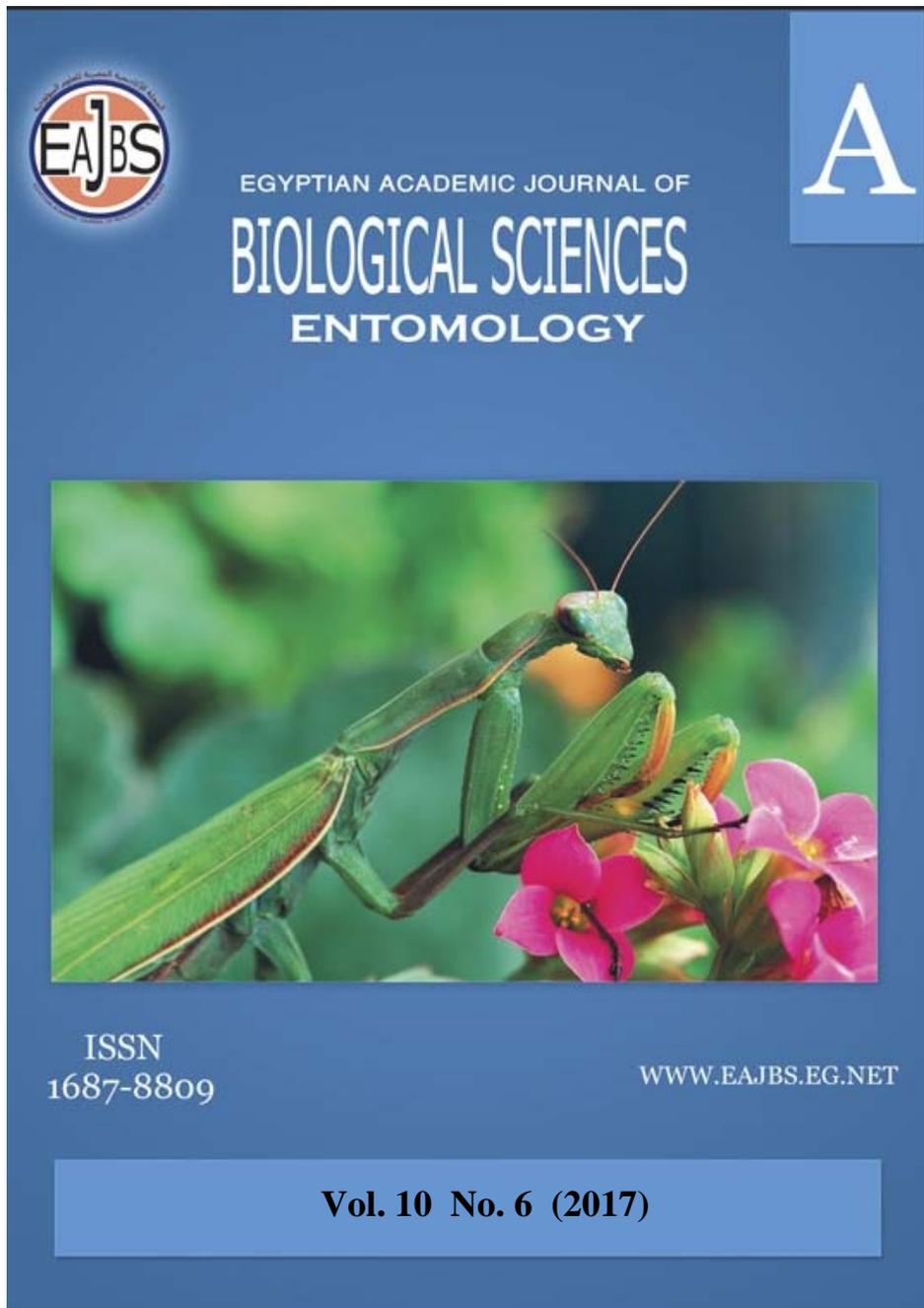


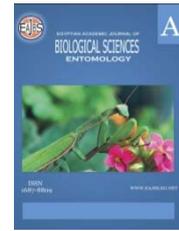
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**Disruptive Impact of Precocene I (juvenile hormone-antagonist) on the Adult Performance and Reproductive Potential of the Egyptian Cotton Leafworm *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae)**

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**ABSTRACT**

The cotton leafworm, *Spodoptera littoralis* is destructive pest of cotton and various crops all over the year. The present study was carried out aiming to assess the effects of Precocene I (PI) on the most important parameters of adult performance and reproductive potential of this pest. Five sublethal doses: 150, 120, 90, 30 and 15 µg/larva had been topically applied (once) onto 1-day old larvae of 5<sup>th</sup> (penultimate) instar and 6<sup>th</sup> (last) instar. The adult emergence was slightly, or drastically, blocked, depending on the dose level and larval instar under treatment. PI exhibited a slightly extended toxic effect on the adult females only with the higher two doses. Some adult deformities were produced after treatment of 6<sup>th</sup> instar larvae with PI. With regard to the adult longevity, the major effect of PI was the promotion of adult females to live longer life-time. Both pre-oviposition and oviposition periods had been slightly, or considerably, shortened. After topical application of PI onto 5<sup>th</sup> instar larvae, the oviposition rate was drastically regressed only at the lower two doses. After treatment of 6<sup>th</sup> instar larvae with PI, the oviposition rate was drastically regressed in a dose-dependent course. Both fecundity and fertility were dramatically reduced. Complete sterility was recorded after treatment of 5<sup>th</sup> instar larvae with PI but complete sterility had been recorded after treatment of 6<sup>th</sup> instar larvae only with 150 and 30 µg/larva. The incubation period was remarkably prolonged.

**INTRODUCTION**

The cotton leafworm *Spodoptera littoralis* has been considered as destructive phytophagous lepidopterous pest of cotton and various vegetable and field crops all over the year (Shonouda and Osman, 2000; El-Khawas and Abd El-Gawad, 2002; Adham *et al.*, 2009). Approximately 112 plant species belonging to 44 families are reported as hosts of this pest in tropical and temperate zones of the old world (Magd El-din and El-Gengaihi, 2000). To control the attacks of *S. littoralis*, several types of conventional insecticides have been used over the past 40 years (Casida and Quistad, 1998). The intensive use of broad-spectrum insecticides against *S. littoralis* has led the development of resistance to many registered pesticides making their control

