# *Bioinsecticidal effect of the flavonoids pinocembrin and quercetin against* Spodoptera frugiperda

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**Journal of Pest Science**

ISSN 1612-4758
Volume 88
Number 3

J Pest Sci (2015) 88:629-635
DOI 10.1007/s10340-014-0641-z


Springer

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ORIGINAL PAPER

# Bioinsecticidal effect of the flavonoids pinocembrin and quercetin against *Spodoptera frugiperda*

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Received: 7 March 2014 / Revised: 18 December 2014 / Accepted: 31 December 2014 / Published online: 13 January 2015


**Abstract** Flavonoids function in many aspects of plant–insect interactions, but the responses of insects to these compounds vary greatly. In this study, we determined the effects of two widely distributed flavonoids, pinocembrin and quercetin, on the feeding behavior, survival, and development of the fall armyworm *Spodoptera frugiperda* J.E. (Smith) (Lepidoptera: Noctuidae). In a choice test, *S. frugiperda* larvae strongly rejected leaves treated with pinocembrin at concentrations of 10, 50, or 100 μg/cm$^2$. Larvae fed normally on leaves treated with quercetin at 10 and 50 μg/cm$^2$, but showed 57 % deterrence when fed on leaves treated with 100 μg/cm$^2$ quercetin. At concentrations of 0.01–1 μg/cm$^2$, pinocembrin and quercetin functioned as phagostimulants for *S. frugiperda*. In a multiple-choice experiment, *S. frugiperda* larvae preferred to consume untreated leaves or those treated with 0.1 μg/cm$^2$ pinocembrin, but rejected leaves treated with 5–50 μg/cm$^2$ pinocembrin. In a no-choice feeding experiment, larvae fed on leaves treated with 5 and 50 μg/cm$^2$ pinocembrin consumed less than those fed on leaves treated with 0.1 and 1 μg/cm$^2$ pinocembrin or untreated leaves. Pinocembrin at 1–50 μg/cm$^2$ negatively affected larval weight and survival, thus showing a toxic effect. In contrast, leaf consumption and larval weight were not significantly affected by quercetin at 0.1, 1, 5, and 50 μg/cm$^2$, and mortality rates only slightly increased. Because of its dual activity, pinocembrin could be used for insect control in a stimulo-deterrent diversionary strategy: the same compound could promote both stimulate (low doses) and deter insect activity (high doses).

**Keywords** Flavonoids · Antifeedant · Pinocembrin · Quercetin · Lepidoptera · Noctuidae

## Key message

- The responses of insects to flavonoids vary greatly and many aspects remain unknown.
- Pinocembrin affects feeding behavior and survival of *Spodoptera frugiperda* at 10–50 μg/cm$^2$.
- Quercetin provokes no effect on *Spodoptera frugiperda* up to 100 μg/cm$^2$.
- Both flavonoids were phagostimulant at concentration below 1 μg/cm$^2$.
- Consequently plants treated with a high concentration of pinocembrin may be rejected while those treated with a low concentration may be attractive.
- Pinocembrin may be useful in an stimulo-deterrent diversionary strategy for crop protection.

## Introduction

The fall armyworm *Spodoptera frugiperda* J.E. (Smith) (Lepidoptera: Noctuidae) is an economically important pest in the production of grain and many other crops in North, Central, and South America (Wyckhuys and O'Neil 2006). Because *S. frugiperda* is a late-season pest of late-

S.M. Palacios is a member of the National Research Council of Argentina (CONICET).

Communicated by M. B. Isman.

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planted maize crops in subtropical regions, and of other crops throughout the cropping cycle in tropical regions, insecticide must be applied frequently to maintain its populations below economic thresholds (Storer et al. 2012). *S. frugiperda* is the main corn pest in Brazil and Argentina (Di Blessing et al. 2010; Tavares et al. 2009) and its control has become a serious problem because it has become resistant to many synthetic insecticides (Tomquelski and Martins 2007) and to transgenic Bt-maize (Storer et al. 2012). Also *S. frugiperda* is polyphagous, feeding on a broad range of host plants in different families and genera (Devappa et al. 2012). It has developed the ability to detoxify plant xenobiotics (Schramm et al. 2012), which makes it even more difficult to control, especially using natural insecticides.

