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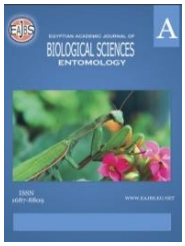

Impairing Effectiveness of Nerolidol, a Sesquiterpene Compound, on Adult Performance and Reproductive Potential of Egyptian Cotton Leafworm, *Spodoptera littoralis* (Lepidoptera: Noctuidae).

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

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ABSTRACT

Although Egyptian cotton leafworm *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) is native in Africa, it is distributed throughout the world. It is a serious polyphagous insect damaging more than 90 host plants of economic importance. The objective of the current study was to evaluate the disruptive impact of Nerolidol, a Sesquiterpene compound, 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 7 concentrations of Nerolidol (400, 200, 100, 50, 25, 12.5 & 6.25 ppm) for 24 hr. The most important results could be summarized as follows. Nerolidol exhibited an adulticidal activity only at the higher concentrations. Nerolidol exerted an anti-morphogenic activity against adult moths since some malformed adults were produced at the higher concentrations. Regardless the treated larval instar, Nerolidol induced the successfully emerged adults to live remarkably shortened total longevity and oviposition period, but the pre-oviposition period was generally prolonged. Nerolidol exhibited an inhibitory effect on the oviposition efficiency since the oviposition rate was deleteriously regressed, in a dose-dependent course. Nerolidol caused a disturbance of the reproductive capacity since fecundity and fertility were dramatically prohibited. After larval treatment with Nerolidol, the successfully mated adult females laid eggs with a significantly prolonged incubation period, especially at the higher concentration levels.

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 and the Middle East countries (El-Aswad, 2007; El-Sabrout, 2013; Azzouz *et al*., 2014). *S. littoralis* caterpillars feed on more than 90 plant species of economic importance belonging to 44 plant families (Kandil *et al*., 2003; Benelli *et al*., 2017), such as vegetables, horticultural crops and ornamental plants (Dahi, 2005; Amin, 2007; Ismail, 2014; Sut *et al*., 2017). Over the years, the number of attacked plants increased to more than 112 species (El-Sinary *et al*., 2008; El-Zoghby *et al*., 2011; Sut *et al*., 2017; Benelli *et al*., 2017; Al-Nagar *et al*., 2020).

In Egypt, Cotton (*Gossypium hirsutum*) 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). It mainly reduces the net productivity and quality of cotton (Amin and Gergis, 2006). In addition, *S. littoralis* is considered the most destructive pest of different Egyptian crops (Magd El-Din and El-Gengaihi, 2000), ornamentals and vegetables (Dahi, 2005; Amin, 2007; Lanzoni *et al*., 2012; Abd El-Razik and Mostafa, 2013). The high fecundity and migratory potential of *S. littoralis* contribute to serious damage which occurs as a result of feeding on leaves, flower buds, fruiting buds, and bolls (Mokbel *et al*., 2019). It is also reported to be a dangerous pest of cotton in Africa, the Middle East and Southern Europe (Abd-el-Aziz and Sayed, 2014). In Egypt, more than 10 million dollars have been spent to combat *S. littoralis* on all crops every year (Temerak, 2006).

Although different mechanical, physical and cultural control measures have been applied against *S. littoralis*, no satisfactory results can be achieved, most farmers, however, prefer using synthetic insecticides for obtaining fast results (Temerak, 2002; Abd El-Mageed and Shalaby, 2011; Ghoneim *et al*., 2012; Fetoh *et al*., 2015). The continuous and extensive use of insecticides to control agricultural pests usually exhibits adverse impacts on beneficial organisms, fish and wildlife, hazards to man and animals by environmental pollution, residues in foods (Abdel-Rahim and Azab, 2008; Osman and Mahmoud, 2009; Ehab, 2012). In spite of these hazards, some synthetic insecticides have already been used for controlling *S. littoralis* (Abd El-Mageed and Shalaby, 2011, Ghoneim *et al*., 2012). 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). Therefore, 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, many research works have been conducted to assess the insecticidal activities of various plant products against *S. littoralis* (Mansour *et al*., 2012; Derbalah *et al*., 2014; Moharramipour and Negahban, 2014; Abdel-Eltawab, 2016; Sammour *et al*., 2018).
Different classes of terpenes, in particular Monoterpenes, phenylpropenes, and Sesquiterpenes, are recognized to involve in several ecological functions in plants, including chemical defense against herbivores and pathogens, the attraction of pollinators and growth inhibition of other plants (Luitgards-Moura *et al*., 2002; Dudareva *et al*., 2006; Qualley and Dudareva, 2008). In Egypt, some studies (Abdelgaleil *et al*., 2008; Abbassy *et al*., 2009; Abdelgaleil, 2010) revealed the insecticidal activities of different monoterpenes, phenylpropenes, and sesquiterpenes against larvae of *S. littoralis*. Moreover, sesquiterpenes were found to possess topical and feeding toxicities against the larvae of *S. littoralis* (Handayani *et al*., 1997). Nerolidol (3,7,11-trimethyl-1,6,10-dodecatrien-3-ol, Molecular Formula: $C_{15}H_{26}O$), also known as peruviol and penetrol, is one of the most important acyclic Sesquiterpenes. It is isolated from essential oils of various plant sources (Botelho *et al*., 2007; Pacifico *et al*., 2008; Silva, 2014; Amaral *et al*., 2017; Chaaban *et al*., 2018; Azzi *et al*., 2018; Negrini *et al*., 2019; Pavela *et al*., 2019). Chemically, Nerolidol exists in two isomers, a *trans* and a *cis* form, which differ in the geometry about the central double bond (Chan *et al*., 2016). Nerolidol is synthesized as an intermediate in the production of (3E)-4,8-dimethy-1,3,7-nonatriene, a herbivore-induced volatile that protects plants against herbivore attacks and attracts some predatory insects (Chan *et al*., 2016).