even more difficult (Miles and Lysandrou, 2002; Aydin and Gurkan, 2006; Davies *et al.*, 2007, Mosallanejad and Smagghe, 2009). As a result of improper and excessive uses, also, these insecticides usually exhibit several adverse impacts on the human health and beneficial animals as well as cause serious toxicological problems to the environmental systems because these chemicals have a long half-life and retention in the environment for long periods (Van Der Gaag, 2000; Costa *et al.*, 2008; Relyea, 2009; Tiryaki and Temur, 2010; Damalas and Eleftherohorinos, 2011; Chowański *et al.*, 2014). Therefore, eco-friendly insecticides have received global attention in recent years as alternative for the conventional insecticides. These alternative compounds are characterized by lower toxicity to non-target organisms than conventional insecticides and they are effective at low concentrations (Attathom, 2002; Gade and Goldsworthy, 2003). Also, they are biodegradable into harmless compounds, which allows for avoiding the problems of environmental pollution (Tiryaki and Temur, 2010; Walkowiak *et al.*, 2015; Li *et al.*, 2017). The potential of juvenile hormone analogues (JHAs) and insect growth regulators (IGRs) for the pest control had been intensively reviewed (Staal, 1982; El-Ibrashy, 1982, 1984; Dhadialla *et al.*, 1998; Gilbert *et al.*, 2000; Tunaz and Uygun, 2004; Chowański *et al.*, 2014).

In insects, Juvenile hormone (JH) is necessary for insect development throughout the immature stages (Staal, 1986). It works alone or in combination with ecdysone and its metabolite 20E (20-hydroxyecdysone) in regulating various functions (Nijhout, 1994). JHs play important roles in several physiological processes, such as reproduction, diapause, behaviour, polymorphism, migration, metabolism and innate immunity (Mitsuoka *et al.*, 2001; Tatar *et al.*, 2001a,b; Truman and Riddiford, 2007; Flatt *et al.*, 2008; Denlinger *et al.*, 2012; Amsalem *et al.*, 2014a). JH functions as gonadotropin in adults (Riddiford, 1994, 2008; Gilbert *et al.*, 2000; Amsalem *et al.*, 2014b).

It has been demonstrated that the design of JH mimics or anti-JH agents is an effective strategy for insecticide discovery (Bede *et al.*, 2001). Compounds with anti-JH activity are considered as new representatives of insect growth regulators (IGRs) lacking some disadvantages of juvenoid-type chemicals (Bowers, 1982; Staal, 1982). These chemicals are potentially efficacious for control of the major insect pests where most of the damage is caused by larval stage (El-Ibrashy, 1982).

The anti-juvenile hormone agents, such as compactin, fluoromevalonate, imidazoles and precocene, are considered as insect growth regulators (IGRs) because they affect either the mevalonate pathway in JH biosynthesis, or the corpora allata (CA) directly, the organ that produces JH (Staal, 1986).

Precocenes are originally plant-derived chromenes (2H-1-benzopyran) with insecticidal activities (Proksch *et al.*, 1983; Isman *et al.*, 1986). On the basis of their functions, precocenes can be described as JH inhibitors or anti-JH agents (Staal, 1986). Precocenes and their synthetic analogues received a great attention by entomologists both doing fundamental and applied work due to their twin advantage; using as a physiological probe in the former avoiding surgical allatectomy and as an effective tool in devising 'fourth generation insecticides' in the latter (Muraleedharan *et al.*, 1986; Sariaslani *et al.*, 1987; Moya *et al.*, 1997; Szczepanik *et al.*, 2005; Singh and Kumar, 2011). Compounds with anti-JH activity are considered as new representatives of IGRs lacking some disadvantages of juvenoid-type chemicals (Bowers, 1982; Staal, 1982). The chemicals having anti-JH activity are potentially efficacious and superior to JH mimics for control of the major insect pests where most of the damage is caused by larval stage (El-Ibrashy, 1982).

On reproduction in adults of several insect orders, precocenes have been shown to prevent normal vitellogenic development of the oocytes or disturb the embryonic development leading to sterility (Staal, 1986; Kumar and Khan, 2004; Ringo *et al.*, 2005; Amiri *et al.*, 2010). The present study was carried out aiming to assess the effects of Precocene I (PI) on the most important parameters of adult performance and reproductive potential of *S. littoralis*.

## MATERIALS AND METHODS

### Experimental insect:

A sample of Egyptian cotton leafworm, *Spodoptera littoralis* Boisduval (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. A culture was raised under laboratory controlled conditions ( $27\pm 2^{\circ}\text{C}$ ,  $65\pm 5\%$  R.H., photoperiod 14h L and 10h D). Rearing procedure was carried out according to Ghoneim (1985) and improved by Bakr *et al.* (2010). Larvae were provided daily with fresh castor bean leaves *Ricinus communis*. The emerged adults were provided with cotton pieces soaked in 10% honey solution as a food source. Moths were allowed to lay eggs on *Oleander* branches. The egg patches were collected daily, and transferred into Petri dishes for another generation.

### Precocene I administration:

Precocene I (PI)(7-methoxy-2,2-dimethyl chromene) was kindly provided by Dr. Heba Hassan, Prof. at Plant Protection Research Institute, Agricultural Research Center, Doqqi, Giza, Egypt. Molecular formula:  $\text{C}_{12}\text{H}_{14}\text{O}_2$ . PI was diluted in acetone to prepare a wide range of doses. In a preliminary experiment, the sublethal doses of PI were found as 150, 120, 90, 30 and  $15\mu\text{g}/\text{larva}$ . Groups of 20 healthy larvae of 1-day old 5<sup>th</sup> (penultimate) and 1-day old (last) instar larvae were used as replicates for each dose. Each dose was topically applied (once) onto the thoracic sternum of each larva using Hamilton micro applicator (NHN 737). Control larvae had been topically applied only with  $1\mu\text{l}$  acetone. All treated and control larvae were kept individually under the previously mentioned laboratory controlled conditions. All larvae were provided with fresh castor bean leaves every day, during the feeding period. Just after the adult emergence, the most important parameters of adult performance and reproductive potential had been recorded.

### Adult performance parameters:

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

$$\left[ \frac{\text{No. of completely emerged adults}}{\text{No. of pupae}} \right] \times 100$$

**Adulticidal activity:** The adulticidal activity of PI was determined by observing the adult mortality.

**Morphogenic efficiency:** It was determined by the impaired adult morphogenesis as appeared in deformed adult females and recorded in %. It was calculated in percentage as follows:

$$\left[ \frac{\text{No. of deformed adults}}{\text{No. of emerged adults}} \right] \times 100$$

**Adult longevity:** Total longevity of adult females and its major compartments: pre-oviposition (ovarian maturation) period and oviposition period (reproductive lifetime) were measured in mean days $\pm$ SD.

