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Bioactivity of Farnesol (a sesquiterpene compound) against the adult life parameters and reproductive potential of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae)

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Abstract

Egyptian cotton leafworm *Spodoptera littoralis* is native in Africa, but it is distributed in different parts of Europe and Asia. It is a dangerous herbivore damaging more than 90 field and ornamental crops of high economic importance. The current study was conducted to assess the impact of Farnesol on the most important parameters of adult performance and reproductive potential of this insect. The newly moulted larvae of 5th (penultimate) or 6th (last) instar larvae fed castor bean leaves previously treated with seven concentrations of Farnesol (400, 200, 100, 50, 25, 12.5 & 6.25 ppm) for 24 hr. The obtained results could be summarized as follows. Farnesol exhibited an adulticidal activity, since various adult mortalities were recorded. The adult morphogenesis was disrupted, since some adult deformities were observed. The total adult longevity and oviposition period were significantly shortened, but the pre-oviposition period was slightly prolonged. Farnesol exhibited an extended inhibitory effect on the oviposition efficiency, since oviposition rate was drastically regressed, in a dose-dependent course. Fecundity was detrimentally prohibited. Fertility was dramatically reduced. The embryonic development was remarkably retarded, since the incubation period of eggs was remarkably prolonged.

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Introduction

Cotton is one of the major sources of fiber. Besides the fibers, cotton plants produce a large amount of seeds (Cai *et al.*, 2010). These seeds are rich in protein and have been considered as a valuable source of oil and fodder (Bertrand *et al.*, 2005). The Egyptian cotton leafworm *Spodoptera littoralis* (Boisduval) is one of the key pests of the cotton plant and many field crops, as well as vegetable and ornamental crops (El-Aswad *et al.*, 2003; Abdel Rahman *et al.*, 2007; Shalaby *et al.*, 2020). This pest is distributed in many parts of Europe (Pineda *et al.*, 2007; Lanzoni *et al.*, 2012; EPPO, 2019), Asia Minor and the Middle East countries (El-Aswad, 2007; El-Sabrout, 2013; Azzouz *et al.*, 2014; Sut *et al.*, 2017). Also, this pest has a very wide host range of at least 90 plant species of economic importance belonging to 44 families (Kandil *et al.*, 2003). Many authors (El-Sinary *et al.*, 2008; El-Zoghby *et al.*, 2011; Bakr *et al.*, 2013; Benelli *et al.*, 2017; Al-Nagar *et al.*, 2020) reported that the number of attacked plants by *S. littoralis* increased recently to more than 112 species.

Although different control measures have been applied for the management of *S. littoralis* in Egypt, no satisfactory results can be obtained, most farmers, however, prefer using synthetic pesticides for obtaining fast results (Temerak, 2002; Abd El-Mageed and Shalaby, 2011; Ghoneim *et al.*, 2012; Fetoh *et al.*, 2015). Insect resistance is one of the major problems for the management of insect pests (Nkya *et al.*, 2014). Over the past 50 years, the indiscriminate and extensive uses of synthetic pesticides had led to the development of quick resistance of *S. littoralis* (Aydin and Gurkan, 2006; Mosallanejad and Smagghe, 2009; Rizk *et al.*, 2010) and other insects (Qayyum *et al.*, 2015) to many conventional insecticides. The development of *S. littoralis* resistance to the synthetic pyrethroids, carbamates, organophosphorus and other synthetic chemicals has been correlated with the development of cross-resistance in many cases (El-Zemaity *et al.*, 2003). In addition the resistance problem, synthetic insecticides cause toxic reactions in mammals (Arslan *et al.*, 2016) and other non-target organisms, such as parasitoids, predators and pollinators (Penagos *et al.*, 2005; Martínez *et al.*, 2018; Catae *et al.*, 2018). They may cause residual contamination of human foods (Abd El-Wahab, 2003; Liu *et al.*, 2011; Martínez *et al.*, 2014; Plata-Rueda *et al.*, 2019) and cause serious environmental problems (Wan *et al.*, 2015; Metayi *et al.*, 2015; Fiaz *et al.*, 2018; Eldesouky *et al.*, 2019). Also, application of synthetic pesticides is financially expensive (Pavunraj *et al.*, 2016). Therefore, searching for new alternative and safer agents for human health, economic animals and environment, is prerequisite need (Damala, 2011; Korrat *et al.*, 2012; Gill and Garg, 2014). Also, it is necessary to develop specific compounds for the pest control which are selective for the non-target organisms (Biondi *et al.*, 2012; Martínez *et al.*, 2019).

Over two decades, biopesticides have attracted a great attention of researchers and institutions for controlling different insect pests (Needham *et al.*, 2004: Anjum *et al.*, 2010; Alves *et al.*, 2014). Plant extracts and products constitute a promising and effective class of biopesticides and, therefore, they have now been established worldwide (Morey and Khandagle, 2020). Because the plant extracts have bioactive compounds, which are basically secondary metabolites (Zahoor *et al.*, 2020), it is difficult for the insects to develop resistance to these materials (Mounika *et al.*, 2020). The plant-based products have little drastic effects on human health, environment and parasites, predators and pollinators owing to their minimal residual activity (Regnault-Roger *et al.*, 2012; Morey and Khandagle, 2020). Use of these products reduces the accumulation of toxic chemicals in the environment (Maia and Moore, 2011; Rehman *et al.*, 2014).

With more than 80 000 plant compounds known to date (Christianson, 2017), terpenes constitute a large class in living organisms. Some well-known terpenes are primary metabolites either in plants (sterols, carotenoids and many hormones) or in insects (juvenile and molting hormones)(Beran *et al.*, 2019). The functions of monoterpenes and sesquiterpenes in plants include their activities as constitutive or induced defense compounds with direct or indirect impacts against herbivores or pathogens (Schnee *et al.*, 2006; Huffaker *et al.*, 2011; Chiu *et al.*, 2017). On the other hand, many monoterpenes, phenylpropenes and sesquiterpenes have reported to exhibit different biological activities against some economic insect pests as they can act as insecticidal compounds (Abdelgaleil *et al.*, 2008, 2009; Abbassy *et al.*, 2009; Abdelgaleil, 2010; Wu *et al.*, 2016; Saad *et al.*, 2018), insect growth regulators (Zahran and Abdelgaleil, 2011), antifeedants (Rajkumar *et al.*, 2019) and repellents (Watanabe *et al.*, 2005; Peixoto *et al.*, 2015). However, few studies examined the antifeedant and growth inhibitory effects of these plant products against *S. littoralis* (Gonzalez *et al.*, 1997; Zapata *et al.*, 2009; Ali *et al.*, 2017; Abdelgaleil *et al.*, 2020). Farnesol (3,7,11-trimethyl-2,6,10-dodecatrien-1-ol) and its derivatives have a necessary function in the signal transmission between plants and other organisms (Dancewicz *et al.*, 2010; Jamalian *et al.*, 2012).

