El Colegio de la Frontera Sur

Compuestos volátiles emitidos por *Cedrela odorata* L. (Meliaceae) como atrayentes de *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae)

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I. RESUMEN

Hypsipyla grandella Zeller (Lepidoptera: Pyralidae) ha sido reportada como una plaga que limita el establecimiento exitoso de plantaciones de cedro y caoba en México. Existen estudios sobre la bioecología, control químico y silvicultural de esta plaga; sin embargo, se conoce poco sobre las interacciones biológicas entre el insecto y su planta hospedera. Por lo tanto, el objetivo de este trabajo fue identificar los compuestos volátiles emitidos por *Cedrela odorata* L. que median la atracción de *H. grandella*. Se realizaron pruebas en jaulas de campo para determinar la actividad comportamental y la respuesta de atracción de *H. grandella* a *C. odorata*. Además, se identificaron los compuestos volátiles de *C. odorata* y se evaluó la respuesta de atracción de las palomillas al extracto de cedro y la mezcla sintética mediante bioensayos en tubo “Y”. Encontramos que las hembras vírgenes y apareadas presentan poca actividad nocturna, con movimientos de antenas frecuentes, vuelos esporádicos, aleteos cortos (<10 s) y largos (> 30 s). Las hembras vírgenes realizaron la postura de llamado, mientras que las hembras apareadas presentaron tres periodos de oviposición. Los resultados indicaron que tanto hembras vírgenes, machos vírgenes, y hembras apareadas fueron atraídos a plantas de cedro. Los volátiles identificados fueron: α-pineno, β-ocimeno, 2-etil-1-hexanol, D-limoneno, nonanal, (*E*)-4,8-dimetil-1,3,7-nonatrieno, α-copaeno, β-cariofileno y germacreno D. La mezcla de compuestos sintéticos atrajo de forma significativa a machos vírgenes y hembras apareadas de *H. grandella*. Los resultados sugieren que los compuestos volátiles identificados en el extracto pueden ser responsables de la atracción de *H. grandella* hacia *C. odorata*.

Palabras clave: señales químicas, compuestos volátiles, interacción insecto-planta, planta hospedera, olfato.

II. INTRODUCCIÓN

El cedro rojo *Cedrela odorata* (Linneo 1759) es una especie forestal tropical de la familia Meliaceae. Debido a sus características de dureza, color, durabilidad y aroma, es la segunda especie de madera preciosa más importante de la industria forestal en México y una de las más valiosas en los trópicos (Larrea et al. 2008; González-Luna y Cruz-Castillo 2021). El interés por la madera de cedro rojo ha ocasionado una intensa tala de árboles, y por esta razón fue incluida como especie amenazada y bajo protección especial en México y a nivel internacional (SEMARNAT 2010; CITES 2021). Sin embargo, el establecimiento y la productividad de plantaciones comerciales con *C. odorata*, durante los primeros años, se ha visto limitado por el ataque del barrenador de los brotes de las meliáceas *Hypsipyla grandella* (Zeller 1848) (Macías-Sámano 2001; Plath et al. 2011). Las larvas de este barrenador destruyen el retoño terminal principal, taladrando las puntas, además de hacer túneles en los tallos jóvenes, provocando bifurcación de los fustes y ramificación excesiva, perdiendo así las características deseables para la industria forestal y reduciendo su valor comercial (Briceño-Vergara 1997; Lunz et al. 2010). Por lo general, el control de esta plaga se hace mediante insecticidas químicos (Goulet et al. 2005), control biológico y el manejo silvícola (podas, raleos, densidad de siembras, etc.) (Ruiz et al. 2016; Pulgarín et al. 2018). Sin embargo, debido a los hábitos crípticos del insecto (una vez que la larva eclosiona penetra en el brote), la naturaleza del daño (interno a la planta), factores climáticos (lluvias intensas en la región de ocurrencia natural del insecto) y al largo periodo de protección requerido a las plantas, su control con insecticidas convencionales resulta ineficiente, económicamente inviables y perjudicial al medio ambiente (Allan et al. 1976; Wylie 2001; Mahroof et al. 2002; Goulet et al. 2005). Por tal motivo, se sugiere utilizar otras estrategias de manejo como el uso de semioquímicos, los cuales están involucrados en las distintas interacciones ecológicas y que median la comunicación entre las especies (Lima-Mendonça et al. 2014).

El reconocimiento de una planta hospedera por los insectos es crucial para asegurar su supervivencia y la de su progenie, dado que este no solo percibe la planta como un sustrato alimenticio, sino también como un lugar apropiado para oviposición y sitios de refugio (Schoonhoven et al. 2005; Rojas 2012). La localización de una planta hospedera

por el insecto no solo puede ocurrir mediante el uso de compuestos específicos de la especie, sino que la mayoría usan mezclas de compuestos ubicuos (Bruce et al. 2005). Durante este proceso un insecto puede usar señales visuales, olfativas y gustativas (Bernays y Champman 1994). Es así que la percepción por olfacción es un proceso de importancia para los insectos, debido a que está involucrado en patrones de comportamiento, como en la selección de alimento (Libert et al. 2007), la percepción de sustancias tóxicas (Fuyama 1976), el reconocimiento y elección de pareja (Billeter et al. 2009) y sitio de oviposición (Hoffmann y O'Donnell 1990; Jaenike 1990). Sin embargo, se conoce poco sobre la ecología, etología y las interacciones biológicas entre el insecto y su planta hospedera.

Hay algunos reportes sobre la infestación de *H. grandella* a *C. odorata* y la variabilidad genética de este barrenador (Cornelius y Watt 2003; Pérez-Salicrup y Esquivel 2008). Existe evidencia sobre la susceptibilidad de *C. odorata* y *Swietenia macrophylla* al ataque de *H. grandella* (Newton et al. 1998), la cual está dada por la variación en la producción de compuestos químicos atrayentes o disuasivos para hembras en oviposición (Honda 1995). Por lo que es importante conocer y estudiar los diferentes compuestos involucrados en las interacciones ecológicas entre plantas e insectos, para entender los fenómenos mediados por compuestos químicos.

