COMPARATIVE EFFECTS OF CERTAIN IGRS ON THE CARBOHYDRATES OF HEMOLYMPH AND FAT BODY OF THE DESERT LOCUST, SCHISTOCERCA GREGARIA (ORTHOPTERA: ACRIDIDAE)

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Abstract

Newly molted last (5th) instar of the desert locust, *Schistocerca gregaria* (Forsk.), was treated through fresh plant food with 2 concentrations: high (1000.0 ppm) or low (62.5 ppm) of 3 IGRs: pyriproxyfen, tebufenozide, and lufenuron. Carbohydrate content was determined in the hemolymph and in the fat body of the early-aged, mid-aged, and late-aged 5th instar, as well as of 1- and 4-d old adult females. Pyriproxyfen prevented the nymphs to gain normal carbohydrate content in the hemolymph. In contrast, tebufenozide induced the nymphs to gain more carbohydrates. Lufenuron caused hemolymph carbohydrate content to decrease slightly in the early-aged nymphs but increased it in older nymphs. All three IGRs significantly affected the hemolymph carbohydrate content of nymphs of all ages. Pyriproxyfen drastically reduced the carbohydrate content of the hemolymph of 1-day old adults, but at the low concentration caused it to increase in the 4-day old adults. Tebufenozide induced adults to attain excess carbohydrates in the hemolymph at the low concentration level only. Lufenuron at both concentrations promoted increases of this metabolite in adults regardless of their age. Pyriproxyfen treatments of nymphs resulted in reduced carbohydrate content in the fat body of 1-d old adults, whereas tebufenozide and lufenuron at both concentrations induced increases in the carbohydrate content in fat bodies of 1- and 4-day old adults. The data from this study suggest that pyriproxyfen, tebufenozide and lufenuron alter the metabolism and storage of carbohydrate in nymphs and adults of the desert locust *S. gregaria*. Because carbohydrate is for all biological processes in nymphs and adults, these IGRs have considerable promise for use in the control of this destructive pest.

Key Words: carbohydrates, fat body, hemolymph, nymph, adult, pyriproxyfen, tebufenozide, lufenuron

Resumen

Ultimos (5 °) estadios de la langosta del desierto, *Schistocerca gregaria* (Forsk.) recién mudados, fueron tratados con alimento fresco de plantas a 2 concentraciones: alta (1,000.0 ppm) o baja (62.5 ppm) de 3 IGR: piriproxifen, tebufenozide y lufenuron. Se determinó el contenido de carbohidratos en la hemolinfa y en la grasa corporal de individuos del 5ª estadio de temprana edad, de mediana edad y de tardía edad, así como en hembras adultas de 1 y 4 dias de edad. El piriproxifeno impedio que las ninfas obtuvieran el contenido normal de los carbohidratos en la hemolinfa. Por el contrario, el tebufenozide indujó que las ninfas obtuvieran más carbohidratos. El Lufenuron causó que el contenido de carbohidratos a disminuyera ligeramente en las ninfas de temprana edad, pero aumentó en las ninfas mayores. Los tres IGR afectaron significativamente el contenido de carbohidratos en la hemolinfa de las ninfas de todas las edades. El Piriproxifeno redujó drásticamente el contenido de carbohidratos en la hemolinfa de adultos 1 día de edad, pero a la baja concentración provoco que aumente en los adultos de 4 días de edad. El Tebufenozide indujó que los adultos obtuvieran un exceso de carbohidratos en la hemolinfa solamente en el nivel bajo de concentración. El Lufenuron en ambas concentraciones promovió incrementos de este metabolito en los adultos, independientemente de su edad. Los tratamientos de piriproxifen en las ninfas resultaron en un contenido de carbohidratos reducido en la grasa corporal de adultos de 1 dia de edad, mientras que tebufenozide y lufenuron en ambas concentraciones resultaron en un aumento en el contenido de carbohidratos en la grasa corporal de los adultos de 1 y 4 días de edad. Los datos de este estudio sugieren que piriproxifen, tebufenozide y lufenuron alteran el metabolismo y el almacenamiento de carbohidratos en las ninfas y adultos de la langosta del desierto *S. gregaria*. Debido a que los carbohidratos son necesarios para todos los procesos biológicos en las ninfas y adultos, estos IGRs son muy prometedores para su uso en el control de esta plaga destructiva.

