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Sub-lethal effects of a Bt-based bioinsecticide on the biological conditioning of *Anticarsia gemmatalis*

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Abstract

Bioinsecticides based on *Bacillus thuringiensis* (Bt) Berliner, 1915 are widely used to control lepidopteran in several crops. However, surviving insects exposed to the sub-lethal concentration of Bt-based bioinsecticides can suffer a multitude of effects on the biological conditioning known as hormesis. Here, we aimed to provide a clearer understanding of the biological conditioning of *Anticarsia gemmatalis* (Hübner, 1818), exposed to different concentrations of a Bt-based bioinsecticide, by assessing life table parameters over three generations. We defined five sub-lethal concentrations (LC_5, LC_{10}, LC_{15}, LC_{20}, and LC_{25}) from the response curve estimate of *A. gemmatalis*. Deionized water was used as a control. We assessed the parameters of eggs-viability and the duration of the stages, incubation, larval, pre-pupal, pupal, adult, pre-oviposition and total biological cycle. Data were used to construct the fertility life table using the two-sex program. The survival curves showed greater variation in the proportion of individuals at each development stage using the LC_{25}. The sub-lethal concentrations did not influence the incubation-eggs period, pre-pupal and pupal. However, the larval and adult stages using LC_{25} and LC_{10} were the most affected. Changes in sex ratio were observed using LC_{20} and LC_5. The toxic effect of Bt-based bioinsecticide interfered mainly in the parameters of fertility, sex ratio, net reproduction rate (R0), and gross reproduction rate (GRR).

Keywords Velvet-bean caterpillar · Microbial control · Life table · Biological development · Hormesis · Hormoligosis

Introduction

Velvet bean caterpillar *Anticarsia gemmatalis* Hübner, 1818, is one of the main defoliating caterpillars in the soybean crop (Haase et al. 2015). However, the losses provided by the species in the field vary from 3 to 75% in conventional soybean cultivars (Silva et al. 2003; Moscardi et al. 2012).

In the 1990s, the control of *A. gemmatalis* in Brazil was carried out, starting with chemical insecticides such as organochlorines and organophosphates. However, problems provided to man and the environment have led to restrictions on the use of these pesticides (Moscardi et al. 2012). Currently, this pest control is carried out with insecticides selective to the environment and cultivars of transgenic soybean that expresses only the toxin Cry1Ac from the bacterium *Bacillus thuringiensis* Berliner, 1915 (Bernardi et al. 2012).

The pressure exerted by the consumer market to reduce dependence on chemical insecticides in agriculture, combined with growing reports of insect resistance to transgenic plants, renewed the worldwide interest in Bt-based bioinsecticides (Lacey 2017; Konecka et al. 2018; Amaral et al. 2019; Horikoshi et al. 2019).

Agriculture over the years has made significant leaps in technology; however, it still faces challenges in microbial control to reach the biologically active product in the target and in the correct concentration (Frye et al. 1973; Sedaratian et al. 2013). Surviving insects, exposed to sub-lethal concentration of Bt-based bioinsecticides due to biotic

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factors (incompatibility with other products, inadequate spray calibration, and drift) and abiotic (temperature, ultraviolet radiation, precipitation, and others) can suffer a multitude of effects in biological conditioning (Van-Rie and Fereé 2000).

The phenomenon is known as hormesis and occurs in surviving insects and their descendants. Studies show that the phenomenon can provide positive consequences, called hormoligosis (Guedes et al. 2009; Guedes and Culter 2013). The theory of hormoligosis is poorly studied; however, part of the assumption that sub-lethal concentration, instead of harming the insect, ends up having the opposite effect, stimulating biological development through, for example, an increase in the fertility parameter (physiological hormoligosis) or oviposition behavior (behavioral hormoligosis) of the species, leading to a significant increase in its abundance (Abivardi 2004; Dutcher 2007).

Studies are evaluating the effects of insecticides on the biological parameters of pests based on the theory of physiological and behavioral hormoligosis, however, there are no studies performed with Bt-based bioinsecticides at this moment. The lack of understanding about the theory prevents us from understanding the flaws in the pest control programs, outbreaks and resurgences of insects, among other factors (Abivardi 2004; Cohen 2006; Dutcher 2007). Thus, this study aimed to evaluate the biological conditioning of *A. gemmatalis* exposed to sub-lethal concentration of Bt-based bioinsecticides Dipel® through the parameters of the life table over three generations.

Material and methods

Insect rearing

The population of *A. gemmatalis* was obtained at the Laboratory of Insect Biology of the College of Agriculture "Luiz de Queiroz" (ESALQ-Piracicaba) and the insect rearing was established at the laboratory of microbial control of arthropod pests at Paulista State University "Júlio de Mesquita Filho" (UNESP - Jaboticabal), maintained on an artificial diet (Greene et al. 1976).

For the colony establishment, 2000 eggs of *A. gemmatalis* were placed in Petri dishes (9 cm Ø) with filter paper moistened in distilled water. The insect colony was kept under 25 ± 1 °C, RH of 70 ± 10%, and 12:12 (L:D).

Commercial formulation lethal concentrations

The commercial formulation toxicity was evaluated using the spore-crystal suspensions of the Bt-based bioinsecticide (Dipel®). The suspensions were defined by plating on nutrient agar to determine the CFU, which was evaluated after seven days (Sedaratian et al. 2013). The curve response was estimated using the Six Error Problems analysis (Sas University 2013). 200 µL on the surface of the artificial diet (4.8 cm^3) were previously distributed in polyethylene cups (3.5 cm Ø). A hundred insects were used to estimate a curve response for each treatment, distributed in 10 repetitions. Deionized water was applied in equal volume as a control (Santos et al. 2019). The bioassay evaluations were carried out after seven days.

