



RESEARCH ARTICLE

Management of the maize weevil (*Sitophilus oryzae* L.) using turmeric (*Curcuma longa*) essential oil

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Abstract

Among the various insect pests infesting stored maize, the rice weevil, *Sitophilus oryzae* L. (Coleoptera: Curculionidae), is one of the most destructive pests, capable of causing 100 % infestation and significant qualitative losses. Essential oils (EOs) from botanicals are considered eco-friendly as they show promise against several stored product pests including *S. oryzae* without leaving any non-toxic residues in the final product. This study aims to evaluate the potential insecticidal effects of essential oil of turmeric, *Curcuma longa* against *S. oryzae* under laboratory conditions. A maximum adult mortality of 90.0 % was recorded in fumigant toxicity tests at 65 µL/96 cm³ after 5 days of exposure. Under contact toxicity conditions, 99.13 % mortality was observed at 70 µL after 5 days. Fumigant and contact toxicity tests revealed an LC₅₀ of 60.39 µL and 65.61 µL, respectively, against adults of *S. oryzae*. At the same concentration (70 µL), turmeric EO observed complete reduction of oviposition and adult emergence. These findings indicate that turmeric EO possesses strong insecticidal properties and could serve as an effective and environmentally safe alternative to synthetic fumigants for the management of *S. oryzae* in stored maize grains.

Keywords: bioassay; fumigant toxicity; mortality; rice weevil; turmeric oil

Introduction

After rice and wheat, maize is the third-most significant cereal crop in India. India supplies over 4 % of the World's maize acreage and 2 % of the total production, ranking fourth in area and seventh in production (1). India's total area under maize cultivation has increased to 9.89 million ha, with an annual yield of 31.65 million tonnes and a productivity of 3199 kg/ha (2). Karnataka, Madhya Pradesh, Maharashtra, Rajasthan, Bihar, Uttar Pradesh, Telangana, Gujarat and Tamil Nadu are the major states where maize is largely cultivated.

Abiotic stresses including drought, temperature extremities and salinity and biotic stresses including insect pest and diseases have a substantial impact on maize yield and output (3). One of the main challenges to achieving food security in emerging and underdeveloped nations is post-harvest loss during storage. Around 60 % of maize grain is lost during storage, in Bangladesh where the harvested grains remain in the open floor due to lack of adequate knowledge among the farmers on stored grain plant protection (4). During storage, roughly 15 % of grains in poor nations suffer harm from insect pests each year (5). Among the various pests attacking stored commodities, coleopterans such as rice weevil *Sitophilus oryzae* Linnaeus, *Rhyzopertha dominica* Fabricius, red flour beetle and *Tribolium castaneum* are the most significant pests (6). Among them, the

rice weevil (*S. oryzae* L.), Coleoptera: Curculionidae, is one of the most destructive primary pests of stored grains in the world, capable of penetrating and infesting intact kernels (7).

The rice weevil consumes grains like rice, maize, sorghum, oats and barley voraciously and renders them unfit for human consumption (8). It results in 100 % damage to maize grain infestation, which over a four-month storage period led to a 14 % decrease in kernel weight (9). The larger grain borer, grain moth, maize weevil and other associated insect pests severely damage more than 70 % of maize stored as cob after 6 to 8 months of storage, according to studies on the magnitude of postharvest losses (10). Additionally, the buildup of frass, exuviae and insect carcasses contaminates maize that has been stored. Additionally, an overabundance of this pest leads to the emergence of secondary pests and the presence of deadly aflatoxins in stored grain (11).

