



Effects of menthol on nutritional physiology and enzyme activities of the lesser grain borer, *Rhyzopertha dominica* (F. 1792) (Coleoptera: Bostrichidae)

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Abstract

This present study aims to evaluate the insecticidal activity of a bioactive molecule, menthol, against a pest species, *Rhyzopertha dominica* (F. 1792) (Coleoptera: Bostrichidae). Effects were examined on mortality, enzymes of intermediary metabolism (ALP, GOT and GPT), nutritional reserves, digestive enzymes, and oxidative stress biomarker. Toxicological tests revealed the insecticide activity of this treatment with a dose–response relationship. In addition, ingestion (LC₅₀ at 24 h: 0.69 µl/ml) is the most effective mode of application compared to fumigation (LC₅₀ at 24 h: 302 µl/L air). The obtained results revealed an increase in the percent repellency as a function of concentrations. Moreover, the biochemical study shows that the treatment decreases the protein content and the energy reserves. In addition, it disrupts the activity of enzymes of intermediary metabolism (ALP, GOT and GPT) in *R. dominica* adult. Finally, menthol also disrupts the digestive enzymes activity in treated adults compared to controls. Indeed, the treatment reduces the specific activity of α-amylase, protease, chitinase, and lipase.

Keywords Menthol · *Rhyzopertha dominica* · Toxicity · Repulsion · Energy reserves · Digestive enzymes · Enzymatic biomarkers

Introduction

Chemical pesticides and fumigants (methyl bromide, phosphine) are crucial tools for controlling stored grain insect pests. However, these compounds led to possible risks to non-target organisms and had contributed to pest resistance development to pesticides (Venkatesan et al. 2016). These issues have prompted scientists to search for new classes of safer pest control agents that would be inexpensive, biodegradable, non-toxic to humans, and environmentally friendly.

Some studies have shown insecticidal and physiological effects of essential oils of aromatic plants and their constituents (Oftadeh et al. 2020; Dutra et al. 2020; Gong and Ren 2020). Insecticidal activity, antifeedant, repellency, and

insect growth regulation are just a few of the many properties that pesticides of a botanical origin might have (Guettal et al. 2021a, b; Sayada et al. 2021a). Before using these substances to combat pests, it is crucial to have a thorough understanding of plant essential oils (EOs), or their active metabolites, and how they interact with the physiology of insect pests (Shahriari et al. 2019). The majority of the reports are based on the fumigant activity of essential oils rather than their constituents. Several studies have confirmed that these activities are due to their compounds (menthol, menthone, carvone, limonene, β-ocimene, and dihydrotagetone), which act on the nervous system of the insect by disrupting the functions GABAergic (Tong and Coats 2012) and aminergic (Enan 2005) systems and by inhibiting acetylcholinesterase (Abdelgaleil et al. 2009).

Plant essential oils are typically composed of complex mixtures of mono- and sesquiterpenoids, such as 1,8-cineole, eugenol, and menthol (El-Saadony et al. 2022). Menthol and its derivatives were reported to exhibit insecticidal (Samarasekera et al. 2008) and antifeedant activity (Rajkumar et al. 2019) against flies, beetles, mosquitoes, and mites and affect also their behavior (Abed-Vieillard et al. 2014; Himmel

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et al. 2019). The insect repellent activity of menthol and its derivatives against stored product pests has been reported (Aggarwal et al. 2001; Shimomura et al. 2020).

So, we have tested the toxicity, the repellent activity, and the biochemical effects of menthol with an emphasis on digestive enzymes such as α -amylase, lipase, and general protease of *Rhyzopertha dominica* (F. 1792) (Coleoptera: Bostrichidae).

Additionally, the effects of this bioactive molecule on the amounts of protein, carbohydrate, and lipid in the treated adult were also taken into consideration under laboratory conditions. Finally, enzymes of intermediary metabolism have been analyzed.

Materials and methods

Insects rearing

The mass rearing of *R. dominica* was carried out in the Laboratory of Water and Environment in Larbi Tebessi University (Tebessa, North east Algeria). The insect rearing carried out in cubic containers with 1 kg wheat was maintained at temperature of 27 ± 1 °C and relative humidity of $65 \pm 5\%$. All experiments used adult insects aged 7 to 14 days.

Menthol

(\pm)- Menthol (> 98%) were purchased from Sigma-Aldrich.

Fumigant bioassay

After preliminary screening, menthol dissolved in acetone (3% w/v) was applied at different concentrations: 83.33, 166.67, 333.33, and 666.67 μ l/L air to disks of Whatman filter paper (2.5 cm in diameter), attached to the underside of plastic vial caps. This test is carried out in plastic vials (60 mL); in each of them 10 adults (both sexes) were released. Insects used as controls were maintained in the same conditions without treatment. Each concentration was replicated three times. The number of dead and alive insects was counted after 24, 48, and 72 h from the start of exposure.