Sub-lethal concentrations

Based on mortality data from bioassays, artificial diet preparations containing sub-lethal concentrations of Dipel® or controls (untreated diet) were prepared and used to study sublethal effects of Bt on *A. gemmatalis*. The sub-lethal concentrations LC_5, LC_{10}, LC_{15}, LC_{20}, and LC_{25} (0.20509, 0.38126, 0.57929, 0.80776, and 1.07438 µg Bt.mL $diet^{-1}$) were chosen by the estimate response curve (Sedaratian et al. 2013).

In these assays, a 200 µL aliquot of each sub-lethal concentration was applied to the surface of the artificial diet (4.8 cm^3), previously distributed in polyethylene cups (3.5 cm Ø) (Sas University 2013). The surviving caterpillars were fed an artificial diet containing their respective sub-lethal concentrations for three generations (F_1, F_2, and F_3). For each generation, 100 insects were used for each treatment, considering each caterpillar as a sampling unit. Deionized water was applied in an equivalent volume in the control. The evaluations were carried out daily.

Sub-lethal effects bioassay

All generations were evaluated daily until the pupae phase, which was sexed for up to 24 h (Butt and Cantu 1962). The newly emerged adults were separated into couples and placed inside a PVC cage (10 cm × 20 cm), lined with white A4 sulfite paper (used as an oviposition substrate). At the bottom, a Petri dish with filter paper was used and an upper part sealed with voile fabric.

The adults were fed with a 10% honey solution moistened with cotton wool, placed in a polyethylene petri dish (49 × 12 mm) at the bottom of the cage. The papers used as a laying substrate were removed daily and the eggs counted with the aid of a stereoscopic microscope (Leica-S8 APO).

Data analysis

Mortality data were submitted to Probit regression analysis and sub-lethal concentrations values LC_5, LC_{10}, LC_{15}, LC_{20}, and LC_{25} were obtained using the SAS software ($P > 95\%$) (Sas University 2013). The experimental design was a completely randomized design (CRD) for the variables

duration of the biological cycle and egg viability, caterpillar, pre-pupa, pupa, adult, and pre-oviposition phases.

The following parameters were recorded in each treatment (LC_5, LC_{10}, LC_{15}, LC_{20}, LC_{25}, and control) and generation (F_1, F_2, and F_3): pre-oviposition period (APOP: period from the adult emergence to the first oviposition), total pre-oviposition (TPOP: period from the egg eclosion to the first oviposition), period of oviposition and daily fertility (Colinet et al. 2015).

The Two-Sex fertility life table program (Chi and Liu 1985) was used to analyze the biological parameters of egg, larva, pupa, adult pre-oviposition period, total pre-oviposition period, and fertility (Chi 1988, 2019). In the age stage, the Two-Sex fertility life table values, *lx*, *mx,* and R_0 are calculated as:

$$lx = \sum_{j=1}^{k} S_{xj} \tag{1}$$

$$mx = \sum_{j=1}^{k} S_{xj} f_{xj} / \sum_{j=1}^{k} S_{xj} \tag{2}$$

$$Ro = \sum_{j=1}^{\infty} l_x m_x \tag{3}$$

where k is the number of stages, s_{xj} is the survival rate of the velvet bean caterpillar, $x =$ age in days, and $j =$ stage. f_{xj} is the stage-specific fertility, l_x is the stage-specific survival rate, m_x is the stage-specific fertility stage, e_{xj} life expectancy, v_{xj} reproductive value in the stage, R_0 is the net reproductive rate, k finite rate of increase, and T is the mean generation.

In this study, the iterative bisection method of the Euler–Lotka formula was used to estimate r (r is the intrinsic rate of increase) using the age indexed to 0 (Goodman 1982), as shown in Eq. (2).

The e_{xj} is defined as the period of duration that an individual or insect of x and j is predictable to live (Chi and Su 2006) as:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} S'_{iy} \tag{4}$$

where S'_{iy} is defined as the probability that individuals and individuals will survive to age and stage and it's found assuming $S_{iy} = 1$. The v_{xj} was estimated following the methodology of Abbas et al. (2014) and was calculated as:

$$v_{xj} = \frac{e^{-r(x+1)}}{S_{xj}} \sum_{i=x}^{\infty} e^{-r(x+1)} \sum_{y=j}^{k} S'_{iy} f_{iy} \tag{5}$$

Standard errors and means were estimated technically using bootstrap (Efron and Tibshirani 1994).

Table 1 Toxicity of *Bacillus thuringiensis*-based bioinsecticide (Dipel®) on neonates of *Anticarsia gemmatalis*

No.[1]	X^2 (*df*)	Slope ± SE[2]
600	1.34 (4)	0.10 ± 0.39
Sub-lethal concentrations (μg Bt.mL diet^{-1})[3]		
LC_5	0.20509	(0.11637–0.31622)
LC_{10}	0.38126	(0.23825–0.54825)
LC_{15}	0.57929	(0.38542–0.79669)
LC_{20}	0.80776	(0.56364–1.07458)
LC_{25}	1.07438	(0.77920–1.39215)
LC_{50}	3.39680	(2.76115–4.12754)
LC_{99}	180.00975	(108.96631–348.70017)

[1]Number of subjects. [2]Slope ± Standard Error. [3]Sub-lethal concentrations and 95% fiducial limits (FL) were estimated using Probit analysis of SAS (2013).