Most infestations caused by stored pests begin in the field and spread to storage facilities (12). The maize weevil, attacks corn during the ripening stage as soon as the colour of the kernels starts to become yellow (13). It is then transported to storage by field-infested grains and is the primary factor in the population build up in grains that have been stored. Unprotected ears at the tip expose corn to severe *Sitophilus* spp. infestation. The amount of infestation in the storage area

is determined by the infestation level in the fields and the higher the infestation in the fields, the higher the infestation in stores (6). Synthetic chemical insecticides, though reduce post-harvest losses during storage, are strongly discouraged due to their negative consequences, including the development of insecticide resistance, environmental risks, chemical residues in food and effects on non-target organisms (14-16). Therefore, adopting an eco-friendly strategy for the management of storage pests will be useful in the long run. Due to their non-phytotoxicity, simple biodegradability and stimulatory nature of the host metabolism, plant products are increasingly being used as innovative chemotherapeutic agents in plant protection in many parts of the world (17). Plant EOs have broad spectrum activity against a wide range of storage insect pests because of their fast penetration and presence of nontoxic residues (18).

Compounds found in plant extracts have ovicidal, repellent, antifeedant, sterilizing and toxic properties on insects (19, 20). Botanicals, primarily the volatile EOs derived from aromatic plants, have been touted as alternatives since they have broad-spectrum activity against a wide range of insect-pests and display insecticidal capabilities (21, 22). Several EOs have both contact and fumigant effects and because they are lipophilic, it is simpler for them to disrupt an insect's physiological, biochemical and behavioral processes (23). Monoterpenoids, which serve as neurotoxicants against certain insect pests and cause rapid knockdown effects or immobilization, are the insecticidal component of many plants EOs (24, 25). Many studies on the neurotoxic, cytotoxic, phytotoxic and mutagenic activities of various edible EOs on storage pests make them a good, inexpensive and safe alternative for protecting and controlling stored product pests (26, 27).

Toxicity of turmeric essential oil on storage insect pests

Turmeric EOs and extracts have demonstrated insecticidal and repellent properties against stored-insect pests of wheat such as *T. castaneum*, *Callosobruchus maculatus* (Fabricius), *Cryptolestes ferrugineus* (Stefens), *Oryzaephilus surinamensis* (Linnaeus), *Corcyra cephalonica* (Stainton) and *S. oryzae*. *C. longa* extracts at 20.0 % concentration completely suppressed the adult emergence of *T. castaneum* (28, 29). EO of *C. longa* at 100-500 mg/L had repellent, contact and fumigant action against *T. castaneum* (30). Reduction in growth rate and food consumption in *S. oryzae* and *R. dominica* were also documented (31).

Extracts of turmeric (*Curcuma longa* Linnaeus) were effective against the angoumois grain moth, *Sitotroga cereaella* (Olivier) (32). The 100 % mortality of *S. zeamais* (Motschulsky) was observed within a day of fumigation at 15 $\mu\text{L}/\text{cm}^2$ (33). EO from *C. domestica* was effective against *Tribolium* spp., *Callosobruchus chinensis*, *C. maculatus*, *S. granarius*, *S. oryzae* and *R. dominica* (34). An LD_{50} of 36.71 $\mu\text{g}/\text{mg}$ against *R. dominica* adults was documented earlier with EO of turmeric (34). At 5.2 mg/cm^2 , turmeric EO inhibited oviposition and egg hatching by 72 % and 80 % in *T. castaneum* (35). Fumigant toxicity was also reported against *S. oryzae* adults which exhibited an LC_{50} of 11.36 mg/L air. About 81 % antifeedant effect at a dose of 40.5 mg of turmeric EO/g food was documented, while reported fumigant action of turmeric EO against *R. dominica* at 0.01 % and 0.05 % concentrations (36).

C. longa extracts caused 49.33 % mortality in *C. maculatus* infesting chickpea, with a repellency index of 0.73 after 5 days of treatment (37). Similar results were observed in *C. longa* had insecticidal toxicity against *C. maculatus* at 80 g/kg at 72 hr of exposure (38). EO of *C. longa* exhibited synergistic effect against *R. dominica* (100 % mortality) when used with *Citrus reticulata* L., *Murraya koenigii* (L.) Spreng. and *Cymbopogon citrinus* L., infesting wheat grains (39, 40). In another study, EO of *C. longa* showed 100 % repellence against *R. dominica* when combined with *M. koenigii*, *Callistemon citrinus* R. Br. and *Citrus limetta* Risso. oils (41). Thus, EOs and extracts derived from *Curcuma* provide ecofriendly solution to post-harvest management of storage insect pests.