After correction of observed mortality (Abbott 1925), lethal concentrations (LC_{25} , LC_{50} and LC_{90}) with their 95% confidence interval (CI) were determined.

Contact toxicity

After preliminary screening, 0.5 ml aliquot of the appropriate dilutions of menthol (0.5; 1; 2 and 4 mg/ml in acetone) was applied to 5 g of wheat grains in plastic bottles. The grains were shaken thoroughly to ensure uniform

distribution product in grains. After complete evaporation of the solvent for 15 min, 10 adults of *R. dominica* without sexing are introduced into the bottle. The bioassay was carried out in four repetitions for each concentration. A control series is conducted in parallel, and the wheat grains receive only acetone solvent (0.5 ml). Insects used as controls were maintained in the same conditions with acetone. The mortalities recorded at 6, 12 and 24 h after treatment were corrected according to Abbott's (1925) correction formula in order to eliminate natural mortalities:

$$\% \text{ Mortality} = [(\%Mt - \%Mc) / (100 - \%Mc)] * 100 \quad (1)$$

where Mt = mortality with treatment

Mc = mortality with control

A nonlinear regression was used to determine the lethal concentrations (LC_{25} , LC_{50} , and LC_{90}) and their fiducial limits (95% FL).

Repellent activity

The Talukder and Howse (1994) method was used to examine menthol's repellency. Filter paper circles of 9 cm in diameter were cut into two halves. On one half of each of the filter-papers, 0.5 ml of each of the four menthol solutions (5, 10, and 20 l/ml) was uniformly applied. On the second halves that acted as the control, acetone was applied. The treated and untreated half-circles are dried until the total evaporation of the solvent; then, they were joined by adhesive tape and placed in the Petri dish. In the center of the dish, ten adults were liberated. Each treatment was replicated five times, and the percentages of insects present on treated (G) and control (P) areas were recorded after 15 min, 30 min, 1 h, 2 h, and 3 h. The repulsion percentage (RP) was calculated using the following formula:

$$RP (\%) = (Nc - 50) \times 2$$

where Nc is the percentage of beetles present in the control half.

The average values were calculated and assigned as ranked by Mc Donald et al. (1970) by a repulsive different class varying from 0 to V [Class 0 (RP < 0.1%), class I (RP = 0.1%–20.0%), class II (RP = 20.1–40.0%), class III (RP = 40.1–60.0%), class IV (RP = 60.1–80.0%), and class V (RP = 80.1–100.0%)].

Determination of biochemical profile

In order to investigate the sublethal effects of menthol on the biochemistry and physiology, insects were treated with LC_{25} and LC_{50} . These two concentrations permit us to obtain a sufficient number of survivors following treatment to

perform different experiments compared to LC_{90} (Kissoum et al. 2020). Samples were collected from control and treated series and subjected to extraction. The method described by Shibko et al. (1966) was used to extract the biochemical components (proteins, carbohydrates, and lipids). The whole body of the control and treated insects (3 replicates each containing ten individual) was weighed and then placed in 1 ml of 20% trichloroacetic acid. Using bovine serum albumin as a standard and Coomassie Brilliant Blue as the reagent, proteins were quantified following the Bradford (1976) technique. Using anthrone as the reagent and glucose as the standard, carbohydrates were determined using the Ducha-teau and Florkin (1959) method. The method of Goldsworthy et al. (1972) was used to measure lipids, with vanillin serving as a reagent and sunflower oil as the standard.

Digestive enzyme assay

Control and treated (LC_{25} and LC_{50}) adults were sampled for digestive enzymes analysis. Dinitrosalicylic acid (DNS) was used as the reagent and 1% soluble starch as the substrate to measure the activity of α -amylase (Bernfeld 1955). According to Garcia-Carreno and Haard's (1993) method, protease activity was measured using casein (1%) as a substrate. The lipase assay was performed according to the method of Tsujita et al. (1989).

Enzymes of intermediary metabolism

A BIOSCAN commercial kit was used to assess the activity of alanine and aspartate aminotransferase. At 340 nm, the absorbance was measured. The alkaline phosphatase was quantified by BIOLABO commercial kit. At 405 nm, the absorbance was measured.

Statistical analysis

The mean \pm SEM are used to present the data. Numbers of individuals and repetitions were also mentioned. Data were analyzed using one-way analysis of variance (ANOVA) and Tukey's post hoc test to compare treatment means using GraphPad Prism v.7.00 for Windows (GraphPad Software, Inc., <http://www.graphPad.com>).

