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Insecticidal and repellent effects of *Pelargonium graveolens* L'Hér., *Salvia rosmarinus* Spenn., and *Mentha* × *piperita* L. essential oils against *Dendroctonus mexicanus* (Coleoptera: Curculionidae)

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Abstract. Bark beetles are insects that help regenerate coniferous forests; however, they can become a devastating pest, causing widespread tree mortality. In Mexico, these insects are one of the most important pests. The use of synthetic insecticides has resulted in environmental damage, human health risks, and increased pest resistance. Aromatic plants offer a potential alternative for forest pest management. This study evaluated the insecticidal and repellent activities of essential oils (EOs) from *Pelargonium graveolens*, *Salvia rosmarinus*, and *Mentha* × *piperita* against *Dendroctonus mexicanus*. EOs were extracted through steam distillation, identified by gas chromatography-mass spectrometry (GC-MS), and tested

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for bioactivity. The major constituents were citronellol (54.0 %) and *trans*-menthone (9.9 %) in *P. graveolens*; 1,8-cineole (32.4 %) and α-pinene (30.7 %) in *S. rosmarinus*, and menthol (37.4 %) and menthyl acetate (20.1 %) in *M.* × *piperita*. The terpene geraniol exhibited the strongest insecticidal effect (LD_{50}= 14.82 µg/insect). *P. graveolens* EO showed significant repellency at 80 µg/cm^2 (50 %). In the acetylcholinesterase inhibition assay, α-pinene showed the most potent effect (IC_{50}=3.49 mg/mL). These findings suggest that the tested EOs are promising natural alternatives to synthetic insecticides for managing *D. mexicanus* infestations.

Resumen. Los escarabajos descortezadores son insectos que ayudan a la regeneración de bosques de coníferas, sin embargo, pueden convertirse en una plaga devastadora, provocando la mortalidad generalizada de árboles. En México estos insectos son uno de los agentes de disturbio más importantes. El uso de insecticidas sintéticos ha generado daños ambientales, riesgos para la salud humana y aumento de la resistencia de plagas. Las plantas aromáticas ofrecen una alternativa potencial para el manejo de plagas forestales. Este estudio evaluó la actividad insecticida y repelente de los aceites esenciales (AE) de *Pelargonium graveolens*, *Salvia rosmarinus* y *Mentha* × *piperita* contra *Dendroctonus mexicanus*. Los AE se extrajeron mediante destilación al vapor, se identificaron por cromatografía de gases-espectrometría de masas y se analizó su bioactividad. Los componentes principales fueron citronelol (54.0 %) y trans-mentona (9.9 %) en el AE de *P. graveolens*; 1,8-cineol (32.4 %) y α-pineno (30.7 %) en el AE de *S. rosmarinus*, y mentol (37.4 %) y acetato de mentilo (20.1 %) en el AE de *M.* × *piperita*. El terpeno geraniol mostró el efecto insecticida más potente (DL_{50}= 14.82 µg/insecto). El AE de *P. graveolens* mostró una repelencia significativa a 80 µg/cm^2 (50 %). En el ensayo de inhibición de la acetilcolinesterasa, el α-pineno mostró el efecto más potente (CI_{50}= 3.49 mg/mL). Estos hallazgos sugieren que los AEs analizados son alternativas naturales prometedoras a los insecticidas sintéticos para el control de infestaciones de *D. mexicanus*.

Introduction

Temperate forests face significant threats, including illegal logging, wildlife trafficking, fires, pollution, and climate change, with the latter expected to cause substantial declines in these ecosystems [1]. Biotic damage, such as insect and pest outbreaks, has environmental, economic, and social impacts, disrupting wood supply and ecosystem services [2]. Several *Dendroctonus* bark beetle species are aggressive, tree-killing pests of pine forests in North and Central America [3]. Among them, *Dendroctonus mexicanus* Hopkins, 1905 (Coleoptera: Curculionidae) is particularly aggressive, ranging from the Southern United States to Southern Mexico. This species can kill healthy trees and trigger large-scale epidemic outbreaks [4,5].

Managed forests employ several control strategies to reduce bark beetle populations and prevent outbreaks, including chemical, biological, and physical methods, or a combination thereof [6,7]. Phytosanitary measures primarily involve clearing windthrows, removing infested trees, and/or using pheromones [8]. Synthetic pyrethroids are commonly used to control these pests because they offer advantages over other chemical insecticides, such as organophosphates and carbamates. However, pyrethroids are known to bioaccumulate in marine mammals and humans, limiting their use in protected areas and non-intervention zones [9-12].