Materials and Methods

Mass culturing of rice weevil

Mass culturing of rice weevil (*S. oryzae*) was carried out at Central Instrumentation Laboratory, TNAU (Tamil Nadu Agricultural University), Coimbatore. *S. oryzae* adults were reared on fresh maize seeds disinfected by sun drying to kill any other existing insect stages. About 50 pairs of freshly emerged adult weevils were released into a 500 mL capacity of plastic container containing 400 g maize seeds with 12 % moisture content. The container was covered with a muslin cloth and culture was maintained at a temperature of 27 ± 2 °C, 65 ± 5 % RH (relative humidity) and 12:12 hr light: dark photoperiod throughout the experiment (42, 43). After 39 to 45 days, the newly emerged F1 generation adults from the culture were utilized for the toxicity studies. Sub culturing was done following the same procedure as above to have continuous supply of insects for the experiments proposed in this investigation.

Evaluation of turmeric essential oils against *S. oryzae*

Laboratory experiments were conducted to evaluate the efficacy of turmeric EO in managing *S. oryzae*. Turmeric oil was selected for the experiment based on the available literature suggesting the efficacy of turmeric EO against storage pests (35, 44, 45).

Essential oil

For the present studies, turmeric EO was procured from commercial sources (Tegraj & Co. and Doddabetta EO & Herbs). The TNAU sweet flag formulation was used as a standard check, alongside an untreated control.

Fumigant toxicity of turmeric essential oils on the mortality of *S. oryzae* adults

The fumigant effect of the turmeric EO was evaluated using filter paper discs (Whatman No. 1 filter paper discs of 9 cm diameter and 63.64 cm^2 surface area) treated with the oils diluted in acetone. The filter paper discs were placed in Petri dishes (9 cm diameter and 1.5 cm height). The concentrations used for fumigant toxicity study are given in Table 1. Toxicity was determined based on a preliminary range finding test, which was diluted in 1 mL acetone and applied uniformly to the filter paper discs using a micropipette. Two other separate Petri dishes with filter paper disc (one with 1 mL acetone alone as solvent control and another without essential oil or acetone as negative control), while 0.8 mL TNAU sweet flag 6 % EC formulation was taken as the standard check thus accounting for a total of eight treatments. The acetone was allowed to evaporate for 20 min

prior to the introduction of insects. In each Petri plate with the filter paper disc, 3-7 day old 20 unsexed adults were released and kept under dark in the laboratory conditions for 24 hr (45, 46). Each treatment was replicated thrice and maintained under laboratory conditions (27 ± 2 °C, 65 ± 5 % RH). Insect mortality was recorded daily up to five days and percentage mortality was subjected to Abbott's correction (47).

Contact toxicity of essential oils on mortality of *S. oryzae* adults

The effect of the EO treatment on adult mortality was studied under laboratory conditions (27 ± 2 °C, 65 ± 5 % RH) following standard methodology (48). The concentrations used for this study are furnished in Table 1, which were diluted in 1 mL acetone for each dose of oil and was mixed with 40 g sample of grains in glass jars using a micropipette and stirred continuously for 1 min manually to ensure even spread of the EO over the grain surface. Samples were kept for 20 min, so that the solvent evaporates completely. Three to seven day old test insects were released in groups of 20 individuals per jar, covered by nylon mesh and fastened with rubber bands. Two more glass jars viz., one with solvent control and negative control, while TNAU sweet flag formulation (0.8 mL) was used as standard check. Each set of treatment was replicated thrice in a completely randomised design (CRD). Percentage insect mortality was subjected to the Abbott's correction (47).

