007; Pashley et al., 1995). More complicated selection pressures are suggested.

The involvement of parasitoids in driving fall armyworm strain divergence and asymmetrical distribution in the field is possible, perhaps likely, given that high (>50%) levels of parasitism are not uncommon and the spectrum of available natural enemies is defined by habitat (Roland, 2000). In this scenario, a generalist feeder becomes associated with specific plant hosts to escape natural enemies found in other habitats or to adapt plant allelochemicals as a defense mechanism. Support for this claim would be provided by the observations that the two strains exhibit different susceptibilities to parasitoid species in a manner influenced by diet.

To test this we examined a parasitoid wasp that is commonly associated with fall armyworm populations in Florida. *Euplectrus platyhypenae* Howard (also in the literature as *E. plathypenae*; Hymenoptera: Eulophidae) is a gregarious ectoparasitic koinobiont that attacks Lepidoptera larvae (Noctuidae, Pyralidae, Sphingidae and Tortricidae) (Luginbill, 1928; Murúa and Virla, 2004; Vickery, 1929; Wilson, 1932). Before oviposition, females inject venom into the larvae to inhibit molting and arrest development (apolysis and ecdysis) without inducing host paralysis (Coudron and Puttler, 1988). Female wasps lay clusters of eggs on the dorsum of hosts, an area used by parasitoids to prevent defensive biting and egg removal by the host. Parasitoid larval development is completed near the oviposition site, and pupation occurs along the ventral side of the now moribund caterpillar, where they spin silky cocoons. *E. platyhypenae* has been proposed as a good candidate for use as a biological control agent for the fall armyworm (Molina-Ochoa et al., 2001), but few studies have been carried out to determine optimal ecological conditions.

The objective of this study was to test the preferences of *E. platyhypenae* towards two fall armyworm host strains fed different host plants and to determine how plant type affects the performance of parasitoid wasps. We compared parasitoid host-preference, brood size, parasitoid larval survival and brood sex ratio in corn and rice strain larvae fed either corn *Zea mays* L. ('Trucker's Favorite') or stargrass (*Cynodon nlemfuensis* var. *nlemfuensis* Vanderyst, ('Florona'). The results of this study lead to a discussion of parasitod-host behavior for biological control.

2. Materials and methods

2.1. Insects

E. platyhypenae was obtained from field populations of fall armyworm collected from corn at the Dairy Research Unit at the University of Florida, Hague, Alachua Co., FL. In May 1008. Parasitoids were reared in the laboratory at 24 °C, 65% humidity and at a photoperiod of L:D 14:10, and were maintained in a 27 × 27 × 27 cm Plexiglas cages. Cages had a screen on one side for ventilation and a 14 cm circular screen hole for access to the colony. Several smears of honey were placed on the roof of the Plexiglas cage and a cotton ball saturated with water was placed in a 1-oz acrylic Solo cup (Solo Cup Co., Urbana, IL) for parasitoid feeding. The colony was maintained in the laboratory for 9 months before experiments were initiated.

Fall armyworm rice strain larvae were collected from pasture fields at the Range Cattle Research and Education Center, Ona, Hardee Co., FL, while the corn strain larvae were collected from corn fields at Hague. The two strains were identified by molecular markers (Levy et al., 2002), as modified by Nagoshi and Meagher (2003) and are currently maintained at the USDA, ARS, CMAVE Behavior and Biocontrol Unit in Gainesville, FL on an artificial pinto bean diet. Cohorts of these colonies were raised on 'Trucker's Favorite' corn and on 'Florona' stargrass in plastic Sterilite tubs (Sterilite Corporation, Townsend, MA) [26 (d) × 12.1 (h) cm] containing metal screens (holes at 0.7 cm). Plant cuttings (15–17 cm long) were wrapped in wet paper towels to keep them hydrated. When plant material was completely consumed, more material was added and the lower stems were placed on the top metal screen to be removed the following day. Previous research showed 'Florona' stargrass to be an excellent host for fall armyworm (Meagher et al., 2007), although rearing parameters can have a negative effect on larval mortality (Hay-Roe et al., 2011). The cohorts were maintained in environmental chambers at 26 °C, 75% humidity and L:D 14:10 photoperiod.