With regard to the commercial uses and medicinal values of Nerolidol, it is frequently incorporated in cosmetics (e.g., shampoos, soaps, and perfumes) (Koudou *et al*., 2005) and non-cosmetic products (e.g., detergents and cleansers) (Lapczynski *et al*., 2008). Besides, Nerolidol is also widely used in the food industry as a flavor enhancer in many food products (Chan *et al*., 2016). In medicine, Nerolidol is currently under testing as a skin

penetration enhancer for the transdermal delivery of therapeutic drugs (Arruda *et al*., 2005; Lapczynski *et al*., 2008; Williams and Barry, 2004). For more information, see Inoue *et al*. (2004), Klopell *et al*. (2007), Nogueira Neto *et al*. (2013), Fonsêca *et al*. (2016) and Javed *et al*. (2016). From the pest control view of point, Nerolidol isomers function as insect attractants (Binder *et al*., 1995), antifeedants (Wheeler *et al*., 2003), larvicidal (Chantraine *et al*., 1998) and ovicidal agent (Priestley *et al*., 2006; Di Campli *et al*., 2012). Recently, Wróblewska-Kurdyk *et al*. (2019) evaluated the effect of Nerolidol isomers on the host-plant selection behaviour of the peach potato aphid *Myzus persicae*. The objective of the current study was to evaluate the disruptive impact of Nerolidol on the most important parameters of adult performance and reproductive potential of *S. littoralis*.

MATERIALS AND METHODS

I. 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.

2. The tested Sesquiterpene compound and larval treatment:

The tested Nerolidol in the present study was provided by Dr. Shady Selim, Faculty of Desert and Environmental Agriculture, Matrouh University, Egypt. Its common name is Nerolidol 98% has the chemical name: (*cis* + *trans*) [3,7,11-Trimethyl-1,6,10-dodecatrien-3-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 Nerolidol. For obtaining a stock solution, 90 ml of distilled water was added to each mixture for preparing a concentration of 4.9% Nerolidol, emulsion (Awad *et al*., 2013). The stock solution was diluted with distilled water in volumetric flasks for preparation of a series of concentrations: 400.0, 200.0, 100.0, 50.0, 25.0, 12.5 & 6.25 ppm.

The newly moulted 5^{th} (penultimate) and 6^{th} (last) larvae were treated with Nerolidol concentration levels *via* the fresh food, as follows. 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, the most important parameters of adult performance and reproductive potential were recorded just after the adult emergence.

3. Criteria of study:

3.1. Adult Performance:

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: 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 a few hours, therefore, no post-oviposition period was recorded.

3.2. 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 the hatching percentage of the laid eggs.

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

$$\text{Sterility Index} = 100 - [(a\ b / A\ B) \times 100]$$

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.

3.3. Incubation Period:

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

4. 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

1. Effect of Nerolidol on the Most Important Parameters of Adult Performance of *S. littoralis*:

1.1. Affected Adult Survival:

After treatment of 5th instar larvae of *S. littoralis* with 7 concentration levels of Nerolidol, data of the most important parameters of adult performance were summarized in Table (1). In the light of these data, no adult emerged after larval treatment with the highest concentration level. The adulticidal activity of Nerolidol was recorded only at the concentration level of 100 ppm (16.67% adult mortality). After treatment of 6th instar larvae, data of adult performance were arranged in Table (2). According to these data, different adult mortalities were recorded only at 200, 100 & 50 ppm (50, 50 & 20% mortality, *vs*. 0% mortality of control adults).

1.2. Imperfect Adult Morphogenesis:

After treatment of 5th instar larvae with Nerolidol, the successfully emerged adults appeared with some deformed features, only at 200 & 100 ppm (50 & 25% deformed adults, respectively, compared to 0% deformity of control adults, see Table 1). After treatment of 6th instar larvae with Nerolidol, some deformed adults emerged only at the higher three concentration levels (50, 50 & 20% deformed adults, at 200, 100 & 50 ppm, respectively, vs. 0% deformity of control adults, see Table 2). As seen in Plate (1), obvious symptoms of adult malformation appeared as curled wings, atrophied mouthparts and crumpled legs.

1.3. Influenced Adult Longevity:

After treatment of 5th instar larvae with Nerolidol, data of adult longevity and its compartments were assorted in Table (1). Depending on these data, total adult longevity was remarkably shortened, at all concentration levels, except the lower two concentration levels (9.67±0.86, 9.96±0.74, 9.98±0.41, 10.07±0.24,10.56±0.44 & 10.60±0.63 days of treated adults, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs*. 10.83±0.41 days of control adults). Also, the oviposition period (reproductive life-time) was generally shortened. On the contrary, the pre-oviposition (ovarian maturation) period was generally prolonged, especially at higher two concentration levels (2.67±0.52 & 2.74±0.17 days of treated adults, at 200 & 100 ppm, respectively, *vs*. 2.22±0.04 days of control adult females).