Contact toxicity of essential oils on oviposition and adult emergence of *S. oryzae*

In a similar experiment, 2 pairs of 3 to 7 days old adults were introduced into 20 numbers of treated and control maize grains. After a period of 3 days, by which time the adults would have oviposited, the adult weevils were removed. The number of eggs laid was counted on the fourth day based on the number of egg plugs secreted over the egg (48). Subsequently, adult emergence was also recorded on 38 - 44 days to arrive at the F2 progeny production.

Statistical analysis

Probit analysis to estimate the lethal concentrations viz., LC_{50} and LC_{95} with their 95 % fiducial limits was carried out using statistical package for social sciences (SPSS) software. The data on percent mortality, egg laying and percent adult emergence were square root transformed and statistically analysed using one-way ANOVA (analysis of variance) in SPSS program version 22.0.

Results and Discussion

Fumigant toxicity of turmeric essential oil on *S. oryzae* adults

There were significant differences in the turmeric oil treated seeds. A maximum mortality of 90.0 % was observed with turmeric oil at 65 μ L/96 cm^3 air at 5 days after treatment. At this highest concentration, more than 80 % mortality was recorded

even after 3 days treatment. Also, at lower concentration, turmeric oil at 55 μ L recorded about 61.67 % mortality at 5 days after treatment. The fumigant activity of *C. aromatica* was observed at an LC_{50} of 2.04 mg/L air against *C. chinensis* and an LC_{50} of 18.18 mg/L air against *T. castaneum* (49). In contrast, the TNAU sweet flag at 0.8 mL registered 68.33 % mortality at 5 days after treatment. The untreated control as well as acetone treatments did not register any mortality during study (Table 2).

The LC_{50} and LC_{95} value of turmeric EO on the mortality of *S. oryzae* adults, due to fumigant toxicity, was evaluated after two days of treatment (Table 3). The data was statistically homogenous as indicated by a chi square value of 0.97. The probit analysis revealed an LC_{50} and LC_{95} of 60.39 μ L and 75.31 μ L, respectively (Fig. 1). A still lower LC_{50} of 11.36 μ g/L of air was also obtained in earlier studies and the difference could be attributed to the source of EO (35).

Contact toxicity of turmeric essential oil on *S. oryzae* adults

At lower concentrations of turmeric EO viz., 62 μ L/40 g seeds, the adult mortality rate due to contact toxicity was nearly negligible (1.67 %) at 1 day after treatment, which reached 86.67 % at 5 days after treatment. With an increase in concentration, there was a matching rise in mortality (Table 4). The highest concentration of turmeric EO, 70 μ L registered an adult mortality of 99.13 % after 5 days after exposure. In contrast, controls with acetone and untreated controls did not record any mortality.

Turmeric EO having high contact action against *R. dominica* was also reported earlier (35). Another species of wild turmeric, *C. aromatica* registered contact toxicity (LC_{50}) of 1.50 mg/ cm^2 against *C. chinensis* and 10.40 mg/ cm^2 against *T. castaneum* (48). At five days after exposure, more than 80 % of adult insects died in all turmeric oil concentrations. Lower adult mortality after 24 hr of exposure may be due to the slow lethal action of EOs. The EOs were typically more lethal and quickly killed insects by reducing respiratory activity or direct toxic effect of EO or its constituents that may penetrate through insect cuticle and encounter the tracheal nerve endings, resulting in neurotoxic activity and more rapid deathlike earlier observations (50). The toxicity might be caused by acetyl cholinesterase being temporarily inhibited by another enzyme occupying its hydrophobic site (51).

The LC_{50} and LC_{95} value of turmeric EO on the adult mortality of *S. oryzae* adults, due to contact toxicity, was statistically homogenous as indicated by a chi square value of 0.08. The probit analysis revealed an LC_{50} of 65.61 μ L and LC_{95} of 75.68 μ L (Table 5).