Plants produce a wide variety of compounds that enable them to defend against herbivore predation. Plant-derived essential oils (EOs) are mixtures of secondary metabolites, mainly terpenoids and phenylpropanoids, which have been studied as alternatives to conventional insecticides due to their insecticidal and repellent properties against insect pests, environmental friendliness, safety for non-target organisms, and low potential for resistance development [13-18]. For example, EOs from species such as *Salvia rosmarinus* Spenn. (Lamiaceae) and *Mentha* × *piperita* L. (Lamiaceae), are well known for their insecticidal properties against insect pests of the order Coleoptera such as *Callosobruchus chinensis* (Linnaeus, 1758) (Coleoptera: Chrysomelidae), *Callosobruchus maculatus* (Fabricius, 1775) (Coleoptera: Chrysomelidae), *Tribolium castaneum* (Herbst, 1797) (Coleoptera: Tenebrionidae), and *Sitophilus zeamais* Motschulsky, 1855 (Coleoptera: Curculionidae) [19-23]. *Pelargonium graveolens* L'Hér. (Geraniaceae) is an aromatic herb recognized for its toxicity against several insect pests, such as *Sitophilus oryzae* (Linnaeus, 1763) (Coleoptera: Curculionidae), *Oryzaephilus surinamensis* (Linnaeus, 1758) (Coleoptera: Silvanidae), *Spodoptera litoralis* (Boisduval, 1833) (Lepidoptera: Noctuidae), and *Bemisia tabaci* (Gennadius, 1889) (Homoptera: Aleyrodidae) [24-28].

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Studies on the neurotoxic effects of EOs as insecticides have identified the enzyme acetylcholinesterase (AChE) as a molecular target because EO metabolites can inhibit AChE activity by hydrolyzing acetylcholine, a neurotransmitter in the central nervous system [29,30]. EOs from *P. graveolens, S. rosmarinus,* and *M.* × *piperita* have been reported as AChE inhibitors in insects such as *C. maculatus, Musca domestica* Linnaeus, 1758 (Diptera: Muscidae), *Culex pipiens* Linnaeus, 1758 (Diptera: Culicidae), and *Reticulitermes dabieshanensis* Wang & Huang, 2018 (Isoptera: Rhinotermitidae) [31-34]. However, the insecticidal and biochemical effects of these EOs on *Dendroctonus* spp. have not been investigated. Therefore, the development of bioinsecticides from EOs represents a promising alternative within integrated pest management in temperate forests [35]. The aim of the present study was to evaluate the insecticidal and repellent potential of *P. graveolens*, *S. rosmarinus,* and *M.* × *piperita* EOs against *D. mexicanus* and their effect on AChE.

Experimental

Plant material and essential oils extraction

The aerial parts of *P. graveolens*, *S. rosmarinus, and M.* × *piperita* were collected from cultivation plots in Ixtacuixtla, Tlaxcala State, Mexico (19°20'17" N, 98°22'26" W), during September 2022. Samples were collected randomly to ensure representative coverage. The identification of the plants was carried out by Prof. Laura García. The voucher specimens (9472, 9473, and 9474) were deposited in the TLXM Herbarium of the Center for Research in Biological Sciences of the Autonomous University of Tlaxcala, Tlaxcala, Mexico.

EOs were obtained by steam distillation using a stainless-steel distillation apparatus at 96 ºC for 3 h. The oil samples were then dehydrated using anhydrous sodium sulfate and stored in amber sealed glass bottles under refrigeration at 4 °C for further analysis.

The terpenes evaluated were citronellol (≥ 95 %), geraniol (98 %), 1,8-cineole (99 %), α-pinene (98 %) and menthol (98 %), all obtained from Sigma-Aldrich Co., Saint Louis, USA.

Insects

D. mexicanus adults were collected from *Pinus leiophylla* Schiede ex Schltdl. & Cham (Pinaceae) logs in Malinche National Park (19°17'46.4" N, 98°05'44.4" W) in Tlaxcala, Mexico, located within the Faja Volcanica Transmexicana, during August and September 2022. Taxonomic identification of the insects was conducted using genitalia analysis [5]. The beetles were maintained on a natural diet of hydrated bark of *P. leiophylla* at 14 ± 1 °C, 65 % relative humidity and in dark conditions and maintained until the third generation. Prior to testing, live adult insects were separated from the bark pieces and placed in groups of 10 unsexed individuals on 90 mm glass plates.

GC-MS analysis and identification of components

The chemical composition of *P. graveolens, S. rosmarinus, and M.* × *piperita* EOs was analyzed using GC-MS [36]. The GC-MS system consisted of a PerkinElmer Clarus gas chromatograph equipped with an Elite 5-ms column (30 m x 0.32 mm, film thickness 0.25 µm) and interfaced with the NIST Mass Spectral Search Program (software version 2.0). The operating conditions were as follows: the injector temperature was set at 250 ºC; helium was used as a carrier gas at a linear velocity of 37 cm/s and a flow rate of 1 mL/min; the sample injection volume was 1 µL; with a split ratio of 50:1; and the ionization energy was 70 eV.