**Criteria of the reproductive potential:**

After pupal stage of control and treated larvae, the emerged adult females of *S. littoralis* were daily collected and released in plastic jars (3L) provided with sterilized cotton pieces, soaked in 10% honey solution, for feeding, as well as suitable *Oleander* branches as an oviposition site. The treated adult females were coupled with normal adult males (1:2) of the same age obtained from the main culture. The eggs were collected daily, and carefully transferred to Petri dishes to count eggs.

**1. Oviposition efficiency:**

Oviposition efficiency could be detected by the oviposition rate as follows:

$$\text{Number of laid eggs per ♀/reproductive lifetime (in days)} \times 100$$

**2. Reproductive capacity:**

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

**Fertility:** The hatchability was usually expressed in hatching percentage of laid eggs.

**Sterility index:** It was calculated according to Topozada *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. Incubation period:**

The laid eggs were kept in Petri dishes under the same laboratory controlled conditions, as previously mentioned. Just after the oviposition, eggs were observed until hatching for recording the incubation period (in mean days $\pm$ SD).

**Statistical analysis of data:**

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

## RESULTS

**Effects of PI on the adult performance of *S. littoralis*:****1. Adult emergence:**

After topical application of PI onto the 5<sup>th</sup> instar larvae, data of the most important parameters of adult performance were assorted in Table (1). Depending on these data, PI exerted a blocking action on this crucial physiological process only at the higher three doses (66.6, 58.3 and 50.0%, at 90, 120 and 150  $\mu$ g/larva, respectively, vs. 100% emergence of control adult females). After topical application of PI onto the 6<sup>th</sup> instar larvae, data of adult performance were arranged in Table (2). In the light of these data, PI exerted a similar arresting action on the adult emergence only at the higher two doses (95.5 and 85.7%, at 120 and 150  $\mu$ g/larva, respectively, vs. 100% emergence of control adult females).

**2. Adult survival:**

As clearly shown in Table (1), PI exhibited a slight extended toxic effect on adult females after treatment of 5<sup>th</sup> instar larvae only with the higher two doses (28 and 30% mortality, at 150 and 120  $\mu$ g/larva, respectively, compared to 0% mortality of control adults). With regard to the survival of adult females successfully emerged from pupae after treatment of 6<sup>th</sup> instar larvae, PI exerted a slightly extended toxic effect only at the higher two doses (10 and 5% mortality, at 150 and 120  $\mu$ g/larva, respectively, compared to 0% mortality of control adults, (Table 2).

### 3. Adult morphogenesis:

After treatment of 5<sup>th</sup> instar larvae, PI failed to exhibit morphogenic efficiency against adults, since no adult deformities were observed (Table 1). In view of data contained in Table (2), topical application of 6<sup>th</sup> instar larvae with PI led to the impairment of adult morphogenesis, since some deformities were produced, in no certain trend (21.4, 25.0, 10.7 and 3.4% deformed adult females, at 150, 120, 90 and 30  $\mu\text{g}/\text{larva}$ , respectively, vs. 0% deformation of control adult females). As obviously seen in Fig. (1), the most important features of the impaired morphogenesis program appeared in adults with curled wings, adults with non-expanded wings and adults failed to completely get rid of the pupal exuvia, at the posterior extremity.

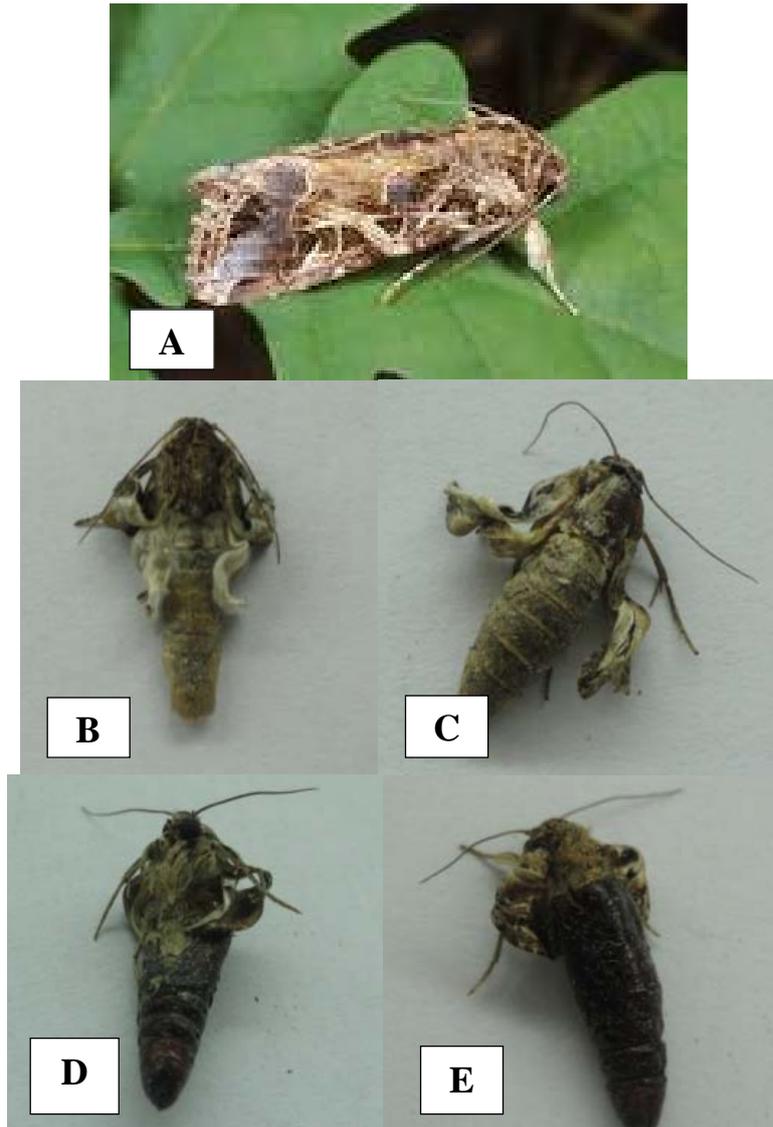


Fig. 1. Deformed adult females of *S. littoralis* after topical application of larvae with the higher four doses of PI. (A) Normal adult. (B & C): Emerged adults with curled wings. (D & E): Moths failed to completely get rid of the pupal exuvia, at the posterior extremity, and the non-expanded wings.

#### 4. Adult longevity:

In the present study, *S. littoralis* is a lepidopteran in which a part of the ovarian maturation has been taken place in the second half of pupal stage and another part has been completed in very few days, or even some hours, after adult emergence. Thus, the pre-oviposition period does not exactly indicate the whole ovarian maturation period. On the other hand, the oviposition period is usually known as 'reproductive life-time'. In addition, the post-oviposition period does not exceed few hours. Therefore, the major compartments of adult longevity are pre-oviposition period and oviposition period.