2.2. *E. platyhypenae* oviposition preference

Three experiments were performed to assess oviposition preferences of *E. platyhypenae* females in response to corn and rice fall armyworm host strains fed either corn or stargrass. The first study examined the timing of oviposition in a choice test. A single newly molted fourth-instar larva of each strain was placed on either corn or star grass in 25 × 25 × 25 cm Plexiglas containers, each with a 7 cm hole covered with 0.15 mm insect screen for aeration. Because fall armyworm larvae are morphologically similar, the second proleg on the right was alternately clipped to facilitate host strain differentiation (Hagler and Jackson, 2001). Three naïve, mated female wasps (females that were not previously exposed to larvae) were released in each cage (Bultman et al., 1997; Coudron et al., 1997). The strain identity of the first larva detected with an egg cluster was recorded. Oviposition generally occurred in the first 24 h period. Eighty larvae fed corn plants (40 larvae from each strain) and 80 larvae fed stargrass (40 larvae from each strain) were used for the choice experiment. The experimental arena was checked at 3–5-h intervals for evidence of oviposition.

The second experiment was a no-choice study in which the number of eggs laid by the wasp was recorded. Clear 18.5 × 13 × 10 cm plastic containers with a 7 cm screened hole for aeration were used as the experimental arena. Each contained a cotton ball saturated with a 20% glucose solution in a 1-oz acrylic cup for adult parasitoid feeding and a 25 ml Erlenmeyer flask with distilled water containing either corn (three cuttings) or stargrass (five to six cuttings), with each cutting approximately 15 cm tall.

A newly molted fourth-instar larva was placed on the plant material and allowed to initiate feeding. Three naïve mated females wasps were then released in each cage and exposed to hosts for 48-h. The experiment was checked two times a day for evidence of oviposition. As soon as a clutch of eggs was observed, the wasps were removed from the experimental arena as female *E. platyhypenae* will scrape and damage other clutches with its ovipositor before laying on the host (Hay-Roe, personal observations). In total 94 corn-fed larvae (47 from each strain) and 80 stargrass-fed larvae (40 from each strain) were used.

The third experiment was a choice study in which the wasp was simultaneously exposed to larvae of both strains. The method was the same as the no-choice experiment except that one larva of each strain was placed on the tested host plant. Larvae were distinguished by foreleg clipping. We allowed 48 h for oviposition and the host larvae were then separated to avoid cannibalization and placed in 1-oz acrylic cups to complete wasp development and pupation. In total 106 larvae fed corn plants were used (53 larvae from each strain) and 80 larvae fed stargrass (40 larvae from each strain) were used. The position on each larva of *E. platyhypenae* egg clutches and the number of eggs laid per larva was recorded for both the no-choice and choice experiments. These last two experiments allowed us to assess egg allocation, host viability, and parasitoid viability and development, under choice and no-choice treatments.

2.3. Developmental metrics of *E. platyhypenae* parasitism

During the choice experiment, head capsule width of the host larvae fed different diets and the wing length of wasp offspring obtained from each treatment were measured using a stage micrometer mounted on a dissecting Wild Heerbrugg M5A microscope to look at the relationships between host size and parasitoid characteristics within strains.

2.4. Statistical analysis

Analysis of variance was performed to compare the number of parasitoid eggs, larval and pupal developmental time, and the number of female and male offspring produced between different treatments. Fisher's LSD multiple comparison tests were performed when appropriate. Oviposition preference by female parasitoids and mortality rates were analyzed by paired Z-test and egg positioning within fall armyworm larvae by Fisher exact test. The size of the larval head capsule from the two fall armyworm host strains fed different diets was transformed to the natural logarithm, as recommended by LaBarbera (1989), before performing the ANOVA test. The statistical program Systat V. 12 was used for the statistical analysis.