The column temperature was programmed 60 ºC for 2 min, 100 ºC at 10 ºC/min for 5 min, 150 ºC at 10 ºC/min for 5 min, 200 ºC at 10 ºC/min for 5 min, and 250 ºC at 10 ºC/min for 20 min. Retention indices were determined relative to the retention times (Rt) of a homologous series of *n-alkanes* (C8-C20) (Sigma-Aldrich, St. Louis, MO, USA) analyzed under the same conditions. Constituents were identified by comparing their retention indices (RI) with published data in the literature. Further identification was achieved by comparing the mass spectra with those stored in the NIST 02 library or referenced from the literature [37]. The relative percentages of the component concentrations were calculated based on the normalized peak area.

Contact toxicity bioassay

The insecticidal activity of EOs against *D. mexicanus* was determined using a contact method [20,21]. *P. graveolens, S. rosmarinus,* and *M.* × *piperita* EOs, as well as their terpenes, were diluted with acetone to obtain

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various concentrations ranging from 27, 55, 110, 221, 442 and 884 µg/mL. A stock solution of each oil (1 µL) was applied to the dorsal surface of the thorax of *D. mexicanus* individuals using a microsyringe (Hamilton). Insects treated with 1 µL of acetone served as the negative controls, while the insecticides bifenthrin (a pyrethroid) and bendiocarb (a methyl carbamate) were used as positive controls. After treatment with the EO or control solutions, cohorts of 10 bark beetles were transferred to glass Petri dishes (90 mm in diameter). The petri dishes containing the beetles were maintained under controlled temperature and humidity conditions (14 ± 2 ºC and 50 ± 10 % RH) for 72 h, in total darkness.

All treatments were conducted in quadruplicate, and insect mortality was recorded at 24, 48, and 72 h post treatment. The percentages of insect mortality were calculated using Abbott's correction formula [38] shown below:

$$\%\ \text{Mortality} = \left[\frac{\%\ Mt - \%\ Mc}{100 - \%\ Mc}\right] x\ 100$$

Where *Mt* = mortality with treatment and *Mc* = mortality with control.

Repellency activity bioassay

The ability of *P. graveolens*, *S. rosmarinus*, and *M.* × *piperita* EOs to repel *D. mexicanus* was evaluated using a modified two-choice assay [39], shown in Fig. 1. Ten minutes prior to introducing the insects, 2 × 2 cm2 Whatman filter papers No.2 were prepared. The filter papers were either impregnated with 10 µL of EO solution or terpene at varying concentrations (10, 20, 40 and 80 µL/cm2) and placed in chamber C, or left without EOs and placed in chamber A. Ten adult insects were then placed in the central chamber (B) and allowed to move freely into either chamber A or chamber C. Repellency activity (%) was recorded after 60 and 120 min of exposure. Each experiment was performed in quadruplicate. Repellency activity was calculated using the following equation:

$$\text{Repellency activity (\%)} = \left[1 - \left(\frac{\text{X}}{10}\right)\right] \text{x } 100$$

Where X represents the number of insects distributed in chamber C.

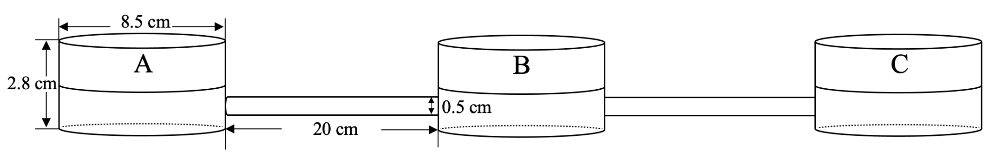

Fig. 1. Apparatus for the repellency assay against *D. mexicanus*. Chamber A: filter paper with acetone (control); Chamber B: chamber where the insects are placed; Chamber C: filter paper with essential oil at different concentrations.

Repellency percentages were classified using the following scale: class 0, <0.1%; class I, 0.1-20 %; class II, 20.1-40 %; class III, 40.1-60 %; class IV, 60.1-80 %; class V, 80.1-100 % [40].

Acetylcholinesterase inhibition assay

Crude protein was extracted from 50 unsexed adult insects. The bark beetles were soaked in 0.1 M Tris-HCl buffer (pH 7.8) containing 20 mM NaCl and 0.5 % Triton X-100. The mixture was centrifuged at 15,000 g for 15 min at 4 °C, and the resulting supernatant was used for the enzymatic assay. AChE inhibitory activity was measured using a modified Ellman's method [41]. EOs or terpene solutions (50 µL at varying concentrations of 12, 24 and 49 mg/mL) were mixed with 20 µL of crude protein extract and incubated at 37 °C for 15 min. Subsequently, 50 µL of acetylcholine iodide (ATCI, 10.0 mM) and 100 µL of 5,5′-dithiobis-(2-nitrobenzoic acid) (DTNB, 5.0 mM) in sodium phosphate buffer (0.1 M, pH 8) were added (Sigma-Aldrich, St. Louis, MO, USA). The mixture was further incubated at 37 °C for 30 min. The absorbance of the reaction mixture was measured at 412 nm using a microplate

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reader (MultiskanTM GO, Thermo Fisher Scientific). The percentage of AChE enzyme inhibition was calculated by comparing the reaction rates of the treated samples with those of the blank sample, using the following equation:

$$\text{AChE inhibition (\%)} = \left(\frac{C - S}{C}\right) \times 100$$

where, C is the activity of the enzyme without the test sample (control) and S is the activity of the enzyme with the test sample. To calculate the IC50, 5 logarithmically spaced concentrations between 98 and 6 mg/mL were evaluated.