Existen algunos estudios sobre la interacción de *H. grandella* e *Hypsipyla robusta* con diferentes especies de Meliaceae, en donde se han reportado algunos compuestos orgánicos volátiles antenalmente activos y que podrían ser los responsables de la atracción de estos lepidópteros. Por ejemplo, se ha reportado que el β-cariofileno liberado por *S. macrophylla* King juega un papel importante en la atracción de *H. grandella* (Soares et al. 2003). Lago et al. (2006), analizaron los volátiles del aceite esencial de *Guarea macrophylla* Vahle, identificaron cinco compuestos antenalmente activos: ledol, 1-cubenol, guai-6-en-10β-ol, 1-*epi*-cubenol, τ-caninol, los cuales podrían ser responsables de la atracción de *H. grandella* a *G. macrophylla.* Esto sugiere que dicha atracción está mediada por sustancias químicas que guían a la hembra a su sitio de oviposición. Así mismo, Borges et al. (2022), identificaron los compuestos volátiles *C. fissilis* de los cuales el nonanal, decanal, salicilato de metilo y β-cariofileno fueron antenalmente activos para

hembras y machos de *H. grandella*. El papel de los compuestos volátiles de *C. odorata* en la atracción de *H. grandella* no ha sido estudiado hasta el momento. Por lo que se desconoce si la hembra virgen, el macho o la hembra apareada de esta especie son atraídos a diferentes compuestos presentes en plantas de cedro rojo. Con ello, se podría anticipar la naturaleza volátil de dichos compuestos, los cuales pueden usarse en el control de dicha plaga. Por lo tanto, el presente trabajo tuvo como objetivo identificar los compuestos volátiles emitidos por *C. odorata* responsables de la atracción de *H. grandella*.

III. ARTÍCULO CIENTÍFICO: ORGANIC VOLATILE COMPOUNDS EMITTED BY *Cedrela odorata* L. (MELIACEAE) AS ATTRACTANTS OF *Hypsipyla grandella* ZELLER (LEPIDOPTERA: PYRALIDAE)

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VOLATILES EMITTED BY *Cedrela odorata* L. (MELIACEAE) AS ATTRACTANTS OF *Hypsipyla grandella* ZELLER (LEPIDOPTERA: PYRALIDAE)

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Abstract-The mahogany shoot borer, *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) is one of the most economically important pests in all American tropical forests because it prevents the establishment of monoculture plantations of the family Meliaceae, such as Spanish cedar, *Cedrela odorata* L. Various studies have focussed on the bioecological aspects and the chemical and silvicultural control of this pest. However, relatively little is known about the biological interactions between this insect and its host plant. In this study, the shoot borer's behavior and attraction response to cedar host plants was evaluated in field cages. We also identified the volatiles emitted by healthy *C. odorata* plants that were attractive to *H. grandella* adults. The attraction to volatile cedar plant extracts and a synthetic blend were evaluated in a Y-glass tube olfactometer. We observed that virgin and mated females exhibited low activity at night, frequent movement of the antennae, sporadic flight activity, and short (< 10s) and long (> 30s) wing-fanning. Virgin females assumed a calling pose, whereas mated females exhibited three periods

of oviposition. The results showed that all evaluated categories – virgin females, virgin males, and mated females – were attracted to cedar plants. We identified the following volatile compounds: α-pinene, β-ocimene, 2-ethyl-1-hexanol, D-limonene, nonanal, (*E*)-4,8-dimethyl-1,3,7-nonatriene, α-copaene, β-caryophyllene, and germacrene D. A synthetic blend significantly attracted virgin male and mated female shoot-borers. Our results suggested that volatile *C. odorata* compounds are responsible for the attraction of *H. grandella*.

Key Words - Chemical cues, host plant volatiles, plant-insect interaction, olfaction, mahogany shoot borer.

INTRODUCTION

The Spanish cedar *Cedrela odorata* (Linnaeus 1759) is one of the most economically and ecologically important tree species of the Meliaceae family in the tropical regions of America due to its productivity, high commercial value timber, and broad natural range (Cavers et al. 2004; Larrea et al. 2008; González-Luna and Cruz-Castillo 2021). Habitat fragmentation and illegal logging of *C. odorata* natural populations have reduced its adaptive and productive potential. Therefore, it has been recognized as a threatened species and has been included in the lists of international organizations such as International Union for Conservation of Nature (IUCN) and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). It is also protected by NOM-059 in Mexico (SEMARNAT 2010; IUCN 2017; CITES 2021).

The establishment and productivity of commercial cedar plantations is compromised by attacks of the mahogany shoot borer *Hypsipyla grandella* (Zeller 1848) (Macías-Sámano 2001; Plath et al. 2011). Mated female shoot borers deposit their eggs on tree leaves (Griffiths 1997). Newly hatched larvae bore into the terminal shoot and create tunnels in the soft stem that ultimately kill

the shoot. The plant will send out new shoots, but the tree will be forked or branched and its commercial value will be reduced (Briceño-Vergara 1997; Floyd and Hauxwell 2001; Lunz et al. 2010).

Chemical (Goulet et al. 2005), biological (Pulgarín et al. 2018), and silvicultural (Ruiz et al. 2016) control methods have been tested against this pest. Aside from being harmful to the environment, the application of conventional pesticides has also proven to be inefficient and economically unsustainable for various reasons, such as: larvae are inaccessible to pesticides since they are concealed in the stem, heavy rainfall washes away the applied pesticides, and a wide pesticide application window is required to protect the plants (Allan et al. 1976; Wylie 2001; Mahroof et al. 2002; Goulet et al. 2005). Therefore, the use of other control strategies is recommended. One such strategy involves semiochemicals, which are compounds involved in various ecological interactions and in chemical communication between species (Lima-Mendonça et al. 2014).

The recognition of a host plant by insects is crucial to guarantee their survival and that of their progeny, since they not only perceive the plant as a food substrate, but also as appropriate sites for oviposition and refuge (Schoonhoven et al. 2005; Rojas 2012). Host plant recognition is mainly mediated blends of ubiquitous compounds, but also by specific compounds (Bruce et al. 2005). Insects are receptive to visual, olfactory, and gustatory cues during this process (Bernays and Champman 1994). Olfactory perception is involved in behavioral patterns associated with the search and selection of food sources (Libert et al. 2007), in the detection of toxic substances (Fuyama 1976), and in the recognition and selection of a partner (Billeter et al. 2009) and oviposition site (Hoffmann and O'Donnell 1990; Jaenike 1990). However, relatively little is

known about the ecology, ethology, and biological interactions between *H. grandella* and *C. odorata*.

