



Integrated evaluation of medicinal plant extracts: phytochemical composition, insecticidal activity, and biochemical impacts on the Angoumois grain moth for sustainable grain protection

Nessma M. Abdeen¹ · Ahmed M. A. Salman¹ · Shaimaa S. Shoman² · Fatma S. Ahmed³

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Abstract

Post-harvest losses from insect pests, such as the Angoumois grain moth (*Sitotroga cerealella*), remain a major constraint on global food security, particularly in stored cereal grains. This study evaluated methanolic extracts of four medicinal plants—*Lantana camara*, *Origanum majorana*, *Ocimum basilicum*, and *Ammi visnaga*. The study assessed their phytochemical constituents, GC–MS chemical profiles, antioxidant and insecticidal activities, physiological effects on *S. cerealella*, and protective effects on stored grains, while exploring correlations among these properties. *O. basilicum* and *O. majorana* were richest in phenolics (2.66 and 2.10 mg GA g⁻¹) and flavonoids (3.19–3.39 mg QE g⁻¹), corresponding with strong antioxidant capacity (IC₅₀ = 75.51 and 80.83 µg mL⁻¹). *L. camara* showed the highest acute toxicity (LC₅₀ = 3.31 mg g⁻¹), whereas *O. basilicum* and *O. majorana* caused the strongest sublethal effects, suppressing adult emergence by > 80% at LC₂₅. Grain protection assays demonstrated that *O. basilicum* provided the best long-term protection at LC₉₀. Enzyme assays revealed that *O. basilicum* and *O. majorana* significantly enhanced antioxidant defenses (SOD, GSH), whereas *A. visnaga* reduced detoxification-related enzymes (ALT, ALP). Pearson correlation analyses revealed strong negative associations between phenolic content and grain weight loss (GWL) and insect-damaged grains (IDGs), as well as between antioxidant potential (DPPH-IC₅₀) and insect emergence reduction (ER). These findings demonstrate the multifunctional value of phenolic-rich extracts for sustainable botanical pest control and grain preservation, supporting their potential incorporation into sustainable post-harvest management strategies.

Keywords Post-harvest · *Sitotroga cerealella* · Phytochemical constituents · GC–MS · *Ammi visnaga* · Grain protection · DPPH-IC₅₀ · Emergence reduction

Key messages

- *Ocimum basilicum* had the richest phenolic profile and strong antioxidant capacity.

- *Lantana camara* showed the highest insecticidal potency against *Sitotroga cerealella*.
- Phenolics and flavonoids were strongly associated with grain protection effects.
- Certain extracts reduced insect survival as well as adult emergence of *S. cerealella*.
- Findings of the study reinforce plant-derived extracts as safe, sustainable pest control options.

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✉ Fatma S. Ahmed
fatma.sherif@cu.edu.eg

¹ Department of Plant Protection, Faculty of Agriculture, Sohag University, Sohag 82524, Egypt

² Department of Biochemistry, Faculty of Agriculture, Cairo University, Giza 12613, Egypt

³ Department of Economic Entomology and Pesticides, Faculty of Agriculture, Cairo University, Giza 12613, Egypt

Introduction

Post-harvest grain losses caused by insect infestation represent a persistent global challenge, with disproportionate impacts on developing countries where storage infrastructures are often inadequate (Oishi 2022; Jasman et al. 2025). The Angoumois grain moth, *Sitotroga cerealella* (Olivier)

(Lepidoptera: Gelechiidae), stands among the most destructive pests of stored cereals, infesting wheat, rice, and maize (Chowdhury et al. 2025). Its infestation reduces grain weight and nutrient content while contaminating stores with frass, rendering produce unfit for consumption or trade (Rhetso et al. 2020; Boamah et al. 2023; Elbehery and Ibrahim 2024). Infestation by *S. cerealella* not only damages the grain directly but also facilitates contamination by mycotoxin fungi, further degrading grain quality and posing health risks (Khan et al. 2023; Khan 2024). The pest's larvae feed inside the grain, destroying the endosperm and germ, which results in substantial reductions in grain quality and marketability (Elbehery and Ibrahim 2024; Keszthelyi et al. 2016; Boamah et al. 2023). Current estimates suggest that post-harvest insect pests can cause up to 20–30% losses annually, threatening food security and economic stability worldwide (Bakthatvatsalam et al. 2022; Mamoon-ur-Rashid et al. 2023).

Conventional management of the Angoumois grain moth relies heavily on synthetic insecticides and fumigants, particularly phosphine and, historically, methyl bromide (Salman et al. 2025). While these chemicals are effective, their extensive use and misuse have raised significant concerns, including environmental contamination, hazardous residues in food, carcinogenicity, and the evolution of resistance in pest populations (Isman 2006; Feng and Zhang 2017; Mostafiz et al. 2021; Ngegba et al. 2022; Ghoorchian et al. 2023; Ahmed et al. 2025). For example, over 98% of sprayed insecticides and 95% of herbicides can reach non-target destinations, causing harm to wildlife and ecosystems, while resistance to phosphine is now a global issue in stored-product pests (Feng and Zhang 2017; Mostafiz et al. 2021). Additionally, exposure to synthetic pesticides has been linked to adverse health outcomes in agricultural workers, such as increased risks of certain cancers and neurological disorders (Curl et al. 2020). The phasing out of ozone-depleting methyl bromide under international agreements has further accelerated the search for sustainable and environmentally friendly pest management alternatives (Mostafiz et al. 2021). As a result, there is growing interest in botanical and other biorational control methods for stored-product pests (Ngegba et al. 2022; Hasan et al. 2025; Jasman et al. 2025; Salman et al. 2025).

In this context, plant-derived insecticides have emerged as promising bio-based alternatives due to their structural diversity, biodegradability, relative safety to mammals, and multiple modes of action that reduce the risk of resistance development (Pavela 2016; Campolo 2022; Elbehery and Ibrahim 2024; Pavela et al. 2025). Numerous botanicals and essential oils, including neem (*Azadirachta indica*), clove (*Syzygium aromaticum*), thyme (*Thymus vulgaris*), garlic (*Allium sativum*), and peppermint (*Mentha piperita*), have demonstrated repellency, ovicidal activity, growth-regulatory effects, and effective grain

protection against *S. cerealella* and related pests (Ghoorchian et al. 2023; Elbehery and Ibrahim 2024; Hasan et al. 2025; Jasman et al. 2025). These studies highlight that these botanicals can induce high adult mortality, suppress oviposition and egg hatchability, and reduce grain damage, supporting their integration into sustainable pest management strategies (Ashamo and Akinlawon 2012; Ghoorchian et al. 2023; Elbehery and Ibrahim 2024; Vaishali et al. 2024; Hasan et al. 2025). However, despite this substantial progress, existing research has largely focused on a limited number of well-studied plant species and formulations, leaving many potentially valuable medicinal plants insufficiently explored, particularly in the context of stored-grain protection (Fouad et al. 2014; Hasan et al. 2025).

More importantly, most previous studies have emphasized acute toxicity or fumigant activity, with relatively few investigations systematically linking phytochemical composition to both lethal and sublethal insecticidal effects, including impacts on reproduction, oxidative balance, and key metabolic enzymes—parameters that are essential for a mechanistic understanding of botanical toxicity (Ghoorchian et al. 2023).

Furthermore, while essential oils and other volatile fractions have been widely reported for their insecticidal efficacy (Nenaah and Ibrahim 2011; Bincy et al. 2023; Gu et al. 2025), the role of non-volatile methanolic phenolic constituents in targeting metabolic and physiological pathways of stored-grain pests remains poorly understood and underexplored.

To address these gaps, this study evaluates the methanolic extracts of four medicinal plants, including *Lantana camara*, *Origanum majorana*, *Ocimum basilicum*, and *Ammi visnaga*, for their phytochemical profiles, major chemical constituents, antioxidant potential, insecticidal efficacy, and biochemical effects on *S. cerealella*. While these species are known for their diverse secondary metabolites, including flavonoids, phenolics, terpenoids, and saponins, their specific contributions to stored-grain protection remain poorly characterized. By linking chemical composition with bioassays of toxicity, reproductive inhibition, grain protection, and enzymatic responses, this work provides new insights into the multi-target actions of plant-derived bioactives. The findings establish a mechanistic basis for their potential use in sustainable post-harvest pest management and contribute to efforts aimed at reducing dependence on synthetic pesticides and safeguarding food security.

Materials & methods

Plants collection and authentication

Four medicinal plants were included in this study: *L. camara*, *O. majorana*, *O. basilicum*, and *A. visnaga*. The

plant materials were collected from various regions within Sohag Governorate, Egypt, primarily from the Sohag University farms (Al-Kawthar and New Sohag). All specimens were authenticated by a taxonomist in the Botany Department, Faculty of Science, Sohag University, and voucher specimens were deposited in the departmental herbarium. Detailed taxonomic information (order and family), plant parts used, and extraction yields (% w/w) are listed in Table 1.