It is a naturally occurring acyclic sesquiterpene alcohol formed from the dephosphorylation of farnesyl pyrophosphate, the key precursor of all sesquiterpenes (Khan and Sultana, 2011; Jung *et al.*, 2018). Farnesol was first isolated from *Vachellia farnesiana*, also known as acacia farnese and occurs in nature with four different isomers (de Araújo Delmondes *et al.*, 2019). It is a constituent of essential oils derived from various higher plants (Schulz, 2013; Azanchi *et al.*, 2014; Krupcik *et al.*, 2015; Eben *et al.*, 2020) and present in numerous herbs, such as lemon grass, rose, chamomile, pine, musk and citrus (Bakkali *et al.*, 2008; Shahnouri *et al.*, 2016). In microorganisms, Farnesol is known as a quorum-sensing molecule that can remarkably increase the extracellular polymeric substances production by promoting polysaccharide biosynthesis (Wroblewska-Kurdyk *et al.*, 2020). At ordinary temperatures, Farnesol is a liquid oil with a sweet odor, and is thus employed in perfumery and cosmetic applications (Schulz, 2013; Lapczynski *et al.*, 2008), as well as in the food industry as a flavoring agent (de Araújo Delmondes *et al.*, 2019). Medically, Farnesol has been reported to regulate the inflammatory responses and has a beneficial effect with edema, allergic asthma, gliosis, skin tumorigenesis, colon oncogenesis, and the immune response system (Qamar *et al.*, 2012; Santhanasabapathy *et al.*, 2015). Farnesol has been recognized to play a necessary role in apoptosis, cell signaling, and proliferation (Hornby *et al.*, 2001; Shea and Del Poeta, 2006; Lorek *et al.*, 2008). For more detail, see Lee *et al.* **(**2015**)**; Jung *et al.* (2018) and Youssefi *et al.* (2020). However, its chemical and biological activity has been reviewed (Gupta *et al.*, 2018). In respect of the pest control, Farnesol was reported as a natural pesticide for mites and several insects (Awad *et al.*, 2013; Schulz, 2013). It can disrupt the normal metabolic function and therefore, affects various life processes of the insects. For example, Farnesol showed a significant dose-dependent increase in mortality of the 4^{th} instar larvae of *Agrotis ipsilon* (Awad, 2012). Also, an inhibitory effect of Farnesol on the food consumption and utilization, digestive enzymes and fat body proteins of the desert locust *Schistocerca gregaria* had been reported by Awad *et al.* (2013). Wróblewska-Kurdyk *et al.* (2020) evaluated the effect of Farnesol on the host-plant selection behaviour of the peach potato aphid *Myzus persicae*. Recently, Ghoneim *et al.* (2020) recorded an insecticidal activity of Farnesol and different drastic effects on growth, development and morphogenesis of *S. littoralis*. The current study was conducted to assess the impact of Farnesol on the most important parameters of adult performance and reproductive potential of *S. littoralis*.

Materials and methods

The insect

In the laboratory of Insect Physiology, Faculty of Science, Al-Azhar University, Cairo, Egypt, a culture the Egyptian cotton leaf worm *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) was established under controlled conditions (27±2ºC, 65±5% R.H., photoperiod 14 h L and 10 h D). Rearing procedure was carried out according to Ghoneim (1985) and improved by Bakr *et al.* (2010). Egg masses were kept in Petri dishes until hatching. The newly hatched larvae were transferred into glass containers and provided daily with fresh castor bean leaves *Ricinus communis*.

The developed pupae were collected and placed in clean jars provided with a layer of moistened saw dust. All jars were provided with branches of fresh Tafla plant, *Nerium oleander*, as oviposition sites.

The emerged adults were provided with 10% honey solution on a cotton wick as a food source. Moths were allowed to mate and lay eggs on branches. The egg patches were collected every day, and transferred into Petri dishes for the next generation.

The tested compound and larval treatment

The tested Farnesol in the present study was purchased from ABCR GmbH, Karlsruhe, Germany. Its common name is Farnesol 96% (mixture isomers) with the chemical name: [(2*E*,6*E*)-3,7,11-trimethyldodeca-2,6,10-trien-1-ol] and Formula: $C_{15}H_{26}O$ Five ml of Tween 60 were added (as emulsifier) to 5 ml of ethyl alcohol (95%). Then, these solvents were mixed thoroughly with 5 ml of the compound. For obtaining a stock solution, 90 ml of distilled water was added to the mixture for preparing a concentration of 4.8 % Farnesol emulsion (Awad *et al*., 2013).

The stock solution was diluted with distilled water in volumetric flasks for preparation of a series of concentrations: 400.00, 200.00, 100.00, 50.00, 25.00, 12.50 & 6.25 ppm.The newly moulted larvae of 5^{th} (penultimate) or 6^{th} (last) instar larvae were allowed to feed castor bean leaves previously treated with the seven concentrations of Farnesol for 24 hr. For this purpose, discs of the fresh leaves were dipped in each concentration for 5 minutes and air dried before introduction to larvae under the aforementioned laboratory conditions. Control larvae received leaf discs after dipping in Tween 60 and alcohol (95 %) solution for 5 minutes. Ten replicates of treated and control larvae (one larva/replicate) were kept separately in glass vials. Then, the most important parameters of adult performance and reproductive potential were recorded just after the adult emergence.

The most important adult life parameters

Adulticidal activity

Mortality of the successfully emerged adults was determined in %.

Adult morphogenesis

The imperfectly emerged adult females had been calculated in % and recorded in photos.

Adult longevity and its compartments

The most important compartments of the longevity of adult females were measured in days: pre-oviposition (gonad maturation) period, oviposition period (reproductive life-time) and post-oviposition period. With regard to *S. littoralis*, the post-oviposition period usually elapses only few hours, therefore, no post-oviposition period was recorded.

Criteria of the reproductive potential

The emerged adult females from each treatment were kept separately in glass jars (1 L) and coupled with normal adult males (1: 2) of the same age obtained from the main culture. Each jar was provided with sterilized cotton pieces soaked in 10% honey solution for feeding, and provided with clean fresh *Nerium oleander* branch, as an oviposition site. The egg-patches were collected daily, and carefully transferred into Petri dishes to count the eggs.

