



# Fitness costs of Cry1F resistance in two populations of fall armyworm, *Spodoptera frugiperda* (J.E. Smith), collected from Puerto Rico and Florida<sup>☆</sup>



Vikash Dangal, Fangneng Huang<sup>\*</sup>

Department of Entomology, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803, USA

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## ABSTRACT

The development of resistance in target pest populations is a threat to the sustainability of transgenic crops expressing *Bacillus thuringiensis* (Bt) proteins. Fall armyworm, *Spodoptera frugiperda* (J.E. Smith), is a major target pest of Bt maize in North and South America. This insect is the first target pest that has developed field resistance to Bt maize at multiple locations in these regions. The objective of this study was to assess the fitness costs associated with the Cry1F resistance in two populations of *S. frugiperda* collected from Puerto Rico (RR-PR) and Florida (RR-FL). In the study, fitness costs were evaluated by comparing survival, growth, and developmental time of seven populations of *S. frugiperda* on (1) non-Bt meridic diet and (2) non-Bt maize leaf tissue and non-Bt diet. The seven populations were RR-PR, RR-FL, a Bt-susceptible strain (Bt-SS), and four F<sub>1</sub> populations developed from reciprocal crosses between Bt-SS and the two resistant populations. Biological parameters measured were neonate-to-adult survivorship, neonate-to-adult developmental time, 10 day larval weight on non-Bt maize leaf tissue, pupal weight, and sex ratios. Results of the study show that the Cry1F resistance in both RR-PR and RR-FL was associated with considerable fitness costs, especially for the Florida population. Compared to the Bt-susceptible population, RR-PR showed an average of 61.1% reduction in larval weight, 20.4% less in neonate-to-adult survivorship, and 3.7 days delay in neonate-to-adult developmental time. These fitness costs for RR-FL were 66.9%, 31.7% and 4.4 days, respectively. The fitness costs of RR-PR and RR-FL appeared to be non-recessive. The results indicate that a diversified genetic basis may exist for the Cry1F resistance in *S. frugiperda*.

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## 1. Introduction

Field maize, *Zea mays* L., is one of the major crops that have been genetically modified to express *Bacillus thuringiensis* (Bt) proteins targeting herbivorous insect pests. Maize is also a major crop in the U.S. with a total area of 37.1 million hectares planted in 2014, out of which 80% was Bt maize (NASS, 2014). Fall armyworm, *Spodoptera frugiperda* (J.E. Smith), is a common pest targeted by Bt maize and Bt cotton in North and South America (Storer et al., 2010; Farias et al., 2014; Huang et al., 2014). It is also a major pest of many other crops in the tropical and subtropical regions. Because of resistance development, most traditional chemical

control tactics are unable to produce satisfactory control results against *S. frugiperda* (Siebert et al., 2008).

Transgenic maize containing the event TC1507 expressing the Cry1F protein was registered in the U.S. in 2001 for controlling various pests including *S. frugiperda* (Siebert et al., 2008). In 2003, Cry1F maize was first commercially planted in Puerto Rico for silage and dairy farms (Storer et al., 2010). However, soon after the commercialization, unprecedented damage of Cry1F maize plants was reported in Puerto Rico (Storer et al., 2010). The unexpected field survival and damage of *S. frugiperda* were then confirmed to be due to resistance development to the Cry1F protein in the plants. Recently, field resistance that resulted in reduced efficacy or control failure of Cry1F maize in *S. frugiperda* has also been documented in Brazil (Farias et al., 2014) and the southeast coastal region of the U.S. (Huang et al., 2014). Until now, *S. frugiperda* is the only target pest that has developed field resistance to commercial Bt crops at multiple locations across different countries and continents. Because Cry1F is a common Bt protein

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<sup>\*</sup> Corresponding author. Tel.: +1 0 225 5780111; fax: +1 0 225 5781643.

E-mail address: [fhuang@agcenter.lsu.edu](mailto:fhuang@agcenter.lsu.edu) (F. Huang).

expressed in many currently used Bt maize and Bt cotton products, the widespread of Cry1F resistance in *S. frugiperda* could represent a great challenge for the sustainable use of the Bt crop technology (Huang et al., 2014).

Fitness costs of Bt resistance occur when insect genotypes conferring at least one allele of resistance has lower fitness than those individuals without any resistance allele in the absence of selection pressure (Gassmann et al., 2009). Fitness costs are regarded as one of the major factors influencing the evolution of resistance (Tabashnik et al., 2008; Carrière and Tabashnik, 2001; Carrière et al., 2010; Gassmann et al., 2009; Huang et al., 2011). In many cases where resistance to Bt has been detected in the laboratory, there has been rapid decline in resistance level after the selection pressure is removed (Gassmann et al., 2009). Mathematical modeling also suggests that fitness costs could play a key role in delaying resistance by selecting against resistant genotypes in the refuges where the Bt protein is not present (Gassmann et al., 2009).

Fitness costs of Cry1F resistance in *S. frugiperda* have recently been investigated in two Puerto Rico populations. The results showed lack of fitness costs in both populations (Vélez et al., 2013; Jakka et al., 2014). The main objective of this study was to determine if fitness costs were associated with Cry1F resistance in two other resistant populations of *S. frugiperda* that were collected from Florida of the U.S. mainland and the southern Puerto Rico. In addition, comparisons of results from this study are made with those from the previous two studies by Vélez et al. (2013) and Jakka et al. (2014) to determine if the lack of fitness costs of the Cry1F resistance is consistent among different populations of *S. frugiperda*. Data generated from this study should be useful in understanding the mechanism of resistance and developing effective strategies for managing the Cry1F resistance in *S. frugiperda*.