In a previous screening program to search for new agrochemicals from plants native to Argentina, the ethanolic extract of aerial parts of *Flourensia oolepis* S.F. Blake (Asteraceae) showed significant antifeedant activity against insects including coccinellids and *Spodoptera* (Palacios et al. 2007). The active compound in *F. oolepis* was identified as the flavanone pinocembrin, which showed a strong antifeedant effect against *S. frugiperda* with an $ED_{50}$ of 8.8 μg/cm$^2$ (Diaz Napal et al. 2009). More recently, we conducted a study (Diaz Napal et al. 2010) comparing the anti-insect effects of pinocembrin and quercetin, the most ubiquitous, abundant, and well-studied flavonol in the plant kingdom (Harnly et al. 2006; Harwood et al. 2007), against the coccinellid *Epilachna paenulata*. When different doses of these compounds were assayed using a choice test for this insect, pinocembrin showed clear antifeedant activity, whereas quercetin elicited variable behavioral responses (phagostimulant or antifeedant) depending on the concentration (Diaz Napal et al. 2010). The antifeedant profile of many flavonoids depends on the dose (Goławska et al. 2014; Simmonds 2003). For instance, the flavonoid rutin (quercetin-3-*O*-rutinoside) has been shown to have both stimulant and deterrent effects against *Spodopteran* insects. At concentrations between $10^{-4}$ and $10^{-5}$ M, rutin was shown to stimulate feeding of *Spodoptera exigua*, *S. exempta*, *S. littoralis*, *Helicoverpa armigera*, and *H. zea*, while it was deterrent for these insects at higher concentrations (Simmonds 2003).

Given these results, we wondered whether the compound pinocembrin also has stimulant and deterrent effects on the feeding behavior of *S. frugiperda*. We also wondered if it affects the development and survival of the insect, and whether pinocembrin has potential as a natural insecticide against this polyphagous pest. Information on the activity and mode of action of this compound will be useful for designing predictable and durable strategies to control pests in the field (Goławska et al. 2014). Consequently, we analyzed the effects of pinocembrin on the feeding behavior, survival, and development of *S. frugiperda* and compared its performance with that of the flavonoid quercetin.

## Materials and methods

### Chemicals

Pinocembrin, quercetin, and azadirachtin were purchased from Sigma Chemical Co. Inc. (St. Louis, MO, USA). Solvents were purchased from Merck (Darmstadt, Germany) and Fisher Scientific (New Jersey, NJ, USA).

### Insects

*Spodoptera frugiperda* larvae were obtained from a laboratory colony, reared on an artificial diet of sterile water, agar, bean meal, yeast extract, wheat germ, sorbic acid, ascorbic acid, and formaldehyde, prepared as described earlier (Céspedes et al. 2000), maintained in a growth chamber at 24 ± 1 °C and 70–75 % relative humidity, with a 16/8 h light–dark cycle, and periodically renewed with field specimens.

### Insect bioassays

#### *Feeding choice assay*

The feeding choice assay of pinocembrin, quercetin, and azadirachtin was carried out according to the previously reported (Carpinella et al. 2002). Two circular sections of *Lactuca sativa* leaves (1 cm$^2$) were placed in a Petri dish and a glass disk with two 1 cm$^2$ holes was placed on top. A starved third instar *S. frugiperda* larva was placed equidistant from a treated (with 10 μl of test solution) and an untreated (with 10 μl of acetone, solvent control) leaf disk, and allowed to feed until 50 % of the available food was eaten. Test solutions were prepared by dissolving the necessary amount of pinocembrin, quercetin, or azadirachtin in 10 ml of HPLC grade acetone. The dosages for each compound, applied with a Hamilton syringe, were 100, 50, 10, 1, 0.1, and 0.01 μg/cm$^2$. Ten replicates were run for each treatment. The relative amounts (recorded in percentages from 0 to 100) of the treated and untreated substrate area eaten by *S. frugiperda* in each test were estimated visually by dividing the food area into imaginary quarters. The measurements were always performed by the same operator. An antifeedant index (FI%) was calculated as $[(C - T)/(C + T)] \times 100$, (Mazoir et al. 2008) where *T* and *C* represent consumption on treated and untreated foods, respectively.