After treatment of 5<sup>th</sup> instar larvae with PI, the total adult longevity of females was remarkably prolonged, in no certain trend (7.96±0.9, 8.06±0.7, 7.15±0.6 and 7.80±0.9 days, at 150, 120, 90 and 30 µg/larva, respectively, vs. 6.90±0.8 days of control adult females). In contrast, the total adult longevity was insignificantly shortened only at the lowest dose. Thus, PI exerted a diverse action on the total longevity, depending on the dose level (see Table 1). After treatment of 6<sup>th</sup> instar larvae, PI enhanced the adult females to live a slightly prolonged period, but in no certain trend (6.33±0.9, 6.72±0.8, 6.50±1.2, 6.00±0.9 and 6.15±0.8 days, at 150, 120, 90, 30 and 15 µg/larva, respectively, vs. 5.75±0.7 days of control adult females).

With regard to the pre-oviposition period, data of Table (1) exiguously revealed that such period was slightly shortened, in no certain trend, after treatment of 5<sup>th</sup> instar larvae (2.0±1.0, 2.3±0.5, 2.3±0.5, 2.1±0.5 and 2.0±0.7 days, at 150, 120, 90, 30 and 15 µg/larva, respectively, vs. 2.4±1.0 days of control adult females). A stronger shortening action of PI was exerted on the pre-oviposition period, after treatment of 6<sup>th</sup> instar larvae, since such period was considerably shortened at the highest dose and the lower two doses (2.3±0.9, 2.0±0.1 and 2.1±0.2 days, at 150, 30 and 15 µg/larva, respectively, vs. 3.4±0.5 days of control adult females, Table 2).

According to the data included in Table (1), the oviposition period was unremarkably or remarkably prolonged, depending on the dose of PI, after treatment of 5<sup>th</sup> instar larvae (5.9±0.9, 5.7±0.8, 4.8±0.9, 5.4±0.8 and 4.7±0.7 days, at 150, 120, 90, 30 and 15 µg/larva, respectively, vs. 4.6±0.4 days of control adult females). Also, the oviposition period was pronouncedly prolonged; regardless the PI dose applied onto 6<sup>th</sup> instar larvae (4.0±0.3, 4.2±0.8, 4.2±0.4, 4.0±0.8 and 3.9±0.7 days, at 150, 120, 90, 30 and 15 µg/larva, respectively, vs. 2.4±0.4 days of control adult females).

**Table 1. Affected adult performance of *S. littoralis* after topical application of PI sublethal doses onto 1-day old penultimate instar larvae.**

Dose (µg/larva)	Adult emergence (%)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days±SD)		
				Pre-oviposition period	Oviposition period	Total longevity
150	50.0	28	0.0	2.0±1.0 a	5.9±0.9 b	7.96±0.9 b
120	58.3	30	0.0	2.3±0.5 a	5.7±0.8 b	8.06±0.7 c
90	66.6	00	0.0	2.3±0.5 a	4.8±0.9 a	7.15±0.6 b
30	100	00	0.0	2.1±0.5 a	5.4±0.8 b	7.80±0.9 b
15	100	00	0.0	2.0±0.7 a	4.7±0.7 a	6.77±0.7 a
Control	100	00	0.0	2.4±1.0	4.6±0.4	6.90±0.8

Mean ± SD followed with the same letter a: insignificantly different (P >0.01), b: significantly different (P<0.05), c: highly significantly different (P<0.01).

**Table 2. Affected adult performance of *S. littoralis* after topical application of PI sublethal doses onto 1-day old last instar larvae.**

Dose ( $\mu\text{g}/\text{larva}$ )	Adult emergence (%)	Adult mortality (%)	Adult deformities (%)	Adult longevity (mean days $\pm$ SD)		
				Pre-oviposition period	Oviposition period	Total longevity
150	85.7	10.0	21.4	2.3 $\pm$ 0.9 b	4.0 $\pm$ 0.3 b	6.33 $\pm$ 0.9 a
120	95.5	05.0	25.0	2.8 $\pm$ 0.9 a	4.2 $\pm$ 0.8 b	6.72 $\pm$ 0.8 b
90	100	00.0	10.7	2.2 $\pm$ 0.9 a	4.2 $\pm$ 0.4 b	6.50 $\pm$ 1.2 a
30	100	00.0	03.4	2.0 $\pm$ 0.1 c	4.0 $\pm$ 0.8 b	6.00 $\pm$ 0.9 a
15	100	00.0	00.0	2.1 $\pm$ 0.2 c	3.9 $\pm$ 0.7 b	6.15 $\pm$ 0.8 a
<b>Control</b>	100	00.0	00.0	3.4 $\pm$ 0.5	2.4 $\pm$ 0.4	5.75 $\pm$ 0.7

a, b, c: See footnote of Table (1).

### Effects of PI on the reproductive potential of *S. littoralis*:

#### 1. Oviposition rate:

After topical application of PI onto 5<sup>th</sup> instar larvae, data of the most important criteria of reproductive potential were assorted in Table (3). Depending on these data, the oviposition efficiency of adult females was drastically prohibited only at the lower two doses, since the oviposition rate was seriously regressed (75 and 85%, at 30 and 15  $\mu\text{g}/\text{larva}$ , respectively, vs. 100% oviposition of control females). Moreover, the suppressing potency of PI on the oviposition rate increased with the increasing dose level, after treatment of 6<sup>th</sup> instar larvae (93.8, 91.5, 86.7, 77.7 and 58.3 %, at 15, 30, 90, 120 and 150  $\mu\text{g}/\text{larva}$ , respectively, vs. 100% oviposition rate of control females, Table 4).

#### 2. Reproductive capacity:

As obviously shown in Table (3), topical application of PI onto 5<sup>th</sup> instar larvae resulted in drastic reduction of fecundity (mean number of eggs/ $\text{♀}$ ), in a dose-dependent course (637.8 $\pm$ 98.2, 521.7 $\pm$ 195.5, 436.7 $\pm$ 96.1, 338.7 $\pm$ 32.5 and 336.5 $\pm$ 30.5 eggs/ $\text{♀}$ , at 15, 30, 90, 120 and 150  $\mu\text{g}/\text{larva}$ , respectively, vs. 943.3 $\pm$ 85.5 eggs/control $\text{♀}$ ). Also, fecundity was severely reduced, in no certain trend, after topical application of PI onto 6<sup>th</sup> instar larvae (678.9 $\pm$ 33.2, 407.2 $\pm$ 118.9, 602.8 $\pm$ 149.4, 098.2 $\pm$ 18.9 and 333.5 $\pm$ 231.7 eggs/ $\text{♀}$ , at 15, 30, 90, 120 and 150  $\mu\text{g}/\text{larva}$ , respectively, vs. 1259.2 $\pm$ 120.3 eggs/control  $\text{♀}$ , Table 4).