3. Results

3.1. Timing of oviposition

Wasps displayed robust parasitism behavior when exposed to fall armyworm larvae in the laboratory assay, with wasp stinging and egg deposition occurring in over 70% of the trials in all treatments (Table 1). The timing of egg deposition showed statistically significant interactions with respect to fall armyworm strain and plant host. Wasps showed a very significant preference for early (<24 h) oviposition on corn-strain larvae when tested on corn plants ($Z = -4.23$; $df = 80$; $P < 0.0001$), with egg deposition occurring during the first day on the corn strain 83% (33/40) of the time compared to 23% (9/40) on the rice-strain on corn plants. Most of the remaining rice-strain larvae were eventually parasitized after another day, indicating that this subgroup was susceptible to parasitism but apparently less immediately attractive than the corn-strain. The same trend was observed on the stargrass diet though there appeared to be a decline in the relative attractiveness of the corn-strain to early oviposition. On stargrass, the corn-strain showed evidence of early parasitism 55% (22/40) of the time versus 40% (16/40) for the rice-strain, however, the results were not statistically significant ($P > 0.05$). Once again, most of the remaining larvae were parasitized within 48 h. The frequencies of larvae showing no parasitism were not affected by diet and were consistently higher in the rice-strain larvae (21/80, 26%) than the corn-strain (11/80, 15%).

Table 1
Euplectrus platyhypenae ovipositional preference when given choice of fall armyworm corn-strain (CS) and rice-strain (RS) larvae grown on either corn or 'Florona' stargrass; timing and order of parasitism.

	Corn host		Stargrass host	
	CS	RS	CS	RS
Number of larvae	40	40	40	40
Parasitized (24 h)	33	9	22	16
Parasitized (48 h)	1	20	12	14
No parasitism	6	11	6	10
First parasitized	75%	13%	38%	20%
Both strains parasitizedwithin 24 h	10%		20%	

3.2. Wasp oviposition preference (egg allocation)

In the no-choice and choice experiments, no consistent, significant differences were observed in the number of eggs oviposited with respect to host strains or host plants (Table 2). One significant interaction between strains and host plants ($F = 4.43$; $df = 1, 124$; $P < 0.05$) was found in the no-choice study, with wasps laying more eggs on corn strain larvae fed stargrass than the other treatments (Table 2A). However, this bias was not repeated in the choice study (Table 2B). In all cases, wasp eggs were laid primarily between the first to fourth abdominal segments and less frequently in the thoracic segments (Table 2C), corroborating previous reports of egg positioning (Murúa and Virla, 2004 and references therein).

3.3. Host viability

Measurement of parasitoid viability was complicated by strain differences in the viability of the larval hosts, as early mortality of parasitized larvae does not permit complete wasp development. Overall, larval mortality of fall armyworm feeding on corn was 19% (19/100) for the corn-strain and 24% (24/100) for the rice-strain (pooled data from choice and no choice studies, Table 2). Mortality for both strains was higher when reared on stargrass, with 40% (32/80) of corn-strain and 63% (50/80) of rice-strain dying as larvae.

This strain bias in mortality was not reflected in size of the larvae. Measurement of head capsule size upon molt of the 4th instar showed little difference between the rice-strain (1.1 mm; $n = 29$) and corn-strain (1.2 mm; $n = 29$) grown on corn or with the rice-strain on stargrass (1.1; $n = 30$). Corn-strain larvae reared on stargrass (1.3 mm; $n = 30$), were significantly larger in comparison to the rice-strain fed the same plant and this was primarily responsible for significant interactions between host strains ($F = 60.88$; $df = 1, 112$; $P < 0.001$), diets ($F = 20.58$; $df = 1,112$; $P < 0.001$), and between strains and diet ($F = 14.88$; $df = 1,112$; $P < 0.001$).

The viability of the host larvae influenced wasp egg deposition in a context-dependent manner. In the no-choice study, where for each trial only a single larva was exposed to wasp parasitism, egg deposition was never observed on the 56 larvae that died prematurely (Table 2A). In contrast, in the choice experiment where

Table 2
Summary of host viability and *Euplectrus platyhypenae* biology when fall armyworm strains were reared on corn or stargrass.