The oviposition efficiency

The oviposition efficiency was denoted by the oviposition rate which was calculated as follows:

Number of laid eggs per ♀/reproductive lifetime (in days).

The reproductive capacity

The most important parameters of reproductive capacity are fecundity and fertility.

Fecundity

The laid eggs were counted for calculating the number of eggs per female.

Fertility

The hatchability was usually expressed in hatching percentage of the laid eggs.

Sterility index was calculated according to Toppozada *et al.* (1966) as follows:

Sterility Index = 100 – [(a b / A B) × 100]

Where: a: mean number of eggs laid per female in the treatment. b: percentage of hatching in the treatment. A: mean number of eggs laid per female in the controls. B: percentage of hatching in the controls.

Incubation period

Just after the oviposition, eggs were kept in Petri dishes under the previously mentioned laboratory conditions. The eggs were observed until hatching to measure the incubation period (in days).

Statistical analysis of data

Data obtained were analyzed by the Student's *t*-distribution, and refined by Bessel correction (Moroney, 1956) for the test significance of difference between means using GraphPad InStat© v. 3.01 (1998).

Results

Effect of Farnesol on the most important adult life parameters of S. littoralis

After treatment of penultimate (5th) instar larvae with seven concentrations of Farnesol, data of the most important parameters of adult performance were arranged in Table (1). Depending on these data, no adults emerged after larval treatment with the higher two concentrations levels. Adulticidal activity of Farnesol was recorded only at the subsequent two concentrations (40.00 & 14.29% adult mortality, at 50 & 25 ppm, respectively, compared to 0% mortality among control adult moths).

After treatment of last (6th) instar larvae with Farnesol concentration levels, data of adult performance were assorted in Table (2). Depending on these data, no adults emerged after larval treatment with the highest concentration level. With exception of the lower two concentrations, other concentrations caused various adult mortalities, in a dose-dependent course (100, 33.33, 25.00 & 16.67% adult mortality, at 200, 100, 50 & 25 ppm, respectively, *vs.* 0% mortality of control adult moths).

Table 1. Affected adult performance of *S. littoralis* after treatment of the newly moulted penultimate (5th) instar larvae with Farnesol.

Conc. (ppm)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days ± SD)		
			Ovarian maturation period	Reproductive life-time	Total longevity
400.00	---	---	---	---	---
200.00	---	---	---	---	---
100.00	0.00	0.00	3.00* d	6.00* d	9.00* d
50.00	40.00	40.00	2.33±0.05 a	5.24±0.58 d	7.56±0.63 d
25.00	14.29	28.57	2.36±0.48 a	6.29±0.45 d	8.67±0.92 d
12.50	0.00	11.11	2.24±0.51 a	7.11±0.67 d	9.33±0.68 d
6.25	0.00	0.00	2.33±0.33 a	7.67±0.44 d	10.01±0.76 c
Control	0.00	0.00	2.22±0.04	8.67±0.52	10.83±0.41

Conc.: concentration levels. ---: no emerged adults. *: only one adult female emerged. Mean ± SD followed with letter: a: insignificant (P >0.05), b: significant (P<0.05), c: highly significant (P<0.01), d: extremely significant (P<0.001).

After treatment of 5th instar larvae with Farnesol, the adult morphogenesis was impaired, since some deformed adults were observed at certain concentrations (40.00, 28.57 & 11.11% malformed adults, at 50, 25 & 12.5 ppm, respectively, *vs.* 0% deformity of control adults, see Table 1). After treatment of 6th instar larvae with Farnesol, no adults survived at the higher two concentrations. With exception of the lowest concentration level, increasing percentage of the deformed adults paralleled to the increasing concentration (33.33, 25.00, 14.29 & 12.50% deformed adults, at 100, 50, 25 & 12.50 ppm, respectively, vs. 0% deformity of control adults, see Table **2**). As seen in Fig. (1), the malformed adult moths could be described as adults with curled wings, atrophied mouth parts and pupal exuvia attached to the adult abdomen.

After treatment of 5th instar larvae with Farnesol, the total adult longevity and its major compartments were listed in Table (1). As clearly shown in this table, the total adult longevity was significantly shortened in no certain trend (9.00, 7.56±0.63, 8.67±0.92, 9.33±0.68 & 10.01±0.76 days of treated adults, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 10.83±0.41days of control adults). One of the major compartments of adult longevity is pre-oviposition (ovarian maturation) period. As obviously shown in the same table, this period was slightly prolonged, with exception of the odd female adult emerged at 100 ppm. On the other hand, the oviposition period (reproductive life-time) was remarkably shortened (6.00, 5.24±0.58, 6.29±0.45, 7.11±0.67 & 7.67±0.44 days of treated adults, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 8.67±0.52 days of the control adult females).

Table 2. Affected adult performance of *S. littoralis* after treatment of the newly moulted last (6th) instar larvae with Farnesol.

Conc. (ppm)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days ± SD)		
			Ovarian maturation period	Reproductive life-time	Total longevity
400.00	---	---	---	---	---
200.00	100.00	---	---	---	---
100.00	33.33	33.33	2.89±0.17 d	5.67±0.41 d	8.56±0.58 d
50.00	25.00	25.00	2.33±0.09 b	6.33±0.48 d	8.56±0.56 d
25.00	16.67	14.29	2.33±0.04 b	6.76±0.17 d	8.56±0.20 d
12.50	0.00	12.50	2.29±0.15 a	7.14±0.45 d	9.46±0.60 c
6.25	0.00	0.00	2.24±0.05 a	7.67±0.52 d	9.95±0.56 a
Control	0.00	0.00	2.19±0.08	8.55±0.39	10.67±0.93

Conc.,---, a, b, c, d: see footnote of Table 1.

After treatment of 6th instar larvae with Farnesol concentration levels, data of the total adult longevity and its compartments were distributed in Table (2). On the basis of these data, a similar trend of total longevity was detected, since the adult longevity was drastically shortened duration (8.56±0.58, 8.56±0.56, 8.56±0.20, 9.46±0.60 & 9.95±0.56 days of treated adults, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 10.67±0.93 days of control adults). Also, the oviposition period was found in a similar trend of shortened duration (5.67±0.41, 6.33±0.48, 6.76±0.17, 7.14±0.45 & 7.67±0.52 days of treated adults, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 8.55±0.39 days of the control adult females). In contrast, the pre-oviposition period was significantly or slightly prolonged, depending on the Farnesol concentration (2.89±0.17, 2.33±0.09, 2.33±0.04, 2.29±0.15 & 2.24±0.05 days of the treated adults, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 2.19±0.08 days of the control adult moths).

