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Bioefficacy of Farnesol, A Common Sesquiterpene, On the Survival, Growth, Development, and Morphogenesis of *Spodoptera littoralis* (Lepidoptera: Noctuidae).

Ghoneim, K.*; Hamadah, Kh.; and Waheeb, H.
1-Department of Zoology and Entomology, Faculty of Science, Al-Azhar University, Cairo, Egypt
*Email: karemghoneim@gmail.com

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ABSTRACT

Egyptian cotton leafworm *Spodoptera littoralis* (Boisduval) is a dangerous pest of many field crops and vegetables in the world. The present study was conducted to evaluate the toxicity of Farnesol and its effects on the growth, development, and morphogenesis of this insect. The newly moulted larvae of 5th (penultimate) or 6th (last) instar larvae were fed on castor bean leaves previously treated with 7 concentrations of Farnesol (400, 200, 100, 50, 25, 12.5 & 6.25 ppm) for 24 hr. The most important results could be summarized as follows. After treatment of 5th or 6th instar larvae with Farnesol, various mortalities were recorded among larvae, pupae, and adults. Depending on LC_{50} values, Farnesol exhibited stronger insecticidal activity after treatment of 6th instar larvae (LC_{50} = 33.67 ppm) than after treatment of 5th instar larvae (LC_{50} = 36.56 ppm). Farnesol caused a serious reduction of larval weight gain and deleterious regression of the growth rate. The larval and pupal durations had been remarkably prolonged, in a dose-dependent course. Disruption of the developmental program was recorded as a failure of ecdysis after treatment of 5th instar larvae and production of larval-pupal intermediates, regardless the treated larval instar. Farnesol exerted considerable suppressing action on the pupation. At higher concentrations, Farnesol interfered with the adult emergence, since eclosion was completely prevented at the highest concentration and partially blocked at other concentrations. Irrespective of the treated larval instar, some deformed pupae were developed only at higher two concentrations of Farnesol.

INTRODUCTION

Although Egyptian cotton leafworm *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) is a native pest to Africa (Shonouda and Osman, 2000; El-Khawas and Abd El-Gawad, 2002), it is distributed in many European countries (Pineda *et al*., 2007; Lanzoni *et al*., 2012; EPPO, 2019), Asia Minor (Brown and Dewhurst, 1975) and the Middle East countries (El-Aswad, 2007; El-Sabrout, 2013; Azzouz *et al*., 2014). Economically, *S. littoralis* is a dangerous pest of many field crops and vegetables in North Africa, Middle East countries including Egypt (Kandil *et al*., 2003) and the glasshouses plant and flower production in Southern Europe (Roques *et al*., 2008; Abdel-Mageed *et al*., 2018), as well as various cash and traditional food crops in Africa

(Capinera, 2008; Khedr *et al*., 2015). In Egypt, cotton cultivation is one of the main resources for the economy. *S. littoralis* represents a key pest of this crop (Raslan, 2002; Ellis, 2004; Ibrahim and Ali, 2018). In addition, it is considered the most destructive pest of more than 60 other crops, ornamentals and vegetables of economic importance (Sannino, 2003; Dahi, 2005; Amin, 2007; Lanzoni *et al*., 2012; Abd El-Razik and Mostafa, 2013).

Different control measures have been applied for controlling of *S. littoralis*, such as the hand-picking of egg patches by children (Abd-El-Aziz and Sayed, 2014). Some physical control measures have been applied to control this pest, such as Ultraviolet light (Vandenbussche *et al*., 2018) and Gamma irradiation (Sallam *et al*., 2000). In addition, some cultural and phytosanitary measures have been carried out, such as cultivating resistant plant varieties (Isman, 2002; Bavaresco *et al*., 2004; Khedr *et al*., 2015) and treatment with compost tea (Ibrahim *et al*., 2016). Although these measures have been applied, no satisfactory results can be achieved for controlling this pest, most farmers, however, prefer using chemically synthetic pesticides for obtaining fast results (Sallam *et al*., 2000; Temerak, 2002; Abd El-Mageed and Shalaby, 2011; Ghoneim *et al*., 2012; Fetoh *et al*., 2015), such as some organophosphates, carbamates, organochlorines and synthetic Pyrethroids (Abo-Elghar *et al*., 1980; Radwan *et al*., 1985; Abd-el-Aziz and Sayed, 2014).

The discriminate uses of many synthetic insecticides lead to the destruction of the natural enemies (like parasites, predators), allowing an exponential increase of pest populations (Naqqash *et al*., 2016) and serious toxicological hazards to humans (Costa *et al*., 2008; Mosallanejad and Smagghe, 2009). Over the past 50 years, the intensive and continuous use of broad-spectrum insecticides against *S. littoralis* had led to the development of its resistance against many registered insecticides and some insect growth regulators (Aydin and Gurkan, 2006; Mosallanejad and Smagghe, 2009; Rizk *et al*., 2010). To avoid the previously mentioned hazards of chemically synthetic insecticides, it is important to search for new effective and safer ways with negligible effects on the ecosystem (Dubey *et al*., 2010; Chandler *et al*., 2011; Korrat *et al*., 2012). In Egypt**,** numerous attempts have been done to assess the insecticidal activities of different plant products against *S. littoralis* (Mansour *et al*., 2012; Derbalah *et al*., 2014; Moharramipour and Negahban, 2014; Abdel-Eltawab, 2016; Sammour *et al*., 2018).

Terpenoids have been shown to have a significant potential for insect control (Copping and Duke, 2007; Alecio *et al*., 2014; Dambolena *et al*., 2016), since they have been reported to act as larvicides, insect growth regulators as well as feeding and oviposition deterrents (Venkatachalam and Jebanesan, 2001a; Venkatachalam and Jebanesan, 2001b). Farnesol is a naturally occurring aliphatic sesquiterpenoid alcohol (Jung *et al.*, 2018). It is a constituent of essential oil derived from various plants (Schulz, 2013; Azanchi *et al*., 2014; Krupcik *et al*., 2015). Commercially, Farnesol is used in perfumery to emphasize the odors of perfumes (Schulz, 2013). For some detail of the pharmaceutical and medical uses of Farnesol, see the review of Jung *et al*. (2018). 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 (Chaudhary *et al*., 2009; Qamar *et al*., 2012; Santhanasabapathy *et al*., 2015). Farnesol is a natural pesticide for mites and several insects (Awad *et al*., 2013; Schulz, 2013). Awad (2012) reported that Farnesol showed a significant dose-dependent increase in mortality on the 4th larval instar of *Agrotis ipsilon*. As reported by Kumar and Gupta (2017), Farnesol can disrupt the normal metabolic function and therefore, affects various life processes of the insects. Wróblewska-Kurdyk *et al*. (2019) evaluated the effect of (*E, E*)-farnesol on the host-plant selection behaviour of the peach potato aphid *Myzus persicae*. Awad *et al*. (2013) recorded the inhibitory effects of Farnesol on the food consumption and utilization, digestive enzymes and fat body proteins of the desert locust *Schistocerca gregaria*. The present study was conducted aiming at the evaluation of toxicity of Farnesol and its drastic effects on growth, development, and morphogenesis of *S. littoralis*.

MATERIALS AND METHODS

Experimental Insect:

A sample of Egyptian cotton leafworm, *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) pupae was kindly obtained from the culture of susceptible strain maintained for several generations in Plant Protection Research Institute, Agricultural Research Center, Doqqi, Giza, Egypt. In the laboratory of Insect Physiology, Faculty of Science, Al-Azhar University, Cairo, a culture was established under laboratory-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 patches were kept in Petri dishes until hatching. The hatched larvae were transferred into glass containers containing a layer of dry sawdust and tightly covered with muslin cloth secured with rubber bands. For feeding, larvae were 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 sawdust. All jars had been kept in suitable cages 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 daily and transferred into Petri dishes for the next generation.

The Tested Sesquiterpene Compound and Larval Treatment:

The tested Farnesol in the present study was provided by Dr. Shady Selim, Faculty of Desert and Environmental Agriculture, Matrouh University, Egypt. 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 each compound. For obtaining a stock solution, 90 ml of distilled water was added to each 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.

Bioassay of Farnesol was carried out against the newly moulted 5th (penultimate) larvae and newly moulted 6th (last) larvae. Discs of fresh castor bean leaves were dipped in each concentration for 5 minutes and air-dried before introduction to larvae as food for 24 hr 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, all biological parameters were recorded daily.