Results

Insecticidal activity

Figure 1 shows the percent mortality in *R. dominica* treated with different concentrations of menthol by fumigation. These mortalities increase significantly according to the applied doses and the time after treatment in *R. dominica*

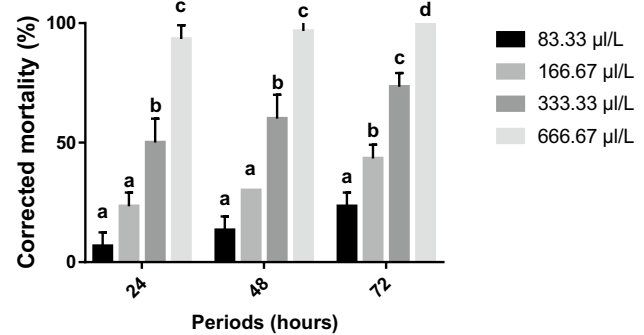


Fig. 1 Efficacy of menthol applied by fumigation on adults of *R. dominica*: corrected mortality (mean \pm SE, n=3 replicates each containing 10 adults)

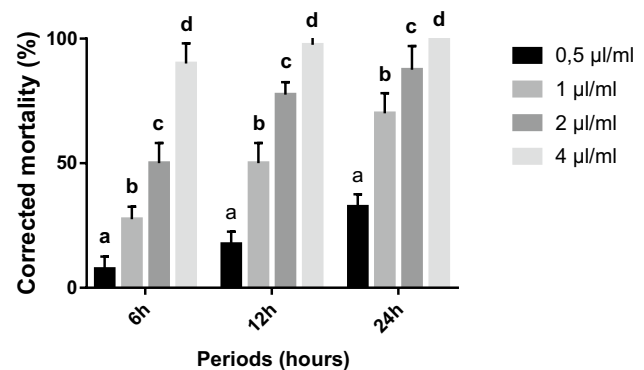


Fig. 2 Efficacy of menthol applied by contact on adults of *R. dominica*: corrected mortality (mean \pm SE, n=4 replicates each containing 10 adults)

treated by fumigation at 24 h ($F_{3,8} = 85.78$; $p < 0.0001$), 48 h ($F_{3,8} = 96.53$; $p < 0.0001$), and 72 h ($F_{3,8} = 136$; $p < 0.0001$). On the lethal times, the concentration of 0.5 μ l/ml of menthol eliminated 50% of the population of *R. dominica* in 42.97 h and 90% during 251.90 h of treatment. When 4 μ l/ml of menthol is applied, LT_{50} was 2.26 h, while the LT_{90} was 6.00 h (Table 2).

Otherwise, application of menthol by contact revealed an increase in mortality as a function of the applied doses and the time after treatment at 6 h ($F_{3,12} = 109.3$; $p < 0.0001$), 12 h ($F_{3,12} = 136.2$; $p < 0.0001$), and 24 h ($F_{3,12} = 75.27$; $p < 0.0001$) (Fig. 2). The results show that menthol applied by contact exerts an insecticidal activity with a dose–response relationship against *R. dominica*. We calculated LC_{25} and LC_{50} values of menthol along with their fiducial limits (Table 1). In addition, it is noted that menthol applied by contact is more toxic compared to fumigation.

On the lethal times, the concentration of 83.33 μ l/L of menthol eliminated 50% of the population of *R. dominica* in the 169.10 h and 90% during 793.40 h of treatment. When

Table 1 Efficacy of menthol applied on adult of *R. dominica*: determination of lethal concentrations and their confidence intervals (95%)

Treatment	Times (hours)	Hill Slope	R ²	LC ₂₅ (95% FL)	LC ₅₀ (95% FL)	LC ₉₀ (95% FL)
Fumigation (µl/L air)	24	2.36	0.97	189.9 (87.54–320.8)	302 (197–453.7)	763.80 (404.90–3055)
	48	2.12	0.97	148.5 (57.45–279.3)	249.1 (154–387.9)	700.50 (329.60–3326)
	72	1.87	0.97	100.4 (29.44–181.9)	72.01 (12.52–185.90)	581.20 (260.40–2963)
Contact (µl/ml)	6	2.05	0.97	1.03 (0.46–1.79)	1.77 (1.15–2.73)	5.17 (2.58–23.78)
	12	2.09	0.99	0.60 (0.44–0.77)	1.02 (0.84–1.23)	2.94 (2.00–4.72)
	24	2.12	0.99	0.41 (0.27–0.53)	0.69 (0.56–0.83)	1.95 (1.32–3.23)