Toxicity of turmeric essential oil on egg laying and adult emergence of *S. oryzae*

There was significant reduction in egg laying and adult progeny emergence in maize grains treated with all concentrations of turmeric EO. At the highest concentration viz. 70 μ L, the egg-

Table 1. List of essential oils used for fumigant toxicity studies against *S. oryzae* adults

Treatments	Fumigant toxicity studies	Contact toxicity studies
	Concentration (per 96 cm^3)	Concentration (per 40 g seeds)
Turmeric essential oil	55, 57.5, 60, 62.5, 65 μ L	62, 64, 66, 68, 70 μ L
TNAU sweet flag formulation 6 % EC	0.8 mL	0.8 mL
Control with acetone	1 mL	1 mL
Untreated control	--	--

Table 2. Fumigant toxicity of turmeric essential oil against *S. oryzae* adults

Treatments (Concentration)	Adult mortality (%)*				
	1 DAT	2 DAT	3 DAT	4 DAT	5 DAT
Turmeric oil at 55 µL	1.67 (7.22) ^f	21.67 (28.1) ^d	43.33 (41.45) ^d	51.67 (46.25) ^{cd}	61.67 (52.1) ^d
Turmeric oil at 57.5 µL	16.67 (24.43) ^d	38.33 (38.54) ^c	51.67 (46.25) ^c	60.00 (51.08) ^{bc}	71.67 (58.1) ^{bc}
Turmeric oil at 60 µL	35.00 (36.57) ^c	51.67 (46.25) ^b	61.67 (52.1) ^b	68.33 (56.07) ^b	76.67 (61.48) ^b
Turmeric oil at 62.5 µL	51.67 (46.25) ^b	56.67 (49.14) ^b	65.00 (54.1) ^b	68.33 (56.16) ^b	78.33 (62.48) ^b
Turmeric oil at 65 µL	61.67 (52.1) ^a	71.67 (58.18) ^a	81.67 (65.15) ^a	86.67 (69.1) ^a	90.00 (72.47) ^a
TNAU sweet flag at 0.8 mL	8.33 (17.13) ^e	8.33 (17.13) ^e	21.67 (28.1) ^e	41.67 (40.47) ^d	68.33 (56.1) ^{cd}
Control with acetone at 1 mL	0.00 (4.05) ^f	0.00 (4.05) ^f	0.00 (4.05) ^f	0.00 (4.05) ^e	0.00 (4.05) ^e
Untreated control	0.00 (4.05) ^f	0.00 (4.05) ^f	0.00 (4.05) ^f	0.00 (4.05) ^e	0.00 (4.05) ^e
SE	2.04	1.67	1.48	3.04	2.36
F value	175.74	306.76	476.02	109.89	176.52
p value (0.05)	0.000	0.000	0.000	0.000	0.000

DAT - days after treatment; SE – standard error, data represents means of three replications.

*Values in parenthesis are arcsine transformed values. Means in a column followed by same letter do not differ significantly at $p = 0.05$ based on Duncan's multiple range test.

Table 3. LC₅₀ and LC₉₅ of turmeric essential oil against *S. oryzae* – Fumigant toxicity

Treatment	Chi square	Regression equation	LC ₅₀ (ppm)	95 % Fiducial limit		LC ₉₅ (ppm)	95 % Fiducial limit	
				LL	UL		LL	UL
Turmeric oil	0.97	$Y = 17.55x - 26.27$	60.39	58.89	61.93	75.31	68.89	84.92

LL – lower limit; UL - upper limit.