Effect of Farnesol on the reproductive potential of S. littoralis

After treatment of 5th instar larvae with Farnesol, data of Table (**3**) revealed that this compound exhibited an extended inhibitory effect on the oviposition efficiency, since oviposition rate was drastically regressed, in a dose-dependent course (46.33, 80.11±1.05, 98.90±3.36, 109.84±7.84 &117.48±5.37 of the treated adult females, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 183.07±18.58 of the control adult females). A similar inhibitory effect of this compound was detected on the oviposition efficiency, after treatment of 6th instar larvae

(32.85±1.91, 39.94±2.58, 52.09±3.04, 73.39±3.98 & 105.46±4.16 of treated adult females, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 184.47±12.96 of the control adult females, see Table 4).

After treatment of 5th instar larvae with Farnesol, data of the reproductive capacity were distributed in Table (3). Depending on these data, fecundity (mean number of egg/♀) was detrimentally prohibited, in a dose-dependent manner (278.00, 424.67±14.79, 632.20±42.67, 782.50±34.43 & 870.43±28.94 eggs/treated♀, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, vs. 1579.50±86.93 eggs/control♀).

Another informative parameter of the reproductive capacity is fertility (hatching% of laid eggs or egg viability) which was dramatically reduced (39.03, 47.87±0.47, 56.19±1.87, 60.33±1.84 & 62.87±1.45 % hatching eggs laid by treated adult females, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 94.02±0.84% hatching eggs laid by control adult females). It may be important to estimate the sterility index which increased proportional to the increasing concentration of Farnesol (for detail, see Table 3).

Table 3. Disrupted oviposition efficiency and reproductive potentiality of *S. littoralis* after treatment of newly moulted penultimate (5th) instar larvae with Farnesol.

Conc. (ppm)	Oviposition rate (mean ± SD)	Reproductive capacity			Incubation period (mean days ± SD)
		Fecundity (mean egg No. ± SD)	Fertility (%)	Sterility index (%)	
400.00	---	---	---	---	---
200.00	---	---	---	---	---
100.00	46.33* d	278.00* d	39.03* d	93.02	4.00* d
50.00	80.11±1.05 d	424.67±14.79 d	47.87±0.47 d	86.92	4.67±0.58 d
25.00	98.90±3.36 d	632.20±42.67 d	56.19±1.87 d	77.15	4.40±0.55 d
12.50	109.84±7.84 d	782.50±34.43 d	60.33±1.84 d	69.63	4.00±0.63 d
6.25	117.48±5.37 d	870.43±28.94 d	62.87±1.45 d	64.79	3.57±0.53 d
Control	183.07±18.58	1579.50±86.93	94.02±0.84	--	2.16±0.41

Conc., ---, a, b, c, d: see footnote of Table 1. *: one female only.

As clearly shown in Table (4), treatment of 6th instar larvae with Farnesol was found to affect the reproductive capacity. Fecundity was drastically prohibited, in a dose-dependent manner (180.00±2.73, 252.00±6.56, 325.22±5.83, 537.36±26.10 & 781.71±30.98 eggs/treated♀, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 1593.83±58.64 eggs/control♀). Also, fertility was severely reduced, in a dose-dependent course (27.24±0.36, 34.91±0.70, 41.09±1.46, 55.93±1.58 & 71.51±2.07% hatching eggs laid by treated adult females, at 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 93.97±0.66% hatching eggs laid by control adult females). The sterility index increased with the increasing concentration. In insects, the incubation period of eggs can be used as a valuable indicator of the embryonic developmental rate, i.e., longer period usually denote slower rate of development and *vice versa.* After treatment of 5th instar larvae with Farnesol, the embryonic developmental rate was remarkably suppressed, since the incubation period of eggs was significantly prolonged (4.00, 4.67±0.58, 4.40±0.55, 4.00±0.63 & 3.57±0.53 days of eggs laid by treated females, at 100, 50, 25, 12.5 & 6.25 ppm, *vs.* 2.16±0.41days of eggs laid by control females, Table 3). A similar retarded embryonic development was indicated by significantly prolonged incubation period of eggs laid by females, after treatment of 6th instar larvae with Farnesol (for detail, see Table 4).

Discussion

Influenced adult life parameters of S. littoralis by Farnesol

Adulticidal activity of Farnesol

Some recent studies have examined the adulticidal activities of plant extracts against various insects, such as the leaf-purple plant extracts of *Ageratum conyzoides* against the mosquito *Aedes aegypti* (Pintong *et al*., 2020); *Thespesia populnea* bark extract against the rice weevil *Sitophilus oryzae* (Viveka and Merin Emerald, 2020); among the extracts of four plants against the beetle *Tribolium castaneum*, the maximum adult mortality was caused by the highest dose of *Zingiber officinale* extract at 10 days exposure interval (Atta *et al*., 2020); among ten essential plant oils, garlic oil (*Allium sativum*) exhibited the most potent adulticidal activity but Rosemary oil (*Rosmarinus officinalis*) showed the least adulticidal activity against the granary weevil *Sitophilus granarius* (Zohry *et al*., 2020). On the other hand, few studies have examined the toxicities of plant compounds on adults of insects. According to these studies, Thymoquinone (among eleven terpene ketones) exhibited the highest toxicity against adults of the maize weevil *Sitophilus zeamais* (Herrera *et al*., 2015). Saad *et al*. (2018) evaluated six monoterpenes and two phenylpropenes against *S. oryzae* adults.

The tested compounds showed varying degrees of contact toxicity, with *trans*-cinnamaldehyde being the most potent compound, followed by (−)-menthone and eugenol. The sesquiterpene compound, Nerolidol, exhibited an adulticidal activity against *S. littoralis*, after treatment of 5th instar larvae only with 100 ppm or after treatment of 6th instar larvae with the higher concentrations (Hamadah *et al*., 2020).

Table 4. Disrupted oviposition efficiency and reproductive potentiality of *S. littoralis* after treatment of newly moulted last (6th) instar larvae with Farnesol.