Palabras Clave: hidratos de carbono, las grasas de cuerpo, hemolinfa, ninfa y adulto, piriproxifen, tebufenozide, lufenuron

The serious effect of the desert locust, *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae), on agriculture and food supply in the Mediterranean area has been well documented. A migratory swarm of this pest usually contains 50 million locusts covering an area of several square kilometers. Such a swarm can fly continuously for 20 h per d for as far as 2400 km. Locusts of only a part of a moderate swarm may devour an amount of food plants sufficient for 2500 persons.

Although chemical pesticides are invaluable in controlling insect populations both in the field and storage facilities, their indiscriminate use has resulted in the destruction of beneficial insects and has caused environmental hazards. Moreover, insecticide resistance has already developed in many insects, and is now a great concern in post-harvest ecosystems throughout the world (Subramanyam & Hagstrum 1995; Arthur 1996). These problems have resulted in the search for alternative control agents that are less toxic to non-target animals and the environment. In this regard, insect growth regulators (IGRs), which disrupt molting and metamorphosis, have captured the interest of entomologists (Mondal & Parween 2000).

Insect growth regulator compounds fall into 2 categories. The first category includes juvenoids (juvenile hormone analogues) and antijuvenoids which mimic the action of authentic JH or inhibit its role in insect growth and development (Slama 1974; Retnakaran et al. 1985). Some of the most effective compounds are methoprene, hydroprene, kinoprene, fenoxycarb, pyriproxyfen and precocenes I and II. The second category comprises compounds inhibiting chitin biosynthesis, such as diflubenzuron, chlorflauzuron, triflumuron, flufenoxuron, hexaflumuron, lufenuron, diofenolan, teflubenzuron, triflumuron, and novaluron, and those that interfere with the molting process in general, such as tebufenozide (RH-5992), methoxyfenozide (RH-2485), halofenozide (RH-0345) and chromofenozide (ANS-118) (Staal 1975; Ghoneim et al. 1992; Dallaire et al. 2004; Doucet et al. 2007; Kebbeb et al. 2008; Ghasemi et al. 2010; Zibaee et al. 2011).

Carbohydrates play an important role in the structure and function of all tissues during insect life (cf. Chippendale 1978). Carbohydrate content in the hemolymph is an important indicator of the level of metabolism in insects, and reflects a dynamic balance of absorption, metabolism, and utilization by different tissues (Zhu et al. 2012). The present study was carried out to evaluate the effects of 3 IGRs, pyriproxyfen, tebufenozide, and lufenuron, on the carbohydrate content of both the hemolymph and fat body of the economically important locust, *S. gregaria*.

Materials and Methods

Experimental Insects

Successive generations of the desert locust *S. gregaria* were maintained for several years under gregarious conditions in the Department of Zoology, Faculty of Science, Al-Azhar University, Cairo, Egypt. This culture originated from a sample provided by the Locust and Grasshopper Research Division, Plant Protection Research Institute, Giza, Egypt. The culture was raised and handled under crowded breeding conditions as described by Hassanein (1965). The hoppers were reared in wooden cages with wire-gauze sides (40 × 40 × 60 cm) and a small door in the upper side to allow the daily feeding and cleaning routine. Each cage was equipped internally with a 60 W electric bulb for lighting at 17:7 h L: D and for warmth at 32 ± 2 °C. The RH in each cage varied from 30-50%, but following the introduction of fresh plant food, the RH ranged between 50 and 70% for several h. Nymphs and adults were allowed to feed on fresh leaves of alfalfa, *Medicago sativa* L.; Fabales: Fabaceae. Routine daily cleaning and routine monthly cleansing with an antiseptic agent of all cages were carried out.