After treatment of 6th instar larvae with Nerolidol, data of adult longevity and its compartments were assorted in Table (2). As clearly seen in this table, total adult longevity was slightly shortened (10.00, 10.11±0.36, 10.50±0.61, 10.51±0.36, 10.49±0.12 & 10.33±0.45 days of treated adults, at 200, 100, 50, 25, 12.5 & 6.25 ppm, *vs*. 10.67±0.93 days of control adult females). In contrast, the pre-oviposition period was considerably prolonged (3.00, 2.67±0.12, 2.51±0.24, 2.36±0.16, 2.25±0.05 & 2.20±0.33 days of treated adults, at 200, 100, 50, 25, 12.5 & 6.25 ppm, *vs*. 2.19±0.08 days of control adult females).

2. Effects of Nerolidol on the Most Important Parameters of Reproductive Potential of *S. littoralis*:

After treatment of 5th instar or 6th instar larvae of *S. littoralis* with 7 concentration levels of Nerolidol, data of the most important criteria of reproductive potential of the successfully mated adult females were assorted in Table (3) and Table (4), respectively.

Table 1: Adult performance of *S. littoralis* as affected by treatment of the newly moulted penultimate (5th) instar larvae with Nerolidol.

Conc. (ppm)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days ± SD)		
			Ovarian maturation period	Reproductive life-time	Total longevity
400.00	---	---	---	---	---
200.00	0.00	50.00	2.67±0.52 b	7.00±0.33 d	9.67±0.86 b
100.00	16.67	25.00	2.74±0.17 d	7.33±0.68 d	9.96±0.74 b
50.00	0.00	0.00	2.27±0.09 a	7.48±0.36 d	9.98±0.41 d
25.00	0.00	0.00	2.11±0.28 a	7.86±0.51 b	10.07±0.24 c
12.50	0.00	0.00	2.24±0.05 a	8.36±0.38 a	10.56±0.44 a
6.25	0.00	0.00	2.25±0.12 a	8.33±0.52 a	10.60±0.63 a
Control	0.00	0.00	2.22±0.04	8.67±0.52	10.83±0.41

Conc.: concentration levels. ---: no emerged 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 2: Adult performance of *S. littoralis* as affected by treatment of the newly moulted last (6^{th}) instar larvae with Nerolidol**.**

Conc. (ppm)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days ± SD)		
			Ovarian maturation period	Reproductive life-time	Total longevity
400.00	---	---	---	---	---
200.00	50.00	50.00	3.00* d	7.00* d	10.00* a
100.00	50.00	50.00	2.67±0.12 d	7.44±0.26 d	10.11±0.36 a
50.00	20.00	20.00	2.51±0.24 c	8.00±0.36 b	10.50±0.61 a
25.00	0.00	0.00	2.36±0.16 b	8.15±0.23 a	10.51±0.36 a
12.50	0.00	0.00	2.25±0.05 a	8.24±0.08 a	10.49±0.12 a
6.25	0.00	0.00	2.20±0.33 a	8.33±0.11 a	10.33±0.45 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). *: only one adult moth emerged

2.1. Prohibited Oviposition Efficiency:

Depending on data listed in Table (3), Nerolidol exhibited an extended inhibitory effect on the oviposition efficiency, since the oviposition rate was conspicuously suppressed, in a dose-dependent course, after treatment of 5^{th} instar larvae (84.00±4.65, 101.26±5.95, 115.66±5.67, 115.35±6.12, 122.65±4.38 & 143.12±6.10 of treated adult females, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 183.07±18.58 of control adult females). A similar inhibitory effect of this compound was detected on the oviposition efficiency since the oviposition rate was deleteriously regressed after treatment of 6^{th} instar larvae (56.00, 69.39±4.30, 74.13±2.23, 98.58±4.01, 141.99±5.40 & 158.59±7.15 of treated adult females, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 184.47±12.96 of control adult females, Table 4).

2.2. Perturbed Reproductive Capacity:

After treatment of 5^{th} instar larvae with Nerolidol, data of the reproductive capacity were distributed in Table (3). Depending on these data, fecundity (mean number of egg/♀) was dramatically prohibited (588.00±32.53, 740.33±15.50, 836.50±20.92, 851.00±20.19, 1000.33±24.91 & 1183.29±23.59 eggs/treated♀, at 200, 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 (53.11±1.27, 65.94±1.56, 67.54±1.75, 72.33±1.91, 78.52±1.52 & 85.51±1.73% hatching eggs laid by treated adult females, at 200, 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 proportionally to the increasing concentration level of Nerolidol (for detail, see Table 3).