The susceptibility of *C. odorata* and *Swietenia macrophylla* (monocultures as well as mixed plantations) to *H. grandella* attack has been documented, and the genetic variability of *C. odorata* has been studied (Newton et al. 1998; Cornelius and Watt 2003; Pérez-Salicrup and Esquivel 2008). These variations have implications in the production of attractants or deterrents for ovipositing *H. grandella* females (Honda 1995), and in morphology and branch formation (Grijpma 1976). To understand these phenomena, it is important to characterize and identify the compounds that mediate plant-insect interactions. Studies focussing on the relation between the moths *H. grandella* and *Hypsipyla robusta* and different Meliaceae species have demonstrated the involvement of volatile compounds. These compounds elicit antennae responses and might be responsible for the attraction of these lepidopterans (Soares et al. 2003; Lago et al. 2006; Abraham et al. 2014; Borges et al. 2022). However, whether *H. grandella* is attracted by the volatiles emitted by cedar plants is still unknown.

In this study, we describe the nocturnal behavior and evaluate the attraction of *H. grandella* to cedar plants in field cages. We identify the volatile compounds emitted by healthy *C. odorata* plants, and evaluate volatile cedar plant extracts and a synthetic blend in a Y-glass tube olfactometer.

MATERIALS AND METHODS

Insects. First- to fourth-instar *H. grandella* larvae were collected from shoots and branches of five-year-old cedar trees. Sampling was conducted in April 2020 at the *Unidad de Manejo para la Conservación de Vida Silvestre* (UMA; registration ID: SEMARNAT-UMA-IN-1009-

CHIS/17), located at the plantation “El Tesoro” (14°44'42.7" N, 92°14'37.2" W; 23.6 m a.s.l.) in Cantón Santa Lucía, municipality of Frontera Hidalgo, Chiapas, Mexico. The collected larvae were transported to the insectarium of the *Laboratorio de Salud Forestal* of *El Colegio de la Frontera Sur* (ECOSUR) in Tapachula, Chiapas, Mexico. They were reared on *C. odorata* shoots and maintained under the following controlled conditions: 25 ± 2 °C, 70 ± 20 % relative humidity (RH), and a photoperiod of 12:12 h (L:D) during larval development (Vargas et al. 2001; Taveras et al. 2004). Pupae were sexed by the morphology of the genital opening (Sharma and Singh 1980). They were separated by sex and transferred to transparent plastic containers (250 ml). Emerging adults were then transferred to mating chambers (20 x 20 x 30 cm) in a 1:1 male:female ratio. Individuals were marked on the dorsal thorax with a Sharpie pen to differentiate females from males (Newell Brands, USA). Copulation was observed during the observation period (0:00–2:00 h), and its success was confirmed by the oviposition of fertile eggs (red color). Virgin female and male moths (1–2 d old) as well as mated females (3–4 d old) were selected for the experiments.

Plants. Cedrela odorata plants were obtained from the Santa Fe commercial plant nursery located in the municipality of Tuxtla Chico, Chiapas, Mexico. The plants were transplanted to containers (13 cm high, 12 cm diameter) filled with local soil, continuously irrigated and fertilized every 15 days with a nutrient solution (Steiner 1961). The plants were maintained under natural environmental conditions and covered with tulle netting to prevent insect damage. All of the plants used in the study were one year old and grown without pesticides.

Chemicals. The standards α-pinene, β-ocimene, 2-ethyl-1-hexanol, D-limonene, nonanal, and β-caryophyllene were purchased from Sigma-Aldrich (Toluca, Mexico) and were of 97–99 % chemical purity according to the manufacturer. (*E*)-4,8-dimethyl-1,3,7-nonatriene (≥ 97 %) was

from Pherobank BV (Wijk bij Duurstede, The Netherlands) and α-copaene (≥ 95 %) from Cayman Chemicals (Ann Harbor, USA).

Volatiles Collection. Volatile compounds were collected by using the dynamic headspace technique. The aerial part of a *C. odorata* plant was carefully enclosed within a 48 x 59 cm nylon oven bag (Reynolds, Lake Forest, USA). Volatiles were collected by passing air previously purified by an activated charcoal filter at a flow rate of 1 l/min with a vacuum pump (Model L-79200-00, Cole-Parmer, IL, United States). The volatiles were captured over a 15 h period in a Super Q adsorbent (50–80 mesh, 30 mg; ARS, Gainesville, USA). At the end of each capture period, volatiles were eluted from the adsorbent with 400 µl of dichloromethane (HPLC-grade; Sigma-Aldrich, St. Louis, USA). Since the cedar plants released only small amounts of volatiles, it was necessary to repeat the extraction process ten times per plant. The collected eluate was then concentrated to a final volume of 100 µl under a gentle stream of N_2 and stored in small vials of 2 ml at -20 °C until analysis. The collection of volatiles were performed at a temperature of 22–28 ºC, 80 ± 10 % RH and a photoperiod of 03:12 h (L:D).

Bioassays

Behavior of Hypsipyla grandella. To determine the behavior of the insect towards the plant, a *C. odorata* plant was placed inside a cylinder-shaped field cage with diameter 3 m and height 2 m (made from anti-aphid netting, mesh 40 x 25, cal. 0.009). A female (virgin or mated) was released into each cage at 18:00 h and observed at 30 min intervals until 6:00 h. The following behaviors were noted: movement of antennae, flight, walking, short (< 10 s) and long (> 30 s) wing fanning, calling pose, and oviposition. The observations were made with artificial red light (Coast-FL13) at a temperature of 22–28 ºC, 50-90 % RH, and 0.10 ± 0.09 lux of ambient light. In total, 10 replicates were performed for each insect category.