Bold value indicates lethal concentration

Table 2 Efficacy of menthol applied on adult of *R. dominica*: determination of lethal times

Treatment	Concentrations	Hill Slope	R ²	LT ₅₀	LT ₉₀
Fumigation (hours)	0.5 µl/ml	1.24	0.99	42.97	251.90
	1 µl/ml	1.30	0.99	12.32	66.02
	2 µl/ml	1.55	0.98	5.86	24.23
	4 µl/ml	2.25	0.99	2.26	6.00
Contact (hours)	83.33 µl/L	1.42	0.98	169.10	793.40
	166.67 µl/L	0.85	0.91	108.30	1433
	333.33 µl/L	0.85	0.93	25.32	330.9
	666.67 µl/L	1.62	0.88	4.78	18.52

666.67 µl/L of menthol is applied, LT50% is 4.78 h, while the LT90% is 18.52 h (Table 2).

Repellent activity

The percentage of repellency shows an increase according to the applied concentrations. The high repulsion rates (93.33%) are observed at 30 min with the highest concentration (20 µl/ml). These percentages increase at 30 min after treatment and decrease thereafter with exposure time. In addition, we note that this treatment is classified in category V of repulsion (Table 3).

Effects on digestive enzyme activities

α-amylase activity decreases significantly ($F_{5,12} = 18.49$; $p < 0.0001$) in the treated adults with menthol without dose effect (LC_{25} Vs LC_{50} ; $p > 0.05$). The results of general protease activity showed a significant reduction in the treated series (LC_{25} and LC_{50}) ($F_{5,12} = 39.75$; $p < 0.0001$) compared to the control with a dose effect at 48 h and 72 h after treatment (LC_{25} vs. LC_{50} ; $p < 0.0001$). Finally, the results of

Table 3 Repellent effect (RP %) and repellent class (RC) of menthol on *R. dominica* adults

Concentrations	Periods	RP %	RC
5 µl/ml	15 min	33.33	II
	30 min	40.00	III
	1 h	26.66	II
	2 h	20.00	II
	3 h	13.33	I
10 µl/ml	15 min	53.33	III
	30 min	66.66	IV
	1 h	53.33	III
	2 h	46.66	III
	3 h	60.00	IV
20 µl/ml	15 min	86.66	V
	30 min	93.33	V
	1 h	86.66	V
	2 h	66.66	IV
	3 h	60.00	IV

lipase activity revealed a significant decrease ($F_{5,12} = 27.79$; $p < 0.0001$) in the treated series with LC_{25} and LC_{50} as compared to control (Table 4).

Effect in enzymes of intermediary metabolism

Treatment of adults with two doses of menthol significantly increased the activity of alanine and aspartate aminotransferases at 12 and 24 h after treatment (ALT: $F_{5,12} = 8.88$; $p = 0.0010$ and AST: $F_{5,12} = 44.17$; $p < 0.0001$). However, the activity of alkaline phosphatases was increased significantly in all treatments compared to the control ($F_{5,12} = 40.53$; $p < 0.0001$) (Table 5).

Table 4 Effect of menthol, applied on adults of *R. dominica* on activity of α -amylase, protease, and lipase (mean \pm SE; n=3 replicates each of 10 insects). Different small letters indicate a significant difference between control and treated series ($p < 0.01$)

Periods	Treatment	α -amylase	Protease	Lipase
48 h	Control	5.36 \pm 0.04 ^a	2.93 \pm 0.15 ^a	6.46 \pm 0.77 ^a
	LC ₂₅	4.90 \pm 0.12 ^b	2.88 \pm 0.06 ^a	4.16 \pm 0.31 ^b
	LC ₅₀	4.52 \pm 0.09 ^b	1.80 \pm 0.09 ^b	2.01 \pm 0.29 ^c
72 h	Control	5.03 \pm 0.04 ^a	3.06 \pm 0.14 ^a	6.71 \pm 0.14 ^a
	LC ₂₅	4.64 \pm 0.08 ^b	2.62 \pm 0.15 ^a	4.76 \pm 0.06 ^b
	LC ₅₀	4.43 \pm 0.17 ^b	1.72 \pm 0.04 ^b	3.68 \pm 0.47 ^b

Table 5 Activities of enzymes of intermediary metabolism (mean \pm SE; n=3 replicates each of 10 insects; U/mg protein) post-treatment of menthol in adults of *R. dominica*. Different small letters indicate a significant difference between control and treated series ($p < 0.01$)