Plant extracts preparation

Freshly collected plant parts were thoroughly rinsed under running tap water (2–3 times) and then with distilled water to remove dust, sand, and other surface contaminants. The materials were shade-dried at room temperature for seven days with regular turning to ensure uniform drying. The dried plant material was ground using an electric blender (BRAUN®, Model JB0123WH, Germany), and the resulting powder was sieved through a 1-mm mesh.

The fine powder was transferred into airtight specimen bottles and stored at 4 °C in a refrigerator until extraction. Crude extracts were prepared by the cold maceration technique. Briefly, 200 g of plant powder was soaked in 800 mL of 70% methanol (powder-to-solvent ratio 1:4 w/v) in a sealed extraction bottle. The mixture was incubated at 4 °C in a cooling shaker incubator for 48 h with intermittent agitation. This low-temperature extraction was selected to minimize thermal degradation and oxidation of thermolabile and volatile phytochemicals.

After incubation, the mixture was filtered through Whatman No. 1 filter paper (Maidstone, Kent, UK) under vacuum filtration (Vacuum Pump Model: VE 115N). The methanolic filtrate was concentrated under reduced pressure with a rotary evaporator (Panchun Scientific Co., Kaohsiung, Taiwan) at 30–40 °C with a rotation speed of 115 rpm until the solvent was completely evaporated.

The concentrated extract was stored at –80 °C for 24 h in an ultra-low-temperature freezer, then lyophilized using a freeze dryer (Alpha 1.2 LD plus) to obtain a dry powder. The final dried extracts were stored at –20 °C until further use.

Analysis of plant extracts

The methanolic extracts of the four selected plant species were characterized by a three-stage analysis: assessment of physical properties, preliminary phytochemical screening (qualitative), and quantitative determination of major phytochemical groups. All experiments were performed in triplicate using standardized protocols with minor modifications.

Physical properties of the plant extracts

Immediately after extraction, the physical properties of each methanolic extract, including color before and after extraction, texture, and pH, were documented. Color and texture were evaluated visually using standardized descriptors such as dark green, powdery, or waxy, thick, and were confirmed independently by two researchers to minimize subjectivity. The pH of each extract was measured in triplicate using a digital pH meter (JENWAY-3205) following the method described by Harborne (1984) (Table 2).

Qualitative phytochemical analysis

The presence of major classes of secondary metabolites in the plant extracts was qualitatively assessed using standard protocols (Harborne 1998; Kebede et al. 2021; Yusuf et al. 2022). The groups analyzed included alkaloids, flavonoids, tannins, glycosides, steroids, phenols, terpenoids, saponins, carbohydrates, and proteins. All tests were performed in triplicate, and reaction intensities were recorded semi-quantitatively as absent (–), low (+), moderate (++), or high (+++) according to the methodologies described by Chukwuma et al. (2022) and Mabadahanye et al. (2022).

Alkaloids were detected using Dragendorff's reagent; the formation of a brownish-red precipitate indicated a positive result (Bouslamti et al. 2024). Flavonoids were identified by the ammonia test, in which the appearance of yellow coloration confirmed their presence (Mwangi et al. 2024).

Tannins and phenols were determined using the ferric chloride test, with a blue-black color indicating a positive reaction (Ndam et al. 2014; Shah and Yadav 2015). Steroids were screened using the Liebermann–Burchard test,

Table 1 Botanical characteristics, plant parts used, and extraction yields of the tested plants

Name	Order	Family	Plant part used	Yield (% w/w)*
<i>L. camara</i>	Lamiales	Verbenaceae	Leaves & flowers	12.58
<i>O. majorana</i>	Lamiales	Lamiaceae	Leaves & flowers	13.38
<i>O. basilicum</i>	Lamiales	Lamiaceae	Leaves & flowers	10.59
<i>A. visnaga</i>	Apiales	Apiaceae	Fruits	8.01

*Yield of plant extract (%) was calculated using the following formula:

Yield (%) = $\text{MF} / \text{MI} \times 100$, where MF is the mass of dried extract after concentration, and MI is the initial mass of the crude plant material

Table 2 Physical properties of methanolic extracts of the tested plant species

Extract	Color before extraction	pH	Color after extraction	Texture
<i>L. camara</i>	Dark green	6.86	Dark green	Powder
<i>O. majorana</i>	Light green	4.42	Dark green	Waxy
<i>O. basilicum</i>	Light brown	5.77	Dark brown	Slightly sticky
<i>A. visnaga</i>	Light yellow	4.34	Dark yellow	Powder

indicated by a rose-red color in the chloroform layer. Terpenoids were detected using the Salkowski test, which produced reddish-brown coloration at the interface after mild heating, indicating their presence (Godlewska et al. 2022).

Glycosides were detected by the Keller–Killiani test, which produced a reddish-brown ring at the interface and a bluish-green coloration in the acetic acid layer, confirming their presence (Sravya et al. 2025). Saponins were screened using the froth test, in which the formation of persistent foam indicated a positive result. Carbohydrates were detected using Molisch's reagent, which produced a violet ring at the tube interface. Proteins were identified using the Biuret test, with a purple color indicating their presence.

Quantitative analysis of major constituents

Total phenolic content Total phenolic content was determined by the Folin–Ciocalteu spectrophotometric assay following Noreen et al. (2017). An aliquot of 100 μL of each extract (1 mg mL^{-1}) was mixed with 150 μL of Folin–Ciocalteu reagent. After incubation for 5–10 min, 500 μL of 7.5% sodium carbonate solution and 400 μL of distilled water were added. The mixture was incubated at room temperature in the dark for 90 min. Absorbance was measured at 760 nm using a UV–Vis spectrophotometer. A standard curve was prepared with gallic acid (GAE; 50–500 $\mu\text{g mL}^{-1}$), and phenolic content was expressed as milligrams of GAE equivalents per gram of dry extract (mg GAE g^{-1} dry extract) (Supplementary Figure S1).

Total flavonoid content The total flavonoid content was measured according to Chohra et al. (2020). For each assay, 100 μL of the extract was mixed with 400 μL of 30% methanol, 100 μL of 1 M potassium acetate, and 100 μL of 0.3 M aluminum chloride hexahydrate ($\text{AlCl}_3 \cdot 6\text{H}_2\text{O}$). After 5 min of incubation, 1 mL of 1 M sodium hydroxide was added. The mixture was vortexed thoroughly, and absorbance was measured at 415 nm. A calibration curve was prepared using quercetin ($10\text{--}1000\text{ }\mu\text{g mL}^{-1}$), and flavonoid results were reported as milligrams of quercetin equivalents per gram of dried extract (mg QE g^{-1}) (Supplementary Figure S2).

Total carbohydrate contents The total carbohydrate content in the plant extracts was quantified using the anthrone method as described by Antunes et al. (2023). Briefly, carbo-

hydrate concentration was measured spectrophotometrically at 620 nm, with glucose ($10\text{--}100\text{ }\mu\text{g mL}^{-1}$) as the standard. Results were expressed as milligrams of glucose equivalents per gram of dried extract (mg glucose g^{-1}) (Supplementary Figure S3).

GC–MS analysis of the plant extracts

The GC–MS/MS analysis of methanolic extracts of *L. camara*, *O. majorana*, *O. basilicum*, and *A. visnaga* was performed using an Agilent 7000 Series (7890B) Triple Quadrupole Gas Chromatograph coupled to a Mass Spectrometer. Chromatographic separation was achieved on an HP-5 ms fused silica capillary column ($30\text{ m} \times 0.25\text{ mm}$ i.d., $0.25\text{ }\mu\text{m}$ film thickness; 5% diphenyl/95% dimethylpolysiloxane). High-purity helium (99.999%) was used as the carrier gas at a constant flow rate of 1.0 mL min^{-1} . A $2\text{ }\mu\text{L}$ sample volume was injected in split mode (split ratio 30:1) with the injector and ion-source temperatures maintained at $250\text{ }^\circ\text{C}$ and $200\text{ }^\circ\text{C}$, respectively. The oven temperature was programmed initially at $40\text{ }^\circ\text{C}$ (held for 2 min), increased at a rate of $4\text{ }^\circ\text{C min}^{-1}$ to $280\text{ }^\circ\text{C}$, and held for 2 min (total run time: 64 min). Mass spectra were acquired in electron ionization (EI) mode at 70 eV, scanning the range of m/z 45–450 with a scan interval of 0.5 s and fragments from 45 to 450 Da.

Compound identification was achieved by matching acquired mass spectra with those in the NIST and WILEY libraries, supported by diagnostic fragmentation pattern analysis following Adams (2017), and by consistency with compounds previously reported in the literature for the same plant species (Bencheraiet et al. 2011; Swamy et al. 2015; Kadhim et al. 2016; Sumitha et al. 2022; Taha et al. 2023; Aziz et al. 2024; He et al. 2024; Abouelela et al. 2024; Harb et al. 2025). As authentic reference standards were not analyzed, all GC–MS identifications are considered putative annotations (Level 2) according to the metabolomics standards initiative guidelines (Sumner et al. 2007).