*Multiple-choice assay*

Five circular sections of *L. sativa* leaves (1 $cm^2$) were placed in a Petri dish. One was treated with 10 µl of acetone (control) and four were each treated with 10 µl of different solutions of pinocembrin in acetone, at doses of 0.1, 1, 5, or 50 µg/$cm^2$. A 2 h-starved *S. frugiperda* larva (third instar) was then placed in the middle of the Petri dish and allowed to feed until 50 % of the available food was eaten (two and a half circular sections). Sixty replicates were run. The area consumed on each piece was recorded in percentages from 0 to 100, and averages between replicas were calculated and normalized in order to express the results as the relative amount of food consumed by a larva in every piece.

*No-choice feeding assay*

One *S. frugiperda* larva (first instar) was placed in a Petri dish and fed on *L. sativa* leaves (1 $cm^2$; renewed every 24 h) on which either pinocembrin or quercetin was applied with a Hamilton syringe at dosages of 0.1, 1, 5, and 50 µg/$cm^2$ or acetone (control). Ten replicates were made for each treatment. Leaf consumption and body weight were recorded every 24 and 72 h, respectively, (Carpinella et al. 2003). The consumption was visually estimated on the 0–100 % scale as indicated above.

*Mortality assay*

A group of 10 *S. frugiperda* larvae (first instar) was continuously fed with leaves treated with either 0.1, 1, 5, and 50 µg/$cm^2$ of pinocembrin, quercetin, or with solvent (acetone) as control. A similar set of larvae was not fed at all and acted as starved controls. Three replicates were performed for each treatment. Mortality was recorded every 24 h. From mortality data, $LD_{50}$ and $LT_{50}$ values for pinocembrin and quercetin were determined by Probit analysis (Carpinella et al. 2003).

Statistical analysis

Results from feeding choice assays were analyzed by the Wilcoxon Signed-Rank Test. Multiple-choice assays were analyzed by the Friedman test (Mangeaud and Videla 2005). When data were not normally distributed or showed heterogeneity of variances, they were subjected to non-parametric tests. Results of no-choice feeding assays, average larval body weight, accumulated consumption values, and average mortality rates, were compared among concentrations by the Kruskal–Wallis non-parametric analysis of variance, followed by the Dunn test, for each compound. Differences were considered significant at $p \leq 0.05$.

## Results

Feeding choice assay

The antifeedant activities of pinocembrin, quercetin, and the positive control, azadirachtin, against *S. frugiperda* are shown in Fig. 1. The *S. frugiperda* larvae ate significantly less when fed on leaves treated with pinocembrin at 10, 50, and 100 µg/$cm^2$ (feeding index (FI) of 70, 91, and 93 %, respectively) (Fig. 1). The *S. frugiperda* larvae consumed similar amounts of control leaves and quercetin-treated leaves. When leaves were treated with quercetin, the FI was 6, 9, and 57 % at concentrations of 10, 50, and 100 µg/$cm^2$, respectively, (Fig. 1). The antifeedant azadirachtin completely inhibited insect feeding at concentrations of 1–10 µg/$cm^2$ (Fig. 1).

Pinocembrin and quercetin at low concentrations (0.01–1 µg/$cm^2$) were phagostimulants for *S. frugiperda,* showing an FI range of −50 to −22 and −68 to −4 %, respectively, (Fig. 1). Azadirachtin at concentrations lower than 1 µg/$cm^2$ did not have a phagostimulant effect (Fig. 1).

Multiple-choice assay

In a multiple-choice experiment, *S. frugiperda* larvae preferred to consume control leaves or those treated with 0.1 µg/$cm^2$ pinocembrin. The food treated with 5 and 50 µg/$cm^2$ pinocembrin was significantly rejected (Fig. 2).

No-choice feeding assay

After 4 days of treatment, the *S. frugiperda* larvae exposed to leaves treated with pinocembrin at 5 and 50 µg/$cm^2$ consumed less food ($H = 9.68$, $P < 0.04$) than did the larvae exposed to untreated leaves (Fig. 3a). The differences in consumption among the treatments increased at day 7 ($H = 19.43$, $P < 0.0001$) and continued over time. The larvae consumed similar amounts of untreated leaves and leaves treated with 0.1 µg/$cm^2$ pinocembrin. In contrast, larvae consumed similar amounts of untreated leaves and quercetin-treated leaves, regardless of the quercetin concentration, during the experiment. The larvae consumed similar amounts of leaves treated with quercetin at phagostimulant concentrations and untreated leaves.