Results

Susceptibility of A. gemmatalis larvae to Dipel®

The results of bioassays with Dipel® incorporated in the artificial diet for neonates of *A. gemmatalis* are presented in Table 1. The estimated value of LC_{50} and LC_{99} after seven days was 3.396 and 180.009 (μg Bt.mL diet^{-1}), while no mortality was recorded in controls. Based on data from these bioassays, we calculated the sub-lethal Dipel® concentrations, from LC_5 to LC_{25}, to use in our study (Table 1).

Sub-lethal effects on the biological parameters of A. gemmatalis

Anticarsia gemmatalis submitted to sub-lethal concentrations LC_5, LC_{10}, LC_{15}, and LC_{20} and the control completed the biological development in the three generations evaluated with different responses in the biological conditioning of the species. The LC_{25} treatment was the only one that did not reach the third generation.

The survival curves show the proportion of *A. gemmatalis* at each development stage related to the first eggs. The overlaps observed are due to differences in the speed of development among individuals. The proportions reached maximum values, with the subsequent reduction due to changes in the next phase or mortality or because they died in adulthood (Fig. 1).

The most significant variation was observed in the proportion of individuals in the LC_{25} in the first generation. In the next generation for the LC_5 and LC_{15}, adult male individuals had a longer survival time than females. Furthermore, in the last generation, the results show an increase in the survival in treatments LC_{15} and LC_{20} (Fig. 1).

The sub-lethal concentrations did not influence the eggs incubation period of *A. gemmatalis* (Table 2). The duration

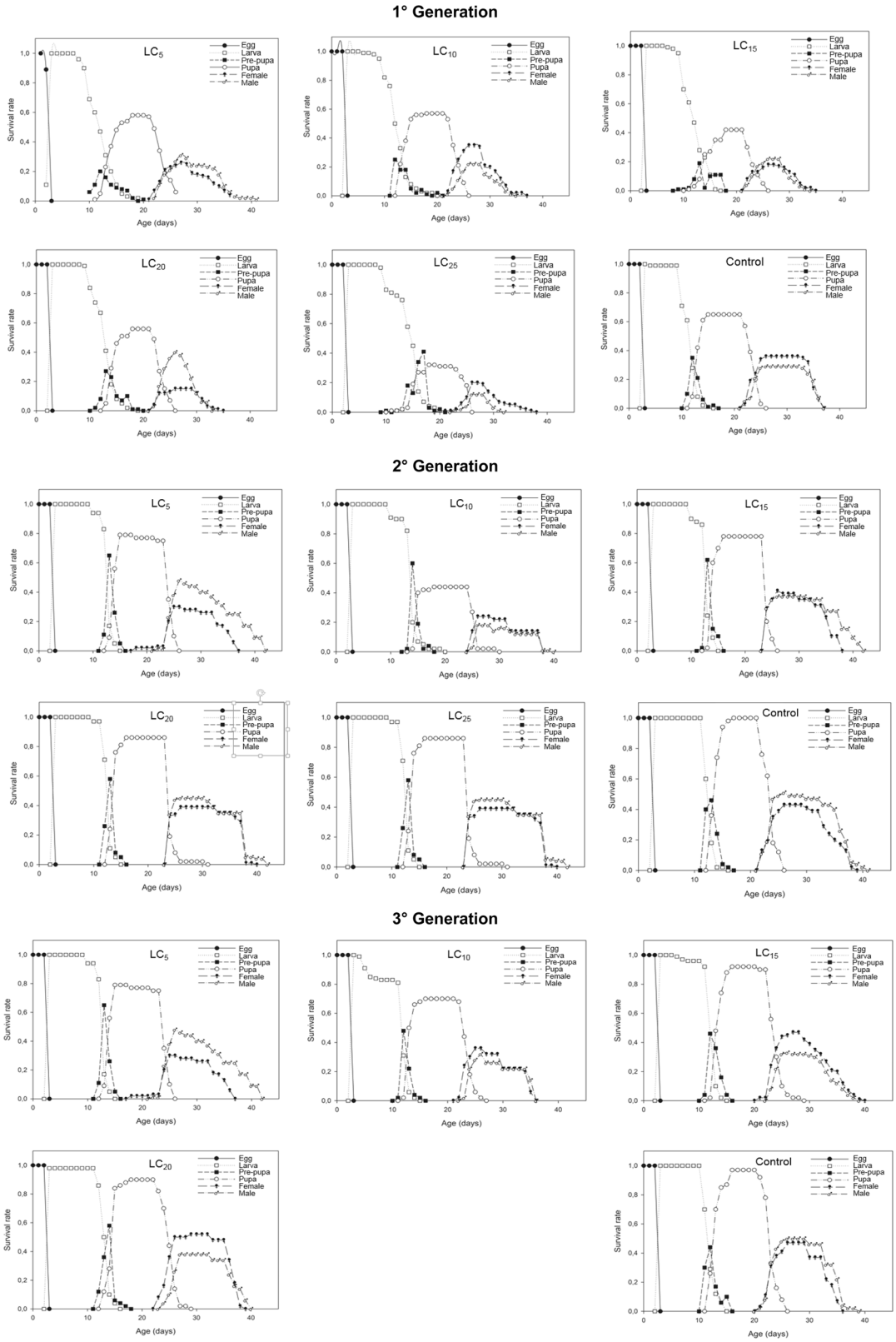

Fig. 1 Survival curves of *Anticarsia gemmatalis* exposed to sub-lethal concentrations of the Bt-bioinsecticide Dipel® over three generations at 25 ± 1 °C, 70 ± 10% RH, and 12:12 h (L:D). The data for each parameter was calculated using the 100,000 sample auto-start procedure.

Table 2 Duration (days) of development phases of *Anticarsia gemmatalis* exposed to sub-lethal concentrations of the bioinsecticide Dipel® over three generations at 25 ± 1 °C, 70 ± 10% RH, and 12:12 h (L:D).