Data analysis

Statistical analysis was conducted using SPSS v25.0. The mortality effect was evaluated at 24 h, 48 h, and 72 h treatment to each EO concentration used in this work. Lethal doses (LD50) for each time point were determined by transforming mortality data using a probit analysis with a logit distribution, based on the binary dependent variable (alive or dead) [42]. For data obtained from repellency bioassays, as well as the AChE inhibition percentages and IC50 analysis, one-way ANOVA followed by a Tukey's post-hoc test at a 95 % confidence level was performed.

Results and discussion

Essential oil yield

Fresh leaves and shoots of *P. graveolens*, *S. rosmarinus*, and *M.* × *piperita* were subjected to steam distillation, EOs with yields of 0.82 ± 0.02 %, 0.88 ± 0.04 %, and 1.02 ± 0.02 % (w/w) respectively, based on fresh weight. These results differ from those reported in some studies where they report yields in *P. graveolens* (0.25 %), *S. rosmarinus* (1-2 %) and *M.* × *piperita* (1.9 %) [43,44,45]. Studies have reported that during the steam distillation process, parameters such as temperature, pressure, and extraction time are important for obtaining longer yield, which is consistent with the results obtained in this work [46,47,48,49].

Chemical composition of the essential oils

Gas chromatography-mass spectrometry (GC-MS) analysis revealed the main components of the EOs studied. For *P. graveolens* EO, we identified citronellol (54.0 %), trans-menthone (9.9 %), aristolene (7.8 %), and geraniol (6.8 %). In *S. rosmarinus* EO, the major constituents were 1,8-cineole (32.4 %), α-pinene (30.7 %) and verbenone (7.0 %). The predominant compounds in *M.* × *piperita* EO were menthol (37.4 %), menthyl acetate (20.1 %) and trans-menthone (16.8 %) (Table 1). These primary terpenes coincide with those previously described for these plant species. In the case of *S. rosmarinus*, although different chemotypes may be present, 1,8-cineole, α-pinene, camphor, and verbenone tend to be the most abundant. Similarly, in *P. graveolens*, there may be a great diversity of terpenes with greater abundance, such as geraniol, linalool, citronellal, trans-menthone, and citronellol. In *M.* × *piperita*, the variability of most terpenes is lower, with menthol and menthone being regularly found [32-35]. Currently, EOs and their main constituents are increasingly used as a sustainable alternative to conventional chemical insecticides [15]. The variation in the percentages of the chemical profiles of these EOs is attributed to several factors, including environmental conditions, nutritional status of the plants, genetic variability, and the specific plant parts used for EO extraction [31,50].

Table 1. Chemical composition of the *P. graveolens*, *S. rosmarinus*, and *M.* × *piperita* EOs.

Rt*	Ri^{C}**	Ri^{L}	Component	Content of the components (%)		
				P. graveolens	*S. rosmarinus*	*M.* × *piperita*
6.19	923	921	α-Pinene	-	30.78	0.35
6.85	936	937	Camphene	-	2.19	-

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Rt*	Ri^{C}**	Ri^{L}	Component	Content of the components (%)		
				P. graveolens	*S. rosmarinus*	*M. × piperita*
9.35	988	988	Myrcene	-	4.58	-
10.83	1026	1028	Limonene	0.25	-	2.20
10.91	1029	1029	1,8-cineole	-	32.42	1.04
11.87	1057	1057	γ-Terpinene	-	1.93	-
13.21	1097	1098	β-Linalool	0.64	2.91	-
13.45	1106	1108	Rose oxide	1.03	-	-
14.21	1137	1138	Camphor	-	3.07	-
14.65	1155	1153	Citronellal	3.40	-	-
14.69	1157	1156	*trans*-Menthone	9.99	-	16.80
14.81	1162	1165	Borneol	-	3.99	-
14.84	1163	1166	Menthofurane	-	-	3.32
15.39	1186	1185	Menthol	0.20	-	37.42
15.83	1202	1204	Verbenone	-	7.04	-
16.53	1222	1227	Citronellol	54.06	-	-
16.54	1223	1223	Pulegone	-	-	2.46
16.86	1229	1241	Piperitone	-	-	2.12
17.01	1233	1233	cis-Geraniol	6.86	-	-
17.73	1252	1274	Menthyl acetate	-	-	20.15
19.84	1408	1415	β-Caryophyllene	-	2.05	-
20.31	1423	1429	Aristolene	7.80	-	-
		Other terpenes		13.57	3.27	10.9
		Total identified (%)		97.7	95.35	96.76

*Retention time (Rt) obtained by chromatogram. **Retention index calculated (Ri^{C}) relative to a series of n-alkanes (C8-C20) on Elite 5-ms capillary columns. Ri^{L} Retention Index of the literature. Identification of the components: Comparison of Ri with published data and comparison of mass spectra with those listed in the NIST 02 and with published data.