As seen in Table (4), the treatment of 6^{th} instar larvae with Nerolidol led to the disturbance of the reproductive capacity. Fecundity was severely prohibited, in a dose-dependent manner (392.00, 507.67±25.93, 593.00±17.87, 843.20±57.25, 1157.83±21.41 & 1311.14±25.91 eggs/treated♀, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 1593.83±58.64 eggs/control♀). Also, fertility was tremendously reduced, in a dose-dependent course (45.61, 50.42±2.06, 66.99±2.32, 73.35±1.73, 81.00±2.31 & 88.19±2.11% hatching eggs laid by treated adult females, at 200, 100, 50, 25, 12.5 & 6.25 ppm, respectively, *vs.* 93.97±0.66% hatching eggs laid by control adult females). In addition, the calculated sterility index ascended with the increasing concentration level of Nerolidol (for detail, see Table 4).

3. Retarded Embryonic Development:

In insects, the incubation period of eggs can be used as a valuable indicator of the embryonic developmental rate, i.e., a longer period usually denotes a slower rate of development and *vice versa*. After treatment of 5th instar larvae with Nerolidol, the successfully mated adult females laid eggs which incubated through a significantly prolonged period, especially at the higher four concentration levels (4.00±0.00, 3.67±0.58, 3.75±0.50 & 3.40±0.55 days of eggs laid by treated females, at 200, 100, 50 & 25 ppm, *vs*. 2.16±0.41 days of eggs laid by control females, Table 3). After treatment of 6th instar larvae with Nerolidol, the successfully mated adult females laid eggs which incubated through a significantly prolonged period (5.00, 4.33±0.58, 3.75±0.50, 3.80±0.45, 3.33±0.52 & 2.85±0.69 days of eggs laid by treated females, at 200, 100, 50, 25, 12.5 & 6.25 ppm, *vs*. 2.33±0.52 days of eggs laid by control females, Table 4). This result indicated remarkable retardation of the embryonic development by Nerolidol.

Table 3: Reproductive potential of *S. littoralis* as affected by the treatment of newly moulted penultimate (5th) instar larvae with Nerolidol.

Conc. (ppm)	Oviposition rate (mean ± SD)	Reproductive capacity			Incubation period (days) (mean ± SD)
		Fecundity (mean egg No. ± SD)	Fertility (%)	Sterility index (%)	
400.00	---	---	---	---	---
200.00	84.00±4.65 d	588.00±32.53 d	53.11±1.27 d	79.91	4.00±0.00 d
100.00	101.26±5.95 d	740.33±15.50 d	65.94±1.56 d	68.59	3.67±0.58 d
50.00	115.66±5.67 d	836.50±20.92 d	67.54±1.75 d	63.65	3.75±0.50 d
25.00	115.35±6.12 d	851.00±20.19 d	72.33±1.91 d	60.40	3.40±0.55 c
12.50	122.65±4.38 d	1000.33±24.91 d	78.52±1.52 d	49.47	2.67±0.52 a
6.25	143.12±6.10 d	1183.29±23.59 d	85.51±1.73 d	34.90	2.43±0.53 a
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).

Table 4: Reproductive potential of *S. littoralis* as affected by the treatment of newly moulted last (6th) instar larvae with Nerolidol.

Conc. (ppm)	Oviposition rate (mean ± SD)	Reproductive capacity			Incubation period (days) (mean ± SD)
		Fecundity (mean egg No. ± SD)	Fertility (%)	Sterility index (%)	
400.00	---	---	---	---	---
200.00	56.00* d	392.00* d	45.61* d	88.50	5.00* d
100.00	69.39±4.30 d	507.67±25.93 d	50.42±2.06 d	83.53	4.33±0.58 d
50.00	74.13±2.23 d	593.00±17.87 d	66.99±2.32 d	74.44	3.75±0.50 c
25.00	98.58±4.01 d	843.20±57.25 d	73.35±1.73 d	60.21	3.80±0.45 d
12.50	141.99±5.40 d	1157.83±21.41 d	81.00±2.31 d	39.66	3.33±0.52 c
6.25	158.59±7.15 d	1311.14±25.91 d	88.19±2.11 d	25.61	2.85±0.69 a
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). *: see footnote of Table (2).