Antioxidant potential evaluation

The free radical scavenging activity of the extracts was evaluated using the DPPH assay, as described by Bhagwat et al. (2025). A stock solution was prepared by dissolving 22 mg of DPPH in 50 mL of 99.5% ethanol and allowing

it to stabilize at 20 °C in the dark for 2 h. A working solution was prepared by diluting the stock to an absorbance of 0.98–1.00 at 517 nm. Three milliliters of the DPPH solution were mixed with 100 µL of the plant extract at concentrations of 30–500 µg mL⁻¹. The mixtures were incubated in the dark at room temperature for 15 min, and absorbance was measured at 517 nm. The DPPH radical scavenging activity (RSA) of each extract was calculated using the following equation:

$$\text{Radical Scavenging Activity (\%)} = \frac{A_c - A_s}{A_c} \times 100$$

where A_c is the absorbance of the control (DPPH solution without samples), and A_s is the absorbance in the presence of the sample. Based on the RSA values at different concentrations, the median inhibitory concentration (IC₅₀) was calculated. The IC₅₀ represents the extract concentration required to scavenge 50% of DPPH radicals. Ascorbic acid (50–250 µg mL⁻¹) served as a positive control (Supplementary Figure S8).

Insects

The initial strain of *S. cerealella* used in this study was obtained from infested wheat grains (*Triticum aestivum* L.) collected from the Laboratory of Insect Biology, Department of Plant Protection, Faculty of Agriculture, Aswan University. The insects were reared on fresh, healthy, uninfested wheat grains that were cleaned of foreign matter and sterilized at 65 ± 5 °C for 8 h to eliminate any hidden infestations. The sterilized grains were stored at –20 °C for 14 days, air-dried, and kept in plastic containers until use.

Adult moths and sterilized wheat grains were introduced into 2-L glass jars, which were covered with muslin cloth and placed inside an insect-rearing cage (150 × 70 × 30 cm). To prevent predatory ants from entering the cage, the cage legs were placed in plastic dishes filled with water (Salman et al. 2025). The *S. cerealella* culture was maintained and periodically renewed with fresh, healthy wheat grains as needed. All insect cultures and experimental setups were kept under controlled laboratory conditions at 28 ± 2 °C and 75 ± 5% relative humidity.

Acute Toxicity assay

The insecticidal activity of plant extracts was evaluated using wheat grains of the Sakha 95 variety. A stock solution of each extract was prepared by dissolving 10 g of crude extract in 100 mL of methanol, yielding a 10% w/v solution (100 mg mL⁻¹). From this stock, working solutions of 10, 30, 50, and 100 mg mL⁻¹ (equivalent to 1%, 3%, 5%, and

10% w/v, respectively) were prepared by serial dilution with methanol.

For grain treatment, 2 mL of each working solution was mixed thoroughly with 20 g of disinfested wheat to ensure uniform coating. This delivered effective doses of 1, 3, 5, and 10 mg of crude extract per gram of grain (equivalent to 0.1, 0.3, 0.5, and 1.0% w/w, respectively). Control grains were treated with methanol alone. Treated grains were spread in a thin layer and allowed to dry completely before insect exposure.

Twenty newly emerged *S. cerealella* adults were introduced into 9 × 18 cm glass jars containing 20 g of treated wheat grains. The jars were covered with muslin cloth to allow aeration and maintained at 28 ± 2 °C and 75 ± 5% relative humidity. Each treatment, including the control, was replicated four times.

Adult mortality was recorded at 24, 48, and 72 h post-exposure. Sublethal and lethal concentrations were calculated at 48 h post-exposure, and the area under the curve (AUC) for cumulative mortality was computed across the time points using the trapezoidal rule as follows:

$$\text{AUC} = \sum_{i=1}^{n-1} \frac{(M_i + M_{i+1})}{2} \times (T_i - T_{i+1})$$

where M_i is the cumulative mortality (%) at time T_i , M_{i+1} is the cumulative mortality (%) at the next time point T_{i+1} , $T_{i+1} - T_i$ is the time interval between observations, and n is the total number of time points. Insects were considered dead if they failed to respond to gentle prodding or did not move when the jar was tilted.

Latent toxicity assay

The effect of extracts on adult emergence of *S. cerealella* was evaluated at two concentrations: sublethal (LC₂₅) and moderately lethal (LC₅₀), derived from the previously described bioassay. For each concentration, four replicates of 20 g of treated grains were placed in 250 mL jars. Each jar was infested with 100 freshly laid (24 h old) *S. cerealella* eggs. Jars were covered with muslin cloth for ventilation and maintained under controlled laboratory conditions (28 ± 2 °C, 75 ± 5% RH) for four weeks. After incubation, adult emergence was monitored daily for 15 days. The percentage reduction in adult emergence was calculated using the following formula:

$$\text{Emergence reduction(\%)} = \frac{A - B}{A} \times 100$$

where A is the number of adults that emerged in the control group, and B is the number that emerged in the treatment group.

Protective effect on stored grains

The protective efficacy of the extracts was assessed using two damage indices: percentage of grain weight loss (GWL) and percentage of insect-damaged grains (IDGs). These indices were evaluated at LC₂₅, LC₅₀, and LC₉₀ concentrations of each extract. After the emergence period, the wheat grains in each jar were sieved to remove debris and all adult moths. The remaining grains were weighed for both the control and treated groups. The percentage of GWL was calculated using the gravimetric (count and weight) method with the following formula:

$$\text{GWL (\%)} = \frac{(\text{Wu} \times \text{Nd}) - (\text{Wd} \times \text{Nu})}{\text{Wu} \times (\text{Nd} + \text{Nu})} \times 100$$

where Wu is the weight of undamaged grains, Nu is the number of undamaged grains, Wd is the weight of damaged grains, and Nd is the number of damaged grains.

Furthermore, the percentage of IDGs was computed using the following formula:

$$\text{IDGs (\%)} = \frac{\text{Number of damaged grains}}{\text{Total number of grains}} \times 100$$

Enzyme assays

Enzyme source preparation

Fourth-instar larvae (12 h old) of *S. cerealella* were fed wheat grains containing the LC₂₅ concentration (w/w) of each plant extract. Enzyme activities were measured in adults freshly emerged from the treated larvae to assess whether larval exposure causes persistent or systemic effects in the subsequent life stage. Three independent biological replicates were prepared for each treatment and control. For each replicate, ten newly emerged adults were pooled and decapitated. Whole-body homogenates were used to determine AST, ALT, SOD, and GSH activities, while midgut tissues were dissected to measure ALP activity.

Adults were homogenized in ice-cold 0.1 M phosphate buffer (pH 7.4) using a Surom™ homogenizer in three bursts of less than 30 s each. Homogenates were then centrifuged at 6000 rpm for 10 min at 4 °C.

Midguts were carefully dissected under a stereomicroscope in distilled water and immediately processed for enzyme extraction. Midgut tissues were homogenized in ice-cold 0.1 M Tris–HCl buffer (pH 9.5) containing 5 mM MgCl₂, then centrifuged at 10,000 rpm for 15 min at 4 °C. The supernatants were collected as crude enzyme extracts, aliquoted, and stored at –20 °C until analysis. Protein

concentrations were determined by the Lowry method (Lowry et al. 1951) with bovine serum albumin as the standard.

Alanine aminotransferase (ALT) and aspartate aminotransferase (AST) activities

ALT (EC 2.6.1.2) and AST (EC 2.6.1.1) activities were measured using colorimetric kits (Biodiagnostic, Dokki, Egypt) following the manufacturer's instructions based on Reitman and Frankel (1957). For each sample, 0.5 mL of substrates (L-alanine and 2-oxoglutarate for ALT; L-aspartate and 2-oxoglutarate for AST) were mixed with 100 µL of homogenate and incubated for 30 min at 37 °C. Then, 0.5 mL of 2,4-dinitrophenylhydrazine was added, and the mixture was incubated for 20 min at room temperature (23 ± 2 °C), followed by the addition of 5.0 mL of 0.4 mol L^{–1} NaOH. After 5 min, absorbance was measured at 546 nm against the appropriate blank. Enzyme activities were calculated using the kit's conversion tables and expressed as U mg^{–1} protein by normalizing to each homogenate's protein content.

Alkaline phosphatase (ALP)

Alkaline phosphatase (ALP; EC 3.1.3.1) activity in midgut homogenates was determined using a colorimetric kit (Biodiagnostic, Dokki, Egypt) based on phenyl phosphate hydrolysis and the 4-aminophenazone reaction (Belfield and Goldberg 1971). For each assay, buffer–substrate (pH 10.0, containing phenyl phosphate) was mixed with the sample homogenate and incubated at 37 °C. After incubation, 4-aminoantipyrine (4-AAP) was added, followed by potassium ferricyanide. The mixture was incubated for 5 min at room temperature in the dark, and absorbance was measured at 510 nm against a reagent blank. A phenol standard was processed in parallel. Enzyme activity was calculated as IU L^{–1} from the absorbance ratio and normalized to sample protein, expressed as U mg^{–1} protein.