Criteria of Study:

1. Insecticidal Activity:

All mortalities of treated and control (larvae, pupae, and adults) were recorded every day and corrected according to Abbott's formula (Abbott, 1925) as follows:

$$\textbf{\% of corrected mortality} = \frac{\text{\% of test mortality - \% of control mortality}}{\text{100 - \% of control mortality}} \times 100$$

The LC_{50} was calculated for total mortality by Microsoft® office Excel (2007), according to Finny (1971).

2. Growth, Development, and Metamorphosis:

Larval Body Weight Gain: Each individual larva (treated or control) was carefully weighed every day using a digital balance for recording the weight gain as follows:
Initial body weight (before the beginning of the experiment) - final body weight (at the end of the experiment).

Growth rate: It was calculated according to Waldauer (1968) as follows**:**

Fresh weight gain during the feeding period/Feeding period x mean fresh body weight of the larva

Developmental Duration and Rate: Dempster's equation (1957) was applied for calculating the developmental duration, and Richard's equation (1957) was used for calculating the developmental rate.

Pupation rate was expressed in % of the successfully developed pupae.

Adult emergence: number of successfully emerged adults was expressed in % according to Jimenez-Peydro *et al*. (1995) as follows:

[No. of completely emerged adults **/** No. of pupae] × 100

Morphogenesis: The deranged metamorphosis and morphogenesis programs were detected and calculated in larval-pupal or pupal-adult intermediates (%). Also, pupal deformation was calculated in %. Features of impaired programs were recorded in photos.

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 the difference between means using GraphPad InStat© v. 3.01 (1998).

RESULTS

In the present study, different activities of the Sesquiterpene compound, Farnesol, were evaluated against *S. littoralis* after treatment of penultimate (5^{th}) and last (6^{th}) instar larvae. In a no-choice test, the newly moulted larvae of both instars were fed on castor bean leaves previously treated with 7 concentration levels (400, 200, 100, 50, 25, 12.5 & 6.25 ppm) for 24 hr. The insecticidal activity and effects on growth, development, metamorphosis, and morphogenesis were recorded as follows.

Insecticidal Activity of Farnesol Against *S. littoralis*:

After treatment of newly moulted penultimate (5^{th}) instar larvae of *S. littoralis* with 7 concentration levels of Farnesol, data assorted in Table (1) revealed that Farnesol exhibited toxicity on the treated larvae only at the higher three concentration levels (30.0, 10.0 & 10.0% larval mortalities, at 400, 200 & 100 ppm, respectively, compared to 0.0% mortality of control larvae). Moreover, the successfully moulted last (6^{th}) instar larvae suffered stronger toxic action of Farnesol, since 100, 77.78, 66.67, 40.0, 30.0 & 10.0% larval mortality were recorded at 400, 200, 100, 50, 25 &12.5 ppm, respectively, *vs*., 0% mortality of control larvae).

Depending on data listed in the same table, Farnesol exhibited chronic toxicity on the successfully developed pupae only at the higher three concentration levels (100, 66.67 & 16.67% pupal mortality, at 200, 100 & 50 ppm, respectively, *vs*. 0.0% mortality of control pupae), because no pupae developed after treatment with the highest concentration level (400 ppm). On the other hand, Farnesol appeared with a weak insecticidal potency against the successfully emerged adult moths, since only 40.0 & 14.29% adult mortalities were observed at 50 & 25 ppm Farnesol. However, the corrected mortality was estimated in a dose-dependent course, with an exception of the lowest concentration level. LC_{50} value was calculated at 36.56 ppm.

After treatment of last (6th) instar larvae with Farnesol concentrations, data of the insecticidal activity were arranged in Table (2). Depending on these data, the larval mortality% was found in a dose-dependent manner, with an exception of the lowest concentration (80, 70, 60, 60, 40 & 20% larval mortality, at 400, 200, 100, 50, 25 & 12.5 ppm, respectively, *vs*. 0% mortality of control larvae). With regard to the toxic effect of Farnesol on the developed pupae, only higher three concentration levels caused mortalities (100, 66.67 & 25.0% pupal mortalities, at 400, 200 & 100 ppm, respectively, *vs*. 0% mortality of control pupae).

Farnesol exhibited an adulticidal effect on the successfully emerged moths, only after larval treatment with the higher four concentration levels (100.0, 33.33, 25.0 & 16.67 % adult mortalities, at 200, 100, 50 & 25 ppm, respectively, *vs*. 0.0% mortality of adult moths). The corrected mortality increased as the concentration was increased. LC_{50} value was 33.67 ppm. As seen in Tables 1 & 2, Farnesol exhibited stronger insecticidal activity after treatment of last instar larvae of *S. littoralis*.

Effect of Farnesol on the Growth, Development, Metamorphosis and Morphogenesis of *S. littoralis*:

After treatment of 5th instar larvae with Farnesol, data of weight gain, growth, development, metamorphosis, and morphogenesis were assorted in Table (3). Data of similar criteria were arranged in Table (4), after treatment of 6th instar larvae with Farnesol.

1. Reduced Weight Gain and Inhibited Growth:

As clearly shown in Table (3), the treatment of 5th instar larvae with Farnesol resulted in a serious reduction of larval weight gain (wtg), in a dose-dependent course. Similarly, the larval growth rate (GR) was regressed proportional to the concentration level. In addition, the successfully moulted 6th instar larvae suffered reducing action of Farnesol as recorded in significantly reduced somatic wtg and severely regressed GR, in a dose-dependent course (21.12±0.48, 18.36±0.65, 13.67±0.24, 9.47±0.53, 6.12±0.18, 5.67±0.33 & 4.29±0.78, at 6.25, 12.5, 25, 50, 100, 200 & 400 ppm, respectively, compared to 25.27±0.56 of control larvae).

After treatment of 6th instar larvae with Farnesol, data of Table (4) revealed a drastic reduction of larval wtg (093.07±3.14, 108.33±4.48, 132.67±5.12, 156.13±4.09, 149.05±1.10, 167.76±3.88 &189.43±2.50 mg, at 400, 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 234.28±2.01 mg of control larvae) and considerable regression of larval GR (3.13±0.09, 5.42±0.57, 8.27±0.74, 11.41±0.52, 16.88±0.17, 19.45±0.29 & 22.36±0.66, at 400, 200, 100, 50, 25, 12.5, 6.25 ppm, respectively, *vs*. 25.27±0.56 of control larvae).

2. Affected Developmental Durations and Rate:

Data of Table (3) revealed that the treatment of 5th instar larvae with Farnesol led to remarkably prolonged duration of the treated larvae (3.74±0.67, 3.25±0.33, 3.33±0.48, 3.12±0.07, 3.21±0.27, 3.07±0.67 & 3.09±0.12 days, at 400, 200, 100, 50, 25, 12.5 & 6.25

ppm, respectively, *vs*. 2.31±0.48 days of control 5th instar larvae), the successfully moulted 6th instar larvae (9.79±0.46, 9.41±0.67, 8.97±0.33, 9.33±0.78, 8.24±0.51, 8.27±0.67 & 8.12±0.58 days, at 400, 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 7.81±0.67 days of control 6th instar larvae), and the successfully developed pupae (8.09±0.36, 7.96±0.05, 7.67±0.33, 7.57±0.46, 7.36±0.09 & 7.00±0.56 days, at 400, 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 6.87±0.33 days of control pupae).

Depending on data assorted in Table (4), treated 6th instar larvae with Farnesol resulted in a significant prolongation of these larvae, in a dose-dependent course (9.24±0.17, 9.33±0.36, 8.87±0.67, 8.68±0.51, 8.25±0.33, 8.63±0.14 & 8.07±0.58 days, at 400, 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 7.20±0.63 days of control larvae). Also, the successfully developed pupae survived markedly prolonged duration, in a dose-dependent course (8.33±0.36, 7.89±0.15, 7.85±0.36, 7.52±0.47, 7.19±0.76 & 7.07±0.12 days, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 6.87±0.33 days of control pupae).

With regard to the developmental rate (DR), data of Table (3) revealed that the treatment of 5th instar larvae with Farnesol resulted in a considerably regressed rate of development. Such regression increased with the increasing concentration (10.21, 10.63, 11.15, 10.72, 12.14, 12.09 & 12.32 days, at 400, 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 12.82 of control larvae). As seen in Table (4), larval DR was suppressed after treatment of 6th instar larvae, in a dose-dependent course.