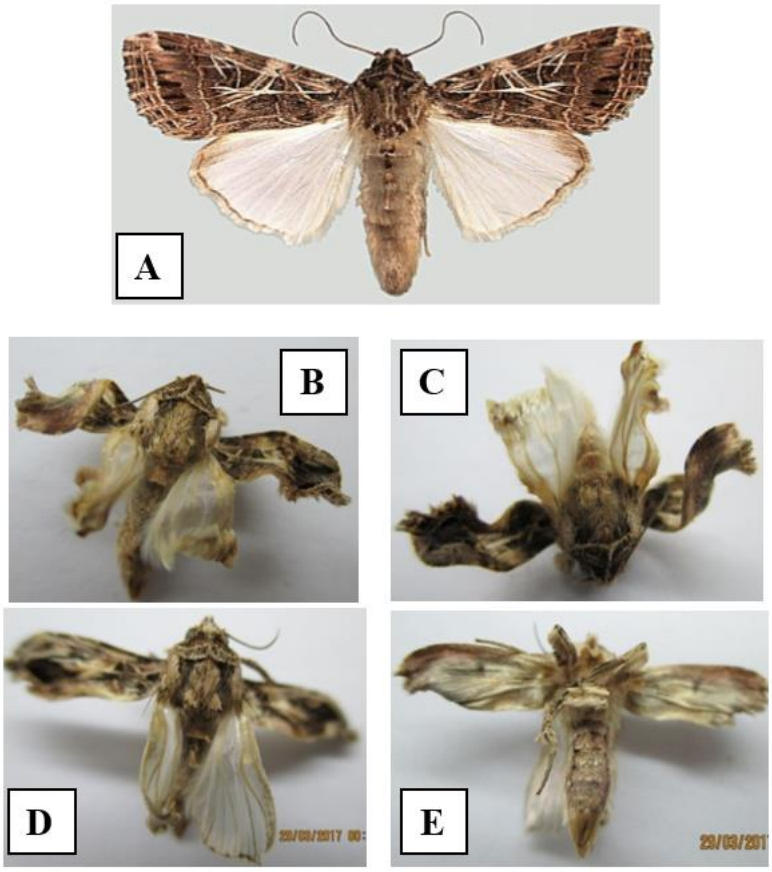

Plate (1): Adult deformities of *S. littoralis* after treatment of 5th or 6th instar larvae with higher concentrations of Nerolidol. (A) Normal adult moth. (B & C): Adult moths with deformed wings and atrophied mouth parts. (D & E): Adult moths with curled wings and crumpled legs.

DISCUSSION

1. Impaired adult performance of *S. littoralis* by Nerolidol:

1.1. Affected Adult Survival:

Depending on the currently available literature, very few studies have examined the toxicity of plant compounds on adults of insects. For example, Thymoquinone (among eleven terpene ketones) exhibited the highest toxicity against adults of the maize weevil *Sitophilus zeamais* by contact and fumigant methods (Herrera *et al*., 2015). In the present study, the sesquiterpene compound, Nerolidol, exhibited an adulticidal activity after treatment of 5th instar larvae of *S. littoralis* only with 100 ppm. After treatment of 6th instar larvae, adult mortality was recorded at the higher three concentrations.

The adult mortality of *S. littoralis* could be explained by the retention and distribution of Nerolidol 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 lethal effect of Nerolidol 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 hindgut may be the cause of untimely adult mortality, as recorded for Nerolidol against *S. littoralis* adults in the current study (Soltani, 1984). Also, the adult mortality may be explicated by a latent prohibitory effect of Nerolidol on feeding leading to continuous starvation and

subsequently death (Ghoneim *et al*., 2000) or adverse effect on the homeostasis leading to increased loss of body water and desiccation and subsequently death (Amer *et al*., 2004).

1.2. Disrupted Adult Morphogenesis:

Many authors (Shekari *et al*., 2008; Jeyasankar *et al*., 2011; Lingampally *et al*., 2013; Nogueira *et al*., 2014**;** Scapinello *et al*., 2014; Bhushan *et al*., 2016; Chinnamani *et al*., 2016) reported detrimental effects of plant extracts or plant compounds on the adult morphogenesis of various insect species, as observed as different morphological aberrations of the whole body or some of its structures. For example, 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). Topical application of Farnesol onto the newly emerged 5th instar nymphs of the red cotton stainer bug *Dysdercus koenigii* led to the metamorphosis of nymphs into adults with malformed wings (Kumar and Gupta, 2017). Treatment of the 5th and 6th instar larvae of the confused flour beetle *Tribolium confusum* with Andrographolide (a terpenoid isolated from the leaves of *Andrographis paniculata*) impaired the adult morphogenesis (Lingampally *et al*., 2013). Feeding of 2nd instar larvae of the tobacco cutworm *Spodoptera litura* on fresh food treated with Allyl isothiocyanate (an isothiocyanate derived from plant Glucosinolates) resulted in the metamorphosis of malformed adults (Bhushan *et al*., 2016). Larval treatment with Pogostone (isolated as the main constituent of essential oil from *Pogostemon cablin*) resulted in some deformities in adult moths of *S. litura* and the beet armyworm *Spodoptera exigua* (Huang *et al*., 2014). Fraction II (300lg/g of diet) from *Vernonanthura nebularum* natural products was found the most active substance causing wing malformations in adults of the fall armyworm *Spodoptera frugiperda* (Sosa *et al*., 2019).

Results of the present study were, to a great extent, in agreement with those reported results, since Nerolidol exhibited an anti-morphogenic activity against the adult moths of *S. littoralis*. Some malformed adults were produced after larval treatment with higher concentrations. These malformed adults appeared with curled wings, atrophied mouthparts, and crumpled legs. For interpretation of the anti-morphogenic action of Nerolidol on the adult moths of *S. littoralis*, in the present investigation, this Sesquiterpene compound might exert an impairing action 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 or even causing inhibition of some physiological processes, such as morphogenesis (Josephrajkumar *et al*., 1999; Cespedes *et al*., 2013). Another suggestion can be appreciated, such as the inhibition of chitin synthase by metabolites of the tested compound (Cohen and Casida, 1980) or inhibition of DNA synthesis and/or inhibition of facilitated diffusion and active transport across cell membranes of nucleosides and amino acids (Mayer *et al*., 1988).