	Corn host		Stargrass host	
	CS	RS	CS	RS
A. No choice study				
Number of larvae	47	47	40	40
Larvae lost (no data)	0	1	4	1
Dead larvae (no egg lay)	7	9	16	24
Dead larvae (egg lay)	0	0	0	0
Larvae not parasitized[*]	9	11	0	0
Larvae parasitized[**]	31	25	20	15
Eggs/parasitized larva	35.6 ± 4.0^{a}	41.7 ± 4.2^{a}	47.2 ± 4.1^{b}	35.9 ± 4.3^{a}
Females/parasitized larva	16.8 ± 2.2^{a}	21.1 ± 2.9^{a}	21.4 ± 2.6^{a}	12.1 ± 2.3^{b}
Males/parasitized larva	8.9 ± 1.5^{a}	8.2 ± 2.0^{a}	7.1 ± 1.7^{a}	5.0 ± 1.6^{a}
Adult recovery	0.72	0.70	0.60	0.48
Sex ratio (F/M)	1.9	3.0	2.6	2.4
B. Choice study				
Number of larvae	53	53	40	40
Larvae lost (no data)	2	1	0	0
Dead larvae (no egg lay)	8	10	3	7
Dead larvae (egg lay)	4	5	13	19
Larvae not parasitized[*]	10	15	7	5
Larvae parasitized[**]	29	23	17	9
Eggs/parasitized larva	36.1 ± 3.5^{a}	35.4 ± 3.8^{a}	36.9 ± 3.7^{a}	38.4 ± 3.9^{a}
Females/parasitized larva	19.3 ± 1.5^{a}	22.4 ± 1.7^{a}	16.9 ± 2.1^{a}	7.6 ± 2.7^{b}
Males/parasitized larva	5.1 ± 0.8^{a}	7.8 ± 0.9^{a}	5.3 ± 1.0^{a}	2.7 ± 1.6^{b}
Adult recovery	0.68	0.85	0.60	0.27
Sex ratio (F/M)	3.8	3.2	2.9	2.8
C. E. platyhypenae egg site				
Eggs on thorax (%)	6.0	10.0	7.0	7.0
Eggs on abdomen (%)	32.0	30.0	31.0	30.0

[*] No eggs and went to pupation.
[**] Produced adult wasp.

two larvae were presented to the wasps (and at least one was usually viable) 59% (41/69) of the dead larvae were found with parasitoid egg clusters (Table 2B). This suggests that the presence of a live host may stimulate more indiscriminate ovipositional behavior in the female wasp.

3.4. Parasitoid viability

The viability of the parasitoids was calculated from the subset of larvae that were sufficiently healthy to allow the development of at least one adult wasp. This was measured as "adult recovery", which describes the proportion of adult wasps recovered from the total number of eggs present on a parasitized larva (Table 2). Comparisons between the no-choice and choice studies found no consistent viability differences with the corn diet. In the no-choice study the two strains were essentially equivalent (72% and 70%), while in the choice study, adult recovery in the rice-strain was higher (85%) than in the corn strain (68%) ($Z = -1.58$; $P = 0.05$).

In contrast, hosts reared on stargrass resulted in a general decline in wasp viability. The wasps developing on corn-strain larvae showed a modest reduction in adult recovery from an average of 72% on corn to 60% on stargrass that was not statistically significant (Table 2B). The decline was more pronounced in the rice strain where the shift from a corn diet to stargrass resulted, in the no-choice test, in a reduction in adult recovery from 70% to 48% and in the choice test from 85% to 27% (Table 2A and B).

The frequency distribution of parasitoid viability in each treatment was graphically displayed by histogram analysis. Wasp viability in corn strain larvae reared on corn approximated a broad bell-shaped pattern with a peak between 0.6 and 0.9 proportion of adult recovery (Fig. 1A). A stargrass diet produced a more irregular configuration with adult recovery levels shifted leftward. These effects were more pronounced with the rice-strain larvae. Wasp viability on rice-strain larvae reared on corn had a clear peak between 0.9 and 1.0 adult recovery, with a long leftward tail. When raised on stargrass, the frequency pattern again became irregular with a pronounced shift toward lower adult recovery values (Fig. 1B).

3.5. Parasitoid development

No differences were observed in the larval and pupal developmental time among experimental treatments. In general, larval developmental time took 6–7 days and pupal developmental time 7–8 days. Males generally emerged on the 7th day after pupation; females emerged on the 8th day.

Larval strain and plant diet had no consistent effect on sex ratio (Table 2A and B). All treatments showed substantial female-bias, with sex ratios that varied from about 2:1–4:1. Statistically significant interactions between host strains and plants were observed with respect to the recovery of wasp males and females, but these were not consistent between experiments. For example, in the no-choice study, the brood size of female wasps generated from rice strain larvae fed on corn was greater than those fed stargrass ($P < 0.05$) and more females were produced in stargrass-reared corn strain larvae than from the rice strain ($P < 0.05$) (Table 2A). Yet neither bias was observed in the choice study (Table 2B).