Another informative parameter of the reproductive capacity is fertility (hatchability= hatching% of laid eggs). Depending on the data distributed in Table (3), treatment of 5<sup>th</sup> instar larvae with PI led to complete sterility of adult females, since complete failure of egg hatching was observed. Similar complete sterility had been recorded for eggs laid by those adult females emerged from 6<sup>th</sup> instar larvae treated only with doses 150 and 30  $\mu\text{g}/\text{larva}$  (see Table 4). At other doses, seriously reduced hatchability was recorded (58.9, 33.1 and 4.2%, at 15, 90 and 120  $\mu\text{g}/\text{larva}$ , respectively, vs. 98.3% of control eggs).

### Effects of PI on the embryonic development of *S. littoralis*:

In insects, incubation period can be used as a valuable indicator of the embryonic developmental rate, i.e., longer period usually denotes slower rate and *vice versa*. In the present study on *S. littoralis*, no incubation period could be measured for eggs of the adult females after treatment of 5<sup>th</sup> instar larvae with PI because no eggs could hatch, regardless of PI dose (see Table 3).

After treatment of 6<sup>th</sup> instar larvae with PI, data of Table (4) clearly revealed a

considerable retarding action of the tested compound on the embryonic rate in the eggs, since the incubation period was remarkably prolonged ( $4.7\pm 0.5$ ,  $4.2\pm 0.7$  and  $4.9\pm 0.6$  days, at 15, 90 and 120  $\mu\text{g}/\text{larva}$ , respectively, vs.  $3.5\pm 0.4$  days of control eggs).

**Table 3. Reproductive potential of *S. littoralis* as influenced by PI after topical application of sublethal doses onto 1-day old penultimate instar larvae.**

Dose ( $\mu\text{g}/\text{larva}$ )	Oviposition Rate (%)	Fecundity (mean eggs $\pm$ SD)	Hatchability (%)	Sterility index (%)	Incubation period (mean days $\pm$ SD)
150	100	336.5 $\pm$ 30.5 c	00.0	100	---
120	100	338.7 $\pm$ 32.5 c	00.0	100	---
90	100	436.7 $\pm$ 96.1 c	00.0	100	---
30	75	521.7 $\pm$ 195.5 c	00.0	100	---
15	85	637.8 $\pm$ 98.2 b	00.0	100	---
<b>Control</b>	100	943.3 $\pm$ 85.5	98.8	---	3.5 $\pm$ 0.5

a, b, c: see footnote of Table (1).

**Table 4. Reproductive potential of *S. littoralis* as influenced by PI after topical application of sublethal doses onto 1-day old last instar larvae.**

Dose ( $\mu\text{g}/\text{larva}$ )	Oviposition Rate (%)	Fecundity (mean eggs $\pm$ SD)	Hatchability (%)	Sterility index (%)	Incubation period (mean days $\pm$ SD)
150	58.3	333.5 $\pm$ 231.7 c	00.0	100	---
120	77.7	098.2 $\pm$ 18.9 d	04.2	97.8	4.9 $\pm$ 0.6 b
90	86.7	602.8 $\pm$ 149.4 c	33.1	82.7	4.2 $\pm$ 0.7 b
30	91.5	407.2 $\pm$ 118.9 b	00.0	100	---
15	93.8	678.9 $\pm$ 33.2 b	58.9	67.7	4.7 $\pm$ 0.5 b
<b>Control</b>	100	1259.2 $\pm$ 120.3	98.3	---	3.5 $\pm$ 0.4

a, b, c: See footnote of Table (1). d: very highly significantly different ( $P < 0.001$ )

## DISCUSSION

### 1. Blocked adult emergence:

Scarce studies have examined the effects of anti-JH compounds on adult emergence in insects. Inhibition of adult emergence in the flesh fly *Sarcophaga ruficornis* was recorded after larval treatment with PII (Khan and Kumar, 2005). The terpenoid imidazoles, KK-42, was reported to inhibit the adult emergence of the mulberry silk moth *Bombyx mori* when applied to the newly formed pupae (Kadono-Okuda *et al.*, 1987). In the present study on *S. littoralis*, the adult emergence was slightly or drastically blocked, especially at the higher three or two doses of PI, depending on the larval instar under treatment, 5<sup>th</sup> or 6<sup>th</sup> instar.

For interpretation of this result, it important to point out that the adult emergence in insects is a crucial physiological process and regulated by the eclosion hormone. The disturbance of this hormone appeared in partial or complete arresting of adults to emerge. The present result of blocked adult emergence can be interpreted by the disruptive effect of PI on the normal metabolism of insect hormones during the development of the juveniles leading to failure of adult emergence (Trigo *et al.*,

1988). In particular, PI may disturb the adult eclosion hormone release and/or inhibition of the neurosecretion (Al-Sharook *et al.*, 1991; Josephraj Kumar *et al.*, 1999). On the molecular basis, anti-JH compounds, like PI, might cause misexpression of certain genes, particularly the *brood* complex (*br-C*) transcription factor gene, leading to symptoms of impaired metamorphosis, like blocking of adult emergence (Wilson, 2004; Nandi and Chakravarty, 2011).

## 2. Affected adult survival:

Toxic effects of different IGRs on the adults have been reported in several insect species of different orders (Pineda *et al.*, 2004; Nasr *et al.*, 2010; Singh and Kumar, 2011; Kamminga *et al.*, 2012; El-Naggar, 2013; Bakr *et al.*, 2013; Hamadah *et al.*, 2015; Tanani *et al.*, 2015; Zhou *et al.*, 2016; Hamaidia and Soltani, 2016; Hassan *et al.*, 2017; Hamadah *et al.*, 2017; Ghoneim *et al.*, 2017a, b).

In contrast, few studies have examined the adulticidal activities of anti-JH compounds against insects. Different doses of PII were topically applied onto the 3<sup>rd</sup> instar larvae of the grey flesh fly *Parasarcophaga dux*. Toxic effects were recorded on adults, in a dose-dependent course (Nassar *et al.*, 1999). Injection of a single dose (of 50 or 150 µg) of PII into 4-day old adults of the desert locust *Schistocerca gregaria* led to high mortality of adults (Tawfik *et al.*, 2014). After exposure of the newly moulted 2<sup>nd</sup> or 4<sup>th</sup> (penultimate) instar nymphs of the grasshopper *Euprepocnemis plorans* to different doses of PII, various mortality percentages were recorded among the emerged adults (Ghoneim and Basiouny, 2017).