Conc. (ppm)	Oviposition rate (mean ± SD)	Reproductive capacity			Incubation period (mean days ± SD)
		Fecundity (mean egg No. ± SD)	Fertility (%)	Sterility index (%)	
400.00	---	---	---	---	---
200.00	---	---	---	---	---
100.00	32.85±1.91 d	180.00±2.73 d	27.24±0.36 d	96.85	5.33±0.58 d
50.00	39.94±2.58 d	252.00±6.56 d	34.91±0.70 d	94.34	4.67±0.58 d
25.00	52.09±3.04 d	325.22±5.83 d	41.09±1.46 d	91.40	3.75±0.50 d
12.50	73.39±3.98 d	537.36±26.10 d	55.93±1.58 d	80.66	3.67±0.52 d
6.25	105.46±4.16 d	781.71±30.98 d	71.51±2.07 d	64.04	3.29±0.49 c
Control	184.47±12.96	1593.83±58.64	93.97±0.66	--	2.33±0.52

Conc., ---, a, b, c, d: see footnote of Table 1.

The camphor and menthol exhibited adulticidal effects against the beetles *Callosobruchus maculates* and *Triboliun confusum*. *C. maculatus* was more susceptible than *T. confusum* to the used compounds (Ahmady *et al*., 2020). Results of the present study were, to a great extent, in agreement with the previously reported results, since Farnesol exhibited an adulticidal activity against *S. littoralis* after treatment of 5th instar larvae with certain concentrations or in a dose-dependent course after treatment of 6th instar larvae.

In the present study, the adulticidal effect of Farnesol against *S. littoralis* could be explained by the retention and distribution of the compound in the insect body as a result of direct and rapid transport *via* the haemolymph to other tissues, and then into different tissues of the successfully emerged adults, and/or by lower detoxification capacity of adults against the tested compound (Osman *et al*., 1984; Smagghe and Degheele, 1992). Also, an extended toxic effect of Farnesol might be due to the disturbance of enzymatic pattern and/or hormonal hierarchy in adults of *S. littoralis* (Kartal *et al*., 2003). Because the adult life in insects depends on healthy immature stages, the digestive disorders, such as starvation, disturbance in metabolism, degeneration of peritrophic membranes and accumulation of faecal materials at the hind gut may be the cause of untimely adult mortality, as recorded for Farnesol against *S. littoralis* adults in the current study (Soltani, 1984). Also, the adult mortality may be explicated by a latent inhibitory effect of Farnesol on the feeding leading to continuous starvation and subsequently death (Ghoneim *et al.*, 2000) or adverse effect on the homeostasis leading to increasing loss of body water and desiccation and subsequently death (Amer *et al.*, 2004).

Anti-morphogenic activity of Farnesol

As reported by many authors (Jeyasankar *et al.*, 2011; Lingampally *et al.*, 2013; Nogueira *et al.*, 2014; Scapinello *et al.*, 2014; Bhushan *et al.*, 2016; Chinnamani *et al.*, 2016), different plant extracts or products exhibited deleterious effects on the adult morphogenesis of several insects, as appeared in various morphological malformations either of the whole body or some of its features. In the present study, treatment of 5th instar larvae of *S. littoralis* with Farnesol resulted in disruption of the adult morphogenesis. The anti-morphogenic activity of Farnesol could be detected by the metamorphosis of some malformed adults at certain concentrations. Moreover, percentage of the deformed adults increased with the increasing concentration, after treatment of 6th instar larvae.

Results of the current investigation were, to a great extent, in corroboration with some reported results of the adult deformities after larval treatments with certain plant products. For example, treatment of the 5th and 6th instar larvae of the beetle *Tribolium confusum* with Andrographolide (a terpenoid) resulted in the production of some deformed adults (Lingampally *et al.*, 2013). Larval treatment of *Spodoptera litura* and *Spodoptera exigua* with Pogostone resulted in some deformities of the adult moths (Huang *et al.*, 2014). Feeding of 2nd instar larvae of *S. litura* on fresh food treated with Allyl isothiocyanate resulted in the metamorphosis of some deformed adults (Bhushan *et al.*, 2016). Topical application of Farnesol onto the newly moulted 5th instar nymphs of the bug *Dysdercus koenigii* led to the metamorphosis of nymphs into adults with malformed wings (Kumar and Gupta, 2017). Sosa *et al.* (2019) isolated some Sesquiterpene lactone compounds from *Vernonanthura nebularum* and evaluated their effects on *Spodoptera frugiperda*. Treatment of *S. frugiperda* larvae with compounds 1, 2 and 3 caused serious wing malformations in adults. Recently, feeding of *S. littoralis* 2nd instar larvae on plant leaves previously dipped in Nano-chitosan solution led to the production of deformed adult moths (Marouf, 2020). After feeding of the newly moulted larvae of 5th or 6th instar larvae of *S. littoralis* on castor bean leaves, previously treated with Nerolidol, an anti-morphogenic activity of this compound against the adult moths, could be confirmed by the production of some malformed adults at the higher concentrations (Hamadah, *et al.*, 2020).

To interpret the anti-morphogenic activity of Farnesol against the adult moths of *S. littoralis*, in the present investigation, this sesquiterpene compound might exert a disturbing effect on the hormonal balance for perfect adult metamorphosis program, in particular the disturbance of ecdysteroid titer which led to changes in the lysosomal enzyme activity causing overt morphological abnormalities (Josephrajkumar *et al.*, 1999; Cespedes *et al.*, 2013). Another suggestion could be accepted, where the metabolites of Farnesol could inhibit the chitin synthase (Cohen and Casida, 1980), the DNA synthesis and/or inhibit the facilitated diffusion and active transport across cell membranes of nucleosides and amino acids (Mayer *et al.*, 1988).

Disturbed adult longevity by Farnesol

Shortened total adult longevity

After the attainment of sexual maturity, insects often show degenerative changes in some tissues and organs which can be called 'senility' or 'aging'. In insects, the affected adult longevity can be considered as an informative indicator for the adult aging, i.e., prolongation of longevity may denote a delay of aging and *vice versa*, although the death is usually the destiny of all creatures (Ghoneim and Bakr, 2018; Ghoneim and Al-keridis, 2019). After treatment of 5th instar or 6th instar larvae of *S. littoralis* with Farnesol, in the present study, the total adult longevity had been significantly shortened.

Fig. 1. Adult deformities of *S. littoralis* after treatment of 5^{th} or 6^{th} instar larvae with Farnesol. (A) Normal adult moth. (B & C): Adult moths with deformed wings, atrophied mouth parts and pupal exuvium attached to abdomen. (D & E): Adult moths with curled wings.