Superoxide dismutase (SOD) activity

Superoxide dismutase (SOD) (EC 1.15.1.1) activity was measured using a colorimetric kit (Biodiagnostic, Dokki, Egypt) that detects inhibition of nitroblue tetrazolium (NBT) reduction, following the method of Nishikimi et al. (1972). For each assay, phosphate buffer (pH 8.5), nitroblue tetrazolium, NADH, and phenazine methosulfate (freshly diluted) were combined with tissue homogenates according to the manufacturer's instructions. The change in absorbance at 560 nm was monitored for 5 min at 25 °C. SOD activity was calculated from the inhibition of NBT reduction, normalized to protein concentration, and expressed as U mg^{–1} protein.

Reduced glutathione (GSH)

Glutathione (GSH) concentration was determined using a colorimetric kit (Biodiagnostic, Dokki, Egypt) based on DTNB reduction (Beutler et al. 1963). The homogenate was mixed with distilled water and trichloroacetic acid, vortexed, incubated at room temperature, and then centrifuged at 3000 rpm for 15 min. The supernatant was combined with buffer and 5,5-dithiobis(2-nitrobenzoic acid) (DTNB), and after incubation, absorbance was measured at 405 nm against a reagent blank. GSH content was calculated using the kit's conversion factor and normalized to protein concentration, with results expressed as $\mu\text{mol mg}^{-1}$ protein.

Statistical analysis

Before analysis, data were assessed for normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test). Probit analysis (Finney 1971) was used to estimate LC-values and their 95% confidence intervals from pooled mortality data across repeated bioassays, using the LDP-line software (<http://ehabsoft.com/ldpline>).

Area under the curve (AUC) values derived from time–mortality data, total phenolic content, total volatile compounds, carbohydrate content, and antioxidant activity (IC_{50} values from DPPH radical-scavenging assays) were analyzed by one-way ANOVA followed by Tukey's HSD post hoc test for multiple comparisons. Enzyme assay data were analyzed using one-way ANOVA with Dunnett's post hoc test for comparisons with the control. Results are presented as mean $\pm$ standard deviation.

Data on adult emergence, GWL, and IDG were analyzed using two-way ANOVA with extract and concentration as fixed factors. When a significant extract $\times$ concentration interaction was detected, Tukey-adjusted pairwise comparisons were performed within each concentration level (LC_{25} and LC_{50} for emergence; LC_{25} , LC_{50} , and LC_{90} for grain parameters).

Pearson's correlation coefficient (r) was used to assess linear relationships among variables. All statistical analyses were performed in SPSS v22.0 (IBM Corp., Armonk, NY, USA), and figures were prepared in GraphPad Prism v9.0 (GraphPad Software, San Diego, CA, USA). Statistical significance was set at $P < 0.05$.

Results

Plant extracts qualitative analysis

The qualitative phytochemical screening of the tested extracts is presented in Table 3. *O. basilicum* and *O. majorana* showed the richest phytochemical profiles, with elevated levels of flavonoids, tannins, phenols, and saponins. *O. majorana* exhibited the highest flavonoid (+++) and tannin (+++) content, while *O. basilicum* contained abundant proteins (+++). *A. visnaga* was characterized by strong steroid (+++) and detectable terpenoid (+) levels but lacked tannins and glycosides. *L. camara* showed high carbohydrate (+++) and moderate phenol (++) content but contained fewer secondary metabolites overall, with only trace levels of alkaloids and saponins.

Plant extracts quantitative measurements

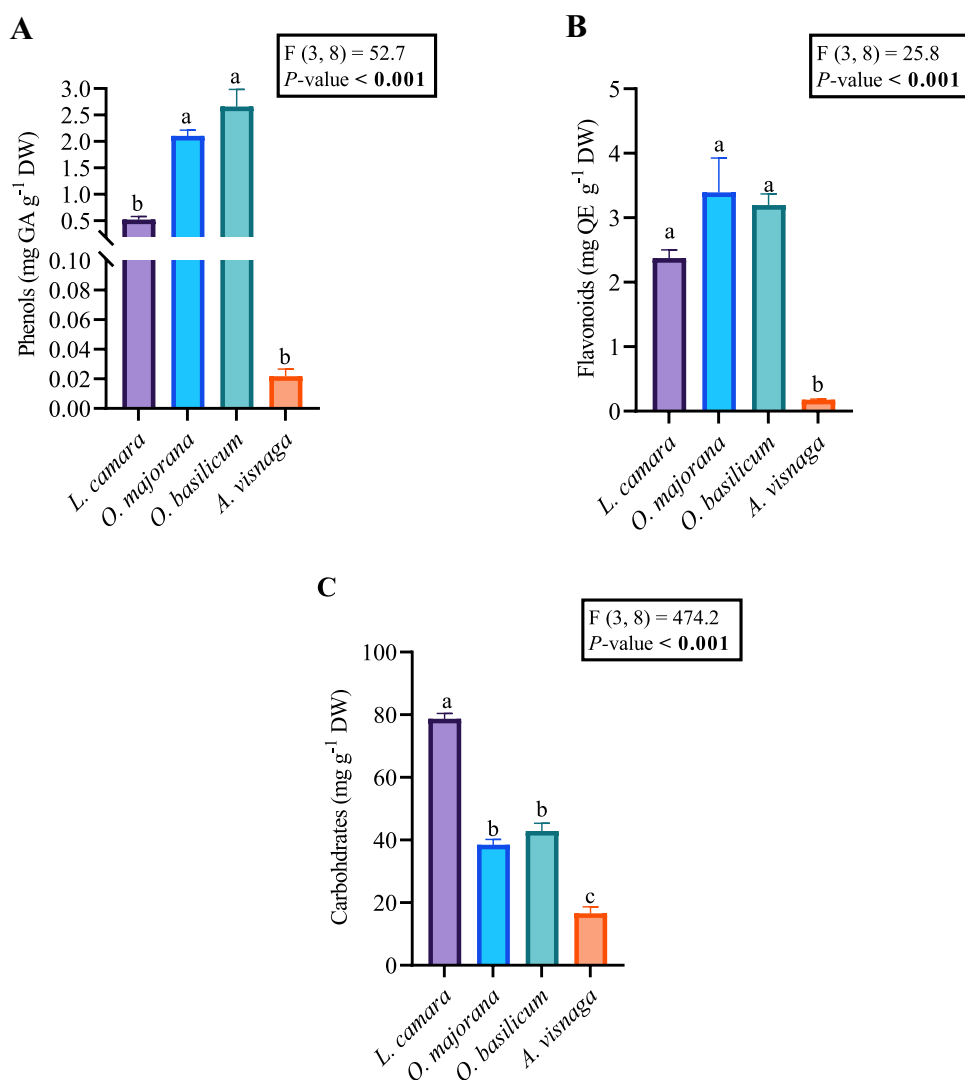
Significant differences were found among the four plant species in their total phenolic, flavonoid, and carbohydrate contents (Fig. 1). *O. basilicum* had the highest phenolic content ($2.66 \text{ mg GAE g}^{-1} \text{ DW}$), followed by *O. majorana* ($2.10 \text{ mg GAE g}^{-1} \text{ DW}$). Both values were significantly higher than those in *L. camara* and *A. visnaga* ($F_{(3,8)} = 52.7$, $P < 0.001$). A similar pattern appeared for flavonoids, with *O. basilicum* and *O. majorana* showing the highest levels (3.19 – $3.39 \text{ mg QE g}^{-1} \text{ DW}$), significantly exceeding those of *L. camara* ($2.37 \text{ mg QE g}^{-1} \text{ DW}$), while *A. visnaga* ($0.18 \text{ mg QE g}^{-1} \text{ DW}$) exhibited the lowest concentrations ($F_{(3,8)} = 25.8$,

Table 3 Qualitative phytochemical screening of crude methanolic extract of the plant species

Chemical constituents	<i>L. camara</i>	<i>O. marjorana</i>	<i>O. basilicum</i>	<i>A. visnaga</i>
Alkaloids	–	–	+	–
Flavonoids	++	+++	++	+
Tannins	+	+++	+++	–
Steroids	+	+	++	+++
Terpenoids	–	–	+	+
Phenols	++	+++	+++	+
Glycosides	+	–	+	–
Saponins	+	+++	+++	++
Carbohydrates	+++	+++	++	+
Proteins	++	++	+++	+

(–) absence; (+) low presence; (++) moderate presence; (+++) high presence

Fig. 1 Phytochemical constituents of *Lantana camara*, *Origanum majorana*, *Ocimum basilicum*, and *Ammi visnaga*. **A** Total phenolic content expressed as mg gallic acid equivalents (GAE) g⁻¹ DW, **B** Total flavonoid content expressed as mg quercetin equivalents (QE) g⁻¹ DW, and **C** Carbohydrate content (mg g⁻¹ DW). Values are presented as mean $\pm$ SD. Different letters above the bars indicate significant differences among species according to Tukey's post hoc test ($P < 0.05$)



$P < 0.001$). In contrast, *L. camara* showed the highest carbohydrate content (78.7 mg g⁻¹ DW), which was significantly higher than that of *O. majorana* and *O. basilicum*, whereas *A. visnaga* contained the lowest level (16.5 mg g⁻¹ DW) ($F_{(3,8)} = 474.2$, $P < 0.001$).

