Impact of *Cotesia flavipes* (Hymenoptera: Braconidae) as an augmentative biocontrol agent for the sugarcane borer (Lepidoptera: Crambidae) on rice

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A B S T R A C T

A 2-year field cage experiment was conducted in Beaumont, Texas to estimate parasitism of sugarcane borer, *Diatraea saccharalis* (F.), by *Cotesia flavipes* (Cameron) on rice. A lab experiment showed that the number of hosts parasitized per female per day reached a maximum (0.961) at 28 °C. Parasitized larvae recovered from the field experiment produced an average of 27.9 ± 19.1 (x ± s.d.) parasitoids, with a 2.57:1 (female/male) sex ratio. A cohort-based age-structured model was developed to simulate the population dynamics and economic impact of sugarcane borer and *C. flavipes* in rice, as affected by overwintering larval density, timing and rate of parasitoid aerial release, and year-to-year climate (temperature and rainfall). The results suggest the cumulative seasonal damaging larval density (3rd or later instars) is negatively correlated with winter temperature, while maximum parasitoid density and maximum proportion parasitized are positively correlated with the cumulative seasonal damaging larval density. *C. flavipes* was most effective when released 40 or 50 days after rice planting, with simulated yield loss reduced by up to 50.9% when the release rate was 10 females and 4 males m⁻². The maximum simulated economic benefit ($59.48 ha⁻¹) is ca. 6.7% of that provided by insecticide-based control, which occurred when the release was 1 female and 0.4 males m⁻².

1. Introduction

The two most important stem-boring pests in the Texas ricebelt are the sugarcane borer, *Diatraea saccharalis* (F.), and the Mexican rice borer, *Eoreuma loftini* (Dyar). The sugarcane borer became the predominant species in both Texas and Louisiana, shortly following its introduction to Louisiana (Bowling, 1967). The Mexican rice borer was first discovered in Texas in 1980 and now causes yield loss across the Texas ricebelt (Reay-Jones et al., 2005). The sugarcane borer was first discovered in Texas in 1980 and now causes yield loss across the Texas ricebelt (Reay-Jones et al., 2005). The occurrence of both species has increased in recent years. Way et al. (2006) reported that stem borer injury resulted in rice yield losses of up to 60% in Texas. Among all stem borers recovered from their field sampling, ca. 60% were sugarcane borers.

Previous research suggests parasitoids can inflict a high level of mortality upon sugarcane borer populations. Browning and Melton (1987) recorded *Trichogramma fuentesi* Torre (Hymenoptera: Trichogrammatidae) parasitized 78.7% of sugarcane borer eggs in sugarcane (*Saccharum officinarum* L.) fields in the Lower Rio Grande Valley of Texas. Parra and Zucchi (2004) studied the efficacy of biocontrol on sugarcane in Brazil when using a number of *Trichogramma* species in combination with *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae), a larval parasitoid. The highest sugarcane borer population reduction (60.2%) occurred when using *Trichogramma galloi* Zucchi and *C. flavipes*. Alam (1980) reported that the introduction of *C. flavipes* and a second larval parasitoid, *Lixophaga diatraeae* (Townsend) (Diptera: Tachinidae), successfully reduced sugarcane borer injury to sub-economic levels in Barbados. The control of the sugarcane borer using *C. flavipes* in sugarcane has also been documented in the Rio Grande Valley of Texas (Meagher et al., 1998).

*T. fuentesi*, *T. galloi*, and *L. diatraeae* coevolved with the sugarcane borer, while *C. flavipes* lacks a long-term association with this species. *C. flavipes* is indigenous to the Indo-Australian region, where its hosts are among the *Chilo* genus (Lepidoptera: Crambidae). Studies of *C. flavipes* as a natural enemy of *Chilo* pests in rice were conducted in Japan (Smith et al., 1993) and China (Song et al., 1996; Zhu et al., 1999; You et al., 2000; Li et al., 2005). However, these studies mainly focused on natural control, and did not evaluate the ability of *C. flavipes* to prevent economic loss. While
C. flavipes has been documented to have a major impact on sugarcane borer populations in perennial hosts, such as sugarcane, which are temporally stable, its ability to control stem borer pests on ephemeral host crops, such as rice, is poorly understood.

The objective of the present research is to determine the potential value of C. flavipes as an augmentatively released biocontrol agent of the sugarcane borer on rice. Life table parameters for both the sugarcane borer and C. flavipes, obtained from published data and experiment presented herein, were incorporated into a simulation model of seasonal population dynamics. A range of overwintering sugarcane borer larval densities and timings and rates of C. flavipes release was simulated. A cost/benefit analysis was conducted by combining estimates of yield loss and parasitoid rearing and release costs.

2. Methods and materials

2.1. Field experiment

A field experiment was conducted in 2005 and 2006 at the Texas A&M University System AgriLife Research and Extension Center at Beaumont. The soil is a fine montmorillonite and thermic Entic Pelludert (Chen et al., 1989). Fields were planted on April 22, and April 19 in 2005, and 2006, respectively, using a 0.18 m-row spacing.

A randomized complete block split–split plot design was used each year. Each of the three blocks contained three plots, one for each cultivar (Cocodrie, Francis, and Jefferson). Cocodrie and Francis were planted at a rate of 120 kg seed ha⁻¹, while Jefferson was planted at 144 kg seed ha⁻¹. The planting rate differed between cultivars because Jefferson has a lower germination rate. Each plot contained three split plots, each representing a growth stage for infestation. Each split plot was 3.25 m in length. The five split–split plots represented a control split–split plot (0 eggs m⁻²) with 0.25 m at each end as buffers. Each split plot in turn consisted of five split–split plots, each 0.5 m in length. The five split–split plots were covered with a 0.85 m (l) × 1.2 m (w) × 1.25 m (h) cage. In 2005, 20 newly emerged C. flavipes females and 5 newly emerged males were released into each cage covering non-zero split–split plots, 15 days after sugarcane borer release. The female/male sex ratio used in each release mimicked the average sex ratio (4:1) of the Beaumont C. flavipes colony. In 2006, the release rate was increased to 100 females and 25 males per cage to increase the parasitoid rate.