## 2. Materials and methods

### 2.1. Sources of insects

Three insect populations, a Bt-susceptible population (Bt-SS) of *S. frugiperda* collected from maize fields near Weslaco, Texas and two Cry1F-resistant populations obtained from Puerto Rico (RR-PR) and Florida (RR-FL) were used as the original insect sources in this study. The Bt-SS strain was collected in 2013 and had never been exposed to Bt proteins or any other insecticides in the laboratory. Laboratory bioassays and greenhouse whole plant tests have shown that Bt-SS was susceptible to both Cry1F plants and purified Cry1F protein in diet (Huang et al., 2014). RR-PR was originated from >300 larvae collected from maize fields in southern Puerto Rico during 2011 (Niu et al., 2013). The field-collected population had been selected on Cry1F maize (Pioneer 31D59) leaf tissue for at least four generations before it was used in the current study. RR-PR is highly resistant to purified Cry1F protein (>769-fold) and Cry1F maize plants (Niu et al., 2013, 2014). RR-FL was developed from an F<sub>2</sub> screen with two-parent families derived from a field population collected from maize plants in south Florida in 2011 (Huang et al., 2014). It was confirmed that RR-FL possessed a major resistance allele to allow the insect to survive and complete normal development on commercial Cry1F maize plants. RR-FL is highly resistant to purified Cry1F protein (>270-fold) in diet-incorporated bioassays (Huang et al., 2014).

To ensure that the three populations have a similar genetic background, both RR-PR and RR-FL were backcrossed to Bt-SS to generate the F<sub>1</sub> generations and then F<sub>1</sub> populations were backcrossed with SS one more time to produce F<sub>2</sub> populations. The F<sub>2</sub> populations were sib-mated to produce F<sub>3</sub> populations. F<sub>3</sub> progeny were selected for Cry1F resistance, by rearing the populations on Cry1F maize leaf tissue for three generations before they were used

in the study. The methods used in the reselection of Cry1F resistance were the same as described in Niu et al. (2013). In the selection process, 2–4 pieces of Cry1F maize leaf tissue were placed in each well of the 32-well C-D International trays (Bio-Ba-32, C-D International, Pitman, NJ). Approximately 5–10 newly hatched larvae were released in each well. For each crossed population, a total of 1000–1500 neonates were selected on Cry1F maize leaf tissue. After 7 days, approximately 120–150 survivors of each population were transferred into 30-ml plastic cups (Fill-Rite, Newark, NJ) containing a meridic diet (Ward's Stonefly Heliiothis diet, Rochester, NY). In the selection, only the survivors with a relatively big body size ( $\geq$ 3rd instars) were transferred and used to develop the next generation (Niu et al., 2013). The larval-rearing cups were held in 30-well trays (Bio-Serv, Frenchtown, NJ) and placed under the room conditions until pupation. In addition, four F<sub>1</sub> hybrid populations were derived from the reciprocal crosses between Bt-SS and the two reselected resistant populations (RR-PR and RR-FL). The two F<sub>1</sub> populations generated from the reciprocal cross between Bt-SS and RR-PR were denoted as PR<sub>m</sub>SS<sub>f</sub> (cross between males of RR-PR and females of Bt-SS) and PR<sub>f</sub>SS<sub>m</sub> (cross between females of RR-PR and males of Bt-SS). The two F<sub>1</sub> populations developed by crossing Bt-SS and RR-FL were denoted as FL<sub>m</sub>SS<sub>f</sub> and FL<sub>f</sub>SS<sub>m</sub>, respectively. Fitness costs associated with the seven insect populations was evaluated using two assays: (1) a non-Bt diet and (2) a combined rearing of non-Bt maize leaf tissue and non-Bt diet.

### 2.2. Maize plants

A non-Bt hybrid maize, Pioneer 31P40 (Pioneer Hi-Bred, Johnston, Iowa), was planted in 5 gallon plastic pots filled with approximately 5 kg of a standard potting mixture (Perfect Mix, Expert Gardener products, St. Louis, MO) as described in Wu et al. (2007). The pots were held in a greenhouse at the Louisiana State University Agricultural Center in Baton Rouge, Louisiana. Two plants per pot were maintained with regular irrigation and fertilization.

### 2.3. Growth and development of *S. frugiperda* on non-Bt diet

To determine if fitness costs were associated with the Cry1F resistance in *S. frugiperda*, growth and development of the seven populations of *S. frugiperda* were first examined on a non-Bt meridic diet. In this assay, approximately 1 g of non-Bt diet (WARD'S Stonefly Heliiothis diet, Rochester, NY) was placed into each cell of the 128-cell bioassay trays (Bio-Ba-128, C-D International Inc. Pitman, NJ) as described in Zhang et al. (2014). One neonate (<24 h old) was placed on the surface of the diet in each cell. The bioassay trays were held in an environmental chamber maintained at 28 °C, ~50% relative humidity (RH), and a photoperiod of 16 h:8 h (L:D). There were four blocks (replications) for each insect population with 32 larvae in each block ( $n = 4 \times 32 = 128$ ) where an individual environmental chamber was treated as a block. After 5 days, larvae were transferred into 30-ml-cups (1 larva/cup) (SOLO, Chicago, IL) containing approximately 8 g of diet and were allowed to develop to the pupal stage. After the first pupa was observed, all cups were checked daily until all insects emerged or died. Pupal weight, insect survival, adult emergence, and sex ratio were recorded for each individual.

### 2.4. Growth and development of *S. frugiperda* in combined rearing of non-Bt maize leaf tissue and non-Bt diet

The combined rearing involved the use of non-Bt maize leaf tissue and non-Bt diet as the food source of the insects. In the combined rearing, leaf tissue was removed at V7–V9 growth stages

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