Table 4 Linear regression equations, coefficient of determination (R^2), and IC_{50} values (μ g mL⁻¹) for the DPPH radical scavenging activity of the tested plant extracts

Extract	Equation	R^2	IC_{50} (μ g mL ⁻¹)
<i>L. camara</i>	$y = 0.1455x + 20.907$	0.86	128.9 ± 3.82 a
<i>O. majorana</i>	$y = 0.307x + 11.144$	0.98	80.83 ± 1.26 c
<i>O. basilicum</i>	$y = 0.2872x + 20.656$	0.91	75.51 ± 1.63 c
<i>A. visnaga</i>	$y = 0.1279x + 25.566$	0.89	122.9 ± 1.53 b
F			436.7
P			< 0.001

Values represent means $\pm$ SD. Different letters indicate significant differences among species according to Tukey's post hoc test ($P < 0.05$)

GC–MS identification of major constituents

The GC–MS analysis of the methanolic extracts of *L. camara*, *O. majorana*, *O. basilicum*, and *A. visnaga* revealed a complex profile of volatile and semi-volatile phytoconstituents belonging mainly to terpenoid, phenolic, flavonoid, and fatty acid classes (Supplementary Tables S1–S4). The chromatograms of the four extracts (Supplementary Figures S4–S7) exhibited distinct chemical fingerprints, and the major constituents were identified by mass spectral matching and retention time data.

In *L. camara*, the dominant compounds were the sesquiterpene alcohol caryophyllene (21.40%) and the flavanone 4',5,7-trimethoxyflavanone (18.66%). The *O. majorana* extract exhibited high relative abundances of the monoterpenoid ester linalyl acetate (12.45%), the flavonoids (–)-galocatechin (10.89%), and 3,7,3',4'-tetrahydroxyflavone (9.83%). The *O. basilicum* extract was characterized by high proportions of the phenylpropanoids methyleugenol

Table 5 Lethal concentrations and Toxicity Indices of different plant extracts against *Sitotroga cerealella* adults

Extracts	LC ₂₅ (mg g ⁻¹) (95% Fiducial limits)	LC ₅₀ (mg g ⁻¹) (95% Fiducial limits)	LC ₉₀ (mg g ⁻¹) (95% Fiducial limits)	Slope ± SE	χ ²	Toxicity index*
<i>L. camara</i>	1.10 (0.57–1.40)	3.31 (2.59–4.17)	32.4 (19.2–80.0)	1.29 ± 0.18	4.45	100
<i>O. majorana</i>	1.36 (0.94–1.76)	3.61 (2.97–4.37)	22.8 (15.4–42.0)	1.59 ± 0.19	2.33	91.7
<i>O. basilicum</i>	2.38 (1.54–3.02)	4.91 (4.12–5.78)	19.6 (13.7–38.6)	2.13 ± 0.36	0.22	67.4
<i>A. visnaga</i>	2.63 (1.75–3.31)	5.57 (4.71–6.67)	23.2 (15.6–50.3)	2.07 ± 0.35	0.14	59.4

*Toxicity index = (LC₅₀ of the most toxic compound/LC₅₀ of other tested compounds) × 100

(15.69%) and estragole (12.36%). In *A. visnaga*, the GC–MS spectrum was dominated by the furochromone khellin (26.37%), the fatty acid methyl ester methyl linoleate (8.22%), the diterpenoid alcohol phytol (7.58%), and the furochromone visnagin (5.52%), reflecting the typical furochromone- and diterpenoid-rich chemotype of this species.

Antioxidant potential

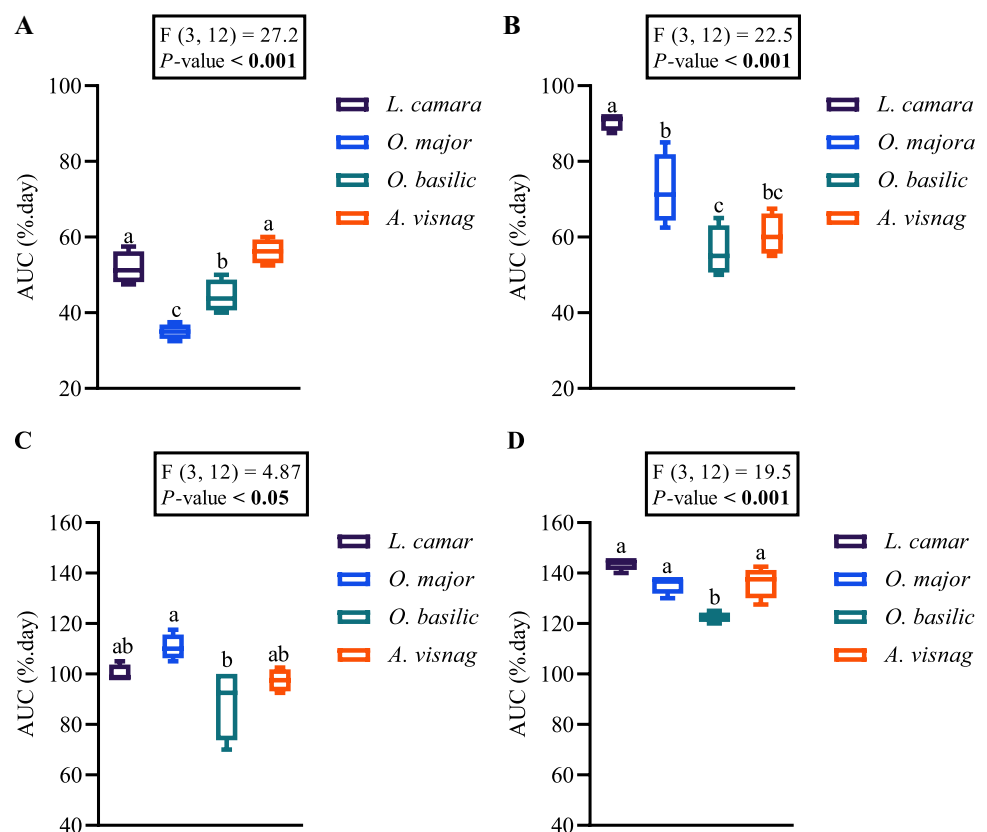
The DPPH radical-scavenging activity of the tested extracts showed dose-dependent inhibition, and IC₅₀ values were derived from the regression equations (Table 4). Among the extracts, *O. basilicum* exhibited the strongest antioxidant activity, with the lowest IC₅₀ value (75.51 µg mL⁻¹), followed closely by *O. majorana* (80.83 µg mL⁻¹). In contrast, *L. camara* (128.9 µg mL⁻¹) and *A. visnaga* (122.9 µg mL⁻¹) showed weaker activity. Statistical analysis indicated significant differences among extracts ($F=436.7$, $P<0.001$).

Insecticidal activity

Acute toxicity assay

The toxicological bioassay of the four plant extracts against *S. cerealella* revealed distinct differences in their lethal concentrations for adults (Table 5). *L. camara* extract exhibited the highest toxicity, with the lowest LC₂₅, LC₅₀, and LC₉₀ values (1.10 mg g⁻¹, 3.31 mg g⁻¹, and 32.4 mg g⁻¹, respectively). Accordingly, the reference extract was assigned a toxicity index of 100. *O. majorana* extract demonstrated slightly lower toxicity, with an LC₅₀ of 3.61 mg g⁻¹ and a toxicity index of 91.7. In contrast, *O. basilicum* and *A. visnaga* extracts were less toxic, with higher LC₅₀ values (4.91 mg g⁻¹ and 5.57 mg g⁻¹, respectively) and lower toxicity indices (67.4 and 59.4, respectively).

Fig. 2 Cumulative mortality of *Sitotroga cerealella* adults expressed as area under the curve (AUC) for *Lantana camara*, *Origanum majorana*, *Ocimum basilicum*, and *Ammi visnaga* extracts at concentrations of **A** = 1 mg g⁻¹, **B** = 3 mg g⁻¹, **C** = 5 mg g⁻¹, and **D** = 10 mg g⁻¹. Bars labeled with different letters indicate statistically significant differences according to Tukey's post hoc test ($P<0.05$)



Cumulative mortality

The cumulative mortality of *S. cerealella* adults over three days, expressed as the area under the curve (AUC, %-day), was assessed for each plant extract at four concentrations (Fig. 2A–D). At 1 mg g⁻¹ (Fig. 2A), there were significant differences among treatments ($F_{(3,12)} = 27.2$, $P < 0.001$), with *L. camara* and *A. visnaga* extracts producing significantly higher AUC values than *O. basilicum* and *O. majorana*. At 3 mg g⁻¹ (Fig. 2B), the extract effect was again significant ($F_{(3,12)} = 22.5$, $P < 0.001$), where *L. camara* had the highest AUC, exceeding all other treatments. At 5 mg g⁻¹ (Fig. 2C), a significant difference was observed ($F_{(3,12)} = 4.87$, $P < 0.05$); *O. majorana* displayed the highest cumulative mortality, while *L. camara* and *A. visnaga* exhibited intermediate effects that were not significantly different from the others. At the highest concentration (10 mg g⁻¹, Fig. 2D), extract effects remained significant ($F_{(3,12)} = 19.5$, $P < 0.001$); *L. camara*, *A. visnaga*, and *O. majorana* all produced comparably high AUC values, each significantly higher than *O. basilicum*, which remained the least effective.