Cages were removed three days after parasitoid release. Tillers within each split–split plot were cut at the base, and returned to the lab for processing. Each injured tiller was slit to check for the presence of larvae. The number of injured tillers and recovered larvae was recorded for each subsample. For the 1st infestation in 2005, instars were estimated based on head capsule widths (Roe et al., 1982). Third or later instars, which were considered as suitable hosts for C. flavipes (Wiedenmann et al., 1992), were placed on artificial diet and reared in the lab (see Sugarcane Borer Colony section) until they either died or pupated, or until parasitoid cocoons were observed. For the 2nd infestation in 2005, all recovered larvae were reared in the lab to confirm that C. flavipes does not parasitize 1st and 2nd instars. Results showed that C. flavipes parasitize sugarcane borer larvae of 2nd instar size. The larval instar might be underestimated because larvae might molt more than once without appreciably increasing in size. As a result of these findings, all larvae recovered from subsequent infestations were classified as either small (head capsule width < 0.93 mm, ca. 2nd and 3rd instars), medium (0.93 mm < head capsule < 1.32 mm, ca. 4th instar), or large (head capsule with ≥ 1.32 mm, ca. 5th instar), and were reared in the lab. Larval developmental duration on rice was estimated as the ratio of the degree-days that recovered larvae experienced in the field and the degree-days for larvae to develop to the same age under lab conditions (King et al., 1975) multiplied by the entire larval developmental duration under lab conditions. The same approach was used to estimate larval developmental variability. Survival of sugarcane borer larvae from hatching to ca. 18 days old was estimated by the ratio of the number of recovered larvae and the egg release rate. C. flavipes cocoons obtained from parasitized larvae were placed in 30 ml plastic cups, as used for the C. flavipes colony (see C. flavipes Colony section). The number and gender of emerging parasitoids was recorded. Parasitization was estimated as the ratio of the number of parasitized larvae and the number of recovered larvae.

2.2. Lab experiment

A lab experiment was conducted at the Texas A&M University System AgriLife Research and Extension Center at Beaumont, to determine the effect of temperature on the maximum number of hosts parasitized per female. The experiment was conducted at 4 temperatures: 22, 25, 28, and 31 C. For each temperature, 10 petri dishes (10 cm dia.) were prepared, each containing a thin layer (ca. 0.5 cm) of sugarcane borer diet (see Section 2.3). Seven 3rd instar sugarcane borers and a pair of newly emerged C. flavipes adults were placed in each petri dish. The number of larvae provided to each female exceeds the observed maximum number of hosts parasitized per female (Potting et al., 1997). The petri dishes were placed in a Conviron 124 L incubator and maintained at a 14:10 photophase. When the C. flavipes adults had all died, the larvae were moved to 30 ml diet cups, and reared separately until they either died, pupated, or C. flavipes cocoons were observed. The number of dead and parasitized larvae was recorded.
2.3. Sugarcane borer colony

Sugarcane borers used in the present study were obtained from a Beaumont colony, established using adult sugarcane borer moths reared from eggs obtained from a USDA-ARS colony maintained by Dr. William White, in Houma, Louisiana. The USDA colony has been maintained in the lab since 1989, with wild moths introduced in 2000 and 2006 from a sugarcane field near Houma. The Beaumont colony was reared in a Conviron 124 L incubator, at 28 ± 1 °C and a 14:10 photophase. Each week, a wax paper lined paper carton (1.9 L) was used as an oviposition container, which holds ca. 15 pairs of pupae. Adults were fed with 5% sugar water, and wax paper was removed and replaced daily for egg collection. Eggs were hatched in plastic bags filled with air and saturated with moisture. Larvae were reared in 30 ml plastic cups (Bio-Serv. Inc., NJ) containing 15 ml of a soybean flour-wheat germ diet produced by Southland Products, Inc.

2.4. C. flavipes colony

A C. flavipes colony was established using adults reared from cocoons obtained from a USDA-ARS colony maintained by Dr. William White, in Houma, Louisiana. This colony was initiated in 2003 with field collected C. flavipes obtained from Weslaco, Texas. The Beaumont colony was maintained as previously described for the sugarcane borer colony. Every 4 days, parasitoid cocoons obtained from 25 parasitized sugarcane borer larvae were placed in 30 ml plastic cups for adult emergence. Individual larvae were each exposed to 5 12-h old C. flavipes females in a Petri dish (10 cm dia.) for parasitization and observed for up to 5 min. Parasitized larva was immediately replaced and reared as described in the Section 2.3. If parasitization did not occur, the larva was replaced. If parasitization did not occur for three consecutive larvae, the C. flavipes were replaced. Parasitism was allowed to continue until ca. 30 parasitized larvae were obtained to maintain the colony, and ca. 100 were produced for each field release.