1° Generation					
Treatments	Egg	Larva	Pre-pupa	Pupa	Adult
LC_5	2.89 ± 0.03 aA[1]	10.44 ± 0.23 abB	1.3 ± 0.07 aA	9.86 ± 0.13 aA	9.36 ± 0.42 aB
LC_{10}	3.00 ± 0.00 aA	10.50 ± 0.21 abB	1.02 ± 0.02 aA	10.02 ± 0.15 aA	7.25 ± 0.25 aC
LC_{15}	3.00 ± 0.00 aA	10.75 ± 0.23 abB	1.17 ± 0.06 aA	8.71 ± 0.21 aA	7.34 ± 0.34 aC
LC_{20}	3.00 ± 0.00 aA	10.87 ± 0.17 aB	1.16 ± 0.06 aA	9.00 ± 0.07 aA	6.55 ± 0.23 bC
LC_{25}	3.00 ± 0.00 aA	12.48 ± 0.18 aA	1.16 ± 0.07 aA	9.62 ± 0.20 aA	5.88 ± 0.46 bD
Control	3.00 ± 0.00 aA	9.41 ± 0.12 bC	1.05 ± 0.03 aA	10.54 ± 0.07 aA	12.71 ± 0.12 aA
2° Generation					
LC_5	3.00 ± 0.00 aA	10.12 ± 0.07 abB	1.18 ± 0.04 aA	10.18 ± 0.15 aA	11.06 ± 0.46 aA
LC_{10}	3.00 ± 0.00 aA	11.27 ± 0.08 aA	1.05 ± 0.03 aA	10.66 ± 0.09 aA	9.43 ± 0.53 bB
LC_{15}	3.00 ± 0.00 aA	10.35 ± 0.07 abB	1.01 ± 0.01 aA	10.05 ± 0.04 aA	12.15 ± 0.37 aA
LC_{20}	3.00 ± 0.00 aA	9.82 ± 0.08 bC	1.04 ± 0.00 aA	10.51 ± 0.11 aA	12.60 ± 0.29 aA
LC_{25}	3.00 ± 0.00 aA	9.89 ± 0.08 bC	1.00 ± 0.00 aA	10.53 ± 0.11 aA	12.63 ± 0.29 aA
Control	3.00 ± 0.00 aA	9.82 ± 0.08 bC	1.16 ± 0.04 aA	9.70 ± 0.07 aA	12.49 ± 0.31 aA
3° Generation					
LC_5	3.00 ± 0.00 aA	10.32 ± 0.20 aB	1.09 ± 0.04 aA	10.55 ± 0.07 aA	10.91 ± 0.31 aA
LC_{10}	3.00 ± 0.00 aA	9.44 ± 0.08 abC	1.00 ± 0.00 aA	10.63 ± 0.08 aA	8.91 ± 0.41 bB
LC_{15}	3.00 ± 0.00 aA	9.57 ± 0.08 abC	1.13 ± 0.04 aA	10.38 ± 0.09 aA	9.83 ± 0.31 abB
LC_{20}	3.00 ± 0.00 aA	10.53 ± 0.09 aB	1.22 ± 0.04 aA	10.69 ± 0.08 aA	11.62 ± 0.19 aA
LC_{25}	–	–	–	–	–
Control	3.00 ± 0.00 aA	9.17 ± 0.11 bC	1.08 ± 0.03 aA	10.10 ± 0.10 aA	12.68 ± 0.26 aA

[1]Mean (days) ± Standard error. 1Means followed by the same lower case letter between treatments and upper case letters between generations do not differ significantly. (Paired startup test: $P < 0.05$).

Standard errors were estimated using 100,000 bootstraps and compared using the paired bootstrap test based on the difference IC.

of the pre-pupa and pupa phases was not affected by the treatments. In the adult phase, treatments LC_{25} in the first generation and LC_{10} in the second and third generations reached the lowest values.

The pre-oviposition period (APOP) was significant in the 2nd generation with the LC_{10} and in the 3rd generation using the LC_5, LC_{10} treatments. In the total pre-oviposition period (TPOP) was observed difference in the third generation with the LC_{10} (Table 3). The greater longevity of females and males in the first generation was observed in the second and third generations. The oviposition period and fertility parameters were affected by the LC_{20} and LC_{25} over the evaluated generations (Table 3). The sex ratio was affected only in the treatments LC_{20} in the first generation and LC_5 in the second generation, since the mean in the generations was 0.47 between the first generation and the second generation and 0.54 in the third generation, respectively (Table 3).

The fertility life table was generated using descendants treated with the respective sub-lethal concentration. The witness had a higher mean in all parameters evaluated over the three generations. In the generation time parameter (T), the CL_{15} treatment reached ~27.93 days, representing the lowest mean among all treatments in the three evaluated generations (Table 4).

The parameters of the life table showed an association with the applied concentration of the bioinsecticide; with the increase in concentration, there is a reduction in the net reproduction rate (R_0) (80.64%), gross reproductive rate (*GRR*) (75.87%), intrinsic population growth rate (r) (35.85%) and the finite population growth rate (λ) (5.87%) (Table 4).

Discussion

Susceptibility of A. gemmatalis larvae to Dipel®

The lethal concentration required to kill 99% of the population of *A. gemmatalis* (LC_{99}) proves differences of 60 (LC_{50}), 180 (LC_{25}), 225 (LC_{20}), 360 (LC_{15}), 600 (LC_{10}), and 900 (LC_5) times about the proportion of the bioinsecticide Dipel®. The results demonstrate, a larger interval between the lethal concentrations of the LC_5 and LC_{10} treatments about the LC_{20} and LC_{25} treatments. Studies determining the susceptibility of *A. gemmatalis* populations revealed that the LC_{50} for the susceptible population was 0.25 µg Bt.mL diet^{-1}, lower than that found in the present study (Gholmie et al. 2018).