In the present study, PI exhibited a slightly extended toxic effect on the adult females after treatment of 5<sup>th</sup> or 6<sup>th</sup> instar larvae of *S. littoralis*, only with the higher two doses. These adult mortalities can be explained by the retention and distribution of PI in the insect body by 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). The adult life in insects depends on healthy immature stages. Digestive disorders, such as starvation, metabolism disturbance, degeneration of peritrophic membranes and accumulation of faecal materials at the hind gut, may be the cause of adult mortality (Soltani, 1984).

## 3. Disrupted adult morphogenesis:

Impaired adult morphogenesis, as expressed in the production of deformed adults, was widely reported in the available literature, after treatment of various insects with different JHAs (Kamaruzzaman *et al.*, 2006; Mojaver and Bandani, 2010; Begum and Qamar, 2016). According to the currently available literature, few studies examined the morphogenic effects of anti-JH compounds on the insect adults. Topical application of the highest dose (1 mg) of PII onto 3<sup>rd</sup> instar larvae of *P. dux* led to the production of adult malformation (Nassar *et al.*, 1999). During the study carried out by Khafagi and Hegazi (1999) on the latent effects of PI and PII on the parasitic wasp *Microplitis rufiventris* reared on its host *S. littoralis*, they observed various morphologically imperfect moths. Deformed adults of the Eri silk *Philosamia ricini* were observed after larval treatment with PII (Khan and Kumar, 2000). Formation of deformed *S. ruficornis* adult flies were recorded after larval treatment with PII (Khan and Kumar, 2005). After topical application of PI and PII onto the 2<sup>nd</sup> instar larvae of the Colorado potato beetle *Leptinotarsa decemlineata*, severe morphological abnormalities were observed (Farazmand and Chaika, 2008). Treatment of the 4<sup>th</sup> instar or 5<sup>th</sup> instar larvae of the red cotton stainer bug *Dysdercus koenigii* with PII or the precocenoid compounds 6-hydroxy-DMC and 6-bromo-

DMC, the emerged adults appeared with small and pale body and underdeveloped wing pads/wings, at certain doses (Banerjee *et al.*, 2008). Deformed adults of the house fly *Musca domestica* were produced after treatment of larvae with PII (Gaur and Kumar, 2009). In addition, the development of some adult structures and organs, as affected by anti-JH compounds, had been investigated. As for example, treatment of 5<sup>th</sup> instar larvae or prepupae of the large fruit tree Tortrix *Archips podana* with 300, 450, and 600 µg Precocene/insect, morphogenesis of the adult antennae was retarded (Triselyova, 2012). After treatment of 5<sup>th</sup> instar larvae of *S. littoralis*, in the current investigation, PI failed to exhibit morphogenic efficiency against adults, since no deformed adults were produced. On the other hand, treatment of 6<sup>th</sup> instar larvae with PI resulted in the impairment of adult morphogenesis, since some adult deformities were produced.

These adult deformities may be explained by an action of PI on the hormonal imbalance during the adult differentiation, in particular the modification of ecdysteroid titer which led to changes in lysosomal enzyme activity causing overt morphological abnormalities (Josephraj Kumar *et al.*, 1999). Other suggestions can be conceivable, such as the interference of PI with JH or ecdysteroid metabolism causing a disruption in the chitin metabolic system (Yu and Terriere, 1975), inhibition of chitin synthase by metabolites of PI (Cohen and Casida, 1980a, b), inhibition of DNA synthesis (Mitlin *et al.*, 1977) and/or inhibition of facilitated diffusion and active transport across cell membranes of nucleosides and amino acids (Mayer *et al.*, 1988).

#### **4. Disturbed adult longevity:**

In *S. littoralis*, the post-oviposition period does not exceed few hours. Therefore, the major compartments of adult longevity can be considered as the pre-oviposition period and oviposition period.

#### **Total adult longevity:**

Diverse effects of IGRs on the adult longevity had been reported in a number of insects. The total adult longevity in some insects was shortened after larval treatment of some insects with some IGRs (Pineda *et al.*, 2009; Luna *et al.*, 2011; Hamadah *et al.*, 2015; Aliabadi *et al.*, 2016). On the contrary, adult longevity in other insects was prolonged after larval treatment with some IGRs (Liu and Chen, 2001; Kandil *et al.*, 2012; Sabry and Abdou, 2016). Furthermore, no effect was exhibited by some IGRs on the adult longevity of a number of insects (Saenz-de-Cabezón *et al.*, 2005; Zarate *et al.*, 2011).

Only few results had been reported in the current literature concerning the affected adult longevity by some anti-JH compounds. Depending on the reported results, the adult longevity was shortened after larval treatment with some anti-juvenoids. For examples, different doses of PII were topically applied onto the 3<sup>rd</sup> instar larvae of *P. dux*, total adult longevity was significantly shortened (Nassar *et al.*, 1999). After topical application of 25 mg l<sup>-1</sup> of the precocenoïd compound 6-hydroxy-DMC onto the 5<sup>th</sup> instar nymphs of *D. koenigii*, the emerged adults lived shorter longevity than control adults (Banerjee *et al.*, 2008). Khafagi and Hegazi (2004) investigated the effects of PI and PII on the parasitoid wasp *M. rufiventris* after topical treatment of the host larvae of *S. littoralis*. Longevity of the parasitoid adult females which developed in hosts treated by Precocenes was shortened. Results of the current investigation on *S. littoralis* disagreed with those previously reported results, since the major effect of PI was the promotion of adult females to

spend longer life-time than control adults. In other words, treatment of 5<sup>th</sup> or 6<sup>th</sup> instar larvae with PI led to remarkably or slightly prolonged longevity, respectively. An exceptional case was recorded as slightly shortened longevity after treatment of 5<sup>th</sup> instar larvae only with the lowest dose (15 µg PI/larva). However, the prevalent prolongation of total adult longevity of *S. littoralis*, as a response to the action of PI, in the present study, was, to some extent, in agreement with those reported results of extended life span in desert grasshoppers, monarch butterflies and the linden bug *Pyrrhocoris apterus*, after surgical allatectomy (Herman and Tatar, 2001; Hodkova, 2008).

In the current study, the affected female adult longevity of *S. littoralis*, after larval treatment with PI, may be attributed to its interference with the hormonal regulation of adult longevity because a close relation between certain hormones and adult longevity was reported in other insects, such as *Drosophila melanogaster* (Broughton *et al.*, 2005; Carbone *et al.*, 2006; Chamseddin *et al.*, 2012) 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). Also, the prolonged longevity may be due to the preventing physiological trade-offs between survival and egg production (Flatt, 2011; Edward and Chapman, 2011). In addition, the extended longevity was associated with resistance to exogenous stress, like PI, as suggested by Wang *et al.* (2004) for *D. melanogaster*.