Latent effects

The reduction in adult emergence of *S. cerealella* following treatment with different plant extracts at LC₂₅ and LC₅₀ concentrations is shown in Fig. 3. Two-way ANOVA revealed significant main effects of extract ($F_{(3,24)} = 112.2$, $P < 0.0001$) and concentration ($F_{(1,24)} = 571.3$, $P < 0.0001$), as well as a significant extract × concentration interaction ($F_{(3,24)} = 15.6$, $P < 0.0001$), Table S5.

At the LC₂₅ level, *O. basilicum* extracts produced the greatest reduction in adult emergence (81.7%), and *O. majorana* also produced a substantial reduction (70.9%). *A. visnaga* and *L. camara* exhibited reductions in emergence of 67.2% and 64.2%, respectively. At the LC₅₀ level, *O. basilicum* was the most effective treatment, resulting in an 89.1%

reduction in emergence. This was followed by *A. visnaga*, *O. majorana*, and *L. camara*, which exhibited emergence reductions (ERs) of 83.9%, 82.5%, and 79.9%, respectively, with no significant differences among these treatments.

Grain protection efficacy

The effects of plant extract type and concentration on GWL and IDGs caused by *S. cerealella* are shown in Fig. 4A and B. The GWL was significantly affected by both extract and concentration, and their interaction was also significant (two-way ANOVA; extract: $F_{(3,36)} = 66.6$, $P < 0.0001$; concentration: $F_{(2,36)} = 876.1$, $P < 0.0001$; interaction: $F_{(6,36)} = 38.0$, $P < 0.0001$; Table S6).

At LC₂₅ and LC₅₀, *O. basilicum* and *O. majorana* caused the greatest reductions in GWL, showing significantly lower values than *L. camara* and *A. visnaga*. At LC₉₀, *L. camara*, *O. majorana*, and *A. visnaga* produced the lowest GWL and did not differ significantly from each other, whereas *O. basilicum* showed a comparatively higher value (Fig. 4A).

The percentage of IDGs was significantly affected by both extract type and concentration, as well as their interaction (two-way ANOVA; extract: $F_{(3,36)} = 180.9$, $P < 0.0001$; concentration: $F_{(2,36)} = 642.3$, $P < 0.0001$; extract × concentration: $F_{(6,36)} = 29.25$, $P < 0.0001$; Table S7).

Across all extracts, increasing the concentration from LC₂₅ to LC₉₀ consistently reduced the proportion of damaged grains (Fig. 4B). At LC₂₅, *L. camara* and *A. visnaga* caused the highest grain damage, while *O. basilicum* showed the least, with *O. majorana* intermediate. At LC₅₀, damage was markedly reduced but remained significantly higher in *L. camara* and *A. visnaga* than in *O. majorana* and *O. basilicum*. At LC₉₀, all extracts suppressed damage, though *A. visnaga* still produced significantly more damaged grains than *O. majorana* and *O. basilicum*, while *L. camara* was intermediate (Fig. 4B).

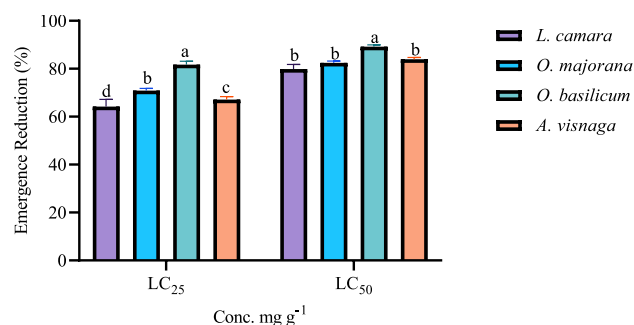


Fig. 3 Reduction in adult emergence of *Sitotroga cerealella* exposed to four plant extracts at two concentration levels: **A** LC₂₅ and **B** LC₅₀. Bars represent mean ± SD. Different letters above bars indicate significant differences among extracts within each concentration, according to one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$)

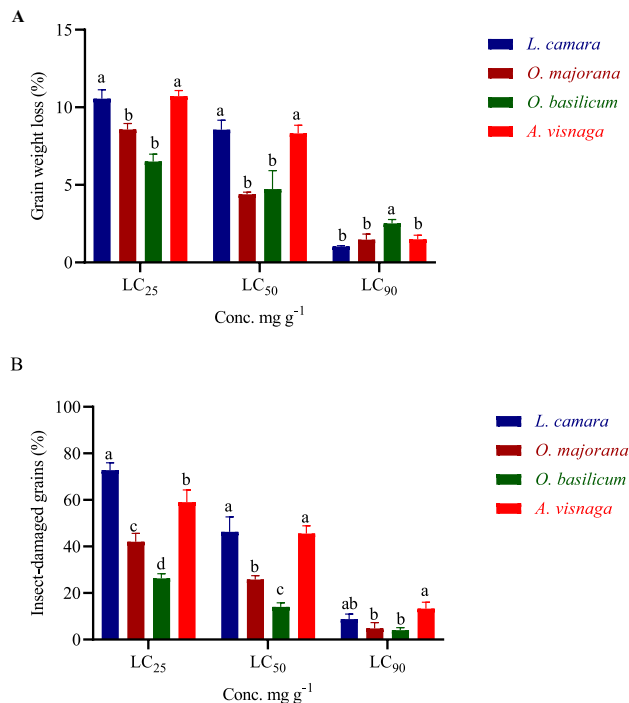


Fig. 4 **A** Grain weight loss (%) and **B** percentage insect-damaged grains of wheat caused by *S. cerealella*, when treated with four plant extracts at three concentration levels (LC₂₅, LC₅₀, and LC₉₀). Bars represent mean $\pm$ SD. Different letters above bars indicate significant differences among extracts within each concentration level according to Tukey's HSD test ($P \leq 0.05$)

Enzyme assays

The impacts of the tested plant extracts on *S. cerealella* enzymes are shown in Fig. 5. One-way ANOVA revealed significant effects of plant extract treatments on all measured biochemical parameters compared with the control.

For ALT activity, there was a significant overall treatment effect, $F_{(4,10)} = 14.18$, $P < 0.001$. Dunnett's post hoc test showed that *A. visnaga* significantly reduced ALT levels ($P < 0.001$), while *L. camara*, *O. majorana*, and *O. basilicum* did not differ significantly from the control ($P > 0.05$). For AST activity, treatment effects were highly significant, $F_{(4,10)} = 106.97$, $P < 0.001$. All tested extracts significantly lowered AST compared to the control ($P < 0.0001$ for all).

For ALP activity, ANOVA indicated a significant treatment effect ($F_{(4,10)} = 10.19$, $P < 0.001$). *O. majorana* ($P < 0.01$) and *A. visnaga* ($P < 0.001$) significantly reduced ALP compared with the control, whereas *L. camara* and *O. basilicum* did not ($P > 0.05$).

For SOD activity, there was a significant overall effect, $F_{(4,10)} = 17.30$, $P < 0.001$. *O. majorana* and *O. basilicum* significantly increased SOD activity ($P < 0.001$ for both),

while *L. camara* and *A. visnaga* did not differ significantly from the control.

For GSH levels, treatment effects were also significant ($F_{(4,10)} = 29.76$, $P < 0.001$). *O. majorana* ($P < 0.001$) and *O. basilicum* ($P < 0.01$) significantly increased GSH compared with the control, whereas *L. camara* and *A. visnaga* showed no significant effects.

Correlation analyses

Correlation analyses were performed to assess associations between the quantitative phytochemical constituents of the extracts and their antioxidant potential (expressed as DPPH-IC₅₀). Furthermore, associations among phytochemical composition, antioxidant potential, insect biology, grain protection parameters, and insect enzyme activities were investigated. The outcomes of these analyses are summarized below.

Correlation between phytochemical constituents and antioxidant activity.

Correlations between bioactive compounds (total phenolic content, total flavonoid content, and carbohydrate content) and antioxidant potential (DPPH radical-scavenging, expressed as IC₅₀) are presented in Table 6. A strong, significant negative correlation was observed between TPC and DPPH-IC₅₀ (Pearson's $r = -0.933$, $P < 0.01$). Flavonoid content also showed a significant negative correlation with DPPH-IC₅₀ (Pearson's $r = -0.693$, $P = 0.012$). In contrast, carbohydrate content showed no significant correlation with DPPH-IC₅₀ (Pearson's $r = 0.236$, $P = 0.459$), indicating that carbohydrates did not contribute to the antioxidant potential of the extracts.

Correlation between phytochemical constituents, antioxidant potential, and insect biological and grain protection parameters.