Table 3 Duration (days) of development parameters, fertility and sex ratio of Anticarsia gem*matalis* exposed to sub-lethal concentrations of the bioinsecticide Dipel® over three generations at 25 ± 1 °C, 70 ± 10% RH, and 12:12 h (L:D)

Treatments	APOP (days)	TPOP (days)	Longevity of females (days)	Longevity of males (days)	Total longevity (days)	Oviposition (days)	Fecundity (egg/female)	Sex Ratio (female/female + male)
1° Generation								
CL_5	3.04 ± 0.17 aA[1]	26.80 ± 0.34 aB	32.67 ± 0.64 bC	34.13 ± 0.64 bB	24.44 ± 1.12 abD	3.52 ± 0.30 aB	299.63 ± 38.62 bB	0.46 ± 0.04 aA
CL_{10}	2.91 ± 0.15 aA	26.70 ± 0.25 aB	31.34 ± 0.41 bC	31.27 ± 0.43 cC	23.24 ± 0.97 bE	3.17 ± 0.21 aB	277.63 ± 28.68 bB	0.61 ± 0.04 aA
CL_{15}	2.27 ± 0.19 aB	25.50 ± 0.44 aB	31.67 ± 0.44 bC	30.17 ± 0.46c dC	19.65 ± 0.97 dF	4.00 ± 0.22 aB	264.00 ± 15.54 bC	0.43 ± 0.04 aA
CL_{20}	3.26 ± 0.11 aA	26.53 ± 0.37 aB	31.73 ± 0.37 bC	29.78 ± 0.28 dD	22.59 ± 0.91 bcE	3.73 ± 0.26 aB	232.67 ± 16.20 bC	0.26 ± 0.04 bB
CL_{25}	2.20 ± 0.19 aB	27.15 ± 0.31 aA	31.65 ± 0.67 bC	29.92 ± 0.29 dD	20.61 ± 0.79 dE	2.80 ± 0.31 bC	139.95 ± 14.44 cD	0.62 ± 0.04 aA
Control	2.63 ± 0.15 aB	26.41 ± 0.23 aB	35.42 ± 0.16 aB	35.96 ± 0.21 aB	26.86 ± 1.20 aD	4.58 ± 0.20 aA	472.86 ± 22.59 aA	0.55 ± 0.04 aA
2° Generation								
CL_5	2.86 ± 0.09 aB	26.73 ± 0.32 aB	34.20 ± 0.51 bB	36.21 ± 0.67 bA	30.68 ± 0.98 cC	4.76 ± 0.33 aA	414.80 ± 53.22 aA	0.38 ± 0.04 bB
CL_{10}	1.91 ± 0.05 bC	27.33 ± 0.12 aA	35.25 ± 0.70 bB	35.20 ± 0.88 bB	23.62 ± 1.07 dE	5.08 ± 0.46 aA	235.00 ± 27.23 bB	0.54 ± 0.04 aA
CL_{15}	2.97 ± 0.05 aA	27.44 ± 0.13 aA	34.98 ± 0.46 bB	38.22 ± 0.46 aA	31.18 ± 1.05b cB	4.78 ± 0.20 aA	150.66 ± 11.29 bD	0.52 ± 0.04 aA
CL_{20}	3.29 ± 0.15 aA	27.90 ± 0.22 aA	37.00 ± 0.33 aA	37.11 ± 0.43 abA	33.70 ± 0.12 abB	3.68 ± 0.21 abB	104.46 ± 9.19 bD	0.47 ± 0.03 aA
CL_{25}	3.70 ± 0.23 aA	28.31 ± 0.27 aA	37.00 ± 0.33 aA	37.11 ± 0.43 abA	30.70 ± 0.87 abC	1.28 ± 0.23 bC	50.93 ± 4.37 cE	0.48 ± 0.03 aA
Control	2.97 ± 0.02 aA	26.60 ± 0.20 aB	34.80 ± 0.47 bB	35.47 ± 0.52 bB	35.17 ± 0.35 aA	5.60 ± 0.26 aA	454.87 ± 26.93 aA	0.45 ± 0.00 aA
3° Generation								
CL_5	2.00 ± 0.00 bB	27.12 ± 0.42 aA	36.15 ± 0.50 aA	35.48 ± 0.42 aB	28.75 ± 1.02 cC	5.81 ± 0.55 aA	352.39 ± 42.21 aB	0.50 ± 0.04 aA
CL_{10}	2.22 ± 0.07 bB	25.68 ± 0.13 bB	32.83 ± 0.52 bC	32.94 ± 0.66 bC	25.74 ± 1.15 dD	4.77 ± 0.39 aA	253.67 ± 26.90 abB	0.51 ± 0.04 aA
CL_{15}	3.45 ± 0.10 aA	27.21 ± 0.20 aA	33.94 ± 0.48 bB	33.86 ± 0.52 bC	31.22 ± 0.74 bB	3.39 ± 0.25 aB	176.10 ± 19.26 bC	0.57 ± 0.03 aA
CL_{20}	4.75 ± 0.34 aA	29.43 ± 0.38 aA	36.81 ± 0.19 aA	37. 26 ± 0.34 aA	34.58 ± 0.76 aA	2.93 ± 0.21 bC	98.92 ± 12.59 cD	0.57 ± 0.03 aA
CL_{25}	–	–	–	–	–	–	–	–
Control	2.00 ± 0.00 bB	25.30 ± 0.19 bB	33.36 ± 0.30 bB	34.64 ± 0.29 abB	35.40 ± 0.41 aA	5.93 ± 0.39 aA	434.04 ± 34.43 aA	0.48 ± 0.01 aA

Mean ± standard error. Averages followed by the same lower case letter between treatments and upper case letters between generations do not differ significantly. (Paired startup test: $P < 0.05$). Standard errors were estimated using 100,000 bootstraps and compared using the paired bootstrap test based on the difference IC.