2.5. Model structure

Cohort-based age-structured models were used to simulate the population dynamics of the sugarcane borer and C. flavipes. A cohort refers to individuals within a species having the same physiological age at a particular time, while physiological age expresses development on a heat unit basis (Gilbert and Gutierrez, 1973) by integrating variability in aging, with some individuals aging faster or slower than the average (Plant and Wilson, 1986). The sugarcane borer population was initiated from overwintering larvae at the time of diapause termination in early spring. Population progression was simulated in rice through the main crop, and in the stubble until the next year’s spring emergence. The majority of rice fields in the southern US have stubble that remains in the fields until the next spring. Because ratoon crop production represents an average of only 11% of the total rice production east of Houston for 2001 through 2009 (Morace et al., 2009), it was not simulated. Rice is rarely replanted in the same field two years in a row. Simulated overwintering larval density provides estimates of the timing of diapause termination and subsequent pupal development, and adult emergence the following spring. The immigration and emigration of sugarcane borer moths was assumed to be equal throughout each year.

C. flavipes population progression was simulated from age-structured data to the last generation each year. White et al. (2004) reported that in subtropical and temperate regions, overwintering sugarcane borer larvae exist in underground internodes of sugarcane in early spring, where C. flavipes are not able to reach. As a result, the 1st generation C. flavipes was not simulated due to the adults failing to find hosts for oviposition and failing to produce future generations.

The functions used in this model to describe major physiological processes, and the corresponding data sources used for parameterization are listed in Table 1. Simulations were conducted using a physiological time scale (degree-days (DD) > 10.4 °C, estimated from King et al., 1975) on a m² area basis, with population progression calculated daily. Major differences between the coefficients of developmental variability for the eggs, larvae, pupae, and adults required that each stage be simulated separately. Developmental variability was incorporated using a modification to the Plant and Wilson (1986) degree-day based distributed maturation algorithm, allowing development to be incremented on a daily instead of a degree-day basis. Sugarcane borers enter diapause at the end of the larval stage during the winter in areas with temperate and sub-tropical climates. Diapause can be induced in 2nd and 3rd instars by decreasing day length and decreasing temperature (Fuchs et al., 1979; Philogène and Hammond, 1984; Rodriguez-del-Bosque et al., 1995). Intrinsic survivorship was estimated as a function of temperature and age using data from King et al. (1975), while abiotic extrinsic survivorship was estimated as a function of sugarcane borer age, host plant age, and rainfall, using data from Bonhof and Overholt (2001), Lv et al. (2008), and from the field experiment reported herein. Fecundity was estimated as a function of temperature and age using data from King et al. (1975) and Bessin and Reagan (1990).

Population progression of C. flavipes was simulated using the same distributed maturation algorithm as described for the sugarcane borer submodel. Oviposition preference quantifies departure from random host selection, and can be used to estimate herbivore oviposition, parasitism, and predation based on the availability of different host species or age/stage classes (Murdoch, 1969; Manly et al., 1972; Chesson, 1978; Wilson and Gutierrez, 1980; Pickett et al., 1989; Murphy et al., 1991; Reay-Jones et al., 2007). Estimates of relative oviposition preference (0–1) by C. flavipes for each host instar were derived from the estimated number of larvae and parasitized larvae in each instar at the time of peak parasitization (ca. 1 day after release of the adult C. flavipes, Potting et al., 1997). The physiological age-class distribution of total and parasitized larvae at the time of parasitism was obtained from the respective age-class distribution at the time of samplings by using a reverse solution of the distributed maturation method. Daily parasitization of sugarcane borer larvae within each age class by C. flavipes was simulated using the Frazer–Gilbert functional response equation (Frazer and Gilbert, 1976), with the maximum number of hosts parasitized per female, and the effective search rate estimated from the lab and field experiments described herein.

For each of the three sugarcane borer generations that occur during main crop development, the normalized yield is expressed as a function of the simulated density of sugarcane borer that entered the 3rd instars, herein referred to as damaging larval density, and the degree-days from rice planting to timing when injury occurred (Eqs. (1a)–(1c), modified from Lv et al., 2008),

\[
Y_i = -5.14 + 0.0191DD_i - 0.00000199\rho_i - 0.0000150DD_i^2 + 0.0000000343DD_i^3\rho_i - 0.000000000199\rho_i^2 + 0.0000000005DD_i\rho_i^2
\]  
(1a)

\[
Y_i = -0.581 + 0.0029DD_i + 0.000000418\rho_i - 0.00000137DD_i^2 - 0.0000000508DD_i^3\rho_i
\]  
(1b)

\[
Y_i = -3.05 + 0.0057DD_i - 0.000000398\rho_i - 0.000000192DD_i^2 + 0.0000000000155\rho_i^2
\]  
(1c)
Table 1
Functions used in the sugarcane borer and *C. flavipes* submodels and corresponding data source for parameterization.