Contact toxicity bioassay

The toxicological activity of EOs extracted from *P. graveolens*, *S. rosmarinus*, and *M. × piperita* against *D. mexicanus* was significantly influenced by the concentration used, with toxicity increasing as the exposure time was extended (Table 2). After 24 h of application, the LD_{50} (lethal dose for 50 % of tested insects) values were calculated as 83.7 µg/insect for *P. graveolens* EO, 119.7 µg/insect for *S. rosmarinus* EO, and 349.5

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µg/insect for *M.* × *piperita* EO. With increasing exposure times (48 and 72 h), the LD_{50} values decreased, with *P. graveolens* EO exhibiting the highest contact toxicity (52.9 µg/insect at 72 h). Similarly, terpenes of *P. graveolens* (citronellol and geraniol), *S. rosmarinus* (1,8-cineole and α-pinene), and *M.* × *piperita* (menthol) followed the same trend, showing increased toxicity with prolonged exposure. Among these, citronellol and geraniol displayed the highest activity (Table 3). The data obtained indicate that geraniol and citronellol exhibit very high insecticidal activity against *D. mexicanus* adults, with LD_{50} around 14-15 µg/insect (72 h). These values are significantly lower than those reported for other insect species such as *M. domestica*, where an LD_{50} value of 99.7 µg/insect was obtained evaluating geraniol and 93.4 µg/insect citronelic acid [51]. This indicates that the toxicity of these monoterpenes depends on the species, the route of exposure and the concentration, and that in the case of *D. mexicanus* the compounds act with greater insecticidal potency. These results demonstrate that all EOs tested exhibited significant contact toxicity, with citronellol and geraniol producing the strongest effects after relatively short exposure times.

Plants produce specific mixtures of chemical compounds in varying proportions, which can be toxic to insect pests of agricultural or forestry importance. The high contact toxicity of EOs from plants such as *Salvia officinalis* L. (Lamiaceae), *Hyssopus officinalis* L. (Lamiaceae), *Origanum acutidens* (Hand.-Mazz.) Ietsw. (Lamiaceae), *Origanum vulgare* L. (Lamiaceae), *Monarda fistulosa* L. (Lamiaceae), *Tanacetum cinerariifolium* (Trevir.) Sch. Bip. (Asteraceae), *Thymus vulgaris* L. (Lamiaceae), *Foeniculum vulgare* Mill. (Apiaceae), and *Pimpinella anisum* L. (Apiaceae) has also been documented against other bark beetle species, including *Dendroctonus micans* (Kugelann, 1794) (Coleoptera: Curculionidae) and *Ips typographus* (Linnaeus, 1758) (Coleoptera: Curculionidae) [10,52,53]. Furthermore, the effect of EOs on insect morphology and behavior has been reported. This is the case with *Aphis craccivora* Koch, 1854 (Hemiptera: Aphididae), where morphological alterations were observed in the antennal flagellar segments and sensilla after 96 h of treatment with *Tagetes minuta* L. (Asteraceae) EOs using scanning electron microscopy [54]. Another mechanism of action linked to insecticidal activity is the inhibition of the enzyme glutathione S-transferase, which can be inhibited in *Aphis craccivora* by *Triadica sebifera* (L.) Small (Euphorbiaceae) seed oil [55]. Notably, this study represents the first report of the insecticidal efficiency of EOs and terpenes against *D. mexicanus*.

Table 2. Toxicological activity of *P. graveolens*, *S. rosmarinus*, and *M.* × *piperita* essential oils against *D. mexicanus* adults.

Essential oil	Time (h)	LD_{50} µg/insect (50% C.I.)	Slope[a]	Intercept[b]	χ^{2c}	*p*-value[d]	*df*[e]
P. graveolens	24	83.71 (80.38 - 87.04)	0.380 ± 0.01	18.47 ± 0.01	18.40	0.001	4
	48	58.33 (53.16 - 63.50)	0.332 ± 0.03	30.61 ± 2.29	18.34	0.001	4
	72	52.99 (50.01 - 55.97)	0.349 ± 0.00	31.51 ± 0.50	18.16	0.001	4
S. rosmarinus	24	119.70 (66.58 - 172.82)	0.160 ± 0.01	30.49 ± 8.43	15.92	0.003	4
	48	95.14 (69.94 - 120.34)	0.172 ± 0.01	33.39 ± 5.08	18.75	0.001	4
	72	53.02 (30.05 - 75.99)	0.150 ± 0.01	41.73 ± 3.56	17.83	0.001	4
M. × piperita	24	349.53 (319.74 - 379.32)	0.086 ± 0.00	19.85 ± 3.17	10.14	0.038	4
	48	296.61 (273.20 - 320.02)	0.082 ± 0.00	25.46 ± 1.43	7.71	0.102	4
	72	256.38 (234.98 - 277.78)	0.086 ± 0.00	27.78 ± 1.22	8.55	0.73	4