APOP pre-oviposition period, TPOP total pre-oviposition.

Table 4 Two-Sex fertility life table of *Anticarsia gemmatalis* exposed to sub-lethal concentrations of the Bt-bioinsecticide Dipel® over three generations at 25 ± 1 °C, 70 ± 10% RH and 12:12 h (L:D)

1° Generation					
Treatments	*T* (day)	R_0 (individual descendant^{-1})	*GRR* (descendant)	*r* (n° dia^{-1})	λ (n° day^{-1})
LC_5	28.88 ± 0.34 aB[1]	80.90 ± 16.79 bC	166.49 ± 31.54 bB	0.15 ± 0.01 bB	1.16 ± 0.01 bB
LC_{10}	28.72 ± 0.32 aB	97.17 ± 16.50 bB	232.17 ± 36. 87 aA	0.15 ± 0.00 bB	1.17 ± 0.01 bB
LC_{15}	27.34 ± 0.41 bB	47.52 ± 10.48 cD	132.32 ± 23.70 bC	0.14 ± 0.01 bB	1.15 ± 0.01 bB
LC_{20}	28.59 ± 0.31 aB	34.90 ± 8.64 dE	89.09 ± 19.39 cD	0.12 ± 0.01 cC	1.13 ± 0.01 cC
LC_{25}	28.98 ± 0.51 aB	27.99 ± 6.28 dE	148.51 ± 20.93 bB	0.11 ± 0.01 cC	1.12 ± 0.01 cC
Control	29.53 ± 0.22 aA	170.23 ± 24.16 aA	261.92 ± 31.83 aA	0.18 ± 0.00 aA	1.19 ± 0.01 aA
2° Generation					
LC_5	29.47 ± 0.52 aA	124.44 ± 24.79 bB	178.51 ± 33.74 bB	0.16 ± 0.01 aA	1.17 ± 0.01 aB
LC_{10}	31.17 ± 0.15 aA	56.4 ± 11.87 cD	163.55 ± 27.62 bB	0.12 ± 0.01 bC	1.13 ± 0.01 bC
LC_{15}	27.35 ± 0.41 cC	47.51 ± 10.48 cD	84.29 ± 10.94 cD	0.14 ± 0.01 bB	1.15 ± 0.01 bB
LC_{20}	28.61 ± 0.31 bB	34.89 ± 8.64 cE	50.87 ± 7.21 dE	0.12 ± 0.01 bC	1.13 ± 0.01 bC
LC_{25}	28.99 ± 0.51 bB	27.99 ± 6.28 dE	26.13 ± 3.59 eF	0.11 ± 0.01 cC	1.12 ± 0.01 cC
Control	30.54 ± 0.22 aA	170.14 ± 24.11 aA	232.86 ± 28.81 aA	0.17 ± 0.00 aA	1.19 ± 0.01 aA
3° Generation					
LC_5	30.32 ± 0.30 aA	116.29 ± 21.52 bB	189.57 ± 31.64 aB	0.15 ± 0.01 bB	1.16 ± 0.01 bB
LC_{10}	29.24 ± 0.20 bA	91.32 ± 15.47 bB	168.75 ± 25.52 aB	0.15 ± 0.00 bB	1.16 ± 0.01 bB
LC_{15}	29.11 ± 0.31 bA	84.53 ± 12.68 bC	131.37 ± 18.22 bC	0.14 ± 0.00 bB	1.16 ± 0.01 bB
LC_{20}	30.66 ± 0.20 aA	51.44 ± 8.14 cD	58.55 ± 8.90 cE	0.12 ± 0.00 cC	1.13 ± 0.01 cC
LC_{25}	–	–	–	–	–
Control	31.44 ± 0.14 aA	204.00 ± 26.93 aA	215.26 ± 27.94 aA	0.18 ± 0.00 aA	1.20 ± 0.00 aA

Mean ± standard error. Averages followed by the same lower case letter between treatments and upper case letters between generations do not differ significantly. (Paired startup test: $P < 0.05$). Standard errors were estimated using 100,000 bootstraps and compared using the paired bootstrap test based on the difference IC. *T* mean duration of one generation (day), R0 net reproduction rate (individual descendant-1), GRR gross reproductive rate (descending), *r* intrinsic rate of increase (n ° day-1), λ finite rate of increase (n ° day-1).

These differences are attributed to the genetic variability between the populations collected in the state of Parana and that of the present study in Sao Paulo, Brazil. Dipel® is composed of *B. thuringiensis* var. kurstaki, line HD-1, and presents the toxins Cry1Aa, 1Ab, and 1Ac, having in more significant quantities Cry1Ab and Cry1Ac. The toxins can also act individually or together, which can potentiate the individual toxicity of each toxin (Xue et al. 2005; Wei et al. 2015) or the combination of the toxins can reduce the insecticidal effect (Ameen et al. 1998; Garbutt et al. 2011), probably due to competition for the same receptor in the intestine of the caterpillar (Gómez et al. 2007).

Differences in susceptibility may be the main cause of the presence or absence of specific receptors for Cry toxins in the apical microvilli of columnar cells in the caterpillar's midgut (Gómez et al., 2007). Any interference associated with the mode of action of Bt helps in the survival of the insect and, therefore, in the development of resistance (Tabashnik, 1994).