<table>
<thead>
<tr>
<th>Submodel</th>
<th>Process</th>
<th>Functions</th>
<th>Parameter and description</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugarcane borer</td>
<td>Developmental duration</td>
<td>( D_{ij} = \frac{D_{ij,\text{min}}}{(\tau_j - \tau)} ) ((\tau &gt; \tau_{ij,\text{min}}))</td>
<td>( D_{ij} ): mean developmental duration of the ( j )th stage, at temperature ( \tau ) (DD &gt; 10 °C) ( D_{ij,\text{min}} ): minimum developmental duration for the ( j )th sugarcane borer stage at optimal temperature ( \tau ): daily average temperature (°C) ( \tau_{ij,\text{min}} ): optimal temperature for the ( j )th stage ( \beta_{ij,1} ): empirical constants</td>
<td>King et al. (1975); the field experiment</td>
</tr>
<tr>
<td></td>
<td>Distributed maturation</td>
<td>( N_{ij} = N_{ij,k-1} + \eta_i + N_{ij,k-1}(1 - 2\delta_i) + N_{ij,k-1}\delta_i ) ( \delta_i = \frac{n_i(t_j)}{2D_{ij}} )</td>
<td>( N_{ij} ): sugarcane borer density in the ( i )th age class of ( j )th stage on the ( k )th day ( \eta_i ): probability of aging either faster or slower than the mean developmental rate ( \delta_i &lt; 0.33 ) ( n_i ): number of age classes within the ( j )th stage ( \eta_i ): variance of developmental duration for the ( j )th stage at temperature ( \tau ) ( \delta_i ): variance of the timing of diapause initiation</td>
<td>King et al. (1975); the field experiment</td>
</tr>
<tr>
<td></td>
<td>Diapause</td>
<td>( p_d = \text{Min}(1, \text{Max}(0, (\beta_1 + \beta_2(1 + \beta_3(t_i)))) ) ( \beta_1 ): proportion of 2nd and 3rd instars induced to enter diapause at the end of larval stage ( \beta_2 ): proportion induced on the ( k )th day ( t_i ): day length (h) ( p_{d1} ): number of age classes sensitive to diapause induction</td>
<td>( p_d ): proportion of 2nd and 3rd instars induced to enter diapause at the end of larval stage</td>
<td>Fuchs et al. (1979); Philiogène and Hammond (1984) and Rodriguez-del-Bosque et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>Survival</td>
<td>( S_{ij,k} = \left( \frac{\beta_i \tau_i}{\beta \tau} \right)^{\frac{k}{\tau_i}} \right)_{\text{egg stage}} ) ( \beta ): oviposition preference for the ( i )th age class sugarcane borer larvae. ( \beta ): density of ( i )th age class sugarcane borer larvae when parasitism occurred at the ( k )th instar across the three crop growth stages</td>
<td>( S_{ij,k} ): intrinsic survivorship in the ( i )th age class of ( j )th stage on the ( k )th day at temperature ( \tau )</td>
<td>King et al. (1975), Bonhoff and Overholt (2001) and Lv et al. (2008)</td>
</tr>
<tr>
<td></td>
<td>Fecundity</td>
<td>( F_{i,\text{ej}} = (\text{Max}(C_{ij}))^{\text{Max}(C_{ij})/\tau} ) ( \tau ): day length (h) ( \text{Max}(C_{ij}) ): maximum number of larvae parasitized per female per day at temperature ( \tau )</td>
<td>( F_{i,\text{ej}} ): cumulative fecundity per female to the ( i )th age class of adult stage at temperature ( \tau )</td>
<td>Bessin and Reagan (1990)</td>
</tr>
<tr>
<td><em>Cotesia flavipes</em></td>
<td>Oviposition preference</td>
<td>( x_{m,\text{ej}} = \frac{n_{m,j}\text{ej}}{n_{m,j}\text{ej} + n_{m,j}\text{ej}} ) ( n_{m,j}\text{ej} ): average oviposition preference for the ( m )th instar across the three crop growth stages and two years ( n_{m,j}\text{ej} ): number of parasitized sugarcane borer larvae at peak parasitism in the ( m )th instar when parasitism occurred at the ( k )th crop growth stage and the ( k )th year</td>
<td>( x_{m,\text{ej}} ): oviposition preference for the ( m )th instar when parasitism occurred at the ( k )th crop growth stage and the ( k )th year</td>
<td>The field experiment</td>
</tr>
<tr>
<td></td>
<td>Functional response</td>
<td>( N_{p,i} = N_p \frac{n_{i,j}}{n_{i,j} + n_{i,j}} ) ( n_{i,j} ): density of <em>C. flavipes</em> females attacking the ( i )th age class ( n_{i,j} ): oviposition preference for the ( i )th age class ( N_p ): <em>Cotesia flavipes</em> female density ( N_{p,i} ): density of ith age class sugarcane borer larvae ( N_{p,i} ): density of parasitized ith age class sugarcane borer larvae ( b_i ): number of larvae parasitized per female per day at temperature ( \tau ) ( b_{i,\text{max}} ): proportion of development completed at the end of egg stage</td>
<td>The field and lab experiments</td>
<td></td>
</tr>
</tbody>
</table>
where:
\[ Y_i = \text{normalized yield as affected by the } i\text{th generation of } C. \text{ flavipes} \]
\[ Y_u = \text{yield in the absence of injury} \]
\[ \text{DD}_i = \text{degree-days from rice planting to the time when injury occurred} \]
\[ \rho_i = \text{density (ha}^{-1}) \text{of sugarcane borer larvae reaching the } 3\text{rd instar} \]

The impact of sugarcane borer injury on rice yield was assumed to be multiplicative across the three generations and was estimated as the product of yield in the absence of injury and normalized yield as affected by each generation (Eq. (2)). The average yield for the three cultivars used in our experiment in the absence of injury was 6776.4 kg ha\(^{-1}\) (Lv et al., unpublished data). When \( C. \text{ flavipes} \) were released, the yield loss prevented was estimated as the difference in yield with and without \( C. \text{ flavipes} \) release.

\[ Y = Y_u \prod_{i=1}^{3} Y_i \quad (2) \]

where:
\[ Y = \text{rice yield (kg ha}^{-1}) \text{as affected by three generations of sugarcane borer injury} \]