This result was in accordance with some reported results of shortened total longevity of some insects after larval treatment with certain plant extracts or products, such as domestic mosquito *Culex pipiens* after treatment of 4^{th} instar larvae with Saponin (Djeghader *et al.*, 2018); the brown planthopper *Nilaparvata lugens* after treatment of nymphs with Jasmonic acid (plant growth regulator)(Senthil-Nathan *et al.*, 2009); injection of higher doses of Abscisic acid (plant growth regulator) into the haemocoel of *G. mellonella* larvae resulted in shortened adult longevity (Er and Keskin, 2015). Recently, feeding of the newly moulted larvae of 5^{th} or 6^{th} instar larvae of *S. littoralis* on castor bean leaves, previously treated with nerolidol, led to remarkably shortened total longevity of the successfully emerged adults (Hamadah, *et al.*, 2020). Also, treatment of the bug *Nezara viridula* nymphs with certain concentrations of ethanolic extract of *Taxodium distichum* caused considerable shortening of the total longevity of males and females of (El-Gendy, 2020).

The total adult longevity of *S. littoralis* was shortened after treatment of 4^{th} instar larvae with LC_{50} of chloroform/ methanol extract of *Conyza dioscoridis* (Matloub *et al.*, 2021).

To explicate the remarkably shortened adult longevity of *S. littoralis* after treatment of larvae with Farnesol, in the current study, some conceivable scenarios could be suggested. (1) Farnesol might exert a general accelerating action on these adult females to quickly pass aging ending in death. However, this result can be interpreted by the accumulation of toxic xenobioties in the adult body which upsets a complicated balance of factors, such as absorption, excretion and detoxification (Abdel-Aal, 1996). (2) Shortened longevity (or acceleration of adult aging) of *S. littoralis* might be due to the action of Farnesol on the hormonal regulation because a close relation between certain hormones and adult longevity was reported in other insects, such as *Drosophila melanogaster* (Carbone *et al*., 2006; Toivonen and Partridge, 2009; Chamseddin *et al*., 2012; Yamamoto *et al*., 2013). In this fly, representatives of peptide hormone, lipophilic hormones and bioactive amines have been shown to modulate longevity by manipulations that directly decrease the hormone production, through inactivating mutations in hormone receptors or their downstream targets (Clancy *et al*., 2001; Simon *et al*., 2003; Broughton *et al*., 2005) or by polymorphic alterations in the genes required for the hormone production (Carbone *et al*., 2006). (3) As reported by Yamamoto *et al*. (2013), juvenile hormone (JH) controls aging, to some extent, because it directly affects mechanisms of somatic survival. Therefore, Farnesol might affect the JH level and/or functions leading to the shortening of adult longevity of *S. littoralis,* in the present study.

However, the exact mode of action of Farnesol on the biochemical sites in adults of *S. littoralis* is unknown until now. Also, more information on the adult endocrine system of *S. littoralis* is required to clarify the mechanism by which Farnesol can affect the adult longevity. (4) In insects, the fat body serves many important functions (Arrese and Soulages 2010) and it is therefore not surprising that longevity mechanisms may occur within the fat body (Hwangbo *et al*., 2004). Thus, Farnesol might adversely affect the fat bodies resulting in shortened longevity of *S. littoralis* adults.

Shortened oviposition period

To the best of our knowledge, the available literature has no results of effects of plant compounds on the oviposition period in adult females of insects except a recent study of Hamadah *et al*. (2020) who recorded significantly shortened oviposition period of *S. littoralis* after treatment of the newly moulted larvae of 5^{th} or 6^{th} instar larvae with nerolidol. In the present study, our finding coincided with this result, because treatments of the 5^{th} instar or 6^{th} instar larvae of *S. littoralis* with Farnesol led to significantly shortened oviposition period (reproductive life-time) of the successfully mated female moths. This result could be interpreted by an enforcing effect of Farnesol on the adult females of *S. littoralis* to quickly lay eggs during a very short time interval to avoid this toxic xenobiotic factor (Tanani and Ghoneim, 2017). However, the exact mechanism of this enforcing action is still unknown to us.

Prolonged pre-oviposition period

In the present study, treatment of 5^{th} instar or 6^{th} instar larvae of *S. littoralis* with Farnesol resulted in slightly prolonged pre-oviposition (may be ovarian maturation). This result was in agreement with that result reported for the locust *Locusta migratoria* by Abdellaoui *et al*. (2009), since treatment with Gibberellic acid, a plant growth regulator, led to the prolongation of the pre-oviposition period. Also, Hamadah, *et al*. (2020) recorded a general prolongation of the pre-oviposition period of the successfully emerged adults of *S. littoralis* after treatment of the newly moulted larvae of 5^{th} or 6^{th} instar larvae with nerolidol.

It may be important to point out that the prolongation of pre-oviposition period in insects can be used as a good indicator of the retarded ovarian maturation or slow rate of the maturation. For some detail, many lepidopterous insects have a relatively short adult stage, or even non-feeding adults. In these insects, adult female emerges with most of her eggs ready to be fertilized and oviposited within hours. This life style constrains these insects to a program of ovarian organogenesis and/or follicle development that must occur at stages earlier than the adult (Ghoneim and Al-keridis, 2019). The determinants required for germ cell formation are similar in moths, but there are spatial differences in their localization within the presumptive germ band (Richard *et al.*, 1998). In the light of this information, delaying or retarding effect of Farnesol on the ovarian maturation (pre-oviposition period) in *S. littoralis* may be understood by the influenced germ band or the number of germ cells formed in the embryo (Hodin and Riddiford, 1998).

In addition, the ovarian development in insects is known to be under endocrine control (Kaur and Rup, 2002). The retarded ovarian development in *S. littoralis* by Farnesol, in the current study, appears to be related to interference with the inhibition of ecdysteroid production, since very small amounts of ecdysone, or ecdysteroids, exist in the developing ovaries of adult females (Acheuk *et al.*, 2012). These ecdysteroids remarkably increase toward the end of terminal oocyte maturation, and passed to the eggs at the beginning of embryonic development. In locusts, as an example, the ovarian ecdysteroid content sharply declines at time of oviposition. This phenomenon occurs regularly during the successive ovarian cycles. Thus, occurrence of considerable amount of ecdysteroids in the freshly laid eggs suggests a transfer of maternal ecdysteroids into eggs for regulating the embryonic development (Abdellaoui *et al.*, 2015). However, the exact mode of retarding action of Farnesol on the ovarian maturation rate of *S. littoralis*, in the present study, is unfortunately not available right now. The interference of this Sesquiterpene compound with the hormonal regulation of this crucial physiological process needs further investigation in the future.