The size of the adult wasps emerging from each treatment was estimated from the measurement of wing length. A statistically significant interaction across host strains ($F = 28.35$; $df = 1{,}166$; $P < 0.001$), diet ($F = 30.84$; $df = 1{,}166$; $P < 0.001$) and between strain and diet was observed ($F = 14$; $df = 1{,}166$; $P < 0.001$). An average wing length of 2.1 mm was observed for both strains grown on corn and for the corn-strain reared on stargrass. This contrasts with a wing length of 1.7 mm for adult wasps emerging from rice-strain larvae grown on stargrass.

4. Discussion

Previous parasitoid surveys of the fall armyworm (Ashley, 1979; Molina-Ochoa et al., 2001) have described the need to identify parasitoid performance in relation to the host plant attacked by the

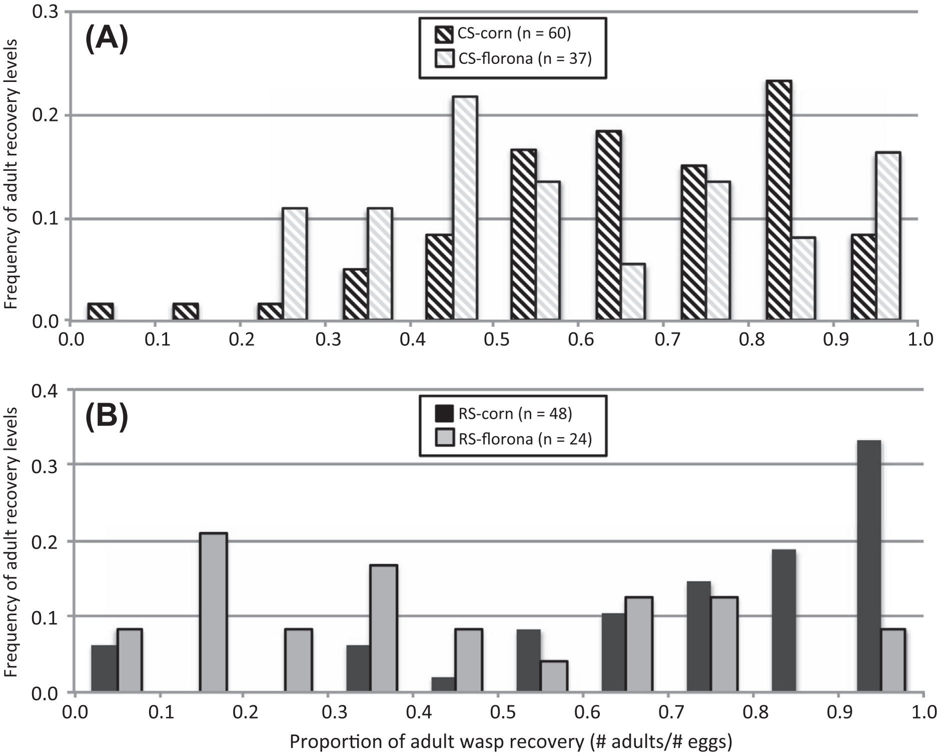


Fig. 1. Frequencies of different *Euplectrus platyhypenae* viability levels in fall armyworm larval hosts grown on either corn or 'Florona' stargrass diets. (A) Histogram of viability levels in individual corn-strain (CS) larvae grown on corn or stargrass. (B) Histogram of viability levels in individual rice-strain (RS) larvae grown on corn or stargrass. Only larvae still alive at the emergence of the parasitoid adults or after 5 days post-egg lay were included.

herbivore pest (Molina-Ochoa et al., 2003). The present study found that fall armyworm larval strain and plant diet had significant effects on the timing of *E. platyhypenae* oviposition, the numbers of eggs laid, and wasp juvenile mortality levels. Most striking was the wasp preference for corn-strain fall armyworm in choice tests when both larvae were raised on corn (Table 1). In most cases the corn-strain larva was parasitized first and we frequently observed the early clustering of the wasps around this strain larva despite the presence of a rice-strain larva in the same cage.