Sub-lethal effects on the biological parameters of A. gemmatalis

The effect of sub-lethal concentration on *A. gemmatalis* varied according to treatments. This observation suggests that sub-lethal must be considered and can be used as a tool in integrated pest management (Bauce et al. 2006). The ingestion of different sub-lethal concentrations of *B. thuringiensis* by caterpillars of the second instar of *A. gemmatalis* had several consequences on biological conditioning and resulted in the prolongation of the larval period in some treatments. These observations occurred in other species, such as *Lymantria dispar* L., 1758 (Erb et al. 2001), *Sesamia nonagrioides* Lefèbvre, 1827 (Eizaguirre et al. 2005) and *Helicoverpa armigera* Hübner, 1808 (Sedaratian et al. 2013).

As a survival strategy, organisms can start to inhibit food, prolong development time, or even increase the incidence of polymorphism with the aim of biological compensation (Moreau and Bauce 2003). Fast and Regniere (1984) found that fourth-instar caterpillars of *L. dispar* can

recover their development when exposed to *B. thuringiensis*, with an increased number of instars without changing the pupae weight (Ramachandran et al. 1993). Also, in field conditions, the behavior may be different due to the continuous inlet of the sub-lethal concentration over the generations, which may make it difficult to acquire a lethal dose due to organoleptic properties that cause food inhibition (Van-Frankenhuyzen et al. 2000).

Intoxication caused by the bacterium *B. thuringiensis* can result in physiological changes resulting from complex interactions between δ endotoxin and the intestinal epithelium of the insect pest (Fathipour et al. 2019). A process that can occur after the death of enterococci caused by the action of δ endotoxin is the activation of the healing mechanism in the damaged regions of the intestine. This process is regulated by proteins that control larval development, justifying the prolongation of this phase (Retnakaran et al. 1983; Sedaratian et al. 2013). Digestibility reduction due to changes in the number of proteases is another justification for slow development. Larvae exposed to δ endotoxin may have a prolonged stage to compensate for the costs associated with recovery from sub-lethal exposure, with increased food consumption (Martinez-Ramirez et al. 1999; Gujar et al. 2001; Dmitriew 2011).

Another fact that can occur is the change in the number of instars in response to the nutritional quality of the food (Sehnal 1985; Kidd and Orr 2001; Mayntz et al. 2003; Verdinelli and Sanna-Passino 2003). Studies carried out with *S. nonagrioides* showed that larvae fed with sub-lethal concentrations of the Cry1Ac toxin increased seedlings and had a longer development period. This larval delay can interfere with the emergence of resistant populations in the agroecosystem, providing susceptible insects to mate with resistant insects (Liu et al. 1999; Eizaguirre et al. 2005). When the larval stage is prolonged in field conditions, the likelihood of predation or parasitism may increase. This is observed in transgenic plants, the positive effect in generalist predators, as in *Podisus nigrispinus* Dallas, 1851 due to the indiscriminate reduction in the application of pesticides that directly contributes to the permanence, constancy and increase in the population of these natural enemies in field conditions. (Malaquias et al. 2014; Malaquias et al. 2014).

In addition, development parameters, such as survival and fertility, can be affected due to reduced digestibility of the food eaten (Erb et al. 2001; Janmaat et al. 2014). In the present study, our results using LC_{25} corroborate these findings.

Studies carried out with *Choristoneura fumiferana* Clemens, 1865 exposed to sub-lethal concentration of *B. thuringiensis* demonstrated that the pupal phase did not affect longevity since the larvae recovered from the exposure (Fast and Regniere 1984; Ramachandran et al. 1993). These studies corroborate our results; however, even with recovery, there was a reduction in adult longevity. The emerged moths showed a reduction in longevity with variation in egg production according to the treatment. Changes in fertility after treatment with the bacterium *B. thuringiensis* have also been reported for other species such as *C. fumiferana* and *Spodoptera littoralis* Boisduval, 1833 (Salama and Zaki 1986; Pedersen et al. 1997).

The reduction in fertility impacted the pest species' population, affecting the population dynamics of the pest in the field. The reduction in egg production caused by the bacteria has been reported in other species such as *S. littoralis* and *C. fumiferana* (Salama and Zaki 1986; Bauce et al. 2006). These observations prove that the treatments have a direct effect on the reproductive system of *A. gemmatalis*. Another factor observed was deformations in the pre-pupa, pupa and adult phases, mainly in the anterior and/or posterior wings, increasing according to the increase in sub-lethal concentration. Insects have basic nutritional requirements such as lipids, carbohydrates and proteins (Dadd 1983). These nutria nts are required for the production of structural proteins and specific enzymes. However, some fatty acids are not synthesized by insects, such as linoleic and linolenic acid and must be ingested from the diet (Parra et al. 2012; Cohen 2015). These fatty acids are referred to as essential for the orders Orthoptera (Dadd 1960), Coleoptera (Vanderzant and Richardson 1964) and, mainly, Lepidoptera (Meneguim et al. 1997).

The insecticidal capacity of *B. thuringiensis* possibly caused some physiological imbalance in the insect pest, contributing to the lack of these fatty acids, which resulted in pre-pupae, pupae and deformed adults (Levinson and Navon 1969; Sivapalan and Gnanapragasam 1979; Bracken 1982; Dadd 1983). Physiologically, a greater energy allocation is expected for processes, such as growth with less allocation for metabolism and/or reproduction. The change in the allocation pattern can have positive or negative consequences depending on each individual (Dadd 1983). Under stress conditions, insects exposed to concentrations of bioinsecticides based on *B. thuringiensis*, spend more energy responding to infection. These additional energy expenditures result in less energy available for reproduction (Parsons 2000).