Disrupted reproductive potential of S. littoralis by Farnesol

Prohibited oviposition efficiency

Few studies investigated the effects of plant compounds on the oviposition efficiency of insects. In the present study, Farnesol exhibited an extended inhibitory effect on the oviposition efficiency of *S. littoralis*, since the oviposition rate was drastically regressed, in a dose-dependent course, after treatment of 5th instar or 6th instar larvae. This finding coincided with a recent reported result of Hamadah *et al.* (2020) who recorded deleterious inhibition of the oviposition efficiency of the same insect after treatment of the newly moulted larvae of 5th or 6th instar larvae with Nerolidol (a sesquiterpene compound). Our result was, also, in corroboration with some reported results of reduced oviposition efficiency of some insects by certain plant products or extracts, such as *S. oryzae* by Eugenol (major constituent of EO from *Cinnamomum tamala*) (Chaubey, 2016) and the melon worm *Diaphania hyalinata* by Rotenone (Silva *et al.*, 2016). Recently, the oviposition of *Drosophila suzukii* was reduced by citral, eugenol and lemongrass oil (Eben *et al.*, 2020). For the interpretation of inhibited oviposition efficiency of *S. littoralis* adults females after larval treatment with Farnesol, in the present study, it is important to mention that the reproduction in insects is mainly controlled by corpus allatum hormone (JH), which is also responsible for the protein metabolism which specifically needed for the egg maturation (Ghoneim *et al.*, 2014). On the other hand, ecdysteroids have an essential role in controlling the processes involved in insect reproduction, i.e., vitellogenesis, ovulation of matured eggs and spermatocyte growth (Wigglesworth, 1984; Hagedorn, 1985). The prohibited oviposition efficiency of *S. littoralis*, in the current study, may be understood by the inhibition of ovarian DNA synthesis or interference of Farnesol with vitellogenesis *via* certain biochemical processes. However, this sesquiterpene compound might exert a reverse action to those exhibited by the ecdysteroids which induce the neurosecretory cells to release a myotropic ovulation hormone (Smagghe *et al.*, 1996; Parween *et al.*, 2001).

Perturbed reproductive capacity

Prohibited fecundity

As reported in the available literature, various different plant products had been reported to prohibit the fecundity (mean number of egg/♀) of different insects. For example, fecundity of *Schistocerca gregaria* was significantly inhibited after treatment of the newly moulted last (5^{th}) instar nymphs with Farnesol (Awad *et al.*, 2013). The adult fecundity of *Aphis* sp. was remarkably reduced, in a dose-dependent course, after treatment with jasmonic acid (a plant growth regulator) (Gong *et al.*, 2010). Fecundity of *G. mellonella* was inhibited after injection of higher doses of Abscisic acid (a plant growth regulator) into the haemocoel of larvae (Er and Keskin, 2015). A deleterious reduction in fecundity of the mosquito *Culex pipiens* had been recorded after treatment of 4^{th} instar larvae with Saponin (Djeghader *et al.*, 2018). Results of the present study were in agreement with those reported results, since the female fecundity of *S. littoralis* was detrimentally prohibited, in a dose-dependent manner, after treatment of 5^{th} instar or 6^{th} instar larvae with Farnesol. Our result corroborated, also, with the findings of some studies, such as dramatic inhibition of fecundity of *S. littoralis* adult females after treatment of the newly moulted larvae of 5^{th} or 6^{th} instar larvae with Nerolidol (Hamadah *et al.*, 2020); the fecundity of *S. littoralis* was seriously inhibited after larval treatments with certain monoterpens, phenylpropenes and sesquiterpenes (Abdelgaleil *et al.*, 2020); treatment of *Drosophila suzukii* with limonene led to zero fecundity of the adult females but treatment with citral, eugenol, and lemongrass oil led to significantly reduced fecundity (Eben *et al.*, 2020).

In addition, the present result agreed with the reported results of inhibited fecundity of some insects and mites after treatment with extracts or oils of certain plants. For example, the adult fecundity of *S. littoralis* had been reduced after treatment of the 2^{nd} instar larvae with Jojoba oil (*Simmondsia chinensis*) and Jatropha oil (*Jatropha curcas*)(EL-Sabagh *et al.*, 2019). The female fecundity of *S. littoralis* was significantly reduced after treatment of 4^{th} instar larvae with LC_{50} (0.3%) of chloroform/ methanol extract of *Conyza dioscoridis* (Matloub *et al.*, 2021). A remarkable inhibitory effect on the fecundity of Mexican mite *Tetranychus mexicanus* was recorded for Nerolidol (isolated from essential oil of *Derris floribunda* roots) (Amaral *et al.*, 2017). To interpret the inhibition of *S. littoralis* fecundity by Farnesol, in the current investigation, it is important to point out that some plant products are known to inhibit the ovarian growth and development, as well as the testes growth (El-Zoghaby, 1992; El-Sabrout, 2013). The remarkably prohibited fecundity of *S. littoralis*, after treatment of the penultimate or last instar larvae with Farnesol, in the present study, might be due to the interference of this compound with one or more processes of the reproductive physiology, from the ovarian follicle development to egg maturation. In this context, some scenarios could be described herein. (1) The inhibition of fecundity might be due to the undifferentiated ovarioles in adult female moths of *S. littoralis* as an action of larval treatment with Farnesol, as reported by some authors for other plant products (Martinez and Van Emden, 2001; Abdelgaleil and El-Sabrout, 2018). (2) The inhibition of *S. littoralis* fecundity, in the current investigation, might be due to the direct disruptive effect of Farnesol on the reproductive behavior of adult moths (Magierowicz *et al.*, 2019). (3) Farnesol might cause some disorders in the developing ovarioles during the immature stages (Davey, 1993) including cell death in the germarium and resorption of oocytes in the pre-vitellarium and vitellarium before oviposition (Zhou *et al.*, 2016). Formation of the vitellin envelops and undue proliferation of the follicle cells sometimes result in malformation of the whole ovary (Lucantoni *et al.*, 2006; Khan *et al.*, 2007). (4) Farnesol might prohibit the developing ovarioles by inhibition of synthesis and metabolism of proteinaceous constituents during the vitellogenesis (Salem *et al.*, 1997). (5) Farnesol might exert an inhibitory action on the ecdysone activity, threshold of which is necessary for the normal oogenesis (Smagghe *et al.*, 1996; Salem *et al.*, 1997; Terashima *et al.*, 2005). (6) Farnesol might disturb the production and/or function of the gonadotropic hormone (juvenile hormone, JH) responsible for the synthesis of vitellogenins (yolk precursors) and regulation of vitellogenesis, in general (Di Ilio *et al.*, 1999). (7) Eggs might develop normally in ovaries, but they could not be laid, owing to the adversely deformed ovipositor of adult females or to the reduced mechanical strength (Moreno *et al.*, 1994) or their rebsorption before oviposition (Zhou *et al.*, 2016). (8) It may be conceivable to suggest that the prohibited fecundity of *S. littoralis*, in the current work, might be due to inhibitory effects of Farnesol on synthesis of both DNA and RNA, suboptimal nutrition owing to reduced feeding, altered mating behaviour as a result of sublethal intoxication, or a combination of factors.