Table 4. Contact toxicity of turmeric essential oil on mortality of *S. oryzae* adults

Treatments	1 DAT	2 DAT	3 DAT	4 DAT	5 DAT
Turmeric oil at 62 µL	1.67 (7.22) ^f	25.00 (30.26) ^e	50.00 (45.29) ^e	76.67 (61.48) ^d	86.67 (69.11) ^c
Turmeric oil at 64 µL	16.67 (24.43) ^d	40.00 (39.50) ^d	65.00 (54.06) ^d	86.67 (69.31) ^c	96.67 (76.1) ^b
Turmeric oil at 66 µL	35.00 (36.57) ^c	51.67 (46.25) ^c	76.67 (61.48) ^c	91.67 (73.95) ^b	95.00 (77.75) ^b
Turmeric oil at 68 µL	51.67 (46.25) ^b	66.67 (55.05) ^b	85.00 (67.62) ^b	95.00 (77.75) ^b	97.67 (82.24) ^b
Turmeric oil at 70 µL	61.67 (52.05) ^a	91.67 (73.95) ^a	91.67 (73.95) ^a	97.67 (82.24) ^a	99.13 (87.23) ^a
TNAU sweet flag at 0.8 mL	8.33 (17.13) ^e	8.33 (16.77) ^f	18.33 (25.67) ^f	45.00 (42.41) ^e	63.33 (53.1) ^d
Control with acetone at 1 mL	0.00 (4.05) ^f	0.00 (4.05) ^g	0.00 (4.05) ^g	0.00 (4.05) ^f	0.00 (4.05) ^e
Untreated control	0.00 (4.05) ^f	0.00 (4.05) ^g	0.00 (4.05) ^g	0.00 (4.05) ^f	0.00 (4.05) ^e
SE	2.042	2.36	1.54	1.96	3.26
F value	175.74	221.22	642.47	528.73	181.141
p value (=0.05)	0.000	0.000	0.000	0.000	0.000

DAT - days after treatment; SE - standard error; data represents means of three replications.

*Values in parenthesis are arcsine transformed values. Means in a column followed by same letter do not differ significantly at $p=0.05$ based on Duncan's multiple range test.