[a]: Slope of regression line ± SE.
[b]: Intercept of the regression line ± SE.
[c]: Pearson χ^2 goodness-of-fit test on the probit model (p=0.05)
[d]: Significant effect at p-value < 0.05.
[e]: degrees of freedom.

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Table 3. Toxicological activity of terpenes against *D. mexicanus* adults.

Compound	Time (h)	LD_{50} µg/insect (50% C.I.)	Slope[a]	Intercept[b]	χ^{2c}	*p*-value[d]	*df*[e]
Citronellol	24	25.72 (25.61 - 25.83)	1.116 ± 0.27	25.44 ± 14.1	8.53	0.74	4
	48	20.38 (20.27 - 20.49)	1.166 ± 0.23	30.82 ± 9.31	10.06	0.39	4
	72	14.89 (14.24 - 15.54)	1.122 ± 0.19	36.95 ± 7.22	14.28	0.006	4
Geraniol	24	22.13 (20.68 - 23.58)	0.911 ± 0.06	29.89 ± 0.19	6.66	0.155	4
	48	20.53 (14.37 - 26.69)	1.019 ± 0.17	32.10 ± 3.20	9.20	0.56	4
	72	14.82 (9.50 - 20.14)	1.033 ± 0.06	34.26 ± 5.26	9.20	0.56	4
1,8-cineole	24	113.85 (101.91 - 125.07)	0.254 ± 0.03	31.07 ± 6.20	12.66	0.13	4
	48	103.00 (85.99 -117.25)	0.254 ± 0.01	23.03 ± 1.52	6.98	0.137	4
	72	101.98 (78.52 -118.18)	0.279 ± 0.43	25.44 ± 6.86	14.28	0.006	4
α-pinene	24	128.56 (96.41 - 160.71)	0.240 ± 0.01	19.25 ± 5.25	9.16	0.057	4
	48	78.59 (60.43 - 96.75)	0.271 ± 0.00	28.67 ± 4.20	6.98	0.137	4
	72	70.34 (47.55 - 93.13)	0.241 ± 0.03	36.99 ± 9.32	5.00	0.287	4
Menthol	24	62.13 (55.59 - 68.67)	0.705 ± 0.10	9.21 ± 7.39	14.77	0.005	4
	48	55.77 (55.59 - 68.67)	0.749 ± 0.04	11.18 ± 3.39	15.90	0.003	4
	72	33.62 (26.90 - 40.34)	0.572 ± 0.06	30.50 ± 5.75	9.36	0.053	4

[a]: Slope of regression line ± SE.
[b]: Intercept of the regression line ± SE.
[c]: Pearson χ^2 goodness-of-fit test on the probit model (p=0.05)
[d]: Significant effect at *p*-value < 0.05.
[e]: degrees of freedom.

Repellency activity bioassay

The olfactometric response of *D. mexicanus* to EOs indicated a strong repellent effect. Among the tested EOs, *P. graveolens* and *S. rosmarinus* demonstrated the most effective repellent activity at 80 µg/cm^2, achieving 50 % (class III) repellency after 120 min (Fig. 2). In contrast, the repellent activity of *M.* × *piperita* EO was significantly lower, with only 20 % (class II) repellency observed at the same time point. Additionally, main terpenes of *P. graveolens* (citronellol and geraniol) and *S. rosmarinus* (1,8-cineole) exhibited the highest repellent activity of 36-40 % (class II) against *D. mexicanus* adults at 80 µg/cm^2 after 120 min of treatment. This result is consistent with studies in other insects, such as *Aedes aegypti* (Linnaeus, 1762) (Diptera: Culicidae) and *Anopheles gambiae* Giles, 1902 (Diptera: Culicidae), where geraniol has shown repellency rates of 70-90% at similar or slightly higher concentrations, especially when used in combination with other monoterpenes. This suggests that geraniol has high potential as a base compound in repellent formulations and that its efficacy could be enhanced through synergies with other terpenes such as citronellol. Furthermore, the observation of partial immobility in treated insects supports the hypothesis that the repellent effect is not only olfactory but also neurophysiological [56,57]. Terpenes α-pinene and menthol showed a repellent effect of around 25 % (class II) at 20 µg/cm^2 after 120 min of treatment. Although