3. Disrupted Developmental Program:

Data listed in Table (3) displayed a criterion of disrupted development program, failure of ecdysis, after treatment of 5th instar larvae with Farnesol. For some detail, 20% of the treated larvae failed to completely moult into the nest instar, only at the highest concentration level (400 ppm). As seen in Plate (1), only one symptom of failure was observed as the incompletely ecdysed 6th instar larvae with attached old exuvia of 5th instar larvae.

Another feature of the disrupted developmental program is the production of larval-pupal intermediates. Depending on the data of Table (3), the treatment of 5th instar larvae with Farnesol induced the production of some larval-pupal intermediates. With an exception of the lowest concentration level, the production of these intermediates was increasingly induced with the increasing concentration (85.71, 70.00, 66.67, 30.00, 30.00 & 10.00% intermediates, at 400, 200, 100, 50, 25 & 12.5 ppm, respectively). A similar feature of the disrupted developmental program was recorded after the treatment of 6th instar larvae since Farnesol induced the production of some larval-pupal intermediates (see Table 4). The percentages of these intermediates ascended as the concentration level was ascended, with an exception of the lowest one (70.0, 60.0, 50.0, 50.0, 20.0 & 20.0% intermediates, at 400, 200, 100, 50, 25 & 12.5 ppm, respectively). Regardless of the treated larval instar, these larval-pupal intermediates had been observed with the pupal abdomen and larval head and thorax (see Plate 2).

4. Disturbed Metamorphosis:

Pupation: As shown in Table (3), no pupae developed at the highest concentration level of Farnesol after the treatment of 5th instar larvae. In respect of the pupation, Farnesol exerted considerable suppressing action on the pupation rate, proportional to the concentration with an exception of the lowest one (20.00, 22.22, 60.00, 70.00, 90.00 & 100% pupation, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, vs. 100% pupation of control congeners). A similar suppressing action of Farnesol was exerted on treated 6th instar larvae to pupate, with an exception of the lowest concentration level (20.0, 30.0, 40.0, 70.0, 80.0 & 100% of pupation, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 100% pupation of control congeners, see Table 4).

Adult Emergence: It may be important to mention that adult emergence is a prerequisite process of insect metamorphosis. At the higher three concentration levels, Farnesol intervened in this process, since eclosion was completely prevented at the highest concentration level and partially blocked at the other two concentration levels, regardless the larval instar under treatment (00.00, 50.00 & 83.33% adult emergence, at 200, 100 & 50 ppm, respectively, *vs*. 100% emergence of control adult moths, after treatment of 5th instar larvae, see Table 3; 00.00, 50.00 & 75.00% adult emergence, at 400, 200 & 100 ppm, respectively, *vs*. 100% emergence of control adult moths, after treatment of 6th instar larvae, see Table 4).

5. Impaired Morphogenesis Program:

Irrespective of the larval instar under treatment, Farnesol exerted an anti-morphogenic action only at its higher two concentration levels, since 50.0 & 50.0% deformed pupae were recorded after treatment of 5th instar larvae with 200 & 100 ppm, respectively, compared to 0.0% deformity of control pupae (see Table 3). Also, 66.67 & 50.00% deformed pupae were recorded after treatment of 6th instar larvae with 400 & 200 ppm, respectively, *vs*. 0.0% deformity of control pupae (see Table 4). As shown in Plate (3), some of the malformed pupae appeared with different constrictions at the head thorax, and other malformed pupae were seen hump-backed, regardless of the larval instar under treatment.

Table (1): Insecticidal activity (%) of Farnesol against *S. littoralis* after treatment of newly moulted penultimate (5th) instar larvae.

Conc. (ppm)	Larval mortalities		Pupal mortality	Adult mortality	Total mortality	Corrected mortality	LC_{50} (ppm)
	5th instar	6th instar					
400.00	30.00	100.00	---	---	100.00	100.00	36.56
200.00	10.00	77.78	100.00	0.00	100.00	100.00	
100.00	10.00	66.67	66.76	0.00	90.00	90.00	
50.00	0.00	40.00	16.67	40.00	70.00	70.00	
25.00	0.00	30.00	0.00	14.29	40.00	40.00	
12.50	0.00	10.00	0.00	0.00	10.00	10.00	
6.25	0.00	0.00	0.00	0.00	0.00	0.00	
Control	0.00	0.00	0.00	0.00	0.00	--	

Conc.: concentration level, ---: no developed pupae or adults.

Table (2): Insecticidal activity (%) of Farnesol against *S. littoralis* after treatment of newly moulted last (6th) instar larvae.

Conc. (ppm)	Larval mortality	Pupal mortality	Adult mortality	Total mortality	Corrected mortality	LC_{50} (ppm)
400.00	80.00	100.00	---	100.00	100.00	33.67
200.00	70.00	66.67	100.00	100.00	100.00	
100.00	60.00	25.00	33.33	80.00	80.00	
50.00	60.00	0.00	25.00	70.00	70.00	
25.00	40.00	0.00	16.67	50.00	50.00	
12.50	20.00	0.00	0.00	20.00	20.00	
6.25	0.00	0.00	0.00	0.00	0.00	
Control	0.00	0.00	0.00	0.00	--	

Conc.: see footnote of Table (1). ---: no emerged adult moths.

Table (3): Growth and development of *S. littoralis* after treatment of the newly moulted penultimate (5th) instar larvae with Farnesol.

Conc. (ppm)	Larval instar									Pupal stage			Adult emergence (%)
	5th				6th								
	Weight gain (mean mg ± SD)	Duration (mean days ± SD)	Growth rate (mean± SD)	Failure of ecdysis (%)	Weight gain (mean mg ± SD)	Duration (mean days ± SD)	Growth rate (mean± SD)	Develop. Rate	Larval-pupal Inter. (%)	Pupation (%)	Pupal deformities (%)	Pupal duration (mean days ± SD)	
400.00	36.33±1.17 d	3.74±0.67 d	2.86±0.12 d	20.00	112.33±2.14 d	9.79±0.46 d	4.29±0.78 d	10.21	85.71	---	---	---	---
200.00	39.67±2.58 d	3.25±0.33 d	3.00±0.08 d	0.00	127.68±3.11 d	9.41±0.67 d	5.67±0.33 d	10.63	70.00	20.00	50.00	8.09±0.36 d	0.00
100.00	45.67±1.47 d	3.33±0.48 d	3.76±0.21 d	0.00	145.67±4.02 d	8.97±0.33 c	6.12±0.18 d	11.15	66.67	22.22	50.00	7.96±0.05 d	50.00
50.00	53.25±1.07 d	3.12±0.07 c	5.19±0.27 d	0.00	158.14±1.78 d	9.33±0.78 c	9.47±0.53 d	10.72	30.00	60.00	0.00	7.67±0.33 d	83.33
25.00	61.78±2.33 d	3.21±0.27 d	6.09±0.92 d	0.00	181.68±3.05 d	8.24±0.51 a	13.67±0.24 d	12.14	30.00	70.00	0.00	7.57±0.46 d	100.00
12.50	72.27±0.97 d	3.07±0.67 b	8.55±0.16 d	0.00	210.07±2.36 d	8.27±0.67 a	18.36±0.65 d	12.09	10.00	90.00	0.00	7.36±0.09 d	100.00
6.25	77.15±2.33 d	3.09±0.12 c	10.16±0.37 c	0.00	217.67±2.33 d	8.12±0.58 a	21.12±0.48 d	12.32	0.00	100.00	0.00	7.00±0.56 b	100.00
Control	86.19±2.71	2.31±0.48	12.49±0.53	0.00	230.68±2.55	7.81±0.67	25.27±0.56	12.82	0.00	100.00	0.00	6.87±0.33	100.00

Conc.: concentration levels. Develop.: Developmental. Inter.: Intermediate. ---: no developed pupae or adults. 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).