The economic impact of parasitoid release was estimated as the difference between the value of the yield loss prevented by releasing \( C. \text{ flavipes} \) and the cost of the control action (Eq. (3)). The estimated cost of a \( C. \text{ flavipes} \) release consists of the cost of rearing, shipping, handling, and release. The cost of \( C. \text{ flavipes} \) rearing is \( \$100.00 \) for 10,000 females (ca. 14,000 males + females), including 66.5% for diet (Southland Products, Inc.) and 33.5% for rearing trays and plastic sheet covers (Hall, personal communication). The estimated shipping cost is \( \$0.29 \) per 10,000 cocoons, derived from Van Driesche et al. (2002), adjusted for the weight difference of \( C. \text{ flavipes} \) pupae. The cost of aerial-release is \( \$1.00 \) per 10,000 parasites, plus an additional \( \$24.72 \) per hectare for the aerial application (Penn, personal communication). The market value of rough rice is ca. \( \$0.28 \) per kg (Chicago Board of Trade May 2011 futures price estimated on May 26, 2010).

\[ E = vY_p - c \quad (3) \]

where:
\[ E = \text{economic impact of } C. \text{ flavipes \ release ($} \text{ha}^{-1}) \]
\[ v = \text{market value of rough rice per unit of product ($} \text{kg}^{-1}) \]
\[ Y_p = \text{yield loss prevented by } C. \text{ flavipes \ release (kg} \text{ha}^{-1}) \]
\[ c = \text{cost of pest control ($} \text{ha}^{-1}) \]

2.7. Statistical analyses

Analyses of variance (ANOVAs) were conducted to evaluate the effect of year, cultivar, crop growth stage, and associated interactions on larval developmental duration, parasitoid progeny produced per parasitized larva, and parasitoid sex ratio, and to evaluate the effect of the same main factors, initial egg density, and associated interactions on survival and proportion parasitized larvae. Survival and proportion parasitized larvae were log transformed to meet the assumptions of normality. ANOVAs were also conducted on simulated cumulative seasonal damaging larval density, maximum seasonal proportion parasitized, maximum seasonal density of \( C. \text{ flavipes} \) adults, rice yield, and economic impact of \( C. \text{ flavipes} \) release, each as affected by year, overwintering larvae density, \( C. \text{ flavipes} \) release rate and release timing, and the corresponding interactions.

Main factors or interactions with \( P < 0.05 \) were considered to be statistically significant. For ANOVAs conducted on field data, statistically significant main factors and interactions that explained more than 5% of variability were discussed in detail. For ANOVAs conducted on simulated results and economic impact, all main factors and interactions that were statistically significant were discussed in detail. Means for each level within each significant main factor or interaction were compared using Tukey’s HSD.

3. Results and discussion

3.1. Field experiment

A total of 2710 and 722 sugarcane borer larvae were recovered in 2005 and 2006, respectively. In 2005, 13 larvae were recovered from the zero control treatment, which implies a low level of natural infestation.

The larval developmental duration was significantly affected by year, stage, cultivar, and year \( \times \) stage interaction (Table 2). Developmental duration was longer in 2005 (658.0 ± 51.8 DD) than in 2006 (545.1 ± 86.6 DD), and was longer at 3rd tiller (611.5 ± 51.1 DD) and panicule differentation (639.9 ± 76.8 DD) than at heading (548.5 ± 94.9 DD). Developmental duration was greater in Francis (631.7 ± 80.0 DD) than in Cocodrie (587.9 ± 79.9 DD) and Jefferson (580.6 ± 94.2 DD). In 2005, developmental duration was longer at panicule differentation (709.1 ± 28.4 DD) than at 3rd tiller (636.8 ± 82.8 DD), and heading (625.0 ± 56.3 DD). In contrast, in 2006, developmental duration was greater at 3rd tiller (593.7 ± 95.0 DD) and panicule differentiation (566.4 ± 79.3 DD), followed by heading (467.9 ± 79.4 DD). The estimated developmental duration from our field experiment was 40.5% to 85.5% longer than reported by King et al. (1975) for lab conditions.

Larval survival was affected by year, stage, density, stage \( \times \) density, and year \( \times \) cultivar \( \times \) density interactions. Survival was higher in 2005 (0.144 ± 0.106) than in 2006 (0.034 ± 0.055), and was higher at 3rd tiller (0.160 ± 0.126) than at panicule differentiation (0.051 ± 0.055) and heading (0.056 ± 0.063). In contrast, in an open-field experiment in the immediately adjacent field
ANOVAs for developmental duration of sugarcane borer larvae, larval survival, proportion parasitized, number of progeny per parasitized larva, and sex ratio of progeny.

Source of variances

<table>
<thead>
<tr>
<th>Development duration of sugarcane borer larvae</th>
<th>Larval survival</th>
<th>Proportion parasitized</th>
<th>Number of progeny per parasitized larva</th>
<th>Sex ratio of progeny</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
<td>P&gt;F</td>
<td>% Explained</td>
<td>df</td>
<td>P&gt;F</td>
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<td>11.51</td>
<td>0.399</td>
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<td>Error</td>
<td>108</td>
<td>108</td>
<td>5.62</td>
<td>23</td>
</tr>
</tbody>
</table>

Significance levels: *P < 0.05.

Fig. 1presents the density of parasitized larvae as a function of sugarcane borer larval density. The estimated effective search rate from the field experiment is 2.2 tillers d^{-1} per parasitoid. The low effective parasitoid search rate was likely due to the larvae being concealed in tunnels within stems. Rice has smaller stems in comparison to many sugarcane borer host plants, such as sugarcane, corn, and sorghum. When C. flavipes females are exposed to frass under laboratory conditions, they generally spend 5–15 min seeking an opening to the larva before giving up (Potting et al., 1999). When larvae feed inside rice stems, the tunnels are often blocked by frass, which can prevent C. flavipes from reaching them (Lv, personal observation).