An analysis of larval weight showed that the body weight of larvae fed on untreated leaves steadily increased, while that of larvae fed on pinocembrin-treated leaves increased more slowly. On day 18, the body weight of larvae fed on leaves treated with 1, 5, and 50 µg/$cm^2$ pinocembrin was 1.3, 1.4, and 2.6 times lower, respectively, than that of the control group 18 (Fig. 3b).

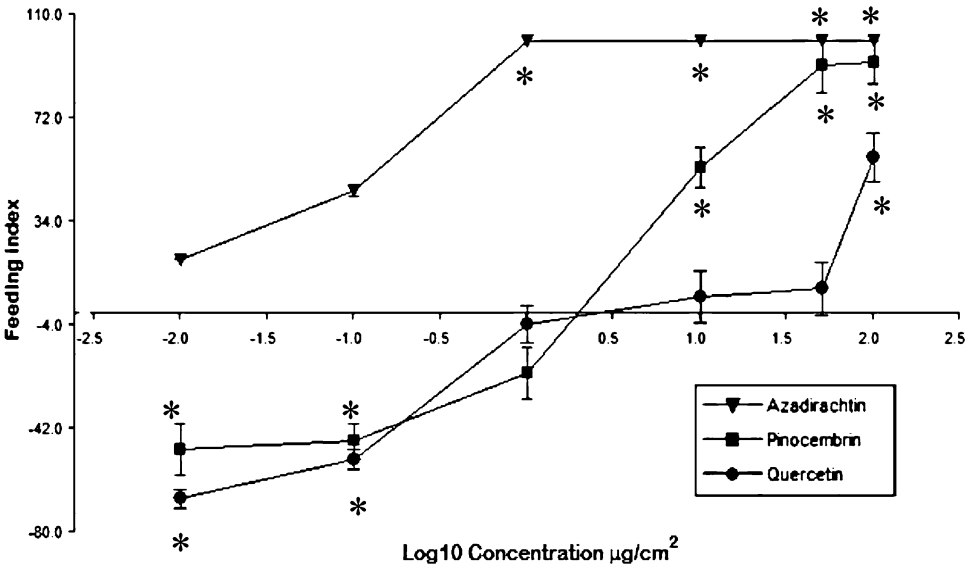


**Fig. 1** Effects of pinocembrin, quercetin, and azadirachtin on feeding behavior of *S. frugiperda* in a choice test. Negative value indicates a phagostimulant effect; positive value indicates an antifeedant effect. *Asterisks* indicate significant differences ($P < 0.05$) between consumption of treated and control leaves (Wilcoxon signed-rank test), $n = 10$

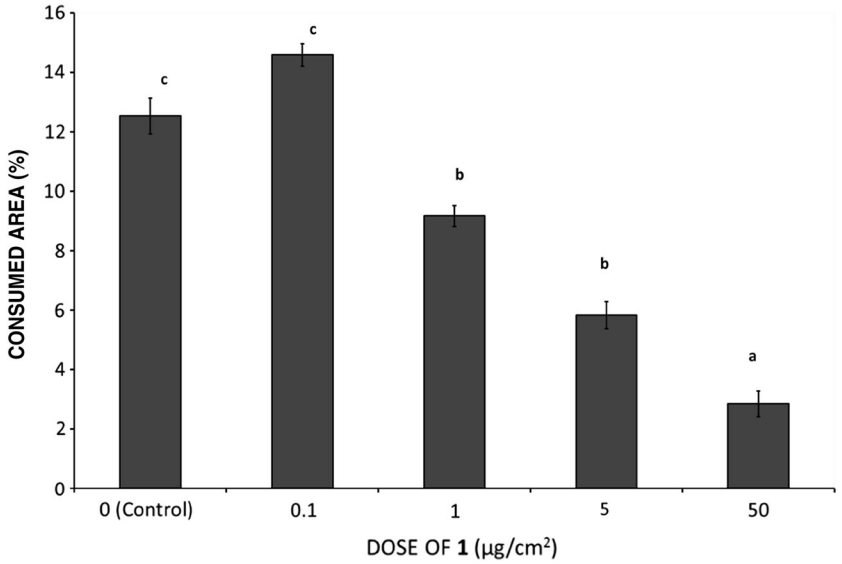


**Fig. 2** Effect of pinocembrin on feeding behavior of *S. frugiperda* in a multiple-choice assay. Different letters indicate significant differences ($P < 0.05$; Friedman test), $n = 60$

The body weight of larvae fed on leaves treated with 0.1 µg/cm$^2$ pinocembrin was not significantly different ($H = 0.96$; $P = 0.1967$) from that of the control group. The body weight of *S. frugiperda* larvae was not affected by quercetin at any concentration.