1.3. Influenced Adult Longevity:

***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).

Regardless of the treated larval instar of *S. littoralis*, Nerolidol induced the successfully emerged adult females, in the present study, to live remarkably shortened total longevity at all concentration levels, except the lower two concentration levels. This result was in accordance with some reported results of shortened total longevity of some insects after larval treatment with a number of plant compounds, such as domestic mosquito *Culex pipiens*

after treatment of 4th instar larvae with Saponin (Djeghader *et al*., 2018); the brown planthopper *Nilaparvata lugens* after nymphal treatment with Jasmonic acid (JA) (Senthil-Nathan *et al*., 2009) and *G. mellonella* after injection of higher doses of Abscisic acid (ABA) into the haemocoel of larvae resulted in shortened adult longevity (Er and Keskin, 2015).

To understand the shortened adult longevity of *S. littoralis* after larval treatment with Nerolidol, in the current study, some conceivable scenarios could be suggested, as follows. (**1**) Nerolidol 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 Nerolidol on the hormonal regulation because a close relationship between certain hormones and adult longevity was reported in other insects, such as *Drosophila melanogaster* (Carbone *et al*., 2006; Chamseddin *et al*., 2012; Yamamoto *et al*., 2013). At least one of the *Drosophila* insulin-linked peptides expressed in the median neurosecretory cells (which produce prothoracicotropic hormone) is likely to contribute to the endocrine regulation of longevity (Toivonen and Partridge, 2009). In this fly, representatives of a peptide hormone, lipophilic hormones and bioactive amines have been shown to modulate longevity by manipulations that directly decrease the hormone production (Broughton *et al.*, 2005), through inactivating mutations in hormone receptors or their downstream targets (Clancy *et al*., 2001; Simon *et al*., 2003) or by polymorphic alterations in the genes required for 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, Nerolidol 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 Nerolidol 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 Nerolidol can affect adult longevity. (**4**) In insects, the fat body serves many vital functions (Arrese and Soulages 2010) and it is therefore not surprising that longevity mechanisms occur within the fat body (Hwangbo *et al*. 2004). Thus, Nerolidol might adversely affect the fat bodies resulting in shortened longevity of *S. littoralis* adults.

***Shortened Oviposition Period*:**

The currently available literature has no results of the effects of plant compounds on the oviposition period in insects. In the present study, Nerolidol induced the adult female moths to pass remarkably shortened oviposition period, regardless the treated larval instar of *S. littoralis*. This result could be interpreted by an enforcing effect of Nerolidol on the ovipositing 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 current investigation, Nerolidol inhibited the adult female moths to pass generally prolonged pre-oviposition period, regardless the treated larval instar of *S. littoralis*. This result was in agreement with that result reported for *L. migratoria* by Abdellaoui *et al*. (2009), since treatment with Gibberellic acid, a plant growth regulator, led to the prolongation of the pre-oviposition period.

It is important to mention that the prolongation of the pre-oviposition period in insects may be a good indicator of a delay or retardation of the ovarian maturation rate. For some detail, many lepidopterous species 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 lifestyle constrains these insects to a program of

ovarian organogenesis and 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 Nerolidol 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, ovarian development in insects is known to be under endocrine control (Kaur and Rup, 2002). The retarded ovarian development in *S. littoralis* by Nerolidol, 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, Abdellaoui *et al*. (2015) reported that the ovarian ecdysteroid contents drop sharply at the time of oviposition. This phenomenon occurs regularly during successive ovarian cycles. Thus, occurrence of considerable amount of ecdysteroids in freshly laid eggs suggests a transfer of maternal ecdysteroids into eggs for regulating the embryonic development.

However, the exact mode of retarding action of Nerolidol 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 physiological process needs further investigation in the foreseeable future.

2. Deteriorated Reproductive Potential of *S. littoralis* by Nerolidol:

2.1. Prohibited Oviposition Efficiency of *S. littoralis*:

Very few studies investigated the effects of plant compounds on the oviposition efficiency of insects. In the present study, Nerolidol exhibited an extended inhibitory effect on the oviposition efficiency of *S. littoralis*, since the oviposition rate was deleteriously regressed, in a dose-dependent course, irrespective of the treated larval instar. This result was in corroboration with those results of the oviposition inhibition activity of Eugenol (a major constituent of EO from *Cinnamomum tamala*) against adults of the maize weevil *Sitophilus oryzae* (Chaubey, 2016) and Rotenone against adults of the melon worm *Diaphania hyalinata* (Silva *et al*., 2016).

For interpretation of the inhibited oviposition efficiency of *S. littoralis* adults after larval treatment with Nerolidol, in the present study, it is important to point out that reproduction in insects is mainly controlled by corpus allatum hormone (JH), which is also responsible for protein metabolism and is specifically needed for egg maturation (Ghoneim *et al*., 2014). On the other hand, ecdysteroids have essential functions 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 Nerolidol 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).