Host defensive behavior also plays a role in reducing successful parasitization. Potting et al. (1997) reported 30–40% of C. flavipes females were killed by the spitting and biting of stem borer larvae when larvae were confined within artificial tunnels. The majority of C. flavipes were killed if they approached the larvae from the head end. Takasu and Overholt (1997) reported parasitoid mortality due to aggressive defensive behavior was significantly higher when older larvae were attacked, with 26.7%, 53.3%, and 66.7% of C. flavipes killed when attacking 3rd, 4th, and 5th instars, respectively. In the present study, C. flavipes relative oviposition preference was estimated to be 0, 0.337, 0.385, 0.718, and 1 for 1st to 5th instar larvae, respectively. The greater preference for large larvae results in a higher risk of being killed. However, it is reasonable to speculate that the higher mortality must be at least partially offset by a greater reproductive success.
Significant main effects and interactions were not observed for either *C. flavipes* progeny produced per parasitized larva or *C. flavipes* sex ratio (Table 2). Parasitized larvae produced an average of 27.9 ± 19.1 *C. flavipes* adults, with 5.1% of the larvae parasitized by unfertilized females, which only produce male offspring. The mean sex ratio produced by fertilized *C. flavipes* was 2.57:1 (females/males), with a 2.13:1 sex ratio recorded for all females combined. The average number of *C. flavipes* progeny per parasitized larva was lower than reported in previous studies, which ranged from 35 to 53 (Alam, 1980; Potting et al., 1997; Wiedenmann et al., 1992). Similarly, the progeny sex ratio was considerably less than previously reported (Potting et al., 1997; Wiedenmann et al., 1992). Takasu and Overholt (1997) reported the majority of *C. flavipes* adults killed by sugarcane borer larval defensive behavior completed parasitism successfully. However, it is unknown whether the defensive behavior of host larvae reduces the clutch size. The oviposition behavior generally takes several seconds (Potting et al., 1997). In our lab experiment, sugarcane borer larvae were observed interrupting *C. flavipes* ovipositioning ca. 10% of the time.

3.2. Simulation analyses

Parameters used by the simulation model are presented in Tables 3 and 4. Table 3 summarizes statistics for minimum developmental duration, maximum fecundity, and sex ratio for sugarcane borer and *C. flavipes*, and *C. flavipes* oviposition preference for each host instar. Table 4 summarizes parameters used to estimate sugarcane borer developmental duration and fecundity, and maximum number of hosts parasitized per *C. flavipes*, each as a function of temperature, with sugarcane borer survival also a function of host plant age and rainfall.

### Table 3

Summary of statistics for minimum developmental duration, maximum fecundity, and sex ratio for sugarcane borer and *C. flavipes*.

<table>
<thead>
<tr>
<th>Life table parameters</th>
<th>Sugarcane borer</th>
<th><em>C. flavipes</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Egg Larval Pupal Adult Immature Adult</td>
<td></td>
</tr>
<tr>
<td>Minimum developmental duration (DD &gt; 10.4 °C)</td>
<td>86.2 562.0 123.8 103.3 277.4 69.8</td>
<td></td>
</tr>
<tr>
<td>Developmental variability</td>
<td>14.2 8236.3 72.5 279.5 – –</td>
<td></td>
</tr>
<tr>
<td>Temperature (°C) when the minimum developmental duration was observed</td>
<td>27.0 27.1 27.0 28.0 – –</td>
<td></td>
</tr>
<tr>
<td>Temperature (°C) when the maximum fecundity was observed</td>
<td>– – – 427.1 – –</td>
<td></td>
</tr>
<tr>
<td>Proportion of female offspring</td>
<td>0.50 0.72</td>
<td></td>
</tr>
</tbody>
</table>

### Table 4

Parameters used to estimate sugarcane borer developmental duration and fecundity, and maximum number of host parasitized per *C. flavipes*, each as a function of temperature, and sugarcane borer survival as a function of temperature, host plant age, and rainfall.