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 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. As reported by Yamamoto *et al.* (2013), JH controls aging, to some extent, because it directly affects mechanisms of somatic survival. Therefore, PI may affect the JH level and/or functions leading to prolongation of adult longevity of *S. littoralis*, in the present study, i.e. PI exerted a delaying action on *S. littoralis* aging. However, the exact mode of action of PI on the biochemical sites in adults is unknown until now. More information on the adult endocrine system of *S. littoralis* is required to clarify the mechanism by which PI prolong the adult longevity and delay aging.

### **Pre-oviposition period:**

*S. littoralis* is a lepidopteran in which the ovarian maturation takes place partially in pharate pupal stage and completes during the pre-oviposition period of the adult females (El-Ibrashy, 1971, 1982). Thus, pre-oviposition period may partially indicate the ovarian maturation rate, i.e. longer period may denotes slower rate and *vice versa*. The currently available literature contains many reported results of the effects of different IGRs on pre-oviposition period in various insect species (Rashad *et al.*, 2006; Aref *et al.*, 2010; Kandil *et al.*, 2013; Salem, 2015; El-Khayat *et al.*, 2015; Zhou *et al.*, 2016; Hassan *et al.*, 2017; Hamadah *et al.*, 2017). As far as our literature survey could ascertain, no information was available on the effects of anti-JH compounds on the pre-oviposition period in insects.

In the present study on *S. littoralis*, treatment of 5<sup>th</sup> instar larvae with PI led to a slight shortening in the pre-oviposition period of adult females, while treatment of 6<sup>th</sup> instar larvae led to a slight or considerable shortening in this period, depending on the dose. This shortened pre-oviposition period may indicate a faster ovarian maturation rate as a response to the action of PI. Depending on this result, PI failed to exhibit anti-gonadotropic activity against *S. littoralis* but it might exert an

enhancing action on this reproductive process. The present result corroborated with Kelly and Fuchs (1978) who reported that precocene is not a specific antigonadotropic agent in adult female *Aedes aegypti*. Recently, Oliveira *et al.* (2017) recorded the failure of precocene to affect the ovary development of workers of a highly eusocial wasp. On the contrary, our result was inconsistent with many reported results of inhibitory action of different anti-JH compounds on the ovarian maturation in insects, such as the Mediterranean splendid grasshopper *Heteracris littoralis* after topical application of PII (20-100 µg/insect) onto 3<sup>rd</sup> instar nymphs (Alrubeai, 1986); *M. domestica* after topical application of 20 µg/fly of PII onto the newly-emerged females (Li *et al.*, 1993); the brown plant hopper *Nilaparvata lugens* after exposure of 5<sup>th</sup> instar nymphs to different doses of PII (Pradeep and Nair, 2000); *D. cingulatus* after topical application of PII onto eggs of different ages (Gayathri-Elayidam and Muraleedharen, 2001) and the wing-dimorphic cricket *Velarifictorus ornatus* after injection of PI (dose over 50 µg) into short-winged females (Zhao and Zhu, 2013). However, the exact mode of the enhancing action of PI on the pre-oviposition period and the ovarian maturation rate in *S. littoralis* is unfortunately available right now!!

### **Oviposition period:**

No reliable information has been obtained regarding the effects of anti-JH compounds on the oviposition period in insects. On the other hand, few reported results of affected oviposition period by IGRs are available. This period was shortened or prolonged, depending on different factors, such as the susceptibility of treated insect, potency of the tested compound, concentration level, time and method of treatment, etc. (For examples, see Kandil *et al.*, 2005; Shahout *et al.*, 2011; Salem, 2015; Hassan *et al.*, 2017).

In the present study on *S. littoralis*, the oviposition period of adult females was slightly or significantly prolonged, depending on the PI dose and the larval instar under treatment, 5<sup>th</sup> or 6<sup>th</sup> instar. The shortened oviposition period can be interpreted by the enforcing action of the IGR on the adult females to lay eggs as quickly as possible for avoiding this xenobiotic factor. On the other hand, the prolonged oviposition period in *S. littoralis*, as a response to the action of PI, in the current investigation, cannot be interpreted right now!! However, PI may interfere with the hormonal control of egg deposition, since every physiological process in insects has been regulated by certain hormone(s). It is important to keep in mind that PI is usually considered anti-JH compound.

## **2. Disrupted reproductive potential of *S. littoralis* by PI:**

Reproduction in insects is mainly controlled by the juvenile hormone (JH), which is also responsible for protein metabolism, and is specifically needed for egg maturation (Ghoneim *et al.*, 2014). Effects of IGRs on the insect reproduction can be grouped into: i) reproductive behaviour, ii) oviposition, iii) egg hatchability (ovicidal and embryocidal), and iv) sterilization of adults (Mondal and Parween, 2000). 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).

### **1. Inhibited oviposition efficiency of adult females:**

In insects, the oviposition rate can be used as an informative indicator for the oviposition efficiency (Ghoneim *et al.*, 2014). Depending on the current literature,

oviposition rate of different insect species has been regressed by various IGRs (Al-Dali *et al.*, 2008; Ghoneim *et al.*, 2014; Bakr *et al.*, 2005; Al-Mekhlafi *et al.*, 2011; Hassan *et al.*, 2017; Hamadah *et al.*, 2017). However, very few studies have examined the effects of anti-JH compounds on this important reproductive parameter. Exposure of *D. melanogaster* females to 0.14  $\mu\text{mol}$  of PI resulted in remarkably regressed oviposition rate (Ringo *et al.*, 2005). Larval treatment of the Sunn pest *Eurygaster integriceps* with PI led to decreasing egg laying rate (Amiri *et al.*, 2010).

Results of the present study were well in agreement with those reported findings, since topical application of PI onto 5<sup>th</sup> instar larvae of *S. littoralis* resulted in serious inhibition of the oviposition efficiency of adult females, i.e., oviposition rate was drastically regressed only at the lower two doses. Moreover, treatment of 6<sup>th</sup> instar larvae with PI resulted in pronouncedly reduced oviposition efficiency, in a dose-dependent course. The prohibited oviposition efficiency of *S. littoralis*, in the current study, can be explained as a result of the inhibition of ovarian DNA synthesis or the interference of PI with vitellogenesis *via* certain biochemical processes. However, anti-JH compounds may exert a reverse action to that exerted by the ecdysteroid agonists which stimulate the neurosecretory cells to release a myotropic ovulation hormone (Parween *et al.*, 2001).