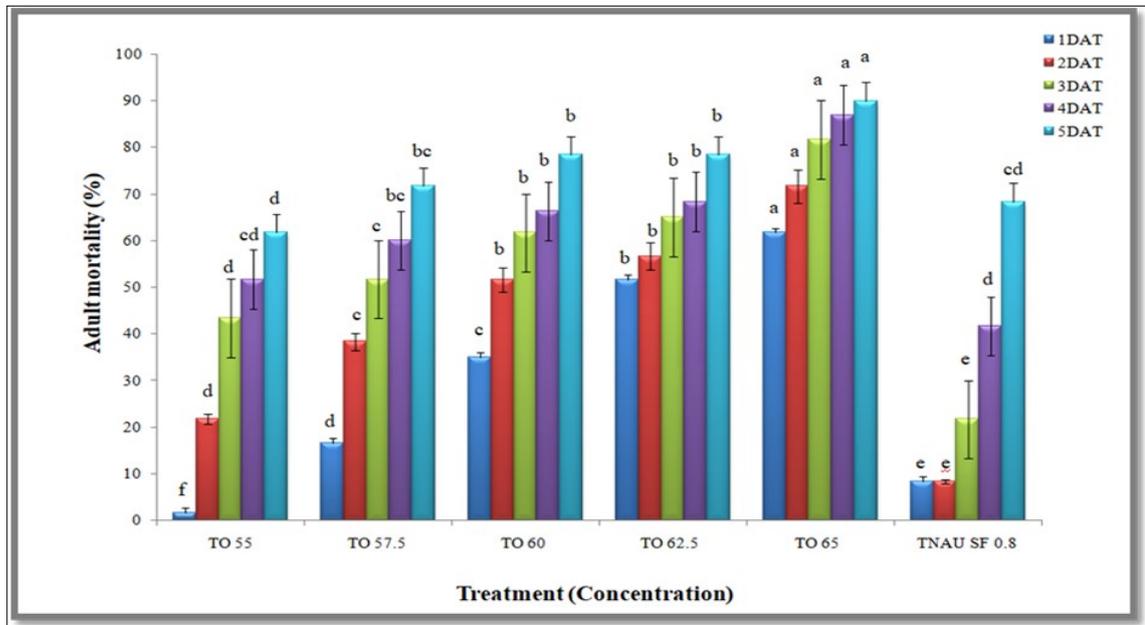


Fig. 1. Fumigant toxicity of turmeric essential oil on *S. oryzae* adults TO 55- turmeric oil at 55 μ L; TO 57.5- turmeric oil at 55 μ L; TO 60- turmeric oil at 60 μ L; TO 62.5- turmeric oil at 62.5 μ L; TO 65- turmeric oil at 65 μ L; TNAU SF0.8- TNAU sweet flag 0.8 mL; DAT- days after treatment.

Table 5. LC₅₀ and LC₉₅ of turmeric essential oil against *S. oryzae* - Contact toxicity

Treatment	Chi square	Regression equation	LC ₅₀ (ppm)	95% Fiducial limit		LC ₉₅ (ppm)	95% Fiducial limit	
				LL	UL		LL	UL
Turmeric oil	0.08	Y = 36.28 x - 60.82	65.61	64.3	66.59	75.68	70.74	80.96

LL – lower limit; UL - upper limit.

laying was entirely inhibited (0.00/20 seeds). The control with acetone and untreated control recorded 20.00 and 23.33 eggs, respectively, while the standard check (TNAU sweet flag formulation 0.8 mL) registered 7.00 eggs/20 seeds (Table 6) (Fig. 2). *C. longa* exhibited oviposition reduction to an extent of 72 % at a concentration of 5.2 mg/cm²(34).

At higher concentrations of turmeric oil viz, 68 and 70 μ L, the adult emergence was completely inhibited (0.00 %), while at lower doses, adult emergence was observed to the extent of 41.67 - 75.93 %. The interference by acetone in adult emergence was negligible (91.74 %) as against 95.83 % adult emergence in untreated control. Turmeric EO (20 % concentration) completely

suppressing the adult emergence of *T. castaneum* and its ability to reduce oviposition and egg hatching rate of *T. castaneum* to an extent of 72 and 80 % were also documented earlier (28, 35).

Conclusion

The present study demonstrates significant insecticidal potential of turmeric EO against the rice weevil, *S. oryzae*, a major pest of stored maize grains. High adult mortality was observed for turmeric EOs, with an LC₅₀ of 60.39 ppm and 65.61 ppm for fumigant and contact toxicity studies, indicating strong bioefficacy even at relatively low concentrations. Additionally, the

Table 6. Toxicity of turmeric essential oil on *S. oryzae* egg laying and adult emergence

Treatment	Eggs laid (per 20 seeds) *	Adult emergence (%) **
Turmeric oil at 62 μ L	8.33 (2.97) ^d	75.93 (60.62) ^c
Turmeric oil at 64 μ L	6.33 (2.61) ^c	79.37 (63.17) ^c
Turmeric oil at 66 μ L	4.00 (2.03) ^b	41.67 (40.00) ^b
Turmeric oil at 68 μ L	0.33 (0.88) ^a	0.00 (0.64) ^a
Turmeric oil at 70 μ L	0.00 (0.71) ^a	0.00 (0.64) ^a
TNAU sweet flag at 0.8 mL	7.00 (2.74) ^{cd}	47.62 (43.63) ^b
Control with acetone at 1 mL	20.00 (4.53) ^e	91.74 (73.44) ^d
Untreated control	23.33 (4.88) ^f	95.83 (79.88) ^d
SE	0.12	3.95
F value	351.73	119.99
p value (=0.05)	0.00	0.00

SE- standard error; data represents mean of three replications. *Values in parenthesis are square root transformed values. **Values in parenthesis are arcsine transformed values. Means in a column followed by same letter do not differ significantly at $p=0.05$ based on Duncan's multiple range test.