Table 4: Growth and development of *S. littoralis* after treatment of the newly moulted last (6th) instar larvae with Farnesol

Conc. (ppm)	Larval instar					Pupal stage			Adult emergence (%)
	Weight gain (mean mg ± SD)	Duration (mean days ± SD)	Growth rate (mean± SD)	Develop. Rate	Larval-pupal Inter. (%)	Pupation (%)	Pupal deformities (%)	Pupal duration (mean days ± SD)	
400.00	093.07±3.14 d	9.24±0.17 d	3.13±0.09 d	10.82	70.00	30.00	66.67	---	00.00
200.00	108.33±4.48 d	9.33±0.36 d	5.42±0.57 d	10.72	60.00	20.00	50.00	8.33±0.36 d	50.00
100.00	132.67±5.12 d	8.87±0.67 d	8.27±0.74 d	11.27	50.00	40.00	0.00	7.89±0.15 d	75.00
50.00	156.13±4.09 d	8.68±0.51 d	11.41±0.52 d	11.52	50.00	40.00	0.00	7.85±0.36 d	100.00
25.00	149.05±1.10 d	8.25±0.33 c	16.88±0.17 d	12.12	20.00	70.00	0.00	7.52±0.47 d	100.00
12.50	167.76±3.88 d	8.63±0.14 d	19.45±0.29 d	11.52	20.00	80.00	0.00	7.19±0.76 d	100.00
6.25	189.43±2.50 d	8.07±0.58 c	22.36±0.66 d	12.39	0.00	100.00	0.00	7.07±0.12 b	100.00
Control	234.28±2.01	7.20±0.63	25.27±0.56	13.89	0.00	100.00	0.00	6.87±0.33	100.00

Conc., Develop., Inter., a, b, c, d: see footnote of Table (7).

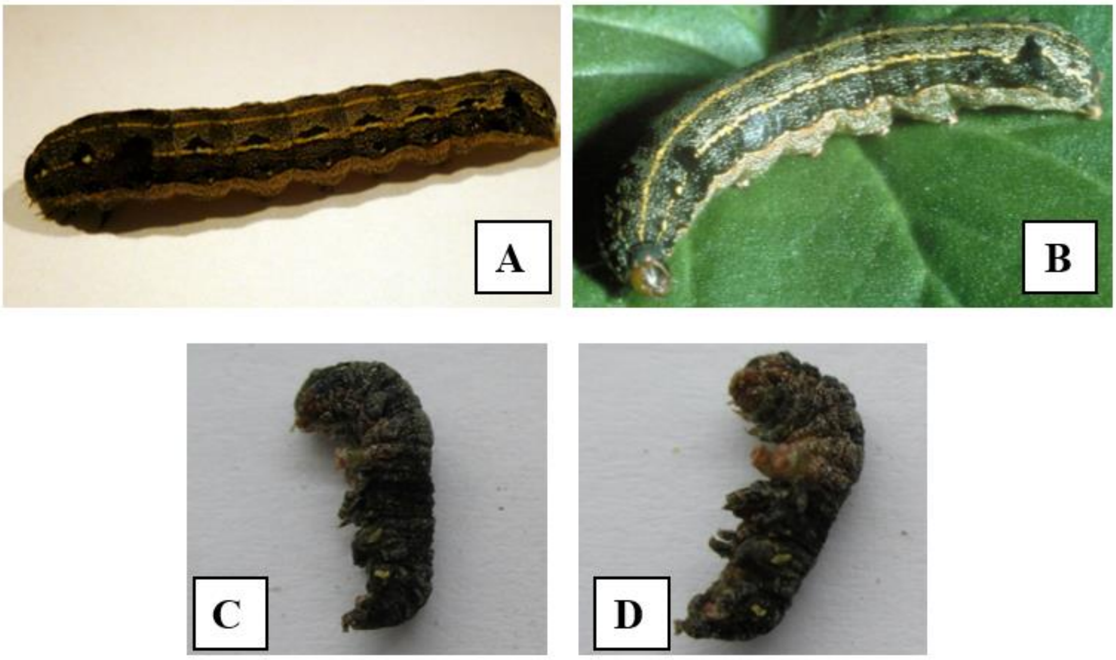

Plate (1): Failure of ecdysis of *S. littoralis* 5th instar larvae after treatment with 400 ppm Farnesol. (A) Normal 5th instar larva. (B) Normal 6th instar larva. (C) Lateral and ventral (D) views of incompletely ecdysed 6th instar larva with attached old cuticle

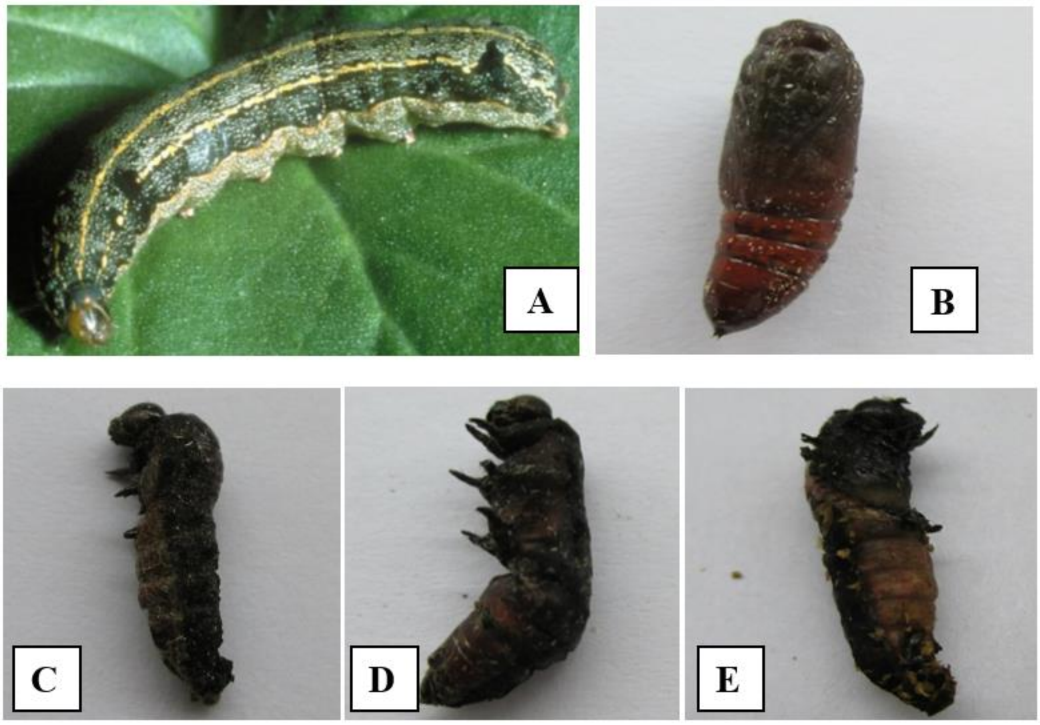

Plate (2): Larval-pupal intermediates of *S. littoralis* as features of disturbed metamorphosis program by Farnesol, regardless the concentration or treated larval instar under. (A) Normal last instar larva. (B) Normal pupa. (C, D & E): Various larval-pupal intermediates (pupal abdomen with larval thorax and head).

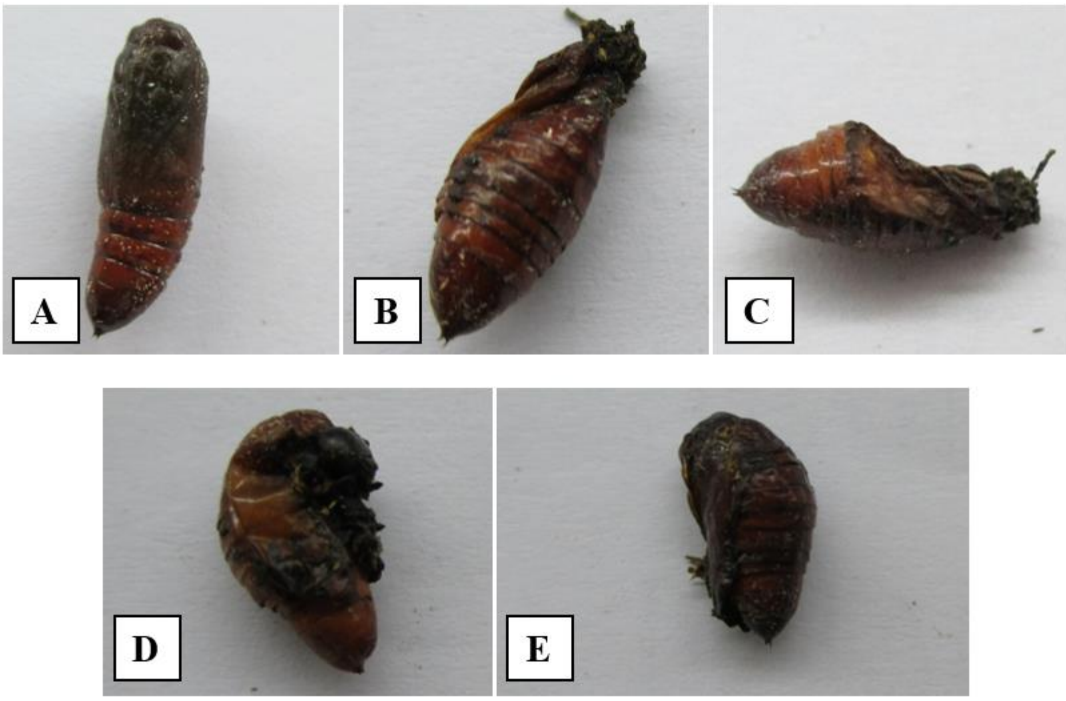

Plate (3): Pupal deformations of *S. littoralis* produced by Farnesol at higher concentrations, regardless the larval instar under treatment. (A) Normal pupa. (B & C) Pupa constricted at head and thorax. (D & E) Hump-back pupae.