Periods	Series	ALT	AST	ALP
48 h	Control	0.243 \pm 0.034 ^a	0.108 \pm 0.004 ^a	0.416 \pm 0.026 ^a
	LC ₂₅	0.316 \pm 0.012 ^a	0.148 \pm 0.007 ^a	0.540 \pm 0.007 ^a
	LC ₅₀	0.373 \pm 0.022 ^b	0.170 \pm 0.003 ^a	1.069 \pm 0.050 ^b
72 h	Control	0.258 \pm 0.009 ^a	0.117 \pm 0.011 ^a	0.399 \pm 0.099 ^a
	LC ₂₅	0.291 \pm 0.023 ^a	0.258 \pm 0.016 ^b	0.561 \pm 0.073 ^a
	LC ₅₀	0.373 \pm 0.034 ^b	0.337 \pm 0.032 ^c	0.955 \pm 0.036 ^b

Effect in nutritional reserves

A significant reduction in the total protein content is noted after treatment with the two concentrations applied ($F_{5,12} = 106.1$; $p < 0.0001$). A dose effect was observed at 24 h (LC₂₅ vs. LC₅₀; $p < 0.0001$) and 48 h (LC₂₅ vs. LC₅₀; $p = 0.0132$) (Fig. 3A). The results mentioned in Fig. 3B showed a significant decrease in lipid content in the treated series at LC₂₅ and LC₅₀ ($F_{5,12} = 537.6$; $p < 0.0001$) with a dose effect at 24 h (LC₂₅ vs LC₅₀; $p = 0.0132$) and 48 h (LC₂₅ vs. LC₅₀; $p < 0.0001$). The carbohydrate content revealed a significant decrease in the treated series at LC₂₅ and LC₅₀ ($F_{5,12} = 85.77$; $p < 0.0001$) compared to the controls, with a dose effect at 48 h (LC₂₅ vs LC₅₀; $p < 0.0001$) (Fig. 3C).

Discussion

Insecticidal activity

In our study, menthol applied on *R. dominica* was evaluated. Mortality increases with the concentration and the exposure time. The fumigant activity of menthol and 1,8-cineole, on different stored product pests, was demonstrated (Erler 2005). They achieved less than 99% mortality against many insect species tested. Menthol was most effective as

fumigant against *Tribolium castaneum* and *Callosobruchus maculatus* (Tripathi et al. 2001). The fumigant activity of six main monoterpenoids of EOs from aromatic plants grown in Turkey such as 1,8-cineole, γ -terpinene, carvacrol, menthol, thymol, and terpinene-4-ol was tested against *Tribolium confusum* adults and *Ephesia kuehniella* larvae. The results showed a variation in the fumigant activity of these molecules with the most active constituent being carvacrol (Erler 2005). In terms of LT₅₀ values (h) at 46.2 mg/l air, the following monoterpenoids had the highest levels of activity against *T. confusum* adults: carvacrol, 3.9; thymol, 15.1; γ -terpinene, 19.1; terpinene-4-ol, 162.2; 1,8-cineole, and menthol, both of which were quite potent. However, *Mentha piperita* oil and menthol showed either less or no activity against *Aedes aegypti* (Samarasekera et al. 2008).

Effect in digestive enzymes

Currently, one of the most important aspects of pest control is the selective inhibition of digestive enzymes of many insect pests (Yazdani et al. 2013). In the midgut, digestive enzymes hydrolyze food macromolecules into smaller molecules, thus facilitating their absorption. Proteins, carbohydrates, and lipids constitute the majority of food macromolecules and are hydrolyzed by proteases, amylases, and lipases, respectively. The application of menthol disrupts the activity of digestive enzymes in adults of *R. dominica* compared to controls with a dose–response relationship. The activity of three enzymes studied was significantly reduced. These results are consistent with previous studies which were demonstrated the reduction of α -amylase, proteases, and lipases activities in pests such as *R. dominica* treated with *Lavandula angustifolia* EO (Sayada et al. 2021a), *Trogoderma granarium* treated with *Eucalyptus globulus* EO (Tine et al. 2021a), and *R. dominica* treated with *Schinus molle* EO (Tine et al. 2021b). α -amylase is a midgut and salivary enzyme involved in the metabolism of starch and other carbohydrates, and its level of activity is diet dependent (Shekari et al. 2008). Some plant extracts and plant-derived molecules inhibited α -amylase activity in vitro (Yazdani et al. 2013). The reduced activity of α -amylase by plant-based compounds could imply their cytotoxic effect on the midgut epithelial cells those synthesize insect α -amylase (Senthil-Nathan et al. 2006; Zibae and Bandani 2010). This result is consistent with previous studies which were demonstrated the reduction of α -amylase activities in pests such as *E. kuehniella* (Shahriari et al. 2017), *Ectomyelois ceratoniae* (Ramzi et al. 2014), *Glyphodes pyloalis* (Yazdani et al. 2013), *Pieris rapae* (Hasheminia et al. 2011) after treatment with botanical toxins.