A second instance of significant strain and plant host interaction was observed with adult wasp recovery. Substantially fewer adults of both sexes emerged from stargrass-raised rice-strain larvae than from corn-strain reared on stargrass or either strain raised on corn (Table 2). This was due at least in part, to the higher larval mortality exhibited by our rice-strain colony (though we note that the adult recovery frequencies were calculated only from larvae still viable at the time of adult wasp emergence). The differential viability of the fall armyworm colonies was previously observed in our earlier study showing that 'Florona' stargrass possesses high concentrations of cyanogenic glycoside relative to corn plants (Hay-Roe et al., 2011), presumably indicating strain differences in the capacity to tolerate these compounds. If so, this could explain the observed differences in parasitoid recovery, either by reducing the overall health of the host population or by an allelochemical tritrophic interaction in which toxins ingested by the host or their metabolic byproducts are detrimental to the parasitoid. With respect to the latter possibility we note that in certain species of Zygaenidae, 30% of ingested cyanogenic glycosides were found to accumulate in the hemolymph (Davis and Nahrstedt, 1985; Nahrstedt and Davis, 1983, 1985), the nutrient source of *Euplectrus* juvenile stages (Coudron et al., 1994). However, we do not discard the possibility that herbivore-induced plant volatile (HIPV) might be causing behavioral and/or physiological responses in this parasitoids. For example, benzyl cyanide detected in lima beans (*Phaseolus lunatus*) and potato plants is known to mediate the attraction of predator mites and potato beetle (Qualley and Dudareva 2008). In other cases aromatic compounds such as methyl salicylate attracts mites in a dose-dependent manner, but at hight amounts repels the predators (De Boer and Dicke, 2004). Although we have not tested the effect of hydrogen cyanide on *Euplectrus* the high concentration of cyanide released by 'Florona'' stargrass might mediate the attraction of *Euplectrus* to the fall armyworm strains fed on this grass. The results for the timing of oviposition seems to indicate that *Euplectrus* female might be mildly repelled by HIPV, since no clear preference was shown, when both strains were feeding on this grass.

The combination of rice-strain larvae and a stargrass diet appears to be particularly detrimental to the larval host and parasitoid, as it is associated with higher mortalities and smaller sizes for both. The reasons for this are unclear, but it does not appear to be due to differences in larval size. The rice-strain larvae grown on stargrass were equal in size to both strains reared on corn, indicating that size was not a determining factor for the observed differences in parasitoid mortality and adult size. Furthermore, the largest larvae were found with the corn-strain grown on stargrass (by approximately 30%), yet this treatment was not associated with higher attractiveness to parasitism, wasp viability, or adult wasp size. These observations suggest that the quality rather than size of the larvae is more determinative of parasitoid performance. Of particular interest is the possibility of tritrophic interactions where the corn diet increases the relative attractiveness of the corn strain (but not rice strain) to parasitism.

The use of natural enemies such as parasitoids to control agricultural pests becomes more attractive as concerns about the ecological and health effects of chemical pesticides increase and naturally occurring resistance to current control methods develop. However, the economical viability and effectiveness of such biological control methods are dependent upon understanding the environmental and biological factors that influence parasitism frequency and optimize parasitoid populations. This is particularly true for a generalist parasitoid like *E. platyhypenae,* where the sympatric presence of competing host populations would likely compromise its effectiveness at controlling a specific pest. A review of the literature on fall armyworm parasitoids found that *E. platyhypenae* was mainly collected in corn fields and not commonly collected in pastures (Molina-Ochoa et al. 2001, Hay-Roe unpublished results). In this context, our results might explain the compartmental distribution of this parasitoid among the two different habitats. Since the rice strain is better adapted to cyanogenic plants (Hay-Roe et al. 2011), a good host strategy would lead to a movement to cyanogenic fields, to temporarily escape parasitism in times when overpopulated corn fields attract a diversity of parasitoids.

In this paper we demonstrated that while *E. platyhypenae* will parasitize both fall armyworm strains in the laboratory, it is likely to be significantly less effective against rice-strain larvae in turf grass and pasture habitats where stargrass and related *Cynodon* spp. grasses are abundant. A higher probability of significant biological control by augmentative release of *E. platyhypenae* would be expected in corn monocultures where the corn strain is mostly present. In fact, the quickness with which corn-strain larvae are parasitized when reared on corn under laboratory conditions suggests that this could be a very effective method of fall armyworm control in this habitat.