<table>
<thead>
<tr>
<th>Submodel</th>
<th>Function</th>
<th>Stage</th>
<th>Equation</th>
<th>Parameter</th>
<th>Estimate</th>
<th>$r^2$</th>
<th>df</th>
<th>$P &gt; F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugarcane borer</td>
<td>Developmental duration</td>
<td>Egg 1 $\beta_1$</td>
<td>$\beta_2$</td>
<td>– 0.794</td>
<td>0.837</td>
<td>2, 3</td>
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<td></td>
<td></td>
<td>Larval 1 $\beta_1$</td>
<td>$\beta_2$</td>
<td>– 0.015</td>
<td>0.975</td>
<td>2, 3</td>
<td>0.004</td>
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<td></td>
<td></td>
<td>Pupal 1 $\beta_1$</td>
<td>$\beta_2$</td>
<td>– 0.536</td>
<td>0.909</td>
<td>2, 3</td>
<td>0.027</td>
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<tr>
<td></td>
<td></td>
<td>Adult 1 $\beta_1$</td>
<td>$\beta_2$</td>
<td>0.159</td>
<td>0.266</td>
<td>2, 3</td>
<td>0.628</td>
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<td></td>
<td>Diapause induction</td>
<td>Larval 4a $\beta_1$</td>
<td>$\beta_2$</td>
<td>21.07</td>
<td>0.921</td>
<td>2, 3</td>
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<td></td>
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<td>$\beta_4$</td>
<td>$\beta_5$</td>
<td>– 0.78</td>
<td>0.861</td>
<td>2, 3</td>
<td>0.052</td>
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<td></td>
<td></td>
<td>$\beta_6$</td>
<td>0.06</td>
<td>– 0.64</td>
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<td></td>
<td>Intrinsic survival</td>
<td>Egg – adult 5a $\beta_1$</td>
<td>$\beta_2$</td>
<td>0.964</td>
<td>0.954</td>
<td>4, &lt;0.001</td>
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<td></td>
<td></td>
<td>$\beta_3$</td>
<td>– 0.323</td>
<td>10</td>
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<td></td>
<td>$\beta_4$</td>
<td>10.142</td>
<td>0.344</td>
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<td>$\beta_5$</td>
<td>0.024</td>
<td>0.986</td>
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<tr>
<td></td>
<td></td>
<td>$\beta_6$</td>
<td>112.063</td>
<td>25.793</td>
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<td>$\beta_7$</td>
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<td></td>
<td>Host plant induced survival</td>
<td>Larval 5b $\beta_1$</td>
<td>$\beta_2$</td>
<td>0.024</td>
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<td>4, 2</td>
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<td>$\beta_3$</td>
<td>112.063</td>
<td>25.793</td>
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<td>$\beta_4$</td>
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<tr>
<td></td>
<td>Rainfall induced survival</td>
<td>Egg, larval 5c $\beta_1$</td>
<td>$\beta_2$</td>
<td>– 0.359</td>
<td>0.953</td>
<td>1, 4</td>
<td>0.001</td>
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<td></td>
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<td>Adult 6a $\beta_1$</td>
<td>$\beta_2$</td>
<td>0.228</td>
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<td>2, 6</td>
<td>&lt;0.001</td>
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<td></td>
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<td>$\beta_3$</td>
<td>– 0.512</td>
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<td>$\beta_4$</td>
<td>– 1.956</td>
<td>0.985</td>
<td>2, 4</td>
<td>&lt;0.001</td>
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<td></td>
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<td>$\beta_5$</td>
<td>– 1.476</td>
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<td></td>
<td>C. flavipes</td>
<td>Maximum number of hosts parasitized per female as affected by temperature</td>
<td>Adult 8c $\beta_1$</td>
<td>$\beta_2$</td>
<td>0.028</td>
<td>0.736</td>
<td>2, 2</td>
<td>0.264</td>
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<td></td>
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<td>$\beta_3$</td>
<td>1.920</td>
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Table 5

<table>
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<th>Source of variances</th>
<th>df</th>
<th>F</th>
<th>% Explained variability</th>
<th>F</th>
<th>% Explained variability</th>
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<th>% Explained variability</th>
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<tr>
<td>Simulated damaging larval density</td>
<td>29</td>
<td>2922.20</td>
<td>22.44</td>
<td>56.33</td>
<td>2782.31</td>
<td>22.50</td>
<td>55.58</td>
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<tr>
<td>Overwintering larval density</td>
<td>9</td>
<td>3715.72</td>
<td>23.35</td>
<td>456.22</td>
<td>9</td>
<td>22.62</td>
<td>456.22</td>
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<tr>
<td>C. flavipes release rate</td>
<td>10</td>
<td>44.38</td>
<td>0.31</td>
<td>83.37</td>
<td>1.71</td>
<td>56.78</td>
<td>0.38</td>
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<tr>
<td>Overwintering larval density/C2</td>
<td>7</td>
<td>217.27</td>
<td>1.06</td>
<td>482.90</td>
<td>7.68</td>
<td>233.28</td>
<td>1.10</td>
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<tr>
<td>Timing of C. flavipes release</td>
<td>70</td>
<td>4.48</td>
<td>0.22</td>
<td>6.11</td>
<td>0.87</td>
<td>6.34</td>
<td>0.30</td>
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<tr>
<td>Error</td>
<td>25491</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For each response variable, all P values except for the overwintering larval density release rate by C. flavipes release rate interaction was <0.001, while the P value for this interaction is >0.999.

The simulated cumulative seasonal damaging larval density, maximum parasitoid adult density, and maximum seasonal proportion parasitized were each affected by year, overwintering larval density, parasitoid release rate, timing of release, and all two-way interactions (Table 5). The highest damaging larval density (716.9 ± 401.3 m⁻²) was simulated in 1978, while the lowest damaging larval density (30.1 ± 16.0 m⁻²) was in 1998. Year resulted in a 23.8-fold range in damaging larval density, which contributed 56.3% of the total variability for this response variable. When temperatures are low during larval diapause, as evident by lower rates of DD accumulation, larvae terminate diapause later in the year, adults emerge later from overwintering, and eggs are laid on rice plants at later crop growth stages, which afford higher survival of subsequent larvae and higher damaging larval densities (Fig. 2). Moths deposit eggs on rice, even when the plants are small (M. O. Way, unpublished data) and larval survival is close to zero. This assumes alternative weed hosts for the sugarcane borer are limited early in the spring, which is correct for most grassy weed hosts for the Upper Gulf Coast region of the US.

The highest seasonal parasitoid adult density (458.5 ± 647.9 m⁻²) and the highest seasonal proportion parasitized (0.403 ± 0.380) were observed in 1978, while the lowest maximum seasonal parasitoid adult density (4.62 ± 6.30 m⁻²) and the lowest maximum seasonal proportion parasitized (0.027 ± 0.021) were observed in 1998. Year resulted in a 99.1-fold range in maximum seasonal parasitoid adult density (20.0% explained variability) and a 14.9-fold range in maximum seasonal proportion parasitized (22.4% explained variability), respectively. When simulated early season larval densities were higher, C. flavipes densities increased more rapidly, and higher maximum seasonal proportion parasitized were observed in later generations.