## Mortality assay

In the mortality assay, all larvae fed on leaves treated with 50 µg/cm$^2$ pinocembrin died 16 days after the beginning of the experiment, while food-deprived larvae died on day 10 (Fig. 4a). The control experiment in which larvae were deprived of food represented the response of larvae exposed to a compound with total antifeedant activity. Larvae fed on leaves treated with 1 and 5 µg/cm$^2$ pinocembrin showed 20 and 50 % mortality, respectively, at day 21. The control group and those consuming leaves treated with 0.1 µg/cm$^2$ pinocembrin showed no mortality in this assay (Fig. 4a). The lethal time 50 ($LT_{50}$) was 9.5 and 21.3 days for pinocembrin at 50 and 5 µg/cm$^2$, respectively, while it was impossible to calculate this parameter accurately for pinocembrin at 1 µg/cm$^2$. The $LT_{50}$ for food-deprived larvae was 4.73 days.

Throughout the experiment, no more than 10 % mortality was observed for larvae fed on leaves treated with quercetin at any concentration. All treatments had effects that were significantly different from those caused by starvation. These results show that quercetin did not affect the life cycle of the insect.

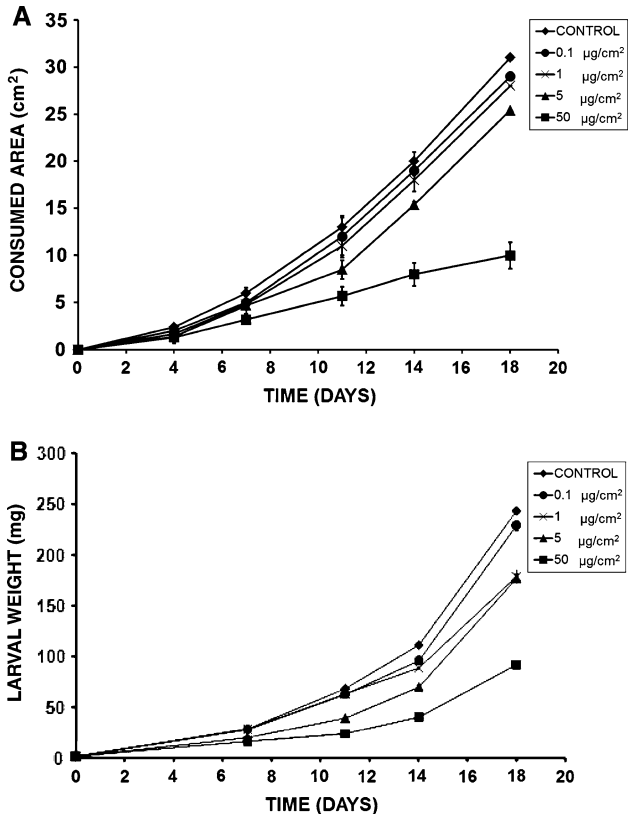


**Fig. 3** Average leaf area consumed (**a**) and average body weight (**b**) of *S. frugiperda* larvae fed on leaves treated with pinocembrin in a no-choice feeding assay. *Error bars* <60 and <2 for area consumed and body weight, respectively, are embedded in symbols