Acknowledgments

We gratefully acknowledge the assistance of Michael W. Gates, Systematics Entomology Laboratory, ARS, USDA, Washington, DC in identifying *Euplectrus platyhypenae* Howard, to A. Rowley and N. Fieleke for plant and insect colony maintenance and to J. Sivinski and H. Frank for early reviews of the manuscript.

References

Ashley, T.R., 1979. Classification and distribution of fall armyworm parasites. Florida Entomologist 62, 114–123.

Barbosa, P., Grossand, P., Kemper, J., 1991. Influence of plant allelochemicals on the tobacco hornworm and its parasitoid, *Cotesia congregata*. Ecology 72, 1567–1575.

Bultman, T.L., Borowicz, K.L., Schneble, R.M., Coudron, T.A., Bush, L.P., 1997. Effect of fungal endophyte on the growth and survival of two *Euplectrus* parasitoids. Oikos 78, 170–176.

Campbell, B.C., Duffy, S.S., 1979. Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control. Science 205, 700–702.

Casmuz, A., Juárez, M.L., Socías, M.G., Murúa, M.G., Prieto, S., Medina, S., Willink, E., Castaminza, G., 2010. Revisión de los hospederos del gusano cogollero del maíz, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Revista de la Sociedad Entomológica Argentina 69, 209–231.

Coudron, T.A., Puttler, B., 1988. Response of natural and factitious hosts to the ectoparasite *Euplectrus plathypenae* (Hymenoptera: Eulophidae). Annals of the Entomological Society of America 81, 931–937.

Coudron, T.A., Jones, D.J., Jones, G., 1994. Premature production of late larval storage proteins in larvae of *Trichoplusia ni* parasitized by *Euplectrus comstockii*. Archives of Insect Biochemistry and Physiology 26, 97–109.

Coudron, T.A., Brandt, S.L., Raqib, A., 1997. Comparison of the response of *Heliothis virescens* to parasitism by *Euplectrus comstockii* and *Euplectrus plathypenae*. Comparative Biochemistry and Physiology 116, 197–202.

Davis, R.H., Nahrstedt, A., 1985. Cyanogenesis in insects. In: Kerkut, G.A., Gilbert, L.I. (Eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology, vol. 11. Pergamon Press, Oxford, pp. 635–654.

De Boer, J.G., Dickle, M.A., 2004. Experience with methyl salicylate affects behavioral responses of a predatory mite to blends of herbivore-induced plant volatiles. Entomologia Experimentalis et Applicata 110, 181–189.

Drès, M., Mallet, J., 2002. Host races in plant-feeding insects and their importance in sympatric speciation. Philosophical Transactions of the Royal Society of London B 357, 471–492.

Fatouros, N.E., van Loon, J.J.A., Hordijk, K.A., Smid, H.M., Dicke, M., 2005. Herbivore-induced plant volatiles mediate in-flight host discrimination by parasitoids. Journal of Chemical Ecology 31, 2033–2047.

Hagler, J.R., Jackson, C.G., 2001. Methods for making insects: current techniques and future prospects. Annual Review of Entomology 46, 511–543.

Hay-Roe, M.M., Meagher, R.L., Nagoshi, R.N., 2011. Effects of cyanogenic plants on fitness in two host strains of the fall armyworm (*Spodoptera frugiperda*). Journal of Chemical Ecology 37, 1314–1322.

LaBarbera, M., 1989. Analyzing body size as a factor in ecology and evolution. Annual Review of Ecology and Systematics 20, 97–117.

Levy, H.C., Garcia-Maruniak, A., Maruniak, J.E., 2002. Strain identification of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) insects and cell line: Pcr-Rflp of cytochrome oxidase C subunit I gene. Florida Entomologist 85, 186–190.

Lill, J.T., Marqui, R.J., Ricklefs, R.E., 2002. Host plant influence parasitism of forest caterpillars. Nature 417, 170–173.

Lu, Y.-J., Adang, M.J., 1996. Distinguishing fall armyworm (Lepidoptera: Noctuidae) strains using a diagnostic mitochondrial DNA marker. Florida Entomologist 79, 48–55.

Luginbill, P., 1928. The fall armyworm. United States Department of Agriculture, Technical Bulletin 34, 1–91.

Meagher, R.L., Mislevy, P., Nagoshi, R.N., 2007. Caterpillar (Lepidoptera: Noctuidae) feeding on pasture grasses in central Florida. Florida Entomologist 90, 295–303.