Proteases are a class of enzymes that catalyze the hydrolysis of peptide bonds in proteins to release their corresponding amino acids (Pascual-Ruiz et al. 2009). They can be

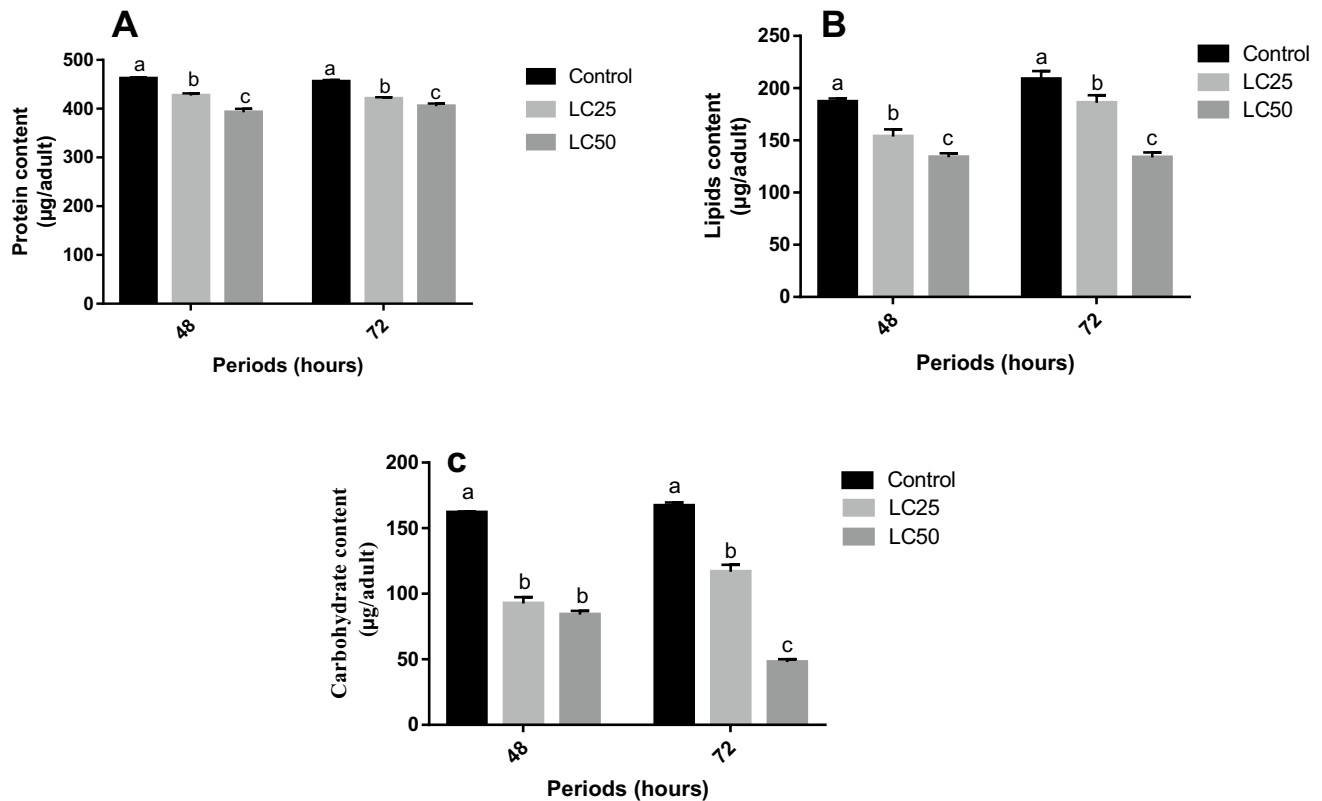


Fig. 3 Effect of menthol (LC₂₅ and LC₅₀) on the protein (A), lipid (B), and carbohydrate (C) contents at different times in adults of *R. dominica* (mean ± SEM; n = 3 pools each containing 10 individuals)

altered by botanical insecticides which interfere with the production of certain types of proteases and prevent them from digesting ingested proteins (Senthil-Nathan et al. 2006). Similar results have been reported in *Periplaneta americana* (Paranagama et al. 2001) and *G. pyloalis* (Khosravi and Sendi 2013) treated with azadirachtin, in *T. granarium* larvae treated with *E. globulus* EO (Tine et al. 2021a), in *R. dominica* treated by *S. molle* EO (Tine et al. 2021b), and *Lavandula angustifolia* (Sayada et al. 2021a). Many insect species have reported a decrease in protease activity after exposure to botanical insecticides (Paranagama et al. 2001).