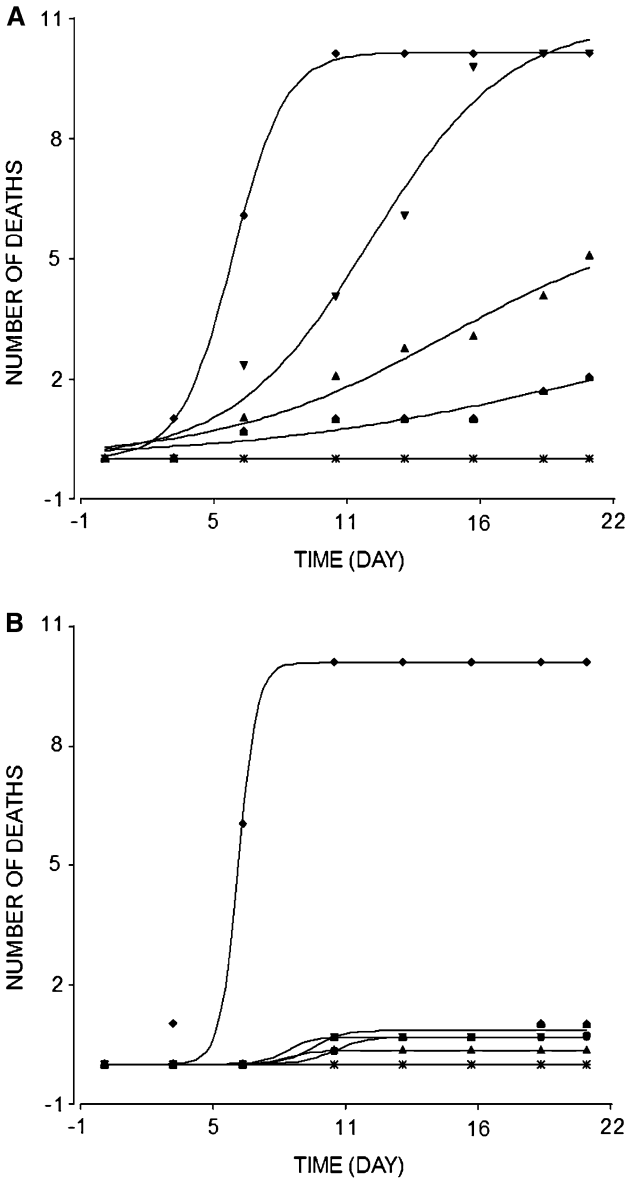


**Fig. 4** Cumulative mortality rates of *S. frugiperda* larvae fed with leaves treated with pinocembrin (**a**) and quercetin (**b**). *Filled diamond* food-deprived treatment, *inverted filled triangle* 50 µg/cm$^2$, *filled triangle* 5 µg/cm$^2$, ⬟ 1 µg/cm$^2$, ✳ control. Concentration of 0.1 µg/cm$^2$ produced no mortality and these values were not plotted in order to avoid superposition with control values. Data were subjected to non-linear correlation (SD 0.1, $P < 0.001$). Symbols represent experimental means and continuous lines correspond to predicted values

## Discussion

A compound can negatively affect insects in two ways; it may not be acceptable (deterrent), so that the insect is essentially deprived of food, or it may have toxic effects once consumed (Akhtar et al. 2012). The flavonoid pinocembrin showed both of these negative effects. In the choice test, it functioned as a strong feeding deterrent at concentrations of 10–100 µg/cm$^2$. This antifeedant effect differed from that of quercetin. Nevertheless, the effect of both flavonoids changed from phagostimulant to deterrent as their concentrations in the treated food increased (Fig. 1). These results are similar to those reported for *Epilachna paenulata* (Diaz Napal et al. 2009), although in that case, pinocembrin showed only antifeedant activity, while quercetin showed both antifeedant and toxic effects.

Other studies on the effects of flavonoids against *S. frugiperda* reported that luteolin (Tringali et al. 2001) was inactive against this insect, while tricin, tricin 7-*O*-glucoside, and isoorientin were phagostimulants (Bouaziz et al. 2001). Comparing those results with the results of the present study, we conclude that pinocembrin functions differently to other flavonoids.

The multiple-choice experiment showed that the rejection of food and the stimulus to eat according to the concentration of pinocembrin were unchanged when the insect had many food options. *S. frugiperda* larvae significantly rejected food treated with pinocembrin at 10–50 µg/cm$^2$ (Fig. 2), but were attracted to food treated with low concentrations of pinocembrin. This finding suggests that in the field, plants treated with a high concentration of

pinocembrin may be rejected, while those treated with a low concentration may be attractive.

The no-choice assay revealed that pinocembrin negatively affected *S. frugiperda* larvae, especially those that consumed large amounts (i.e., leaves treated with 50 μg/cm$^2$ pinocembrin). The larvae consumed similar quantities of leaves treated with pinocembrin at 1 and 5 μg/cm$^2$ and control leaves. However, the body weights of larvae that consumed leaves treated with 1 and 5 μg/cm$^2$ pinocembrin were significantly lower than that of the control group, showing that pinocembrin had toxic effects.

The larvae consumed similar amounts of leaves treated with 0.1 μg/cm$^2$ pinocembrin and untreated leaves, indicating that in a no-choice situation, pinocembrin did not result in increased intake, as observed in the choice test. However, this was consistent with the results observed in the multiple-choice test, in which there was no significant difference in consumption between leaves treated with 0.1 μg/cm$^2$ pinocembrin and untreated leaves. One explanation for this behavior could be that different larval instars were used in the choice and no-choice assays. Lower instars are relatively sensitive to defensive compounds until they adapt to them.