The correlation analyses between phytochemical constituents, antioxidant potential, and insect biological and grain protection parameters are shown in Table 7.

The total phenolic content exhibited a strong positive correlation with ER ($r = 0.807$, $P < 0.01$) and strong negative correlations with AUC mortality ($r = -0.806$, $P < 0.01$), GWL ($r = -0.915$, $P < 0.001$), and IDGs ($r = -0.852$, $P < 0.001$).

Flavonoids were moderately correlated with ER ($r = 0.469$, $P = 0.124$, ns) but showed significant negative correlations with AUC mortality ($r = -0.719$, $P = 0.008$) and GWL ($r = -0.628$, $P = 0.029$). Carbohydrates

Fig. 5 Effects of plant extracts (*Lantana camara*, *Origanum majorana*, *Ocimum basilicum*, and *Ammi visnaga*) on **A** ALT, **B** AST, **C** ALP, **D** SOD, and **E** GSH levels in *Sitotroga cerealella*. Data are presented as mean $\pm$ SE. Statistical analysis was performed using one-way ANOVA followed by Dunnett's post hoc test comparing each treatment to the control. $P < 0.05$ is considered significant. Significance levels: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

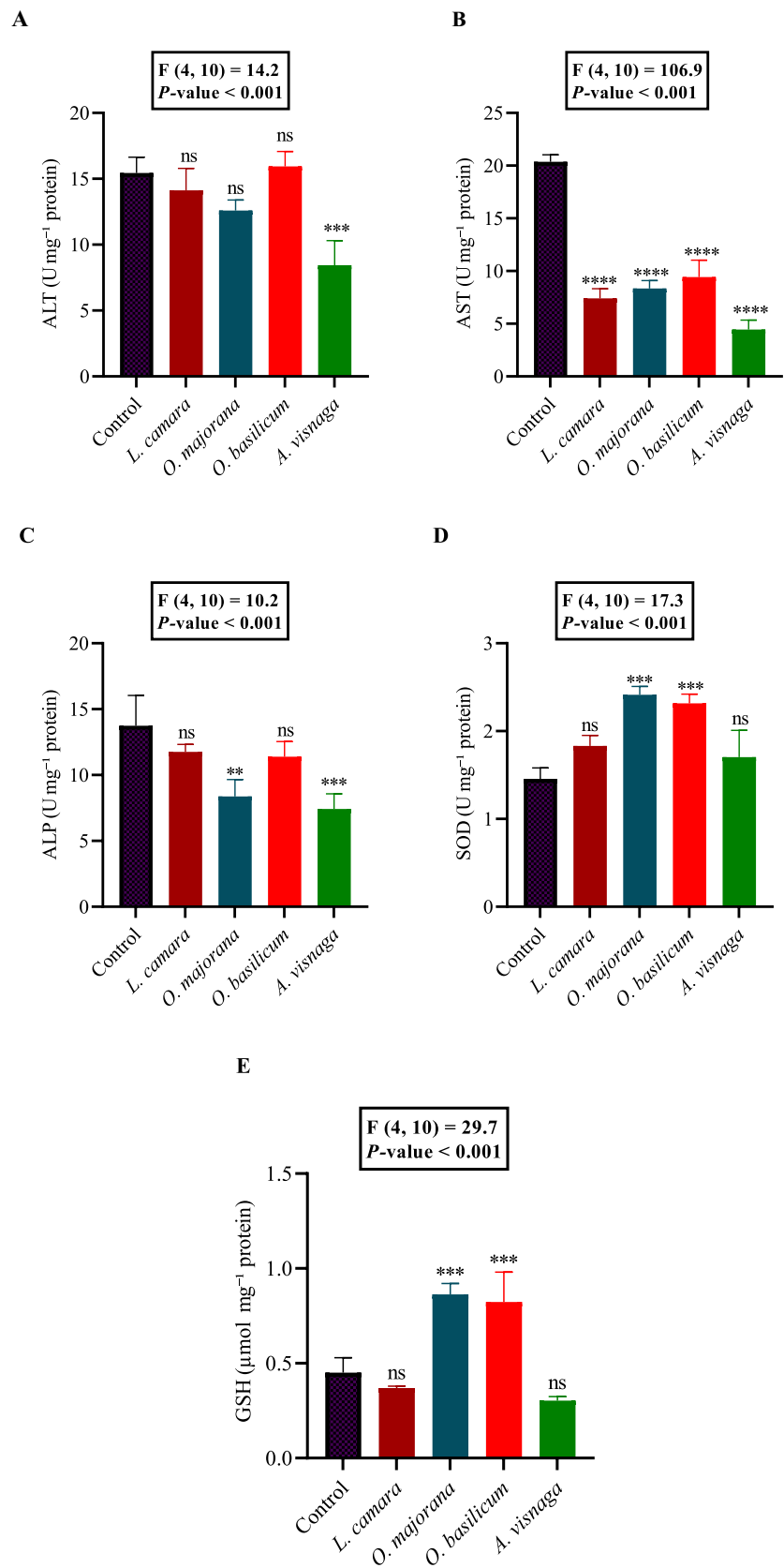


Table 6 Pearson's correlation coefficients (r) among phytochemical contents and antioxidant activity (DPPH-IC₅₀)

Variables	TPC	Flavonoids	Carbohydrates	DPPH-IC ₅₀
Phenolics	1	—	—	−0.933**
Flavonoids	—	1	—	−0.693*
Carbohydrates	—	—	1	0.236 (ns)
DPPH-IC ₅₀	−0.933**	−0.693*	0.236 (ns)	1

* $P < 0.05$, ** $P < 0.01$ **Table 7** Pearson's correlations between phytochemical constituents, antioxidant potential and insect biological and grain protection parameters

Variables	ER ^a (LC ₂₅)	AUC ^b (1 mg g)	GWL ^c (LC ₂₅)	IDG ^d (LC ₂₅)
Phenolics	0.807**	−0.806**	−0.915**	−0.852**
Flavonoids	0.469(ns)	−0.719**	−0.628*	−0.489(ns)
Carbohydrates	−0.208(ns)	0.088(ns)	0.116(ns)	0.390(ns)
DPPH-IC ₅₀	−0.816**	0.867**	0.891**	0.922**

^aEmergence reduction; ^bArea Under Curve; ^cGrain Weight loss; ^dinsect-damaged grains(* $P < 0.05$; ** $P < 0.01$)**Table 8** Pearson's correlations between phytochemical constituents, antioxidant potential, and enzyme activities in *Sitotroga cerealella*

Variables	ALT	AST	ALP	SOD	GSH
Phenols	0.633*	0.808**	0.306	0.821**	0.957**
Flavonoids	0.737**	0.823**	0.437	0.740**	0.747**
Carbohydrates	0.620*	0.406	0.744**	−0.017	−0.074
DPPH-IC ₅₀	−0.464	−0.682*	−0.049	−0.859**	−0.936**

 $P < 0.05$ (*), $P < 0.01$ (**)

displayed weak or nonsignificant associations with these parameters. DPPH-IC₅₀ was negatively correlated with ER ($r = -0.816$, $P < 0.01$) and positively correlated with AUC mortality ($r = 0.867$, $P < 0.001$), GWL ($r = 0.891$, $P < 0.001$), and IDGs ($r = 0.922$, $P < 0.001$), confirming that extracts with lower antioxidant potential were less effective at protecting grains.

Correlation between phytochemical constituents, antioxidant potential, and enzyme activities

The correlation analyses between phytochemical constituents, antioxidant potential, and *S. cerealella* enzyme activities are shown in Table 8. The analyses revealed significant relationships between phytochemical constituents

of the tested plant extracts, their antioxidant potential (DPPH-IC₅₀), and enzyme activities in *S. cerealella* adults.

Total phenolic content showed significant positive correlations with ALT ($r = 0.633$, $P = 0.027$), AST ($r = 0.808$, $P = 0.001$), SOD ($r = 0.821$, $P = 0.001$), and GSH ($r = 0.957$, $P < 0.001$), but not with ALP ($r = 0.306$, $P = 0.333$). Similarly, total flavonoids were strongly correlated with ALT ($r = 0.737$, $P = 0.006$), AST ($r = 0.823$, $P = 0.001$), SOD ($r = 0.740$, $P = 0.006$), and GSH ($r = 0.747$, $P = 0.005$), with no significant association with ALP ($r = 0.437$, $P = 0.155$).

Total carbohydrate content was positively associated with ALT ($r = 0.620$, $P = 0.032$) and ALP ($r = 0.744$, $P = 0.006$), but not with AST, SOD, or GSH. Antioxidant potential (DPPH-IC₅₀) exhibited strong negative correlations with SOD ($r = -0.859$, $P < 0.001$) and GSH ($r = -0.936$, $P < 0.001$), and a moderate negative correlation with AST ($r = -0.682$, $P = 0.015$), but no significant correlations with ALT or ALP.