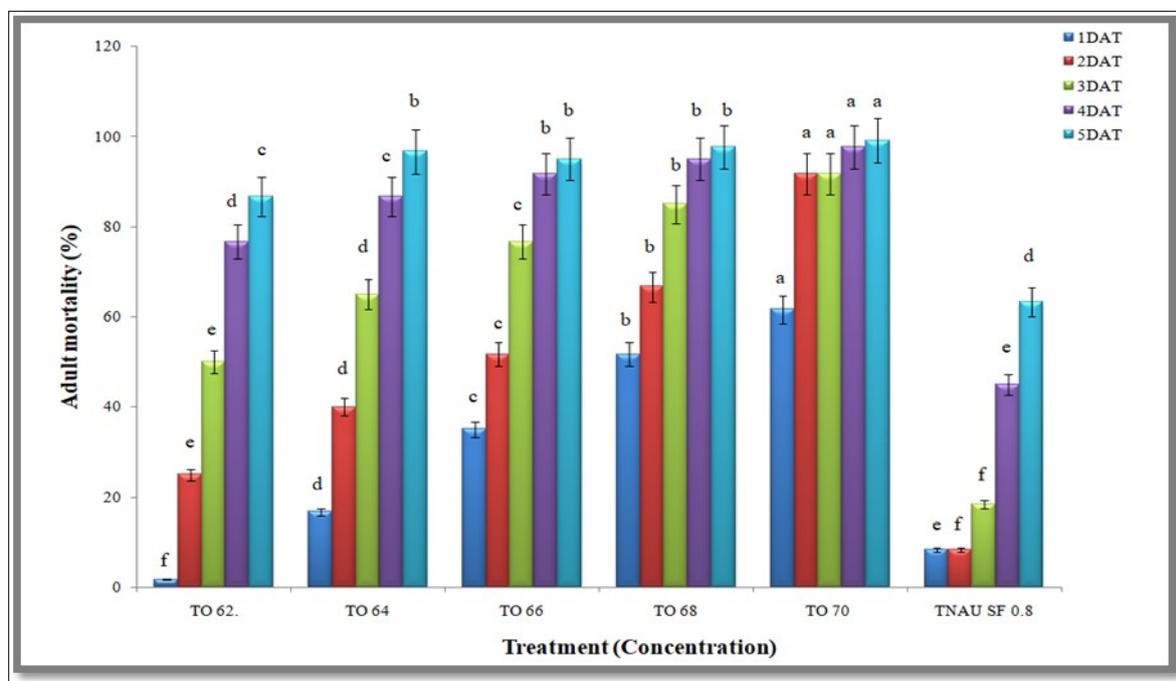


Fig. 2. Contact toxicity of turmeric essential oil on *S. oryzae* adults. TO 62- turmeric oil at 64 μ L; TO 66- turmeric oil at 68 μ L; TO 70- turmeric oil at 60 μ L; TNAU SF 0.8- TNAU sweet flag 0.8 mL; DAT-days after treatment.

complete inhibition of oviposition and adult emergence at 70 μ L highlights the oil's potential as a reproductive inhibitor. Given its high efficacy, eco-friendly nature and absence of toxic residues, turmeric EO presents a promising alternative to conventional synthetic insecticides for the sustainable management of stored grain pests. Further studies focusing on formulation development, mode of action and long-term storage effects are recommended to facilitate its practical application in grain storage systems.

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Authors' contributions

All authors contributed to the study conception, design and manuscript preparation. RAR carried out the experiments, recorded and analysed the data and wrote the manuscript. ST structured and supervised the experiments and edited the manuscript. JMN, NMS, DB, ET, RA, AS, PSS, VB and MA critically reviewed the manuscript. All authors provided feedback on earlier versions of the manuscript and have read and approved the final version.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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