Reduced Fertility

Fertility (hatching% of laid eggs or egg viability) represents an informative parameter of the reproductive capacity in insects. However, decreasing fertility denotes the increasing sterility. Depending on the available literature, few studies have examined the effects of plant compounds in general and sesquiterpene compounds, in particular, on the fertility of insects. Among these few studies, Abdelgaleil *et al.* (2020) recorded seriously reduced fertility of eggs deposited by adult females of *S. littoralis*, after larval treatments with certain monoterpens, phenylpropenes and sesquiterpenes. Hamadah, *et al.* (2020) treated the newly moulted larvae of 5^{th} or 6^{th} instar larvae of *S. littoralis* with nerolidol and recorded a detrimentally reduced fertility of the eggs deposited by the successfully mated adult females.

Results of the present study were in agreement with those reported reduction of fertility, since treatment of 5^{th} instar or 6^{th} instar larvae of *S. littoralis* with Farnesol resulted in dramatically fertility. In other words, the sterility index of *S. littoralis* increased proportional to the increasing concentration of Farnesol. This result was, also, in corroboration with some reported results after treatments with plant compounds or extracts, such as reduced egg hatchability in the brown planthopper *Nilaparvata lugens* after treatment with jasmonic acid (a plant growth regulator) (Senthil-Nathan *et al.*, 2009) and reduced hatchability in *C. pipiens* after treatment of 4^{th} instar larvae with Saponin (Djeghader *et al.*, 2018). With regard to the plants extracts, treatment of the 2^{nd} instar larvae of *S. littoralis* with Jojoba oil (*Simmondsia chinensis*) and Jatropha oil (*Jatropha curcas*) led to considerable reductions of fertility (EL-Sabagh *et al.*, 2019). Also, fertility of *S. littoralis* was remarkably reduced after treatment of 4^{th} instar larvae with LC_{50} of chloroform/ methanol extract of *Conyza dioscoridis* (Matloub *et al.*, 2021).

For understanding the reduction of *S. littoralis* fertility after larval treatment with Farnesol, in the present study, some suggestions could be provided as follows, (1) It is well known that maturation of the eggs in insects depends basically on the vitellogenins, precursor materials of vitellins including lipids, proteins and carbohydrates, all of which are necessarily required for the embryonic development (Chapman, 1998). These materials are synthesized primarily by fat bodies of the immature stages (Telfer, 2009) or by the ovary *in situ* (Indrasith *et al.*, 1988). Farnesol might disrupt the production and/or accumulation of these materials in the adult females of *S. littoralis* resulting in the reduction of fertility in the present study (Taibi *et al.*, 2003; Pineda *et al.*, 2006; Osorio *et al.*, 2008). (2) In the present study, also, Farnesol might indirectly affect the fertility *via* its disruptive effect on the opening "potency" of intracellular spaces in follicular epithelium or generally inhibited the role of gonadotropic hormone responsible for vitellogenesis, or disturbed the regulation of vitellogenin deposition into oocytes (Davey and Gordon, 1996). (3) The reduction of fertility might be due to the penetration of residual amounts of Farnesol in *S. littoralis* mothers into their eggs and disturbance of the embryonic cuticle synthesis. So, the fully mature embryos had weakened chitinous mouth parts that were insufficiently rigid to perforate the surrounding vitellin membrane and free from the eggs (Sallam, 1999; Sammour *et al.*, 2008). (4) Moreover, the developing embryos in eggs of *S. littoralis* suffered some morphological deformations and incomplete development of some body parts after larval treatment with Farnesol. (5) The reduced fertility of *S. littoralis*, in the current study, might be due to serious effect of Farnesol on survival of the developing embryos at certain stages, as recorded in decreasing hatching percentage. (6) Because some molecular studies revealed the effects of some exogenous materials on insect reproduction owing to the impairment of gene expression in the hierarchy cascade of vitellogenesis and/or choriogenesis (Sun *et al.*, 2003), Farnesol might interfere with the gene expression resulting in a reduction of the developed embryos in *S. littoralis*, in the present study.

However, the exact mode of action of Farnesol on the fertility of S. *littoralis* is still debatable and needs further investigation in future.

Retarded embryonic development

In the current study, no experiments had been conducted to investigate the effect of Farnesol on the embryogenesis of *S. littoralis*. Therefore, the affected embryonic development could be indicated by the affected incubation period of eggs because longer incubation period of eggs usually denotes slower rate of development and *vice versa*. To our knowledge, there was no reliable information in the available literature regarding the effects of plant compounds on the embryonic development in insects, except a recent study of Hamadah, *et al.* (2020) who recorded a considerable prolongation of the incubation period of the eggs deposited by adult females of *S. littoralis*, after treatment of 5^{th} or 6^{th} instar larvae with Nerolidol. Results of the present study, on the same insect, coincided with that reported result, since the embryonic development was seriously retarded, as indicated by the remarkably prolonged incubation period of eggs, after treatment of 5^{th} instar or 6^{th} instar larvae with different concentrations of Farnesol. The retarded embryonic development in *S. littoralis*, in the present study, might be due to an impairing effect of Farnesol on the ecdysteroids responsible for the regulation of certain stages of embryogenesis, especially those ecdysteroids originating from the ovary *in situ* (Chapman, 1998).

Conclusion

Depending on the present study on *S. littoralis*, Farnesol exhibited an adulticidal activity, anti-morphogenic effect, retardation of the egg maturation and dramatic reduction of fecundity and fertility leading to the reduction of population. Therefore, Farnesol could be recommended to play an effective role in the integrated pest management of this dangerous pest.

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