2.2. Perturbed reproductive capacity:

Prohibited Fecundity of S. littoralis:

Different plant products had been reported to prohibit the fecundity of various insects. For example, treatment of the newly moulted last (5^{th}) instar nymphs of the desert

locust *Schistocerca gregaria* with farnesol led to inhibited fecundity (decreased egg-pod production and number of eggs/pod)(Awad *et al*., 2013). A great reduction in fecundity of the domestic mosquito *Culex pipiens* had been recorded after treatment of 4th instar larvae with Saponin (Djeghader *et al*., 2018). The adult fecundity of the wolfberry aphid *Aphis* sp. was significantly reduced after treatment with JA, a plant growth regulator, in a dose-dependent course (Gong *et al*., 2010). The injection of higher doses of ABA, a plant growth regulator, into the haemocoel of *G. mellonella* resulted in a reduction of fecundity (Er and Keskin, 2015). A remarkable inhibitory effect on the fecundity of Mexican mite *Tetranychus mexicanus* was recorded for Nerolidol (isolated from the essential oil of *Derris floribunda* roots) (Amaral *et al*., 2017). Results of the present study were in corroboration with the previously reported results because fecundity of *S. littoralis* was dramatically prohibited after treatment of the 5th or 6th instar larvae with Nerolidol, in a dose-dependent manner.

To explicate the present inhibition of *S. littoralis* fecundity, it is important to point out that some plant products act as hormonal regulators of moulting process and metamorphosis in insects due to a blockage and /or delay in the release of ecdysteroid and juvenile hormone from their neurohaemal organs. Therefore, the plant products are known to inhibit ovarian growth, testes growth and development (El-Zoghaby, 1992; El-Sabrout, 2013). The drastically prohibited fecundity of *S. littoralis*, after treatment of the penultimate or last instar larvae with Nerolidol, in the present study, might be due to the interference of this compound with one or more processes of reproductive physiology, from the ovarian follicle development to egg maturation. In this context, this prohibited fecundity could be explained by some scenarios, as discussed herein.

(**1**) The reduction in fecundity might be due to the undifferentiated ovarioles in adult female moths of *S. littoralis* as an action of larval treatment with Nerolidol, as reported by some authors for other plant products (Martinez and Van Emden, 2001; Abdelgaleil and El-Sabrout, 2018). (**2**) The reduction of *S. littoralis* fecundity, in the current investigation, might be due to the direct disruptive effect of Nerolidol on the reproductive behavior of adult moths (Magierowicz *et al*., 2019). **(3)** Nerolidol might cause some disorders in the developing ovarioles during the immature stages (Davey, 1993) including cell death in the germarium, resorption of oocytes in the pre-vitellarium and vitellarium before oviposition (Zhou *et al*., 2016), the formation of vitellin envelops and undue proliferation of follicle cells sometimes resulting in malformation of the whole ovary (Lucantoni *et al*., 2006; Khan *et al*., 2007). **(4)** Nerolidol might prohibit the developing ovarioles by inhibition of synthesis and metabolism of proteinaceous constituents during the vitellogenesis (Salem *et al*., 1997). **(5)** Nerolidol exerted an inhibitory action on the ecdysone activity, threshold of which is essential for the normal oogenesis (Smagghe *et al*., 1996; Salem *et al*., 1997; Terashima *et al*., 2005). **(6)** Nerolidol 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 (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 rebsorpion before oviposition (Zhou *et al*., 2016). **(8)** It may be acceptable to suggest that the prohibited fecundity of *S. littoralis*, in the current work, might be due to inhibitory effects of Nerolidol on a 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 of S. littoralis:

Chemosterilants are used to control economically destructive or disease-causing insect pests by causing temporary or permanent sterility of one or both of the sexes (Navarro-Llopis, *et al*., 2011; Wilke *et al*., 2009). Fertility (hatching% of egg viability) represents an informative parameter of the reproductive capacity in insects. However, decreasing fertility

denotes increasing sterility. Depending on the currently available literature, scarce studies have examined the effects of plant compounds in general and sesquiterpene compounds, in particular, on the fertility of insects. In the present study**,** treatment of 5th or 6th instar larvae of *S. littoralis* with Nerolidol resulted in a dramatic reduction in fertility, in a dose-dependent course. Also, sterility increased proportionally to the increasing concentration of the tested compound. This result was in agreement with the reported reduction of fertility in few insects after larval treatment with plant products, such as reduced egg hatchability in the brown planthopper *Nilaparvata lugens* after treatment with JA, a plant growth regulator (Senthil-Nathan *et al*., 2009) and reduced hatchability in *C. pipiens* after treatment of 4th instar larvae with Saponin (Djeghader *et al*., 2018).

For explicating the fertility reduction in *S. littoralis* after larval treatment with Nerolidol, in the present study, some suggestions could be provided herein. **(1)** Maturation of the insect eggs depends basically on the vitellogenins, precursor materials of vitellins including proteins, lipids, and carbohydrates, all of which are necessarily required for the embryonic development (Soltani and Mazouni, 1992; Chapman, 1998). These materials are synthesized primarily by the fat body during the immature stages (Telfer, 2009) or by the ovary *in situ* (Indrasith *et al*., 1988). Nerolidol might disturb the production and/or accumulation of vitellogenins in adult females of *S. littoralis* leading to the reduction of fertility (for some detail, see Taibi *et al*., 2003; Pineda *et al*., 2006; Osorio *et al*., 2008). **(2)** Nerolidol might indirectly affect the fertility *via* its disruptive effect on opening "potency" of the intracellular spaces in the follicular epithelium or generally inhibited the role of JH (gonadotropic hormone) responsible for vitellogenesis, the regulation of vitellogenin deposition into oocytes (Davey and Gordon, 1996). **(3)** The reduction in fertility might be due to the penetration of residual amounts of Nerolidol in *S. littoralis* mothers into their eggs and disturbance of 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 (Marco and Vinuela, 1994; Sallam, 1999; Sammour *et al*., 2008). (**4**) Moreover, the developing embryos in eggs of *S. littoralis* suffered morphological deformation and incomplete development of some body parts after larval treatment with Nerolidol. **(5)** The reduced fertility of *S. littoralis*, in the current study, might be due to the serious effect of Nerolidol on the 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 perturbation of gene expression in the hierarchy cascade of vitellogenesis and/or choriogenesis (Sun *et al*., 2003), Nerolidol 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 Nerolidol on the fertility of *S. littoralis* is still obscure and needs further investigation to be clearly understood.