In contrast, larvae fed on leaves treated with quercetin did not differ significantly from those in the control group at any time-point during the experiment. Once again, larvae exposed to this phagostimulant at all concentrations did not show higher consumption than that of control larvae. These results were similar to those reported for *E. paenulata* (Diaz Napal et al. 2009).

The slower growth rate of larvae exposed to pinocembrin implied that their growth was delayed and their development time increased. This may result in higher mortality in the field, as a result of biotic and abiotic factors such as increased exposure to predators, diminished immunity, increased sensitivity to pathogens, and/or lower resistance to high or low temperatures (Akhtar et al. 2012).

The mortality assay also confirmed that consuming pinocembrin had negative effects leading to death. This effect of pinocembrin was very strong at a high concentration (50 μg/cm$^2$), and mortalities of 20–50 % were also observed at lower concentrations. Quercetin did not have these effects on the insects.

The push–pull strategy (Pickett et al. 1997), or stimulodeterrent diversionary strategy (SDD) (Miller and Cowles 1990), is a comprehensive approach to insect control. This approach combines different behavioral stimuli to manipulate the pest response, resulting in reduced damage to the treated crop (Björkman et al. 2011).

Pinocembrin may be useful in an SDD strategy for crop protection because of its feeding deterrent and feeding stimulant properties. A feasible SDD strategy would be to apply pinocembrin at deterrent concentrations (push) to the crop that needs protection, but at lower concentrations to an adjacent trap crop or trap rows of the main crop to generate the phagostimulant effect (pull), as observed in the choice feeding and multiple-choice assays. A mobile insect such as *S. frugiperda* would likely abandon the protected crop and move to another plant some distance away, as a result of behavioral manipulation (Akhtar et al. 2012). Although this is an environmentally friendly strategy, the compound at phagostimulant concentrations could increase the rate of pest growth. However, our no-choice assay demonstrated that pinocembrin at the phagostimulant dose did not increase larval performance compared with that of untreated (control) larvae.

It is also important to consider the potential for herbivory damage if the concentration of pinocembrin decreased to the phagostimulant level because of degradation or leaching. Our results indicated that this situation would not differ greatly from that of insects feeding on an untreated crop, as observed in the no-choice assay (compare control vs. 0.1 μg/cm$^2$ pinocembrin; Fig. 3a). In that assay, the larvae consumed the same amounts of leaves with pinocembrin at the phagostimulant dose and untreated leaves. This finding suggests that crops would not suffer greater damage as the concentration of pinocembrin decreased.

In the field, natural insecticides degrade relatively quickly. Therefore, to guarantee crop protection, the use of pinocembrin in pest control programs must be accompanied by pest monitoring before deciding on new applications. As shown by the multiple-choice experiments, if the insect can choose among leaves treated with pinocembrin at concentrations ranging from 0.1 to 50 mg/cm$^2$, it prefers the lower concentration. In other words, the pull action would be effective, suggesting that pinocembrin has potential for use in a DDS strategy.

## Conclusions

Pinocembrin inhibited feeding and negatively affected the survival of the fall armyworm *S. frugiperda*. It showed lower activity than that of another well-known antifeedant, azadirachtin, but its availability in a variety of plant species and its molecular simplicity mean that it has the potential for use as a feeding deterrent. It could also be a target for plant improvement programs. That is, introducing the genes for biosynthesis of pinocembrin could increase natural crop resistance to herbivory, and/or produce high-yielding cultivars as a source of natural botanical insecticides.

Pinocembrin can be extracted from numerous plants or from propolis (Kumazawa et al. 2004), and can be synthesized easily using established methods because of its molecular simplicity. Compared with commercial synthetic

insecticides, pinocembrin may represent a more environmentally friendly insecticide, and its potential availability makes it a useful alternative.

## Author contribution

SMP conceived and designed research. GNDN conducted experiments and analyzed data. SMP wrote the manuscript. Both authors read and approved the manuscript.

**Acknowledgments** Financial support for this work was provided by the Agencia Nacional de Promoción Científica y Técnica, FONCYT, PICT 33593 and CONICET PIP 11220100100236. We thank Joss Heywood for revising the English language.

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