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repellent percentages of 50 % were observed, it is recommended to evaluate higher concentrations of terpenes and EOs, as well as their mixtures, to induce higher repellent values. There are studies that both EOs and terpenes can act together antagonistically or synergistically with respect to different types of biological activity [58,59]. The repellent effect of monoterpenes such as α-pinene and verbenone has been demonstrated in *Dendroctonus pseudotsugae* Hopkins, 1902 (Coleoptera: Curculionidae). Doses close to 100 µg/cm² were evaluated, and significant effects in reducing attraction and locomotor activity were observed [60]. In this study, α-pinene showed moderate repellency (~25%) as early as 20 µg/cm², suggesting an effect consistent with that observed in other species of the same genus. Furthermore, the repellency of mixtures of plant volatiles, including 1,8-cineole and verbenone, against *Dendrcotonus armandi* Tsai & Li, 1963 (Coleoptera: Curculionidae) was evaluated and repellency levels greater than 60 % were reported at concentrations of 200 µg/cm² [61]. In comparison, 1,8-cineole achieved repellency of up to 40 % at only 80 µg/cm², highlighting the efficacy of this compound even at lower doses. In studies with *I. typographus*, EOs from *T. vulgaris* and *O. vulgare* were observed to generate significant repellency (greater than 70 %) at concentrations between 100 and 250 µg/cm² [52]. The results of this study, with 50% repellency at 80 µg/cm², are within a lower effective range, suggesting good relative efficiency of the EOs evaluated in this study. Additionally, repellency of 60-90 % has been reported with Lamiaceae oils at concentrations of 100-200 µg/cm² against *I. typographus* [50]. In contrast, the EOs evaluated in this study achieved a moderate effect (50%) at a lower concentration, which could be explained by differences in sensitivity between species or by the specific chemical composition of the oils used. Taken together, these data indicate that the EOs of *P. graveolens* and *S. rosmarinus* possess comparable or superior repellent activity to other oils reported in the literature, even at relatively low concentrations (≤80 µg/cm^2). Furthermore, it was observed that the EOs of *P. graveolens* and *S. rosmarinus* caused slower movements and partial or total paralysis in the insects, probably affecting the recorded repellency percentages. This finding is relevant, since achieving an effective repellent effect at lower concentrations reduces formulation costs and minimizes environmental risks, which is desirable for integrated forest pest management.

The findings of this study corroborate this association, as *P. graveolens* and *S. rosmarinus* EOs demonstrated strong repellent effects and the highest contact toxicity. Taking advantage of their dual repellent and insecticidal action, EOs can be used strategically to control *D. mexicanus*. For direct applications, EOs could be formulated in microcapsules or emulsions that can be sprayed on tree trunks, combining polymers such as chitosan to improve adherence and prolonged release. Additionally, they could be implemented in a "push-pull" system, where diffusers with repellent EOs are placed on healthy trees while pheromone traps are located in peripheral areas. For greater persistence, EOs can be incorporated into absorbent rings around the trunks or encapsulated in lipid nanoparticles. Applications should be made at early stages of infestation, avoiding extreme weather conditions, and always assessing potential phytotoxic effects. This integrated approach offers a sustainable alternative to the use of synthetic insecticides in forest pest management.

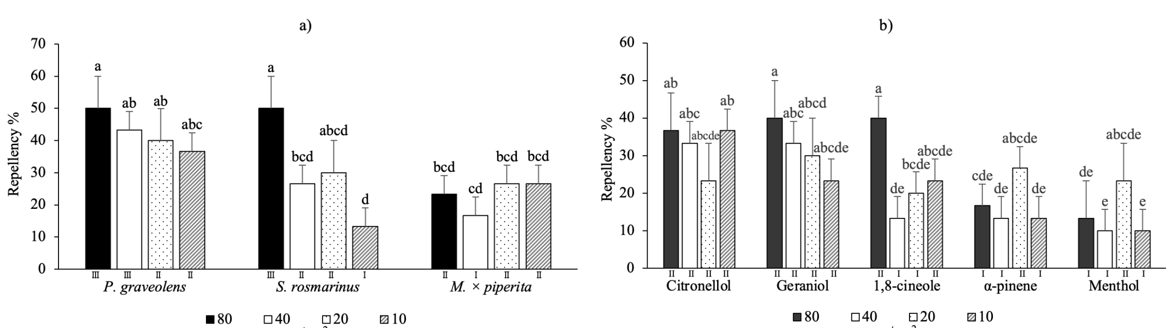

Fig. 2. Repellency of EOs **(a)** and terpenes **(b)** against *D. mexicanus* adults at different concentrations after 120 min of treatment. Different letters indicate statistically significant differences (p<0.05; Tukey's test). Bars represent the standard deviation. Results are the mean of four replicates (*n*=4). Roman numbers indicate the repellency class by EO and terpenes [40].

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AChE inhibition assay

EOs and terpenes effect on enzyme inhibition in *D. mexicanus* is summarized in Fig. 3, where the three EOs showed a concentration-dependent inhibition response. EOs of *S. rosmarinus* and *M.* × *piperita* exhibited moderate inhibition with IC_{50} of 30.2 and 44.8 mg/mL, respectively. Among the terpenes tested, α-pinene and 1,8-cineole displayed good inhibitory effect with IC_{50} of 20.0 and 3.4 mg/mL, respectively (Table 4).