142 *Attraction to* Cedrela odorata *Plants.* Cylinder-shaped field cages (diameter 3 m, height 2 m)
143 were used to determine the attraction of *H. grandella* to the volatiles emitted by *C. odorata*. The
144 test consisted of placing a cedar plant and a dummy control (cedar plant replica made from
145 polyethylene) within the cage separated 1 m from each other as a stimulus. A *H. grandella* moth
146 (either virgin male, virgin female, or mated female) was released at a 1 m distance from the
147 stimulus source. The moth was observed for 5 min and its preference for the stimuli was
148 recorded. These experiments were carried out between 19:00–23:00 h. The observations were
149 made with artificial red light (Coast-FL13) at 25 ± 2 °C, 80 ± 10 % RH and 0.03 ± 0.01 lux of
150 ambient light. Moths, cedar plants, and dummy controls were used only once. In total, 50
151 replicates were performed for each insect category.

152 *Attraction to Volatile* Cedrela odorata *Extracts and Synthetic Blend.* A two-way ‘‘Y’’
153 olfactometer (borosilicate glass, stem 15.52 cm; arms 12 cm, angled 45°, 2.5 cm i.d.) was used to
154 evaluate the attraction behavior of *H. grandella* towards volatile *C. odorata* extracts and a
155 synthetic blend; 5 µl of volatile extract or 1 µl synthetic blend (stimulus) was loaded on a piece of
156 Whatman No. 1 filter paper of 0.25 cm^2 (Whatman International Ltd., Maidstone, UK). The
157 stimulus was placed in one of the sample chambers, and 5 or 1 µl of dichloromethane (control)
158 was placed in the second sample chamber. The synthetic blend was formulated in
159 dichloromethane according to component proportions found in the volatile cedar extracts
160 (compounds 1-8) (Table 1). Activated charcoal filtered air at a rate of 0.5 l/min was pumped into
161 each sample chamber. The flow was regulated with a pair of flow meters and the air was
162 humidified by passing it through a water jar placed before the olfactometer. Virgin males and
163 females and mated females were tested in the bioassay. The moths were placed individually in
164 the base of the stem of the Y-tube olfactometer. The attraction of the insect was registered if it

crossed either of the two arms of the olfactometer (6 cm after intersection) within a 5 min period. The bioassay was stopped if the insect did not choose one of two samples within 5 min, in which case the moth's response was recorded as non-responding. After each trial, the olfactometer was washed with distilled water and neutral soap, and dried in the oven at 120 ºC for 2 h. At the end of each bioassay, the position of the stimulus was changed to avoid experimental bias. The bioassays were conducted in a dark room between 19:00–23:00 h, and observation was facilitated by a red light (Coast-FL13) placed at a distance of 120 cm (0.4 lux) so the insects would not be disturbed (25 ± 1 °C and 65 % RH). In total, 50 replicates were performed for each insect category.

Identification of Volatiles. The volatile compounds from cedar plant extracts were identified with a Shimadzu GCMS-TQ8040 system (Shimadzu, Kyoto, Japan), composed of a TQ-8040 triple quadrupole mass spectrometer interfaced with a GC-2010 Plus gas chromatograph. A split-splitless capillary inlet system and a DB5-MS capillary column (30 m x 0.25 mm i.d.) were utilized for the analyses. All samples were injected in the splitless mode using the following temperature conditions: initial temperature of 50 ºC for 3 min, afterwards the temperature was increased by 15 °C/min to 280 ºC, and kept at a maximum of 280 °C for 10 min. Helium was utilized as the carrier gas at a constant flow rate of 1 ml/min. The injector port was set at 250 ºC. Electron ionization mass spectra were generated at an ionization energy of 70 eV and 250 ºC. The software GC/MS Solution (version 4.20) was used for data processing. Each compound was identified preliminarily using the library of the National Institute of Standards and Technology (NIST, version 2014). The retention times and mass spectra of the identified compounds were compared with those of available synthetic standards to confirm their identification, and the retention index of each compound was determined. The concentrations of the identified

compounds were determined by the external standard method and the release rate of each compound per plant per day was calculated (Sufang et al. 2013).

Statistical Analysis. The responses of *H. grandella* were analyzed by the G test with Williams' correction in the R project software package (version 4.0.5; R Core Team 2021). Moths that did not choose either arm of the olfactometer within the 5 min observation period were excluded from analysis.

RESULTS

Behavior of Hypsipyla grandella. Virgin and mated females spent most of their time resting. The first recorded activity was the movement of antennae, which began at 18:40 h, reached its activity peak at 19:00–23:30 h, and was registered for the last time one hour before the end of the experiment. The first and last recorded flight activities occurred at 18:50 h and 4:00 h, respectively, and peaked at 19:50–22:00 h. Walking activity was observed for the first time at 19:50 h and reached its maximum between 21:00 h and 22:50 h, after which sporadic activity bursts were registered until 2 hours before the end of the experiment. Short wing-fanning was recorded for the first and last time at 19:00 h and 3:00 h, respectively. Maximum short wing-fanning activity was observed at 20:00–21:00 h, whereas long wing-fanning peaked between 3:00 h and 4:00 h. Virgin females assumed a calling pose (by bending the abdomen dorsally up between the wings) at 23:50 h. This activity reached its peak at 1:50–3:30 h and ended at 3:40 h. Mated females had three oviposition periods: the first at 23:00 h, the second from 1:30–2:00 h, and the last at 3:00 h (Fig. 1).

Attraction to Cedrela odorata *Plants.* Virgin females ($\chi^2 = 40.34$; df = 1; $P \leq 0.001$), virgin males ($\chi^2 = 11.28$; df = 1; $P < 0.001$), and mated females ($\chi^2 = 17.45$; df = 1; $P < 0.001$) were

significantly more attracted to cedar plants than to the control (dummy). It should be noted, however, that almost half of the mated females did not respond (48 %, Fig. 2).

Attraction to Volatile Cedrela odorata E*xtracts and Synthetic Blend.* Volatiles from the plant extract caused significantly greater responses in virgin females (χ^2 = 18.29; df = 1; $P < 0.0001$), virgin males (χ^2 = 10.71; df = 1; $P \leq 0.001$), and mated females (χ^2 = 6.86; df = 1; $P < 0.001$) than the control. However, as in the attraction bioassays of *H. grandella* to *C. odorata* plants, the number of non-responding mated females was relatively high (74 %, Fig. 4).