The adult pre-oviposition period (APOP) and the total pre-oviposition period (TPOP) were affected by the sub-lethal concentrations and changes in the proportion of males and females were observed. It is believed that these changes may be associated with differential susceptibility between the sexes and physiological effects on egg fertilization (Alix et al. 2001; Desneux et al. 2007).

Other studies showed sexual distortion in the face of insecticides (Morais et al. 2016; Delpuech and Meyet 2003). However, this is the first report on *Bt*-based bioinsecticides to act in the ratio between males and females. It should be noted that this study was carried out under laboratory conditions,

where insects are subjected to maximum exposure to the bioinsecticide. Thus, it is possible that under field conditions, the effects on the sex ratio are lower than those observed in the present study. However, field studies must be carried out to verify the sub-lethal effects in the *A. gemmatalis* population and subsequent generations.

The Two-Sex fertility life table parameters of *A. gemmatalis* that characterize possible adequacy costs were significantly affected over the three generations assessed. These parameters can also be used to estimate the product's effectiveness related to the target insect (Özgökçe et al. 2018; Rostami et al. 2018). The longer the period of development, the lower the survival rate, which results in less population increase. Therefore, population projection using the two-sex life table helps estimate variations in the different stages of the population development of the species under study and observe the separate behavior between both sexes (Chi 1990; Koner et al. 2019).

The gross reproductive rate (*GRR*) indicates the rapid increase in the population that depends on the number of eggs, hatched eggs and emergence of adults affected by the nutritional quality of the food eaten observed in the present study (Khaliq et al. 2007). Green leafhoppers *Nephotettix virescens* Distant, 1908 and *Nephotettix cincticeps* Uhler, 1896 exposed to sub-lethal concentrations of imidacloprid had a lower reproductive rate than those exposed to untreated and hormoligosis did not occur (Widiarta et al. 2001). Studies of behavioral hormoligosis, evaluating the oviposition preference of *Bemisia tabaci* Gennadius, 1889 revealed changes in the biochemical components of cotton leaves treated with insecticides. The results revealed that the plants treated with Carbaril and Endosulfan caused significant changes in the total phenols, in the pH value of the plants, reduction in total sugars and increase in the total free amino acids (Abdullah et al. 2006).

However, when using Fenvalerate, whiteflies preferred them for oviposition because these biochemical changes do not occur, which may be one of the causes of their resurgence in plants repeatedly treated with these insecticides (Abdullah et al. 2006). As the present study was conducted under laboratory conditions, there is a need to evaluate the effects of sub-lethal concentrations of Bt-based bioinsecticides in field conditions. Because the different sub-lethal concentrations can alter the biochemical components of the leaves of the plant and cause positive or negative effects on the pest. Hormoligosis can occur whenever the pest is exposed to a sub-lethal concentration. And pesticides, applied in lethal concentrations, tend to be reduced to sub-lethal concentrations over time and exposure to climatic conditions in the field (Dutcher, 2007).

The intrinsic population growth rate (r) is a useful parameter to describe the dynamic population of the pest species, which encompasses survival, development and reproduction, and the finite population growth rate (λ) revealed the total population decrease over a while under exposure to the treatments used (Farhadi et al. 2011; Rostami et al. 2018; Das et al. 2019). The life table parameters provided evidence of the sub-lethal effects of the *Bt*-based bioinsecticides in *A. gemmatalis*.

Hormoligosis is a phenomenon that occurs in the measurement of the dose-response to a series of concentrations of a treatment. A low dose (sub-lethal concentration) causes a stimulating response, and a high dose (recommended concentration) causes an inhibitory response (Calabrese and Baldwin, 2003). In these cases, the LC_{25} treatment showed an inhibitory response. For the other treatments, even with the alterations observed in the parameters of biological development, according to the theory of hormoligosis, the surviving insects are looking for new ways or improve the ones that have survived to deal with the exposure to sub-lethal concentrations, contributing to the emergence of populations with average levels of tolerance (Abivardi, 2004).

For integrated pest management, it means the permanence of insects in the field that will cause damage to the crop or the subsequent ones with the possibility of acquiring resistance due to hormoligosis. However, the lack of studies on the sub-lethal effects leaves this possible method unanswered and the adoption of the recommended concentration, together with selective pesticides, conservation of natural enemies and resistance of the host plant, becomes effective *A. gemmatalis* control with a reduction in the possibility of the emergence of resistant insect populations.

Conclusions

The variation of the sub-lethal concentration interfered in the biological parameters of *A. gemmatalis*, with emphasis on the LC_{25} as it did not provide subsequent descendants. The toxic effect of Bt-based bioinsecticide interfered mainly in the parameters of fertility, sex ratio, net reproduction rate (R0), and gross reproduction rate (GRR). It is unlikely that the theory of hormoligosis will not have a substantial impact on the performance of *A. gemmatalis* observed in its population growth rate; however, it should not be neglected because the induction of pest outbreaks in the agroecosystems is challenging to assess since other complex environmental factors are likely to be involved.

Data availability

The authors are available for availability of data and materials.

Author contributions FOF, JAD, and RAP conceived and designed the research. FOF, TDS, and ACS conducted experiments. FOF and TDS analyzed the data. FOF wrote the first draft. NPD and RAP revised and edited the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

Ethical approval Informed consent was obtained from all individual participants included in the study.This study was conducted with a pest species reared under laboratory conditions, in accordance with the standards required by the Department of Agricultural Entomology of the State University "Júlio de Mesquita Filho", Unesp / Jaboticabal, São Paulo - Brazil.

Consent to participate All authors were informed individually and approved the publication of the study result.

Consent for publication Informed consent was obtained from all individual participants included in the study.

Research involving human participants and/or animals' note This study does not involve endangered or protected species

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