## 2. Perturbation of the reproductive capacity:

### 2.1. Prohibited fecundity:

In the present study, topical application of PI onto the 5<sup>th</sup> or 6<sup>th</sup> instar larvae of *S. littoralis* resulted in drastic reduction of the adult fecundity, in a dose-dependent manner or in no certain trend, depending on the larval instar under treatment. These results were, to a great extent, in agreement with those reported results of fecundity inhibition in some insects after treatment of immature with some precocenes and other anti-JH compounds. For examples, topical application of PII doses of 0.125 and 0.0625 mg onto 3<sup>rd</sup> instar larvae of *P. dux* caused inhibition of the female natality (Nassar *et al.*, 1999). Exposure of 5<sup>th</sup> instar nymphs of *N. lugens* to different doses of PII resulted in fecundity reduction, in a dose-dependent manner (Pradeep and Nair, 2000). After treatment of *E. integriceps* nymphs with PI, fecundity of adult females was reduced (Amiri *et al.*, 2010). Repeated daily topical application of PI and PII onto *S. littoralis* larvae led to reduced fecundity of its parasitic wasp *M. rufiventris* (Khafagi and Hegazi, 2004). Apart from precocenes, application of the anti-JH compound H17 reduced the fecundity of *L. decemlineata* (Lehmann *et al.*, 2015). On the other hand, the present findings were inconsistent with those reported results of Precocene failure to affect the fecundity of some insects, such as the bug *Panstrongylus megistus* (Hemiptera: Reduviidae) of which males were treated with PII and ethoxyprecocene (synthesized PII analogue) but the fecundity did not differ statistically from that of the control groups (Cavalcante and Regis, 1992).

To understand the fecundity inhibition of *S. littoralis*, in the present study, it is important to point out that the JH is required for post-eclosion development of the vitellogenin-producing adult fat body. In many insects, including *S. littoralis*, JH modulates fecundity at least in part because JH is necessary to induce yolk proteins uptake into oocytes (Soller *et al.*, 1997), while ecdysone, produced from egg follicles, induces yolk protein mRNA expressed in the fat body (Bownes, 2004; Raikhel *et al.*, 2005; Schwedes and Carny, 2012). In addition, the fecundity inhibition in *S. littoralis* may be due to the interference of PI with one or more

processes from the ovarian follicle development to the egg maturation. (1): PI may cause some disorders in the ovaries, including cell death in the germarium, resorption of oocytes in the pre-vitellarium and vitellarium (Khan *et al.*, 2007; Zhou *et al.*, 2016). (2): PI may inhibit the synthesis and metabolism of proteinaceous constituents during oogenesis (Salem *et al.*, 1997). (3): PI may exert an inhibitory action against the function of authentic gonadotropic hormone (JH in adults) responsible for the synthesis of vitellogenins and vitellogenesis (Di Ilio *et al.*, 1999).

## 2.2. Reduced fertility:

Another informative parameter of the reproductive capacity is fertility (hatchability). In the present study on *S. littoralis*, treatment of 5<sup>th</sup> instar larvae with PI caused complete sterility, since complete failure of egg hatching was observed, regardless the dose. After treatment of 6<sup>th</sup> instar larvae with PI, the egg hatchability was severely reduced. Complete sterility was recorded at the doses 150 and 30 µg/larva. These results were, to a great extent, concomitant to those reported results of sterility and inhibited fertility of some insects after treatment of immature stages with a number of anti-JH compounds. For examples, topical application of PIII onto eggs and 5<sup>th</sup> instar nymphs of the grasshopper *Aiolopus thalassinus* led to sterility of adult females (Osman, 1988). After treatment of *E. integriceps* nymphs with PI, the hatchability of laid eggs was reduced (Amiri *et al.*, 2010). Apart from precocenes, phenolic chromene and hydroxyethyl chromene (isolated from *Ageratum conyzoides*) were found to cause sterility in the bug *Dysdercus flavidus* (Vyas and Mulchandani, 1984; Okunade, 2002). Bowers and Aregullin (1987) isolated an anti-JH compound, polyacetylenic sulfoxide, from *Chrysanthemum coronarium* which produced sterile adults in the large milkweed bug *Oncopeltus fasciatus*.

For explicating the fertility reduction and sterility in *S. littoralis* by PI, in the present study, some suggestions can be provided herein. First: Maturation of the insect eggs depends basically on the vitellogenins, precursor materials of these macromolecules 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 fat body during the immature stages (Telfer, 2009) or by the ovary *in situ* (Indrasith *et al.*, 1988). Wherever the site of their synthesis, PI may disturb the production of these materials and/or accumulation in adult females of *S. littoralis* leading to the reduction of fertility. Second: PI may indirectly affect the fertility *via* its disruptive effect on opening of the intracellular spaces in follicular epithelium or generally inhibited the role of the gonadotropic hormone responsible for the regulation of vitellogenin deposition into oocytes (Davey and Gordon, 1996). Third: The reduction in fertility may be due to the penetration of residual amounts of PI 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 (Sallam, 1999; Sammour *et al.*, 2008). Fourth: The reduced fertility of *S. littoralis* may be due to serious effect of PI on survival of the developing embryos at certain stages as recorded in decreasing hatching percentage. Fifth: Because some molecular studies revealed the effects of some IGRs on insect reproduction owing to the perturbation of gene expression in the hierarchy cascade of vitellogenesis and/or choriogenesis (Sun *et al.*, 2003), PI may interfere with the gene expression resulting in a reduction of the developed embryos in *S. littoralis*, in the present study.

### 3. Retarded embryonic development of *S. littoralis* by PI:

In insects, incubation period can be used as an informative indicator of the embryonic developmental rate, i.e., longer period usually denotes slower rate and *vice versa*. In the present study on *S. littoralis*, effect of PI on the embryonic developmental rate could not be determine after treatment of 5<sup>th</sup> instar larvae because no eggs hatched. After treatment of 6<sup>th</sup> instar larvae, PI exerted conspicuously retarding action on the embryonic rate, since the incubation period was remarkably prolonged.

As far as our literature survey could ascertain, no information was available on the effects of anti-JH compounds on the incubation period or the embryonic developmental rate in insects. Therefore, our result can be considered as the first report in the world concerning the effects of precocenes on the incubation period or the embryonic developmental rate in *S. littoralis*. Unfortunately, a conceivable interpretation of this retardation of embryonic development is not available right now!!

### Conclusion:

According to the obtained results in the present study, Precocene I considerably affected the adult emergence, ovarian maturation rate, oviposition period, and adult longevity of *S. littoralis*. Also, it drastically prohibited the oviposition efficiency, dramatically reduced the reproductive capacity and retarded the embryonic development. Therefore, Precocene I may be a potential control agent being involved in the IPM program against this dangerous polyphagous pest.

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