The synthetic blend was significantly more attractive to mated females (χ^2 = 19.53; df = 1; $P <$ 0.001) and virgin males (χ^2 = 6.90; df = 1; $P < 0.01$) than the control. Virgin females, however, were not significantly more attracted to the synthetic blend than to the control (χ^2 = 1.69; df = 1; $P > 0.05$) (Fig. 5).

Identification of Volatiles. GC-MS analysis of the volatile compounds from cedar plants revealed the presence of 9 compounds (Fig. 3). These are, from highest to lowest relative abundance: 2-ethyl-1-hexanol (23.13 %), nonanal (21.55 %), α-copaene (16.26 %), (*E*)-4,8-dimethyl-1,3,7-nonatriene (12.42 %), α-pinene (16.26 %), D-limonene (5.02 %), germacrene D (4.73 %), β-caryophyllene (4.06 %), and β-ocimene (2.17 %) (Table 1).

The release rates of the compounds from a healthy one-year-old cedar plant were: α-pinene (268.01 ng/d), β-ocimene (109.43 ng/d), 2-ethyl-1-hexanol (6083. 78 ng/d), D-limonene (991.37 ng/d), nonanal (8902 ng/d), (*E*)-4,8-dimethyl-1,3,7-nonatriene (421.27 ng/d), α-copaene (219.75 ng/d), β-caryophyllene (23.46 ng/d), and germacrene D (20.83 ng/d) (Table 1).

DISCUSSION

In this study, we observed that *H. grandella* exhibited low activity during the night, despite being nocturnal insects, and that its antennae were constantly moving, which was also reported by Barradas-Juanz et al. (2016). We also investigated the attraction response of *H. grandella* (virgin males and mated and virgin females) to cedar volatiles. Our results show that virgin males and mated females were attracted to volatiles emitted by *C. odorata* as well as to the synthetic blend.

Adult *H. grandella* moths are good flyers and exhibit remarkable ability to locate their host (Sliwa and Becker 1973; Holsten and Gara 1975; Fasoranti et al. 1982). In our observations, flights (of virgin as well as mated females) occurred between 18:50 and 4:00 h, and peaked at 19:50–22:00 h. However, Gara et al. (1972) recorded flights between 0:00 and 5:00 h, and noted that no flights occurred when night temperatures dropped below 15 ºC. Furthermore, the moths are capable of flying a distance of 31.4 km, although they won't easily leave affected areas (Grijpma and Gara 1970; Fasoranti et al. 1982). Grijpma and Gara (1970) reported that *H. grandella* can be found in ground vegetation during the day, and that it walked from one tree to another. In our study, we frequently observed walking activity and recorded a peak at 21:00–22:50 h. We observed female moths assume a calling pose by exposing the abdominal glands while wing-fanning as part of their circadian rhythm of calling behavior (Barradas et al. 2016; Levi-Zada and Byers 2021). Females remain in the pose for 1.6 h to attract male conspecifics (Grijpma 1971; Samaniego and Sterringa 1976), which approximates our observed duration of 2 h. The moth's wing-fanning behavior was first reported by Grijpma (1971). It is thought that females beat their wings to disperse their pheromones (Levi-Zada and Byers 2021). The wing-fanning behavior that we observed was similar to the behavior reported by Barradas-Juanz et al. (2016), who characterized two different types of wing-fanning – short (< 10 s) and long (> 30 s)

– between 3 h and 4 h. It is currently not clear whether different types of wing-fanning also imply different functions, although both types are likely involved in pheromone dispersion (Barrandas-Juanz et al. 2016).

Volatile compounds are often essential for insects to locate their hosts. To recognize their hosts, insects often use specific compounds or specific blends of ubiquitous compounds (Bruce et al. 2005; Bruce and Pickett 2011). Our results suggest that *H. grandella* moths are attracted by volatiles emitted by the cedar plant. Also, the synthetic blend confirmed that the identified compounds could be responsible for the attractant effect.

We demonstrated that volatile compounds from cedar plants are involved in attracting *H. grandella*; several studies have shown that the attack of this moth is closely related to the foliar phenology of the trees (Newton et al. 1998). Although the localization mechanism of the host plant of this species (*H. grandella*) is still unclear, the orientation by volatiles of the host seems to be the most likely mechanism to localize the plant (Grijpma and Gara 1970; Gara et al. 1972; Grijpma 1976; Howard 1991; Prokopy and Papaj 2001). Males can detect pheromone signals and host plan volatiles that act synergistically to detect females (Yang et al. 2004; Xiang et al. 2019). Compounds released by the plant can stimulate females to oviposit (Grijpma 1976), or release their sexual pheromone and mate with conspecifics (Castrovillo and Cardé 1980; Curkovic and Brunner 2007).

Mated males and females of *H. grandella* showed a different preference for *C. odorata* than virgin females (Newton et al. 1998). The fact than virgin and mated females of *H. grandella* respond differently to cedar volatiles may be related to many factors, for instance the insect olfactory system (Röstelien et al. 2000), or differences in the chemical composition of volatiles from young and mature foliage (Gara et al. 1972). We found that virgin females were not attracted to the synthetic blend, possibly because of the high concentration we used. It is possible

278 that qualitative and quantitative differences in volatile profiles are present in young and mature
279 foliage. However, more studies are needed to know the influence of the concentration of
280 compounds from *C. odorata* on the preference of *H. grandella*. On the other hand, the high
281 number of non-responses of the moths to the evaluated stimuli is possibly due to internal factors
282 such as age, circadian rhythm, sexual status, egg load, or the level of hunger of the evaluated
283 insects (Rojas 2012). In other studies, however, mated female moths responded in greater
284 numbers than virgin female and male moths to volatile compounds (Rojas 1999), as was the case
285 with the synthetic blend we evaluated. This may be due to the fact that the insect is motivated by
286 finding its host plant to lay its eggs.
287 Plants release volatile compounds such as sesquiterpenes that play an essential biological role in
288 insect-plant interactions (Paré and Tumlinson 1999; Das et al. 2013). Sesquiterpenes (including α-
289 copaene, β-elemene, β-caryophyllene and germacrene D) have been identified in the essential oil
290 of terminal shoots and of mature and senescent leaves of *S. macrophylla* (Soares et al. 2003).
291 Abraham et al. (2014) characterized volatile organic compounds in four different mahogany
292 species and found various sesquiterpenes, including α-cubebene, α-copaene, β-elemene, β-
293 caryophyllene, α-humulene, germacrene D, and δ-cadinene. The same sesquiterpenes have also
294 been identified in various Meliaceae, such as *C. odorata*, *Cedrela fissilis*, and *Toona ciliata* (Maia
295 et al. 2000). Lago et al. (2006) detected various sesquiterpenes (including α-cubebene, α-copaene,
296 β-caryophyllene, α-humulene y germacrene D) in the essential oil of *Guarea macrophylla*.