Lipases play a very important role in the storage and mobilization of lipids. These enzymes are also involved in several physiological processes such as reproduction, growth, and defense against pathogens (Lemaitre and Miguel-Aliaga 2013). Similar observations were noted in *Chilo suppressalis* treated with *A. annua* (Zibae et al. 2008), in *Cnaphalocrocis medinalis* treated with azadirachtin (Senthil Nathan et al. 2006), in *T. granarium* larvae treated with *E. globulus* EO (Tine et al. 2021a) and *R. dominica* exposed to *S. molle* EO (Tine et al. 2021b). Decreased lipase activity by botanical insecticide could be due to disturbance of digestion and metabolism processes (Senthil-Nathan et al. 2006; Zibae and Bandani 2010).

Exposure to lethal concentrations considerably affected the enzymatic activities of an organism, reflecting the biochemical disturbances (Kiran et al. 2015). Indeed, any disturbance in the activity of digestive enzymes reduces access to nutrients essential to the functioning of the body. Furthermore, this reduction in nutrient utilization capacity may be related to a conversion of the energy required for biomass production into induction enzymes activity involved in detoxification essential oils and their components (Senthil-Nathan et al. 2005). Inactivation of digestive enzymes leads to poor nutrient utilization, retarded development and death by starvation (Gatehouse and Gatehouse 1999).

Effect on intermediary-involved enzymes

In the body of insects, transamination is the most important physiological process, for formation of protein needed for various functions (Chapman et al. 2013). It also plays an important role in insect energy processes such as alanine to proline conversion (Hakkak et al. 2018; Sugeçti and Büyükgüzel 2018). Transaminase enzymes (GOT and GPT) are mitochondrial enzymes which involved in transamination and found in hemolymph and fat bodies of insects (Nation 2008). They are released in the hemolymph of insects only

when the cells are damaged or destroyed (Abo El Makarem et al. 2015a; b; Pradel and Albert 2021). They are crucial for the Krebs cycle's transformation of aspartate and α -ketoglutarate into oxalate and glutamate, respectively, which enables insects to adapt to oxidative stress (Hakkak et al. 2018). Our results revealed an increase in GOT, GPT, and PAL in *R. dominica* treated with menthol. These results might suggest that menthol application enhanced transaminase enzyme activity due to toxic stress. The study of Abo El Makarem et al. (2015a; b) showed a significant increase in the GPT activity after treatment of *S. granarius* with sublethal concentrations of basil and clove while basil oil increased the activity of GOT indicating of increased synthesis of both enzymes. Significant differences were found among activities of ALT and AST in the hemolymph of *Chrysodeixis chalcites* larvae (Lepidoptera: Noctuidae) reared on lemon balm, corn, and dill, respectively (Mardani-Talaei et al. 2014). Increased transaminase activity might have been required by insects to metabolize amino acids to obtain energy under stress. In fact, the varying effect of plant extracts on GOT and GPT activities might be due to the effect on the synthesis or functional levels of these enzymes directly or indirectly by altering the cytomorphology of the cells (Nath 2000). Our results agreed with some other findings on the effect plant oils on GOT and GPT activities (Abdel-Latif and Al Moajel 2004; Arshad et al. 1999; Hassan 2002; Tabassum et al. 1994). However, decreased enzymatic activity of transaminases was reported in *Helicoverpa armigera* (Lepidoptera: Noctuidae) fed on a diet containing β -cytosterol with dose-dependent (Mishra et al. 2020). The studies of Khater and El-Shafiey (2015) showed a decrease in alanine and aspartate aminotransferase activity in *Tribolium castaneum* treated with *Wedelia trilobata* and *Melissa officinalis* EOs. Decreased alanine aminotransferase activity may be due to lack of energy supply through proline or the need for aminoacids due to tissue damage caused by the compounds used (Goharrostami et al. 2022).

Alkaline phosphatase is hydrolytic enzyme that separate phosphate groups from various molecules such as nucleotides, proteins, and alkaloids in alkaline conditions (Nation 2016). The activity of this enzyme indicates the efficiency of digestion and absorption of nutrients in the stomach and their transfer to fat bodies (Goharrostami et al. 2022). The results of this study revealed an increase in PAL in *R. dominica* adults treated with menthol. Our results disagree with those found in *G. pyralis* larvae treated with thyme EO, thymol, and carvacrol compounds (Goharrostami et al. 2022) and in *E. kuehniella* treated with *Teucrium polium* (Lamiaceae) EO and α -pinene (Shahriari et al. 2019). Significant differences were found among activities of alkaline (ALP) phosphatase in the hemolymph of *Chrysodeixis chalcites* larvae (Lepidoptera: Noctuidae) reared on lemon balm, corn, and dill, respectively (Mardani-Talaei et al. 2014). The lack

of digestive function and decreased metabolism caused by a decrease in the release of phosphate groups for the production of energy can be indicated by a drop in the activity of this enzyme group (Selin-Rani et al. 2016; Senthil-Nathan 2006).