3. Retarded Embryonic Development in *S. littoralis* by Nerolidol:

In insects, the incubation period of eggs can be used as a valuable indicator of the embryonic developmental rate, i.e., a longer period usually denotes a slower rate of development and *vice versa*. From the current literature, no reliable information has been obtained regarding the effects of plant compounds on the embryonic development in insects, as to be denoted by the incubation period of eggs. After treatment of 5th or 6th instar larvae of *S. littoralis* with Nerolidol, the successfully emerged and mated adult females laid eggs which incubated through the significantly prolonged period. This result might indicate remarkable retardation of the embryonic development in eggs by Nerolidol, in the present study.

The retarded embryonic development in *S. littoralis*, in the present study, may be attributed to an impairing effect of Nerolidol on the ecdysteroids responsible for the

regulation of certain stages of embryogenesis, especially those ecdysteroids originating from the ovary *in situ* (Chapman, 1998).

Conclusion:

According to the obtained results, in the present study, Nerolidol exhibited an adulticidal activity against *S. littoralis*. Also, it exerted an anti-morphogenic activity against adult moths and induced the adults to live remarkably shortened longevity. Nerolidol exhibited an inhibitory effect on the oviposition efficiency, fecundity, and fertility beside retardation of the embryonic development. Therefore, it can be recommended to use Nerolidol, as an effective agent in the integrated pest management of this dangerous pest, *S. littoralis***,** since it has developed resistance to the majority of conventional insecticides.

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ARABIC SUMMARY

التأثير الإتلافي لنيروليدول، مركب سيسكويتربيني، في كفاءة اليافعات والكفاءة التكاثرية لدودة ورق القطن المصرية *سبودوبترا ليتوراليس* (حرشفيات الأجنحة: الليليات).

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

تستوطن دودة ورق القطن المصرية *سبودوبترا ليتوراليس* (بويزيوفال)(حرشفيات الأجنحة: الليليات) أفريقيا، أساسا، وبالرغم من ذلك فإنها تنتشر في أنحاء متفرقة من العالم. وتعد هذه الحشرة آفة خطيرة تهاجم وتدمر أكثر من ٩٠ عائل من العوائل النباتية ذات الأهمية الاقتصادية. استهدفت الدراسة الحالية بحث التأثير التدميري لمركب نيروليدول، مركب سيسكويتربيني، في أهم معايير كفاءة اليافعات والكفاءة التكاثرية للحشرة محل الدراسة. ومن أجل ذلك، تمت معاملة أقراص من ورق الخروع الطازج بسبعة تركيزات من المركب المختبر (٤٠٠، ٢٠٠، ١٠٠، ٥٠، ٢٥، ١٢,٥، ٦,٢٥ جزء في المليون) وتغذية يرقات الدور الخامس ويرقات الدور السادس (الأخير) بها لمدة ٢٤ ساعة. وأمكن إيجاز أهم النتائج فيما يلي. أبدى المركب تأثيرا ساما في اليافعات، بعد استعماله فقط بأعلى تركيزاته. كما بذل المركب نشاطا تقويضيا لتشكل الفراشات اليافعة، مادامت أعدادا من الفراشات المشوهة قد ظهرت بعد المعاملات اليرقية بالتركيزات العليا. وبصرف النظر عن الدور اليرقي الذي خضع للمعاملة، فإن اليافعات التي نجحت في البزوغ قد عاشت لأمد زمني قصير قصرا كبيرا، وكذا حدث لفترة وضع البيض، ولكن فترة ما قبل وضع البيض طالت إطالة عامة. بالنسبة للكفاءة التكاثرية، فقد بذل المركب تأثيرا تثبيطيا في فعالية وضع البيض، حيث انحدر معدل وضع البيض انحدارا مواكبا لمستوى التركيز. كما أحدث نيروليدول اضطرابا كبيرا في السعة التكاثرية، إذ انخفضت إنتاجية الإناث للبيض انخفاضا شديدا، واختزلت خصوبة البيض اختزالا عنيفا... وبعد المعاملات اليرقية بالمركب الحالي، قامت الفراشات الإناث التي نجحت في البزوغ والتزاوج بوضع بيضا طالت فترة حضانته إطالة كبيرة، مما دل على تعطيل الإنماء الجنيني تعطيلا ملحوظا، خاصة عند التركيزات العليا.