The insecticidal activity of EOs also points to the inhibition of AChE, since is a potential mechanism in insects generating neurotoxic effects, often characterized by rapid paralysis and death [29]. Furthermore, the acute toxicity of EOs against insect pests has been attributed to their main compounds, generally monoterpenes [29,30,62]. In a similar study, the inhibitory activity of various monoterpenes on AChE was evaluated. In their study, carvacrol, thymol, and α-terpineol presented IC_{50} between 1.1 and 4.5 mg/mL, classified as strong inhibitors, while other compounds such as 1,8-cineole (IC_{50}= 14.6 mg/mL) and eugenol (IC_{50}= 17.2 mg/mL) were considered to have moderate activity. On the other hand, terpenes such as limonene (IC_{50} > 50 mg/mL) were classified as weak inhibitors. These findings reinforce the role of oxygenated monoterpenes as significant contributors to the neurotoxic effects of EOs in pest control strategies [29].

Regarding the *P. graveolens* and *S. rosmarinus* EOs, they show a similar trend as the main terpenes exhibit greater inhibition against AChE than EOs. For *M.* × *piperita* EO, the insecticidal effect could be explained by the presence of its minor compounds including α-pinene. These data suggest that *P. graveolens* and *S. rosmarinus* EOs, and their terpenes, are potential candidates for further open field test against *D. mexicanus*. In addition, its inhibitory effect on AChE allows understanding the mode of action on target insects, which is crucial for the development of novel bioinsecticides [29].

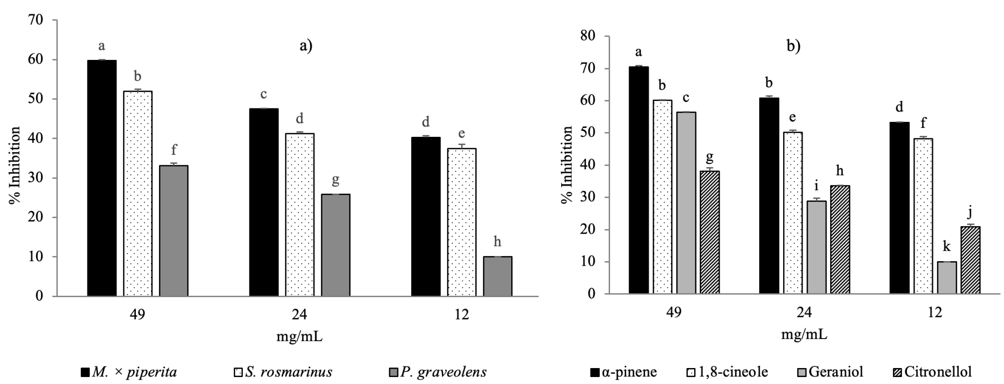

Fig. 3. Dose-dependent inhibitory activity of (a) essential oils and (b) terpenes against AChE. Different letters indicate statistically significant differences (p < 0.05; Tukey's test). Bars represent the standard deviation. Results are the mean of four replicates (n=4).

Table 4. Acetylcholinesterase inhibitory activity of essential oils and identified constituents.

Essential oils	IC_{50} mg/mL
P. graveolens	67.74 ± 1.03^{f}
S. rosmarinus	44.8 ± 0.78^{d}
M. × piperita	30.24 ± 0.08^{c}

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Essential oils	IC_{50} mg/mL
Terpenes	
Citronellol	58.3 ± 1.57[e]
Geraniol	43.37 ± 0.35[d]
1,8-cineole	20.08 ± 1.59[b]
α-pinene	3.49 ± 0.66[a]
Menthol	***
Controls	
Tacrine	137 ± 0.01 μg/mL
Bendiocarb	1.2 ± 0.05 μg/mL

Note. IC_{50} values are mean ± SD (*n=4*). Means within each column followed by the same letter(s) are not significantly different (Tukey's test; $p<0.05$). ***no inhibition.

Conclusions

Extracted EOs and their terpenes exhibited insecticidal, repellent, and AChE inhibition activity. *P. graveolens* EO showed the highest insecticidal activity and repellent effect, while geraniol was the terpene with the greatest insecticidal activity. The highest AChE inhibitory activity was observed with α-pinene. These findings suggest that the insecticidal effects of these EOs and terpenes against *D. mexicanus* could involve mechanisms related to interactions with (neurotransmitter gamma-aminobutyric acid) GABA and octopamine receptors. These results highlight the potential of the evaluated oils and their components as effective control agents against *D. mexicanu*s. However, significant challenges remain, such as the development and evaluation of EO formulations in the search for synergistic or antagonistic responses, as well as the assessment of the activity of these EOs in the field.

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