Cumulative seasonal damaging larval density increased from 42.8 ± 35.2 to 383.2 ± 311.5 m⁻² when overwintering larval density increased from 1 to 10 m⁻² (Fig. 3a), and decreased from 243.6 ± 260.8 to 202.2 ± 206.6 m⁻² when parasitoid release rate increased from 0 to 10 m⁻² (Fig. 3b). The maximum seasonal C. flavipes female density and the maximum seasonal proportion parasitized increased from 3.7 ± 6.6 to 225.1 ± 415.9 m⁻² and 0.029 ± 0.021 to 0.285 ± 0.313, respectively, when overwintering larval density increased from 1 to 10 m⁻² (Fig. 3a), and increased from 0 to 130.9 ± 293.0 m⁻² and 0 to 0.218 ± 0.262, respectively, when release rate increased from 0 to 10 m⁻² (Fig. 3b).

The cumulative seasonal damaging larval density was the lowest (181.9 ± 162.4 m⁻²) when parasitoids were released 40 days after planting, and the highest (243.3 ± 260.4 m⁻²) when released 110 days after planting (Fig. 3c). C. flavipes was most effective when released during the 1st sugarcane borer generation, providing 25.3% average reduction in the cumulative seasonal damaging.
C. flavipes density, mental duration resulted in minor but varying degree of asynchrony interactions (Table 5). The lowest yield ($1481.2 \pm 2130.0$ kg ha$^{-1}$). Yield decreased from $6781.2 \pm 461.1$ to $3732.8 \pm 2313.6$ kg ha$^{-1}$ when overwintering larval density increased from $1$ to $10$ m$^{-2}$. Compensation was detected at the lowest overwintering larval density (1 m$^{-2}$), while yield was reduced by an average of ca. 44.9% at the highest overwintering larval density (10 m$^{-2}$).

Simulated yield increased from $4906.3 \pm 2179.6$ to $5296.9 \pm 1827.2$ kg ha$^{-1}$ when parasitoid release rate increased from $0$ to $10$ m$^{-2}$. Yield was the highest when parasitoids were released 40 days after planting ($5463.9 \pm 1583.9$ kg ha$^{-1}$), and the lowest when parasitoids were released 110 days after planting ($4910.5 \pm 2176.2$ kg ha$^{-1}$). When averaged across years, the maximum C. flavipes release rate and earliest timing of release reduced yield loss by 20.9% and 29.8%, respectively. When C. flavipes were released at the earliest simulated time (40 days after planting) and maximum rate, yield increased to an average of $5857.6 \pm 984.6$ kg ha$^{-1}$, representing a 50.9% reduction of yield loss (Fig. 4a).

### 3.3. Economic impact of larval injury

The economic impact of C. flavipes release was affected by year, overwintering larval density, C. flavipes release rate, timing of release, and all 2-way interactions (Table 5). However, economic benefit was only observed at the three highest overwintering larval densities (8, 9, and 10 m$^{-2}$) at the two earliest releases (Fig. 4b). When averaged across years, the greatest positive economic impact was $59.48 \pm 134.02$ ha$^{-1}$, when the overwintering larval density was in 1978, representing a 78.1% yield loss. The highest yield ($7153.0 \pm 183.1$ kg ha$^{-1}$) was in 1998, which was ca. 5.5% higher than the yield of uninjured rice fields ($6776.4$ kg ha$^{-1}$). Yield decreased from $6781.2 \pm 461.1$ to $3732.8 \pm 2313.6$ kg ha$^{-1}$ when overwintering larval density increased from $1$ to $10$ m$^{-2}$. Compensation was detected at the lowest overwintering larval density (1 m$^{-2}$), while yield was reduced by an average of ca. 44.9% at the highest overwintering larval density (10 m$^{-2}$).

![Fig. 3](image)

**Fig. 3.** Simulated damaging larval density, simulated maximum number of C. flavipes adults, and simulated maximum seasonal proportion parasitized, each as affected by (a) overwintering larval density, (b) C. flavipes release rate, and (c) timing of C. flavipes release.

![Fig. 4](image)

**Fig. 4.** (a) Simulated rice yield and (b) simulated economic impact from C. flavipes release, each as affected by overwintering larval density and C. flavipes release rate, with parasitoids released at the optimal timing.
density was 10 m$^{-2}$, and $C. flavipes$ was released 50 days after planting with a rate of 2 females m$^{-2}$.

For an augmentative release to be economical, the savings must be comparable to that achieved using currently available control methods. Sugarcane borer management inrice in subtropical-temperate regions is entirely achieved through the use of insecticides. Two applications with one of the synthetic pyrethroids gamma-cyhalothrin (Prolex™), lambda-cyhalothrin (Karate Zcides. Two applications with one of the synthetic pyrethroids may exist for the selection of biotypes that emerge later in the spring in areas having colder climates.

4. Conclusions

Herein, we investigate the economic benefit of augmentatively releasing $C. flavipes$ to control the sugarcane borer. The maximum seasonal proportion parasitized observed in our field experiment was 0.119. Simulated results suggest damaging larval density was negatively correlated with winter temperature, while the maximum parasitoid density and maximum seasonal proportion parasitized were positively correlated with the cumulative seasonal damaging larval density. The greatest density resulted in ca. 78.1% yield loss. Although $C. flavipes$ release reduced sugarcane borer induced yield loss by up to 50.8%, the maximum economic benefit provided by $C. flavipes$ was only $59.48, ca. 6.7% of the maximum economic benefit provided by insecticide. The inability of $C. flavipes$ to provide economic control of sugarcane borer in temperate-subtropical areas is due to its high rearing cost, a low effective search rate, a low number of hosts parasitized per female, and failure of early spring emerging parasitoids to find and parasitize first generation hosts in significant numbers.

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References