297 We identified 9 compounds in the volatile profile of *C. odorata*: α-pinene, β-ocimene, 2-ethyl-1-
298 hexanol, D-limonene, nonanal, (*E*)-4,8-dimethyl-1,3,7-nonatriene, α-copaene, β-caryophyllene,
299 and germacrene D. A synthetic blend was prepared that mimicked the composition of *C. odorata*
300 extract to serve as an attractant to *H. grandella* moths. However, due to its unavailability, we

could not include germacrene D in the synthetic blend. β-caryophyllene, one of the constituents of the synthetic blend, triggered an antennal response in female shoot-borers (Soares et al. 2003). According to Borges et al. (2022), nonanal, decanal, methyl salicylate, and β-caryophyllene elicit antennal response in male as well as female shoot-borers. Interestingly, the same authors found that methyl salicylate affected host plant location by *H. grandella* moths, which opens up the potential to integrate this compound in shoot-borer pest management strategies. β-caryophyllene and germacrene D, both identified in our volatile compounds analyses, have been shown to strongly affect insect-plant interactions in other ecosystems (Mozuraitis et al. 2002; Köllner et al. 2008; Hare 2011; Xiao et al. 2012). Abraham et al. (2014), for instance, noted that germacrene D elicited an antennal response in female *H. robusta* moths. Moreover, Lago and Roque (2002) identified α-copaene, β-caryophyllene, and germacrene D in essential oil extracted from the leaves of *G. macrophylla*. Cedar extract also contained β-ocimene, 2-ethyl-1-hexanol and nonanal, which have been reported as antennal active compounds in female *H. robusta* moths (Abraham et al. 2014). Nonanal is a known oviposition attractant for the light brown apple moth *Epiphyas postvittana* Walker (Suckling et al. 1996), and (*E*)-4,8-dimethyl-1,3,7-nonatriene has been used as a lure to catch male and female *Cydia pomonella* (Knight et al. 2011). On the other hand, α-pinene and D-limonene have been reported to influence plant-insect interactions in the order Coleoptera (Tafoya et al. 2011; Romero-Frías et al. 2015; Sánchez-Martínez and Reséndiz-Martínez 2020).

In summary, in this work we observed that virgin and mated female shoot-borers exhibited low activity during the night, frequent antennae movement, sporadic flight activity, and short and long wing-fanning. Virgin females assumed a calling pose, whereas mated females exhibited three periods of oviposition. Virgin males and females as well as mated females of *H. grandella*

were attracted by volatile substances released by the cedar plant. The virgin males and females as well as mated females of *H. grandella* were attracted by volatile substances released by the cedar plant. We also identified nine volatile compounds in the head space of cedar: α-pinene, β-ocimene, 2-ethyl-1-hexanol, D-limonene, nonanal, (*E*)-4,8-dimethyl-1,3,7-nonatriene, α-copaene, β-caryophyllene, and germacrene D. These compounds, with the exception of germacrene D, were combined to prepare a synthetic blend that mimicked the composition of *C. odorata* extract. Male virgin and mated female *H. grandella* moths were attracted to the blend. Future research should be carried out to assess the potential of the synthetic blend in the field. The development of an effective attractant for the *H. grandella* moth would greatly improve our ability to manage this herbivore.

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All authors read and approved the final manuscript.

Competing interests.

The authors declare that no competing interests exist

Table legend

Table 1 Mean relative abundance (% ± SE) and release rate (ng/day ± SE) of *Cedrela odorata* volatiles identified by GC-MS. Samples were collected over a 15 h period using a dynamic volatile collection system (N = 10).

Figure legends

Fig. 1 Observation for 12 h (18.00-6.00h) of virgin (VF) and mated (MF) females in field cages (N = 10): first recorded activity ▲, activity peak ⌐✦¬ , and last recorded activity ▼.

Fig. 2 Attraction of *Hypsipyla grandella* to *Cedrela odorata* plants. NR = Non-responding insects. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$. N = 50.

Fig. 3 GC-MS profile of volatile organic compounds from the plant *Cedrela odorata*.1) α-pinene, 2) β-ocimene, 3) 2-ethyl-1-hexanol, 4) D-limonene, 5) nonanal, 6) (*E*)-4,8-dimethyl-1,3,7-nonatriene, 7) α-copaene, 8) β-caryophyllene, and 9) germacrene D.

Fig. 4 Attraction of *Hypsipyla grandella* by an extract of volatiles from *Cedrela odorata*. NR = Non-responding insects. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$. N = 50.