DISCUSSION

Insecticidal Activity of Farnesol against *S. littoralis*:

It is known from the literature sources that different monoterpenes, phenylpropenes and sesquiterpenes have insecticidal activities against the Egyptian cotton leafworm *Spodoptera littoralis* (Srivastav *et al*., 1990; Handayani *et al*., 1997; Abdelgaleil, 2010; Al-Nagar *et al*., 2020). For example, 5,6-dihydroxy-3,4-7 trimethoxy flavones (isolated from *Artemisia maritima*) were found to be toxic against 2nd and 4th instar larvae of *S. littoralis* (Abdel-Rahim *et al*., 2007). The toxicity of linoleic acid against the larvae of *S. littoralis* was reported by Yousef *et al*. (2013). Different compounds in the essential oil (EO) from *Schinus terebinthifolius*, such as α-pinene, α- and β-phellandrene, α-terpinene, β-ocimene, β-myrcene, limonene, terpinen-4-olα-terpineol, citronellol, carvone, thymol and carvacrol had high insecticidal activities against *S. littoralis* (Caballero-Gallardo *et al*., 2011; Sousa *et al*., 2013; Ennigrou *et al*., 2017). Pavela (2014) evaluated the acute toxicity of 32 volatile compounds against 3rd instar larvae of *S. littoralis* and reported that α-pinene, *p*-cymene, γ-terpinene, thymol and carvacrol (applied at 300µg/larva) caused 100% mortality within 24 h. As recorded by Pavela *et al*. (2019), thymol, carvacrol, geranyl acetate, (E)-Nerolidol or phenolic monoterpenes (isolated from EOs of *Thymus spinulosus* and *Th. Longicaulis*) showed significant toxic effects on larvae of *S. littoralis*.

Apart from *S. littoralis*, many plant compounds had been reported to have toxicities against various insects, such as Biostop Moustiques® (isolated from coconut EO) against 4th instar larvae of susceptible and resistant strains of the African malaria mosquito *Anopheles gambiae* (Ahadji-Dabla *et al*., 2015); Pogostone (isolated as the main constituent in EO from *Pogostemon cablin*) against the tobacco cutworm *Spodoptera litura* and the beet armyworm *Spodoptera exigua* (Huang *et al*., 2014); some sesquiterpene lactones and monoterpenoids (isolated from *Carpesium abrotanoides* fruits) against 4th instar larvae of the fly *Bradysia odoriphaga* (Wua *et al*., 2016); as well as carvacrol, (−)-α-bisabolol and chamazulene (major constituents in *Artemisia absinthium* EO) against the Asian citrus psyllid *Diaphorina citri* (Rizvi *et al*., 2018).

The present results were in corroboration with those previously reported results, since the Sesquiterpene compound, Farnesol exhibited toxicity on 5th instar larvae of *S. littoralis* at the higher concentrations. Also, it exhibited high toxicity on the developed pupae but weak toxic on the emerged adult moths. After the treatment of 6th instar larvae of the same insect with Farnesol, the larval mortality% was found in a dose-dependent manner. Also, Farnesol exhibited high toxicity on both developed pupae and emerged adults, at the higher concentrations.

Also, the present results were in agreement with those reported results on the insecticidal activity of the same tested Sesquiterpene compound against several insects and mites (Awad *et al*., 2013; Schulz, 2013). For examples, (E,E)-α-Farnesene and a mixture of Farnesol isomers caused high mortality among nymphs of the black bean aphid (*Aphis fabae*) and the peach potato aphid (*Myzus persicae*)(Harrewijn *et al*., 2001); Farnesol (isolated from *Stellera chamaejasma*) was recorded with considerably insecticidal activity against the aphids *Aphis craccivora* and *Leucania separata* (Tang *et al*., 2011); Awad (2012) reported that Farnesol showed a significant dose-dependent increase in mortality of the black cutworm *Agrotis ipsilon* 4th instar larvae; the high dose of Farnesol reduced the survival of the nymphs of the red cotton stainer bug *Dysdercus koenigii* to 70% after 24h of exposure and increased mortality during subsequent days (Kumar and Gupta, 2017).

The interpretation of Farnesol insecticidal activity against *S. littoralis*, in the current investigation, could be provided as follows. The larval mortality may be attributed to the failure of larvae to moult owing to the inhibition of chitin synthesis (Abdel Rahman *et al*., 2007; Adel, 2012). The larval mortality may be attributed to the inability of moulting larvae to swallow volumes of air for splitting the old cuticle and expand the new one during ecdysis (Linton *et al*., 1997). Also, the larval deaths might be due to the prevented feeding and continuous starvation (Ghoneim *et al*., 2000). The pupal mortality in *S. littoralis*, in the present investigation, could be directly or indirectly relate to activities of Farnesol against some vital processes, such as suffocation, bleeding and desiccation owing to imperfect exuviation, failure of vital homeostatic mechanisms, *etc*. (Smagghe and Degheele, 1994). The adult mortality of *S. littoralis* could be explained by the retention and distribution of Farnesol in the insect body as a result of direct and rapid transport *via* the haemolymph to other tissues, and/or by lower detoxification capacity of adults against the tested compound (Osman *et al*., 1984).

It may be important to explicate the toxicity of Farnesol, in the present study, leading to mortality of larvae, pupae and/or adults of *S. littoralis*, by its inhibition of Acetylcholinesterase (AchE), one of the most recognized insecticidal mechanisms, since many terpenoid compounds have been reported to inhibit AChE activity in insects resulting in death (López and Pascual-Villalobos, 2010; Yeom *et al*., 2012; Chaubey, 2012a, b). Moreover, toxicity of the tested Sesquiterpene compound, Farnesol, can be mediated through i) inhibition of AChE activity which leads ultimately to impaired neurotransmission, ii) depletion of the activity of antioxidant enzymes leading to accumulation of Reactive oxygen species and peroxidation of membrane lipids and iii) Binding to octopamine receptors or GABA-gated chloride channels and iv) inhibition of cytochrome P450-mediated detoxification (Seo *et al*., 2009; Faraone *et al*., 2015; Kiran and Prakash, 2015)

In respect of LC_{50} values of Farnesol against *S. littoralis*, in the present study, this Sesquiterpene compound exhibited stronger insecticidal activity after treatment of last (6^{th}) instar larvae (LC_{50} = 33.67 ppm) than after treatment of penultimate (5^{th}) instar larvae **(**LC_{50} = 36.56 ppm). However, different LC_{50} values had been determined for various plant compounds against several insects. For examples, the naphtooquinone derivatives, isobutyrylshikonin and isovalerylshikonin (isolated from the root hexane extract from *Onosma visianii*) exhibited different toxicities on *S. littoralis* larvae and isovalerylshikonin was significantly more toxic (LD_{50}= 0.8µg/cm^2) than isobutyrylshikonin (LD_{50}= 7.3µg/cm^2) (Sut *et al*., 2017). Farnesol (isolated from the root powder of *Stellera chamaejasme*) exhibited toxicity against *Aphis craccivora* and *Leucania separate* with LC_{50} values of 20.2 and 15.2 mg L^{-1}, respectively (Tang *et al*., 2011).The 1-desacetylwilforgine, wilforgine, 1-desacetylwilforine and wilforine (isolated Sesquiterpenes from an ethanolic extract of *Tripterygium wilfordii* root bark) showed insecticidal activities to 3^{rd} instar larvae of the common house mosquito *Culex pipiens* (LC_{50}= 25.70, 25.40, 22.58 and 14.57 µg/ml, respectively) and adults of the house fly *Musca domestica* (LC_{50}= 87.29, 70.19, 47.80 and 21.00 µg g/ml, respectively) (Ma *et al*., 2014). Among eleven terpene ketones, thymoquinone exhibited the highest toxicity against adults of the maize weevil *Sitophilus zeamais*, with LC_{50} =16.5µg/cm^2 and LC_{50} 13.8 µL/L air (24h after treatment) of contact and fumigant methods, respectively (Herrera *et al*., 2015). As reported by AlShebly *et al*. (2017), epi-β-bisabolol (one of the major compounds in *Hedychium larsenii* essential oil) showed high toxicity against early 3^{rd} instar larvae of *A. stephensi* (LC_{50}= 14.68 µg/ml), the yellow fever mosquito *Aedes aegypti* (LC_{50}= 15.83 µg/ml) and the southern house mosquito *Culex quinquefasciatus* (LC_{50}= 17.27 µg/ml).