Effect on biochemical composition

Essential oils and their components interfere with several insect functions: metabolic, biochemical, physiological, and behavioral (Mann and Kaufman 2012). Several studies have shown fluctuation of biochemical composition of insect's body treated with EOs and their components (Guettal et al. 2021a, b; Sayada et al. 2021b; Tine et al. 2021a, b). In the present investigation, the application of menthol to *R. dominica* adults resulted in a decrease in the biochemical parameters (carbohydrates, lipids and proteins content) at different periods after treatment. This decline could be due to the reduction in the diet of insects since menthol could have a deterrent effect.

The reduction of proteins is a frequent phenomenon in insects treated with toxic products (Nation et al. 2008); it can be attributed to one or more factors, such as the reduction in their synthesis or increase in their degradation to detoxify the active ingredients present in plant extracts or essential oils (Vijayaraghavan et al. 2010). The breakdown of proteins into amino acids is intended to facilitate their incorporation into the Krebs cycle as ketone acids to compensate for low energy levels caused by stress (Nath et al. 1997). Moreover, the reduction in protein reserve may also be due to the physiological adaptation of the insect to a state of stress caused by insecticides (Ribeiro et al. 2001).

However, an increase in protein levels has been reported in *R. dominica* treated with *S. molle* (Tine et al. 2021a), in *T. granarium* treated with *E. globulus* (Tine et al. 2021b), in *R. dominica* (Tine et al. 2017) and *Sitophilus granarius* treated with azadirachtin (Guettal et al. 2021a, b).

Carbohydrate plays a major metabolic role in the development cycle (Steele 1981) and constitutes an essential source of energy. Our results show a significant reduction in carbohydrate levels in adult of *R. dominica* treated with menthol. Similar results were reported in *S. granarius* treated with citrus oil and azadirachtin (Guettal 2021a), in *T. castaneum* treated with the of *Agastache foeniculum* EO (Ebadollahi 2013), in *S. granarius* treated with *C. limonum* EO (Guettal et al. 2020), in *T. granarium* treated with *S. molle* (Tine et al. 2021b), and in *R. dominica* treated with *E. globulus* (Tine et al. 2021a). Glucose depletion may be due to the stress conditions imposed on these insects which require more energy to cover energy expenditure via induction by neuropeptides (Mojarab-Mahboubkar et al. 2015). It may also be due to an acceleration of glycogenolysis in the fat body, the transport of glycogen from the

fat body to the hemolymph in response to energy depletion when individuals are exposed to toxins (Zibae 2011).

Lipids are the main source of energy in insects (Beenackers et al. 1985). Our results showed that treatment of adult *R. dominica* with menthol induced a significant decrease in lipid content. The same observations were made in *S. granarius* treated with Citrus oil (Guettal et al. 2020), azadirachtin (Guettal et al. 2021b) and combination Aza-EO (Guettal et al. 2021a), in *R. dominica* treated with *E. globulus* EO (Tine et al. 2021a), and in *T. granarium* treated with *S. molle* EO (Tine et al. 2021b). The depletion of this biochemical component after treatment is due to the stress induced following exposure to an insecticide (Sancho et al. 1998) which results in an alteration of their synthesis (Klowden 2007), to hormonal dysfunction that controls lipid metabolism (Steele 1981), to the use of this metabolic reserve (Sak et al. 2006), to the formation of lipoproteins, to the repair of cellular damage, and to the increase lipolysis to provide energy (Lohar and Wright 1993; Steele 1985).

Reducing the amount of energy resources, the proteins, carbohydrates, and lipids considered one of the main strategies in the insect pest management because of their important roles in insect biochemical pathways, growth, metamorphosis, reproduction, and diapause (Arrese and Soulages 2010; Senthil-Nathan 2013).

Conclusions

The menthol exhibited contact and fumigant toxicity against lesser grain borer adults confirming its potential use as a natural alternative to synthetic insecticides against stored-product insect pests. In addition, the strong repellent activity evidence suggests a possible application to flush out insect infestation from empty stores before fresh grain is introduced. Moreover, the perturbation of digestive enzymes affects growth and reproductive events via depressive effects on energy reserves. This study gives additional information on plant derivative products and their use in integrated pest management in the storage sites.

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Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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