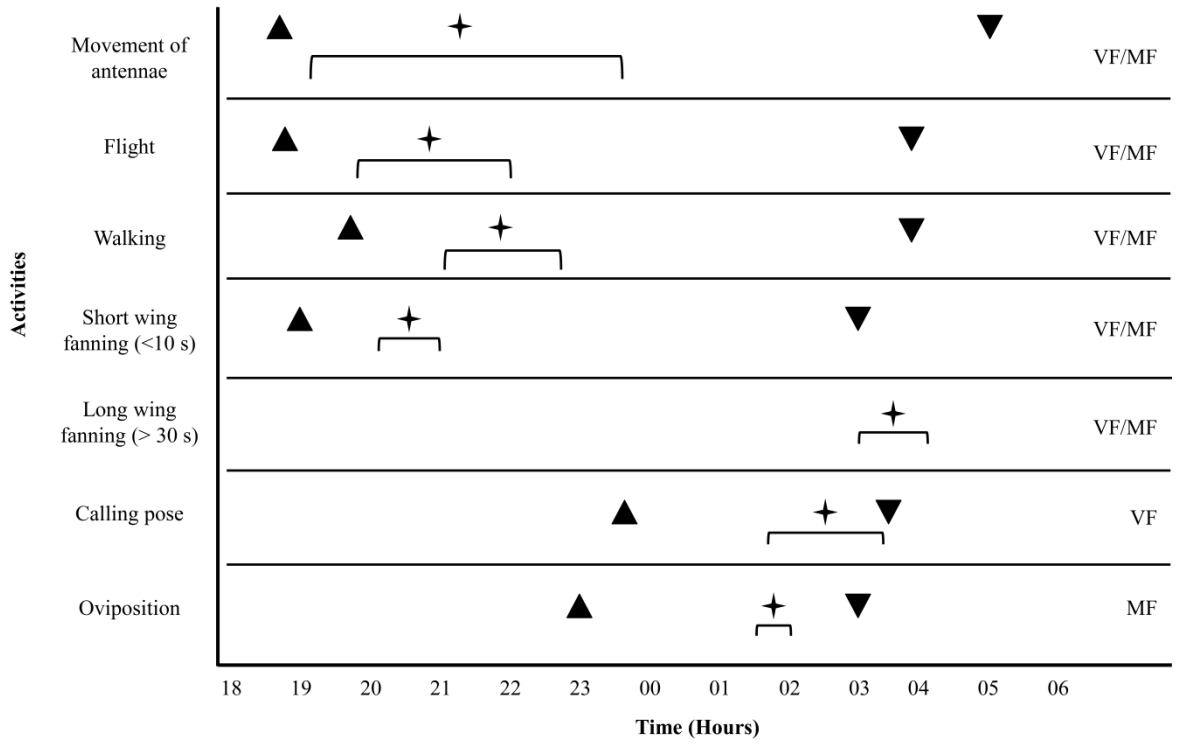
Fig. 5 Attraction of *Hypsipyla grandella* by a synthetic blend that mimics the composition of *Cedrela odorata* extract. NR = Non-responding insects. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$. ns = non-significant difference. N = 50.

Table 1

N°	Compound	RI	Relative abundance (%) ± SE	Release rate (ng/d) ± SE
1	α-Pinene*	940	10.67±3.5	268.01±225.9
2	β-Ocimene*	969	2.17±1.0	109.43±38.1
3	2-Ethyl-1-hexanol*	988	23.13±10.2	6083.78±3002.1
4	D-Limonene*	991	5.02±1.9	991.37±835.9
5	Nonanal*	1065	21.55±14.3	8902±4187.7
6	(*E*)-4,8-Dimethyl-1,3,7-nonatriene*	1071	12.42±6.2	421.27±300.6
7	α-Copaene*	1346	16.26±8.1	219.75±142.5
8	β-Caryophyllene*	1441	4.06±2.0	23.46±8.8
9	Germacrene D	1491	4.73±2.7	20.83±16.2

RI = Retention index. *Verified by comparison with synthetic standards.

Fig. 1


Movement of antennae
Flight
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Short wing fanning (<10 s)
Long wing fanning (> 30 s)
Calling pose
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Activities
VF/MF
VF/MF
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Time (Hours)