Discussion

The chemical characterization of the studied extracts reveals distinct phytochemical profiles that drive their specific biological activities. *O. basilicum* and *O. majorana* are dominated by phenolics and oxygenated monoterpenes, including methyleugenol, estragole, and linalyl acetate, whereas *L. camara* is dominated by sesquiterpenoids such as caryophyllene and the flavanone 4',5,7-trimethoxyflavanone. In contrast, *A. visnaga* exhibited a unique furochromone-rich profile characterized by khellin and visnagin. This chemical diversity underscores that each extract possesses distinct modes of action and potential target mechanisms against *S. cerealella*.

Regarding the acute toxicity assay, *L. camara* demonstrated the most rapid lethality, consistent with its high content of sesquiterpenoids, which are known for their neurotoxic and fumigant activity against stored-product insects (Aisha et al. 2024). Notably, this acute toxicity was not correlated with antioxidant capacity, indicating that *L. camara* likely relies on specific neuroactive compounds rather than oxidative stress mechanisms to achieve rapid mortality. Similar rapid-acting effects have been reported for *Artemisia vulgaris* and *Premna* spp. essential oils, which caused 100% mortality of *S. cerealella* adults within hours of exposure (Adjalian et al. 2015; Song and Lee 2017).

In contrast, *O. majorana* and *O. basilicum* exhibited delayed but potent efficacy, particularly through sublethal reproductive suppression ($> 70\%$ reduction in adult emergence). The strong association between the phytochemicals of these extracts and emergence reduction was supported by observed correlations with increased SOD and GSH activity, indicating oxidative stress as a mode of action. This effect

is consistent with previous reports indicating that secondary metabolites disrupt hormonal regulation and induce oxidative stress during development (Iqbal et al. 2010; Naseri et al. 2017; Ghoorchian et al. 2023; Saha et al. 2024; Ghada et al. 2025; Salman et al. 2025). The decoupling between acute lethality (observed for *L. camara*) and reproductive suppression (recorded for *O. majorana* and *O. basilicum*) underscores the need to consider both immediate and latent effects on insects when evaluating botanical insecticides. Moreover, this emphasizes the importance of integrating phytochemical profiling, particularly GC–MS analysis, to strengthen mechanistic understanding by linking specific constituents to the observed bioactivities.

A critical distinction should be drawn between the methanolic extracts evaluated here and the essential oils commonly reported in literature. Previous studies have attributed the insecticidal activity of *O. basilicum* essential oils primarily to volatile fumigants such as estragole (Bincy et al. 2023; Worku et al. 2024; Gu et al. 2025). In contrast, our findings emphasize the role of non-volatile phenolic compounds, which contribute to pest suppression while simultaneously mitigating oxidative grain deterioration. The strong negative correlation observed between antioxidant capacity and grain protection ($r = -0.915$) demonstrates that these extracts offer a dual benefit by preserving grain quality and reducing pest impact.

This functional separation between acute neurotoxic effects and long-term metabolic or oxidative suppression reinforces the importance of evaluating different solvent fractions when developing integrated pest management (IPM). Consistent with this interpretation, the strong positive correlations between DPPH-IC₅₀ values and grain/insect damage parameters indicate that extracts with lower antioxidant potential are less effective for both pest control and grain protection. This underscores the importance of selecting extracts with high antioxidant activity for IPM strategies (Tourabi et al. 2023; Deffa and Daikh 2024).

Worth noting, the absence of a significant correlation between carbohydrate content and antioxidant activity further highlights the specificity of secondary metabolites—particularly phenolics and flavonoids—in driving antioxidant effects in these extracts. This observation aligns with previous studies indicating that, although certain polysaccharides may exhibit antioxidant activity, the efficacy of plant extracts in oxidative protection and pest control is largely determined by their secondary metabolite composition rather than carbohydrate content (Pateiro et al. 2021; Divekar et al. 2022; Al-Khayri et al. 2023; Takó et al. 2024).

The modulation of key metabolic and antioxidant enzymes in *S. cerealella* by the tested plant extracts provides important mechanistic insights into their insecticidal actions. *O. majorana* and *O. basilicum* significantly increased SOD and GSH activities. This elevation suggests

that phenolic-rich constituents target the midgut epithelial cells, initiating a cascade of reactive oxygen species (ROS) that overwhelms the insect's cellular defence machinery. The ability of phenolics to act as pro-oxidants at high concentrations likely disrupts the mitochondrial electron transport chain in these target tissues, leading to the observed physiological failure. This response is consistent with the mode of action observed for other plant-derived compounds, in which elevated SOD and GSH levels reflect an attempt to counteract oxidative damage caused by phytochemicals (Borzoui et al. 2017; Wu et al. 2020). Such oxidative stress can impair cellular function and contribute to both acute and sublethal toxicity.

In contrast, *A. visnaga* uniquely reduced ALT and ALP activities, suggesting that the fat body and haemolymph are primary target sites of its bioactive compounds. The dominant furochromones of *A. visnaga*, particularly Khellin and visnagin, are likely responsible for this effect, acting as metabolic inhibitors that impair energy mobilization and xenobiotic detoxification (Vrzal et al. 2013; Gad et al. 2025).

This finding distinguishes our work from that of Harmouzi et al. (2024), who reported that *A. visnaga* essential oils exert toxicity against *Sitophilus oryzae* through acetylcholinesterase (AChE) inhibition and disruption of chitin synthesis via volatile compounds. In contrast, our results demonstrate that the methanolic extract, enriched in non-volatile furochromones, primarily targets the detoxification machinery (ALT and ALP) of *S. cerealella*. These findings indicate that *A. visnaga* may possess a dual-action potential: neurotoxicity mediated by volatile essential oil and metabolic disruption mediated by solvent-extracted compounds.

Furthermore, unlike the study of Pavela et al. (2016), which focused on mosquito larvicidal activity, our work provides the first evidence linking *A. visnaga* extract to the suppression of enzymatic defense systems in a stored-product lepidopteran. Inhibition of these enzymes may compromise the insect's ability to detoxify xenobiotics and maintain physiological homeostasis, thereby enhancing its susceptibility to additional stressors.

Several previous studies have demonstrated that plant extracts can modulate digestive and detoxification enzymes in *S. cerealella* and other stored-product pests, leading to impaired development, reduced fecundity, and increased mortality (Fouad et al. 2014; Borzoui et al. 2017; Wu et al. 2020; Shaheen et al. 2024). Building on these findings, our study advances this body of work by providing an integrated mechanistic framework that links phytochemical composition, antioxidant potential, enzymatic modulation, and insecticidal efficacy. This mechanism-guided perspective extends beyond empirical screening and supports the strategic selection of phytochemical-rich botanicals for sustainable pest management and food preservation.

From a practical perspective, the distinct bioactivity profiles observed here suggest complementary roles in IPM. The high acute toxicity of *L. camara* renders it a suitable candidate for rapid ‘clean-out’ treatments to suppress initial infestations before storage. Conversely, the strong correlation between antioxidant capacity and grain protection observed in *O. basilicum* and *O. majorana* suggests these extracts are better suited for long-term preventative applications, where they can simultaneously mitigate oxidative deterioration and exert physiological pressure on pest populations. Integrating these botanical tools could reduce reliance on synthetic fumigants.

While this study demonstrates the promising bioactivity of botanical extracts for post-harvest pest management, it also highlights specific limitations. First, we did not evaluate the impact on the sensory quality (taste and aroma) of treated grains. Given that many plant extracts possess distinctive odors and flavors, future research should systematically assess sensory attributes and analyze volatile compounds to ensure consumer acceptance and commercial viability. Second, regarding safety, the current experimental scope was limited to efficacy against the target pest; toxicity to non-target organisms or mammals was not evaluated. However, as recently reported by Guedes et al. (2026), the natural origin of a compound does not guarantee safety. Consequently, integrating sensory evaluation protocols with rigorous toxicological risk assessments will be crucial for the practical application of these botanicals in sustainable grain protection. Finally, the transition from laboratory success to commercial application faces economic and regulatory hurdles. Future studies must address the scalability of extraction processes and evaluate the cost-effectiveness of mass production compared to synthetic pesticides to verify the financial feasibility of these botanical formulations.

Conclusion

This study identifies distinct bioactivity profiles for the four tested extracts. *O. basilicum* and *O. majorana* exhibited strong antioxidant-linked grain protection, whereas *L. camara* demonstrated rapid acute toxicity. Notably, *A. visnaga* revealed a novel mechanism of action by specifically suppressing detoxification enzymes (ALT and ALP), distinct from the neurotoxic effects of essential oils. These findings posit these botanicals as tailored candidates for sustainable IPM strategies, offering effective alternatives to synthetic fumigants, provided that safety and scalability hurdles are addressed.

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Author contributions NMA, AMAS, and FSA conceived the study and conducted the assays. AMAS provided supervision. SSS performed the GC–Ms analysis. FSA interpreted and analyzed the data and wrote the first draft of the manuscript. All authors reviewed and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding authors upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No approval of the Research Ethics Committee was required to achieve the goals of this study, as the experimental work involved an unregulated invertebrate species.

Consent to participate Not applicable.

Consent for publication Not applicable.

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