Insect Growth Regulators and Nymphal Treatments

The 3 IGRs used in the study are shown in Table 1. Two concentrations of each IGR were prepared with distilled water, i.e., 1000 ppm and 62.5 ppm of active ingredient. The concentration range was chosen depending on preliminary trials carried out on *S. gregaria*. Fresh clean *M. sativa* leaves that had been immersed for 3 min in the appropriate IGR concentration were offered to newly molted last (5th) instars. Control

TABLE 1. Common names, chemical names and suppliers of the IGRs useded in the present study.

Common name and code	Chemical name	Supplier
Pyriproxyfen (S-31183)	2-{1-methyl-2-(4-phenoxy-phenoxy) ethyl}pyridine	Sumitomo Chemical Co.Ltd., Pesticides Division, Osaka, Japan
Tebofenozide (RH-5992)	1-N-t-butyl-1(3, 5-dimethylbenzoyl)-2-(4-ethylbenzoyl)hydrazine	Rohmand Haas Company, Philadelphia, Pennsylvania, USA
Lufenuron (Match, CGA-184699)	N-{{{2,5-dichloro-4-(1,1,2,3,3-hexafluoro-propoxyl)-phenyl}amino}-2,6-difluorobenzamide(CA)}}}	Syngenta CropP rotection Limited, Capital Park, Fulbourn, Cambridge,UK CB2 15XE

nymphs were provided with fresh clean *M. sativa* leaves after they had been dipped in distilled water. Three replicates with 10 nymphs per replicate were carried out for each treatment and the control. Each individual nymph was kept in a suitable glass vial whose bottom was covered with a thin layer of sterilized sand. All vials were carefully located in a cage provided with a suitable electric bulb for lighting and warming.

Determination of Carbohydrates

After treatment as newly molted last instars, locusts were held for various periods to facilitate the drawing of hemolymph of 1-d- old (early-aged), 4-d- old (mid-aged) and 7-d-old (late-aged)] and adult females [1-d- old (newly emerged) and 4-d- old]. The hemolymph was drawn from the coxal joint into an Eppendorff Pipetman containing a few milligrams of phenoloxidase inhibitor (phenylthiourea) to prevent tanning or darkening and then diluted 5 times with 0.7% saline solution. Hemolymph samples were then centrifuged at 2,000 rpm for 5 min, and only the supernatant fractions were used for assay directly or frozen until use. Three replicates were used and the hemolymph of different individuals was never mixed. Then the same nymphs and adults (treated or control) were dissected to collect their fat body (visceral and parietal), which was then homogenized in a saline solution (the fat body of one insect/1 mL 0.7% saline solution) with a fine electric tissue grinder for 2 min. Homogenates were centrifuged at 4000 rpm for 15 min. The supernatant was used directly or frozen until the use for the determination. Three replicates were used and the fat bodies from different individuals were never mixed.

Total carbohydrate (as glycogen) content of hemolymph or fat body was quantitatively determined by using the anthrone reagent with color determined spectrophotometrically at 620 nm according to Singh & Sinha (1977).

Analysis of Data

Data obtained were calculated as mean ± SD and analyzed by Student *t*-distribution. Data analyses were refined by Bessel's correction (Moroney 1956) for testing the significance of differences between means at probabilities of 0.05, 0.01 and 0.001.

RESULTS

Effects of IGRs on the Carbohydrate Content of Nymphs

The data for carbohydrate content of hemolymph of nymphs are shown in Table 2. Pyriproxyfen continuously prohibited the nymphs from gaining normal carbohydrate content in the hemolymph throughout the last instar development. Tebufenozide significantly increased carbohydrate content in 1-d-old and 7-d-old nymphs, but not in 4-d-old ones at 1000 ppm. The low concentration of 62.5 ppm had an insignificant effect on the last instar nymphs. Lufenuron caused an increase in carbohydrate content of nymphal hemolymph in 4- and 7-d-old nymphs, but not in 1-d-old ones at 1000 ppm. The low concentration of 62.5 ppm had no statistically significant effect on hemolymph carbohydrate at any of the measured ages.