668 **Fig. 2**

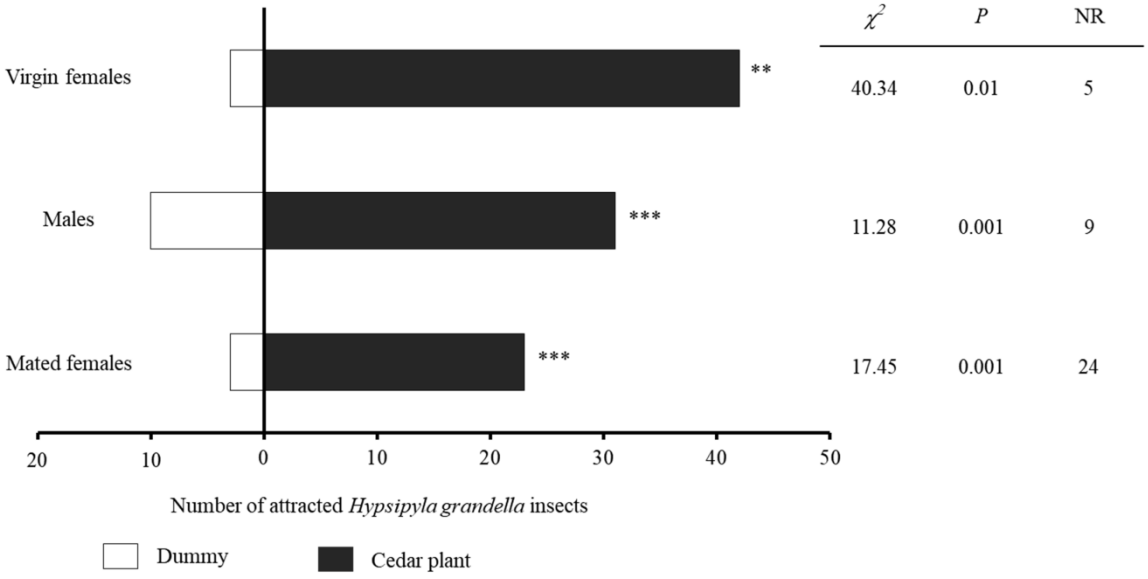

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Fig. 3

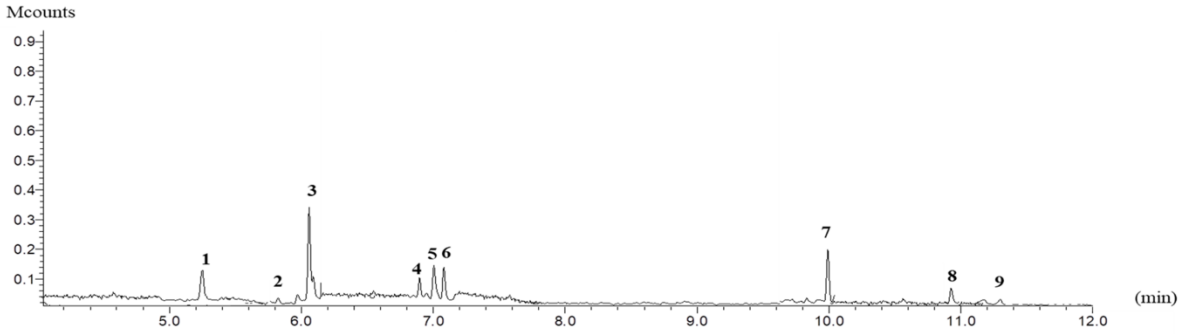
Mcounts
0.9
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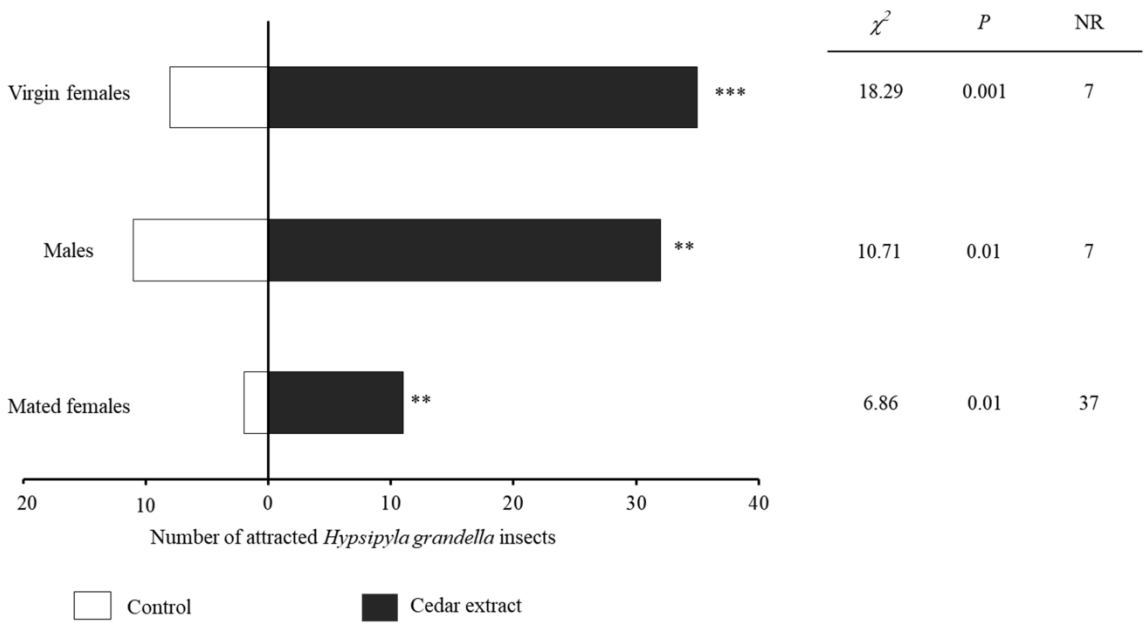
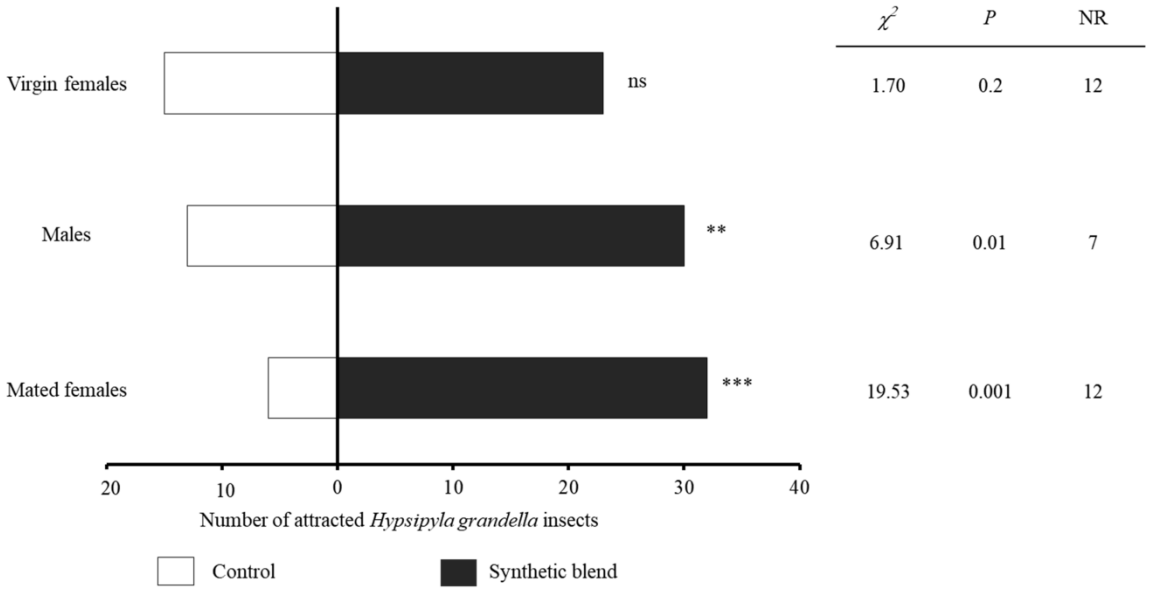
Fig. 4



	χ^2	*P*	NR
Virgin females	18.29	0.001	7
Males	10.71	0.01	7
Mated females	6.86	0.01	37

712 **Fig. 5**



	χ^2	*P*	NR
Virgin females	1.70	0.2	12
Males	6.91	0.01	7
Mated females	19.53	0.001	12

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IV. CONCLUSIONES

En este trabajo encontramos que hembras vírgenes y apareadas presentan poca actividad nocturna, movimientos de antenas frecuentes, vuelos esporádicos, aleteos cortos y largos, las hembras vírgenes realizaron la postura de llamado y las hembras apareadas tuvieron tres periodos de oviposición.

Las hembras vírgenes, machos vírgenes, y hembras apareadas de *H. grandella* fueron atraídos a los volátiles de plantas cedro. Adicionalmente, identificamos nueve compuestos, de los cuales una mezcla sintética de α-pineno, β-ocimeno, 2-etil-1-hexanol, D-limoneno, nonanal, (*E*)-4,8-dimetil-1,3,7-nonatrieno, α-copaeno, β-cariofileno fue atractiva a hembras apareadas y machos vírgenes de *H. grandella.*

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