However, LC_{50} values depend on several factors, such as susceptibility of the insect and its treated stage or instar, lethal potency of the tested compound or product and its concentrations, method and time of treatment or exposure, as well as the experimental conditions (Ghoneim *et al*., 2017). On the other hand, the results of the present study on *S. littoralis* revealed that the 6th instar larvae were more sensitive to Farnesol than 5th instar larvae. Such a result disagreed with many reported results on insects, in particular Lepidoptera, since the earlier larval instars had been recorded more sensitive to the toxic bioactive compounds than the later larval instars. Unfortunately, there is no conceivable interpretation of this finding right now!!

The Disruptive Effect of Farnesol on the Growth, Development, Metamorphosis, and Morphogenesis of *S. littoralis*.

1. Reduced Weight Gain and Inhibited Growth:

Botanical products showed deleterious effects on the growth and development of insects, reducing the weight of larva, pupa and adult stages and lengthening the development stages (Talukder, 2006).

In the present study on *S. littoralis*, the sesquiterpene compound, Farnesol, caused a considerable reduction of the larval weight gain after treatment of 5th instar or 6th instar larvae. The present result was in corroboration with those reported results of reduced larval body weight of *S. littoralis* after treatment with Linoleic acid (= omega-6 fatty acid) (Yousef *et al*., 2013) or allyl cinnamate 0.05% (Giner *et al*., 2012). In addition, feeding of *A. ipsilon* larvae on a food plant treated with Farnesol, the larval body weight was reduced (Awad, 2001). The body weight gain of the lesser mealworm *Alphitobius diaperinus* larvae was reduced after feeding on diet treated with β-damascone (isolated from Bulgarian rose oil) or its synthetic derivatives γ- and δ-halolactones (Szczepanik *et al*., 2016). Feeding of *S. littoralis* larvae and the migratory locust *Locusta migratoria* nymphs on diet treated with Gibberellic acid (GA_3) resulted in significantly reduced larval body weight in both insects (Abdellaoui *et al*., 2009).

To explicate the reduction of weight gain of *S. littoralis* larvae after treatment with Farnesol, in the current investigation, they might suffer gut alterations, suggesting that such larvae stopped feeding and consequently lost weight (Smagghe and Degheele, 1997). Another suggestion is a post-ingestion toxic effect of Farnesol, causing poor utilization of food by these larvae or inhibiting important vital processes, causing weight loss (Giongo *et al*., 2015).

With regard to the growth inhibition of insect larvae after treatment with some plant compounds, the currently available literature contains many results of inhibited growth of *S. littoralis* by various monoterpenes, phenylpropenes, Sesquiterpenes and some terpenoid compounds (Zapata *et al*., 2009; Adel and Zaki, 2010; Pavela, 2011; Pavela and Vrchotova, 2013; Al-Nagar *et al*., 2020). Also, Isobutyrylshikonin and isovalerylshikonin (naphtooquinone derivatives isolated from the root hexane extract of *O. visianii*) inhibited the growth of *S. littoralis* larvae (Sut *et al*., 2017).

Apart from *S. littoralis*, many studies revealed the inhibitory effects of various plant compounds on the larval growth of different insects. For example, treatment of the early larvae of the fall armyworm *Spodoptera frugiperda* with gedunin, photogedunin or Toosendanin resulted in the larval growth inhibition, in a dose-dependent course (Céspedes *et al*., 2000). Some authors (Rabindar and Rup, 1999; Kaur and Rup, 2003) reported a growth inhibition in the melon fly *Bactrocera cucurbitae* larvae after treatment with Gibberellic acid (GA_3) in dose-dependent course or Coumarin (Cn), kinetin, GA_3 and 3-indoleacetic acid (IAA) (Kaur and Rup, 2003). Feeding of *S. litura* larvae on an artificial diet fortified with Miraculan resulted in suppression of larval growth (Bhatnagar *et al*., 2012). Corzo *et al*. (2012) documented a regressed growth rate of *S. frugiperda* larvae feeding on sesquiterpenoids (isolated from *Porella chilensis*). Szołyga *et al*. (2014) showed that α- and β-thujone (the main component of *T. vulgare* EO) inhibited the growth of *A. diaperinus*. Treatment of *S. frugiperda* larvae with Jasmonic acid (JA) consistently reduced the larval growth by rearing on treated cotton and soybean (Gordy *et al*., 2015). Treatment of 3rd instar larvae of *S. litura* with the sesquiterpene compounds, Alantolactone and isoalantolactone, and two eudesmane-type sesquiterpene lactones resulted in the inhibition of larval growth (Kaur *et al*., 2017).

Our results were in agreement with the previously reported results since the treatment of 5th instar or 6th instar larvae of *S. littoralis* with Farnesol resulted in deleterious inhibition of larval growth. In contrast, the present result disagreed with results of few studies which revealed an inducing effect of certain plant compounds on larval growth of some insects, such as cucurbitacin-C (an oxygenated triterpene) which had been appeared to promote the growth of *S. exigua* larvae (Barrett and Agrawal, 2004).

The interpretation of growth inhibition of *S. littoralis* larvae by Farnesol, in the current study, could be provided as follows. The growth inhibition might be a result of the retardation and/or delay in the release of certain peptides from neurohaemal organs, causing an alteration in the hemolymph ecdysteroid and juvenoid titers (Barnby and Klocke, 1990; Ladhari *et al*., 2013). Also, Farnesol might affect the tissues and cells undergoing mitosis (Nasiruddin and Mordue, 1994).

2. Prolonged Developmental Durations and Delayed Development:

In the present investigation of the sesquiterpenoid compound, Farnesol, on *S. littoralis*, both larval and pupal durations had been remarkably prolonged, in a dose-dependent course, regardless the treated larval instar. In addition, the developmental rate was considerably regressed, in a dose-dependent course, indicating delaying or retardation of development. The current results were in partial resemblance with the reported results of prolonged larval and/or pupal duration in different insects after treatment with some plant compounds, such as *S. littoralis* after treatment with 5,6-dihydroxy-3,4-7 trimethoxy flavone (isolated from *A. maritima*) (Abdel-Rahim *et al*., 2007); *A. ipsilon* after feeding on leaves sprayed with Farnesol (Awad, 2001); *S. litura* after treatment with higher concentrations of Alantolactone and isoalantolactone (sesquiterpene compounds isolated from *Inula racemosa*) (Kaur *et al*., 2017) or Erucin (4-Methylthiobutyl isothiocyanate, obtained from *Eruca sativa* seeds) (Gupta *et al*., 2017b); the desert locust *Schistocerca gregaria* after feeding on clover leaves treated with Farnesol (Awad *et al*., 2013); *S. litura* larvae after feeding on an artificial diet fortified with Miraculan (Bhatnagar *et al.,* 2012); the greater wax moth *Galleria mellonella* larvae after injection of Abscisic acid (ABA) into the haemocoel (Er and Keskin, 2015); *A. diaperinus* after feeding on diet treated with β-damascone (isolated from Bulgarian rose oil) or its synthetic derivatives γ- and δ-halolactones (Szczepanik *et al.,* 2016).

On the contrary, the present results disagreed with some reported results of significantly shortened larval and pupal duration after treatment with some plant compounds, such as *S. litura* and *S. exigua* after treatment with Pogostone (the isolated main constituent of EO of *P. cablin*) (Huang *et al*., 2014) and the domestic mosquito *Culex pipiens* after treatment with Saponin (Djeghader *et al*., 2018).