Data from analyses of fat body are presented in Table 3. Pyriproxyfen at 1000 ppm decreased carbohydrate in fat body only in 7-d-old last instar nymphs, and carbohydrate concentration in fat body increased at the lower concentration (62.5 ppm) only in 1-d-old last instar nymphs. Tebufenozideat 1000 ppm caused an increase in fat body carbohydrate in 4- and 7-d-old last instar

TABLE 2. TOTAL CARBOHYDRATE CONTENT (MG/ML±SD) IN THE NYMPHAL HEMOLYMPH AFTER TREATMENT OF THE NEWLY MOLTED LAST INSTAR NYMPHS OF *SCHISTOCERCA GREGARIA* WITH 3 IGRS.

| IGRs | Conc. (ppm) | Last instar nymphs (Age in days) | | | | | |
		1-day old	Change %	4-day old	Change %	7-day old	Change %
Pyriproxyfen	1000.0	31.42 b ± 2.57 b	-15.59	37.32 ± 2.14 d	-22.61	35.47 ± 2.52 d	-40.4
	62.5	35.37 ± 3.51 a	-5.10	42.35 ± 3.70 a	-12.24	48.35 ± 3.77 d	-18.68
	Controls	37.25 ± 2.34	—	48.21 ± 2.56	—	59.46 ± 3.52	—
Tebufenozide	1000.0	48.33 ± 4.98 d	29.91	50.23 ± 1.28 a	4.14	87.20 ± 2.52 d	46.8
	62.5	40.56 ± 2.70 a	8.87	47.72 ± 3.10 a	1.37	55.77 ± 3.71 a	6.22
	Controls	37.25 ± 2.34	—	48.21 ± 2.56	—	59.46 ± 3.52	—
Lufenuron	1000.0	36.21 ± 1.58 a	-26.80	55.35 ± 4.82 b	14.73	68.21 ± 2.38 d	14.81
	62.5	36.36 ± 1.92 a	-2.41	50.62 ± 3.21 a	5.00	60.27 ± 3.57 a	1.34
	Controls	37.25 ± 2.34	—	48.21 ± 2.56	—	59.46 ± 3.52	—

Conc.: concentration; mean ± SD followed with the letter (a): is not significantly different ($P > 0.05$), (b): significantly different ($P < 0.05$), and (d): very highly significantly different ($P < 0.001$).

TABLE 3. TOTAL CARBOHYDRATE CONTENT (MG/G±SD) IN THE NYMPHAL FAT BODY OF *SCHISTOCERCA GREGARIA* AFTER TREATMENT OF THE NEWLY MOLTED LAST INSTAR NYMPHS WITH 3 IGRS.

IGRs	Conc. (ppm)	Last instar nymphs (Age in days)					
		1-day old	Change %	4-day old	Change %	7-day old	Change %
Pyriproxyfen	1000.0	20.71 ± 2.51 a	11.89	25.78 ± 3.26 a	12.71	28.51 ± 1.89 d	-16.17
	62.5	23.45 ± 2.11 b	26.48	23.46 ± 3.50 a	2.67	30.25 ± 2.74 a	-11.17
	Controls	18.52 ± 2.56	—	22.85 ± 3.44	—	34.04 ± 2.81	—
Tebufenozide	1000.0	22.56 ± 1.83 a	21.62	37.25 ± 1.40 d	63.15	50.62 ± 3.96 d	48.82
	62.5	15.46 ± 2.33 a	-16.75	20.62 ± 3.86 a	-9.64	33.64 ± 2.63 a	-1.18
	Controls	18.52 ± 2.56	—	22.85 ± 3.44	—	34.04 ± 2.81	—
Lufenuron	1000.0	20.23 ± 2.11 a	9.18	28.63 ± 2.45 b	25.43	38.61 ± 3.07 a	13.52
	62.5	19.25 ± 1.51 a	3.94	28.34 ± 2.67 b	10.96	36.73 ± 2.51 a	7.93
	Controls	18.52 ± 2.56	—	22.85 ± 3.44	—	34.04 ± 2.81	—

Conc.: concentration; mean ± SD followed with the letter (a): is not significantly different (*P* > 0.05), (b): significantly different (*P* < 0.05), and (d): very highly significantly different (*P* < 0.001).

nymphs, but not in 1-d-old ones. The low concentration of Tebufenozide had no statistically significant effect at any nymphal age. Lufenuron at 1000 ppm and 62.5 ppm had no statistically significant effect on carbohydrate content of fat body in nymphs at 1- and 7-d, but both concentrations increased carbohydrate content slightly in 4-d-old last instar nymphs.