Molina-Ochoa, J., Hamm, J.J., Lezama-Gutierrez, R., Lopez-Edwards, M., Gonzalez-Ramirez, M., Pescador-Rubio, A., 2001. A survey of fall armyworm (Lepidoptera: Noctuidae) parasitoids in the Mexican states of Michoacán, Colima, Jalisco, and Tamaulipas. Florida Entomologist 84, 31–36.

Molina-Ochoa, J., Carpenter, J.E., Heinrichs, E.A., Foster, J.E., 2003. Parasitoids and parasites of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas and caribbean basin: an inventory. Florida Entomologist 86, 254–289.

Murúa, G., Virla, E.G., 2004. Contribution to the biological knowledge of *Euplectrus platyhypenae* (Hymenoptera: Eulophidae), a parasitoid of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Argentina. Folia Entomológica Mexicana 43, 171–180.

Nagoshi, R.N., Meagher, R.L., 2003. FR tandem-repeat sequence in fall armyworm (Lepidoptera: Noctuidae) host strains. Annals of the Entomological Society of America 96, 329–335.

Nagoshi, R.N., Meagher, R.L., Adamczyk, J.J., Braman, S.K., Brandenburg, R.L., Nuessly, G., 2006. New restriction fragment length polymorphisms in the cytochrome oxidase I gene facilitate host strain identification of fall armyworm (Lepidoptera: Noctuidae) populations in the southeastern United States. Journal of Economic Entomology 99, 671–677.

Nagoshi, R.N., Adamczyk, J.J., Meagher, R.L., Gore, J., Jackson, R., 2007. Using stable isotope analysis to examine fall armyworm (Lepidoptera: Noctuidae) host strains in a cotton habitat. Journal of Economic Entomology 100, 1569–1576.

Nahrstedt, A., Davis, R.H., 1983. Occurrence, variation, and biosynthesis of the cyanogenic glucosides linamarin and lotaustralin in the species of Heliconiini (Insects: Lepidoptera). Comparative Biochemistry and Physiology 75, 65–73.

Nahrstedt, A., Davis, R.H., 1985. Biosynthesis and quantitative relationships of the cyanogenic glycosides, linamarin and lotaustralin, in genera of the Heliconiini (Insecta: Lepidoptera). Comparative Biochemistry and Physiology 82, 745–749.

Pashley, D.P., 1988. Quantitative genetics, development, and physiological adaptation in host strains of fall armyworm. Evolution 42, 93–102.

Pashley, D.P., Quisenberry, S.S., Jamjanya, T., 1987. Impact of fall armyworm (Lepidoptera: Noctuidae) host strains on the evaluation of bermuda grass resistance. Journal of Economic Entomology 80, 1127–1130.

Pashley, D.P., Hardy, T.N., Hammond, A.M., 1995. Host effects on development and reproductive traits in fall armyworm strains (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 88, 748–755.

Poelman, E.H., Gols, R., Snoeren, T.A., Muru, D., Smid, H.M., Dicke, M., 2011. Indirect plant-mediated interactions among parasitoid larvae. Ecological Letters 14, 670–676.

Prowell, D.P., 1998. Sex linkage and speciation in Lepidoptera. In: Howard, D.J., Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press, Oxford, United Kingdom, pp. 309–319.

Qualley, A.V., Dudareva, N., 2008. Aromatic volatiles and their involvement in plant defense. In: Schaller, A. (Ed.), Induced Plant Resistance to Herbivory. Springer Science + Business, Media B.V., pp. 409–432.

Reitz, S.R., Trumble, J.T., 1997. Effects of linear furanocoumarins on the herbivore *Spodoptera exigua* and the parasitoid *Archytas marmoratus*: host quality and parasitoid success. Entomologia Experimentalis et Applicata 84, 9–16.

Roland, J., 2000. Landscape ecology of parasitism. In: Hochberg, M.E., Ives, A.R. (Eds.), Parasitoid Population Biology. Princeton University Press, Princeton, pp. 83–99.

Vickery, R.A., 1929. Studies of the fall armyworm in the gulf coast district of Texas. United States Department of Agriculture, Technical Bulletin 138, 63.

Wilson, J.W., 1932. The biology of parasites and predators of *Laphygma exigua* H.B. reared during the season 1932. Florida Entomologist 17, 1–15.