In the present study, prolongation of the larval and pupal durations and retarded development of *S. littoralis*, after larval treatment with Farnesol, could be explained by some scenarios. Farnesol might indirectly interfere with the neuroendocrine organs responsible for the synthesis and release of tropic hormones, like prothoracicotropic hormone (Subrahmanyam *et al*., 1989; Ben Hamouda *et al*., 2015). The final step of the chitin biosynthesis pathway could be inhibited by Farnesol and the precursor was not converted into chitin for moulting leading to a prolongation of the developmental duration (Djeghader *et al*., 2014).

The prolongation of larval duration might be due to decreased food intake, caused by phagodeterrence of Farnesol (Awad and Ghazawy, 2016), or by a deviation of part of the taken food to the detoxification metabolism (Tanzubil and McCaffery, 1990). With decreased food ingestion and low biomass conversion, the insect takes longer to reach the critical weight for ecdysis, leading to the prolongation of larval duration (Giongo *et al*., 2015).

Farnesol might exhibit a delaying effect on the pupal transformation into adults (Linton *et al*., 1997). In other words, the prolongation of pupal duration might be due to an elevated titer of juvenile hormone (JH) in the haemolymph. Only in the absence of JH in haemolymph, ecdysone could be activated and led to the production of the next stage (Kuwano *et al*., 1988).

3. Impaired Development Program:

3.1. Ecdysis Failure of Larvae:

As far as our literature survey could ascertain, no information was available on the failure of ecdysis of larvae, as an effect of sesquiterpene compounds or other plant compounds. In the present study, some 5th instar larvae of *S. littoralis* (20%) failed to completely moult into the next instar, after treatment only with the highest concentration level (400 ppm) of Farnesol. Only one symptom of failure was observed as the incompletely formed 6th instar larvae with attached old exuvia of 5th instar larvae.

For the interpretation of this ecdysis failure of treated *S. littoralis* larvae, it may be important to mention that the moulting hormone "ecdysone" plays a major role in shedding of old cuticle in a phenomenon called "ecdysis" or "moulting". Farnesol might exhibit serious disturbances during larval moulting, indicating that it disrupted the function of the larval endocrine system, thereby preventing completion of moulting (Ben Hamouda *et al*., 2015). For some detail, Farnesol might suppress the activity of ecdysone in larvae leading to the failure of moult and ultimately died (Baskar *et al*., 2009; Baskar *et al*., 2011; Jeyasankar *et al*., 2013; Sivaraman *et al*., 2014; Chennaiyan *et al*., 2016). On the other hand, failure of ecdysis of *S. littoralis* larvae, in the current work, may be attributed to an inhibitory effect of Farnesol on the chitin formation (Abdel Rahman *et al*., 2007; Adel, 2012) or to the inability of larvae to shed their exocuticle during ecdysis (Linton *et al*., 1997).

3.2. Production of Larval-Pupal Intermediates:

The production of larval-pupal or/and pupal-adult intermediates had been reported for different insects by the disruptive effects of some botanicals (Kaur *et al*., 2014; Palanikumar *et al*., 2017), such as the confused flour beetle *Tribolium confusum* after treatment of 5th instar larvae (production of larval-pupal intermediates) or 6th instar larvae or 0 h-old pupae (production of pupal-adult intermediates) with 1µg/µl of Andrographolide (a terpenoid isolated from the leaves of *Andrographis paniculata*) (Lingampally *et al*., 2013). Also, larval treatment of *S. litura* with the same plant compound led to the production of larval-pupal intermediates, at all concentrations (Edwin *et al*., 2016).

Results of the present study on *S. littoralis* were, to a great extent, agreed with these reported results, since some larval-pupal intermediates were produced after treatment of 5th instar or 6th instar larvae with Farnesol. This syndrome of the disrupted developmental program was increasingly induced with the increasing concentration of Farnesol, with an exception of the lowest one.

To explicate the production of larval-pupal intermediates in *S. littoralis* by

Farnesol, in the present study, this Sesquiterpene compound might interfere with the pupal moulting and development *via* the disturbance of hormonal regulation. For example, larval-pupal transformation may be interpreted as an interference with moulting hormone leading to an ecdysteroid reduction (Al-Sharook *et al.,* 1991; Lingampally *et al*., 2013).

However, some conceivable scenarios can be described herein. (**1**) Farnesol might inhibit the development program *via* the interference with the release of the neurosecretion (Josephrajkumar *et al.,* 1999). (**2**) The production of these intermediates might indicate a juvenile hormone-like activity of Farnesol retarding the perfect larval-pupal transformation. (**3**) Farnesol might interfere with the chitin biosynthesis and chitin synthase leading to moulting into non-viable forms between stages (Tateishi *et al*., 1993). (**4**) The production of these mosaic creatures in *S. littoralis* may be explicated by an inhibitory effect of Farnesol on DNA synthesis (Mitlin *et al*., 1977). (**5**) The moult induction had lethal consequences because the induction of a rapid moult did not provide enough time for the completion of larval-pupal transformation. Thus, the insects moulted to non-viable forms between the stages (Tateishi *et al*., 1993). Molts induced during the early phase of the last instar produce larval-like individuals, while those formed in the late phase generate pupal-like individuals (Eizaguirre *et al*., 2007). (**6**) Farnesol might cause misexpression of *br*-C which then leads to improper expression of one or more downstream effector genes controlled by *br*-C gene products. Symptoms of impaired development, like larval-pupal intermediates, are the end results (Wilson, 2004; Nandi and Chakravarty, 2011).

4. Disturbed Metamorphosis:

4.1. Inhibited Pupation:

According to the currently available literature, the pupation rate of different insects decreased after treatment with plant extracts or plant-derived compounds (Jilani *et al*., 2006; Kaur *et al*., 2010; Kaur *et al*., 2017; Gupta *et al*., 2017). In the present study, Farnesol exerted a considerable suppressing action on the pupation rate of *S. littoralis,* almost in a dose-dependent course, regardless the treated larval instar. Moreover, no pupae were developed after the treatment of 5th instar larvae with the highest concentration of Farnesol. This result was in accordance with some reported results of reduced pupation of some insects after treatment with certain plant compounds. For examples, treatment of the *S. frugiperda* larvae with doses 0.2-5.0µg/mL of different phytochemicals, such as eucalyptin, chrysin, eucalyptin, quercetin, luteolin, and betulinic and oleanolic acids (isolated from the methanol extract of *Eucalyptus citriodora* leaves) considerably reduced the pupation (Salazar *et al*., 2015). The addition of alantolactone and isoalantolactone (sesquiterpenes isolated from *I. racemosa*) to the diet of 3rd instar larvae of *S. litura* significantly reduced the pupation% (Kaur *et al*., 2017). A reduction of pupation was recorded in *S. litura* after larval feeding on Miraculan-treated diet (Bhatnagar *et al*., 2012) and in *G. mellonella* after injection of ABA into the larval haemocoel (Er and Keskin, 2015).

To understand the regressed pupation rate of *S. littoralis*, in the current investigation, Farnesol might exert a suppressive action on the chitin synthesis and prevented the normal deposition of the new cuticle during apolysis (Retnakaran *et al*., 1985). For some detail, Farnesol might exert an inhibitory action on the prothoracic gland (ecdysone-producing gland) and hence the ecdysone could not be synthesized and/or released. In other words, Farnesol might block the release of morphogenic peptides, causing a disturbance in titers of both ecdysteroids and juvenoids (Barnby and Klocke, 1990). Also, Farnesol might disrupt the ecdysteroid metabolism or might alternatively act directly to inhibit the release of ecdysis-triggering hormone (Gaur and Kumar, 2010). In addition, reduction of the pupation rate of *S. littoralis* might be due to the inhibitory effect of Farnesol on the synthesis of specific storage proteins in fat body during the last larval instar and their deposition at the time of pupation (Gupta, 1985).

4.2. Blocked Adult Emergence:

It is known from the literature sources that the adult emergence of different insects was completely or partially blocked by various plant extracts or plant compounds (Jilani *et al*., 2006; Baskar *et al*., 2009; Kaur *et al*., 2010; Baskar and Ignacimuthu, 2012; Nogueira *et al*., 2014; Pathak and Tiwari, 2015; Bhushan *et al*., 2016; Kaur *et al*., 2017). In the present study, Farnesol interfered with the process of adult emergence of *S. littoralis*, since eclosion was completely prevented at the highest concentration or partially blocked at other concentrations, regardless the treated larval instar.

The present result was in agreement with many reported results of blocked adult emergence after larval treatment with some plant products, such as significantly blocked adult emergence after treatment of 2nd instar larvae of *S. littoralis* with 5,6-dihydroxy-3,4-7 trimethoxy flavones (isolated from *Eucalyptus* plant) (Abdel-Rahim *et al*., 2007); significantly blocked adult emergence after treatment of the *S. frugiperda* neonate larvae with gedunin, photogedunin epimeric mixture, photogedunin acetates mixture (isolated from *Cedrela salvadorensis*) or Toosendanin (isolated from *Melia azedarach*)(Céspedes *et al*., 2000) or after treatment with eucalyptin, chrysin, eucalyptin, quercetin, luteolin, and oleanolic acids (isolated from the methanol extract of *Eucalyptus citriodora* leaves)(Salazar *et al*., 2015); partially blocked adult emergence after treatment of 5th or 6th instar larvae of *T. confusum* with Andrographolide (a terpenoid isolated from the leaves of *Andrographis paniculata*)(Lingampally *et al*., 2013); blocked adult emergence of *S. litura* and *S. exigua* after larval treatment with Pogostone (isolated as a main constituent of EO of *P. cablin*) (Huang *et al*., 2014); blocked adult emergence after treatment of *H. armigera* and *S. litura* larvae with Flindersine (an alkaloid isolated from *Toddalia asiatica*)(Duraipandiyan *et al*., 2015); blocked adult emergence after feeding of 2nd instar larvae of *S. litura* on fresh food treated with Allyl isothiocyanate (an isothiocyanate derived from plant Glucosinolates)(Bhushan *et al*., 2016) or treatment of 3rd instar larvae of *S. litura* with alantolactone and isoalantolactone (sesquiterpenes isolated from *I. racemosa*) (Kaur *et al*., 2017); and blocked adult emergence after treatment of 4th instar larvae of *C. pipiens* with Saponin (Djeghader *et al*., 2018). In addition, feeding of larvae on artificial diets containing different concentrations of GA_3 hindered the adult emergence of *B. cucurbitae* (Kaur and Rup, 1999). A similar result on this melon fruit fly was recorded by Kaur and Rup (2003) after treatment of the larvae with Cn, kinetin, GA_3, and IAA.

It is important to point out that adult emergence in insects is a crucial physiological process and regulated by the eclosion hormone. Disturbance of this hormone partially or completely arrest the adults to emerge (Josephrajkumar *et al*., 1999).

For interpretation of the blocking of adult emergence after treatment of 5th or 6th instar larvae of *S. littoralis*, in the present study, Farnesol might exhibit a disturbing effect on the normal metabolism of insect hormones during the development of the immatures leading to failure of adult emergence (Trigo *et al*., 1988). In particular, Farnesol might disturb the adult eclosion hormone release and/or inhibition of the neurosecretion (Al-Sharook *et al*., 1991; Josephrajkumar *et al*., 1999). On the molecular basis, Farnesol might cause misexpression of certain genes, particularly the broodcomplex (br-C) transcription factor gene, leading to symptoms of impaired metamorphosis, like blocking of adult emergence (Wilson, 2004; Nandi and Chakravarty, 2011).

2.5. Deteriorated Morphogenesis Program:

As reported in the literature, plant extracts of different families or isolated plant compounds deleteriously affect the morphogenesis of pupae in several insects, as appeared in pupal deformities (Jeyasankar *et al*., 2011; Lingampally *et al*., 2013; Scapinello *et al*., 2014; Ben Hamouda *et al*., 2015; Salazar *et al*., 2015; Bhushan *et al*., 2016; Chennaiyan *et al*., 2016).

In the present study, Farnesol exerted an anti-morphogenic action on *S. littoralis*, since some deformed pupae were developed, at higher concentrations. Some of the malformed pupae appeared with constrictions at head and thorax, while other pupae were seen hump-backed, regardless the treated larval instar. The present result was in agreement with some reported results in different insects after treatment with various plant compounds, such as *S. frugiperda* after treatment with eucalyptin, chrysin, eucalyptin, quercetin, luteolin, and oleanolic acids (phytochemicals isolated from the methanol extract of *E. citriodora* leaves)(Salazar *et al*., 2015) and *S. litura* after treatment with Andrographolide (isolated from ethanol extraction of *A. paniculata*)(Edwin *et al*., 2016).

To understand the impairment of the pupation program in *S. littoralis,* in the present study, Farnesol might suppress the chitin synthesis and prevented the normal deposition of the new cuticle during apolysis leading to the pupal deformities (Retnakaran *et al*., 1985). These abnormalities affect the larval and pupal stages. The anti-morphogenic effect of Farnesol may be attributed to the disturbance of the release of ecdysteroids responsible for the form of developing pupae (Cespedes *et al*., 2013). In this context, Farnesol might block the release of morphogenic peptides, causing an alteration in titers of juvenoids required for the pupal transformation (Barnby and Klocke, 1990).

Conclusion:

Depending on the results of the present study, Farnesol exhibited a toxic effect on *S. littoralis*, caused a serious reduction of larval weight gain and deleteriously inhibited growth and development; disrupted development program, considerably suppressed pupation, completely prevented or partially blocked adult emergence, and deformed pupae. Therefore, Farnesol was found as an insect growth regulator and can be used as a potential agent in the integrated pest management program against *S. littoralis*.

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ARABIC SUMMARY

الكفاءة الحيوية للفارنيزول، مركب سيسكويتربيني عام، ضد القدرة المعيشية، النمو، الإنماء، والتشكل في دودة ورق القطن *سبودوبترا ليتوراليس* (حرشفيات الأجنحة: الليليات).

كارم غنيم، خالد حمادة، وحسن وهيب
قسم علم الحيوان والحشرات، بكلية العلوم جامعة الأزهر، القاهرة، مصر

دودة ورق القطن المصرية *سبودوبترا ليتوراليس* (بويزدوفال) آفة مدمرة لكثير من المحاصيل الحقلية والخضر في العالم. تم إجراء الدراسة الحالية بهدف تقويم (تقييم) سمية فارنيزول وتأثيره في نمو، إنماء، وتشكل الحشرة محل الدراسة. وقد سُمح ليرقات الدور الخامس ويرقات الدور السادس (الأخير) حديثة الانسلاخ بأكل أقراص من ورق الخروع الطازج بعد معاملتها بسبعة تركيزات من فارنيزول (٤٠٠، ٢٠٠، ١٠٠، ٥٠، ٢٥، ١٢,٥، ٦,٢٥ جزء في المليون) لمدة ٢٤ ساعة. وأمكن إيجاز أهم النتائج فيما يلي. تسبب المركب في وقوع وفيات فيما بين اليرقات والعذارى والفراشات اليافعة. واعتمادا على قيم التركيز نصف المميت، فقد أبدى فارنيزول نشاطا ساما بعد معاملة يرقات الدور السادس أشد (٣٣,٦٧ جزء في المليون) منه بعد معاملة يرقات الدور الخامس (٣٦,٥٦ جزء في المليون). كما تسبب فارنيزول في حدوث اختزال بالغ في وزن الجسم المكتسب في اليرقات، كما سبب انحدارا عنيفا لمعدل النمو. أما فترة حياة اليرقات وفترة حياة العذارى فقد طالت كلاهما إطالة ملحوظة، وموازية لمستويات التركيز. وقد اختل برنامج الإنماء اختلالا ظهر بشكلين، أحدهما فشل بعض اليرقات في الإنسلاخ، وإنتاج نسب مئوية من كائنات يرقية- عذراوية وسيطة، بصرف النظر عن الدور اليرقي الخاضع للمعاملة. كما بذل مركب فارنيزول فعلا كابحا قويا في عملية التعذر. وبعد استعماله بالتركيزات العليا، تدخل فارنيزول في عملية بزوغ اليافعات، فمنع البزوغ منعا كاملا عند أعلى تركيز، كما أعاقه إعاقة جزئية عند التركيزات الأخرى. وبصرف النظر عن الدور اليرقي الذي خضع للمعاملة، فقد أدت المعاملة بالمركب الحالي إلى إتلاف برنامج التشكُّل، وقد ظهر هذا واضحا بتكوين عذارى مشوهة، وخصوصا بعد استعمال أعلى تركيزين.