Effects of IGRs on the Carbohydrate Contents of Adults

Carbohydrate contents in adult locust hemolymph that had been treated with IGRs during the last nymphal instar are shown in Table 4. Pyriproxyfen at 1000 ppm greatly reduced the carbohydrate content of hemolymph of 1-d old adults (56.37 ± 2.20 vs. 74.64 ± 2.5 in the control), and no adults survived to 4 d. The low concentration of 62.5 ppm had no statistically significant effect in 1- or 4-d-old adults, but adults did survive to the 4 d. No adults survived to either become even 1-d-old in the 1000 ppm treatment with Tebufenozide. The low dose had no effect at 1-d, but caused a slight increase in carbohydrate in the hemolymph in 4-d-old adults. Lufenuron had no effect at either concentration in 1-d-old adults, but 1000 ppm increased carbohydrate concentration in the hemolymph of 4-d-old adults.

The metabolic effects of the 3 IGRs on the carbohydrate content of fat body of adults are presented in Table 5. These data show that treatments of last instar nymphs with the 1000 ppm pyriproxyfen decreased the fat body carbohydrates of 1-d-old adults, and no adults survived to the 4-d. The low concentration had no effect at either age, and adults did survive to 4-d. No adults survived to the 1- or 4-d age in individuals treated with 1000 ppm Tebufenozide, but the low concentration did not affect fat body carbohydrate

TABLE 4. TOTAL CARBOHYDRATE CONTENT (MG/ML ± SD) IN THE ADULT HEMOLYMPH AFTER TREATMENT OF THE NEWLY MOLTED LAST INSTAR NYMPHS OF *SCHISTOCERCA GREGARIA* WITH CERTAIN IGRS.

IGRs	Conc. (ppm)	Last instar nymphs (Age in days)		
		1-day old	Change %	4-day old
Pyriproxyfen	1000.0	56.37 ± 2.20 d	-24.53	=
	62.5	70.52 ± 2.25 a	-5.49	73.48 ± 3.58 a
	Controls	74.64 ± 2.5	—	69.21 ± 1.89
Tebufenozide	1000.0	=	—	—
	62.5	78.66 ± 3.11 a	5.44	76.81 ± 4.52 b
	Controls	74.64 ± 2.5	—	69.21 ± 1.89
Lufenuron	1000.0	77.48 ± 2.52 a	3.75	75.21 ± 2.34 c
	62.5	75.25 ± 3.57 a	0.82	72.86 ± 2.31 a
	Controls	74.64 ± 2.50	—	69.21 ± 1.89

Conc.: concentration; mean ± SD followed with the letter (a): is not significantly different (*P* > 0.05), (b): significantly different (*P* < 0.05), and (d): very highly significantly different (*P* < 0.001).
=: adults died.

TABLE 5. TOTAL CARBOHYDRATE CONTENT (MG/G ± SD) IN THE ADULT FAT BODY OF *SCHISTOCERCA GREGARIA* AFTER TREATMENT OF THE NEWLY MOLTED LAST INSTAR NYMPHS WITH SOME IGRS.

| IGRs | Conc. (ppm) | Last instar nymphs (Age in days) | | | |
		1-day old	Change %	4-day old	Change %
Pyriproxyfen	1000.0	30.62 ± 2.02 b	-19.04	=	—
	62.5	33.46 ± 2.52 a	-11.46	31.21 ± 3.42 a	-11.68
	Controls	37.85 ± 2.57	—	35.33 ± 1.84	—
Tebufenozide	1000.0	=	—	=	—
	62.5	40.25 ± 2.77 a	6.34	37.63 ± 1.25 a	6.42
	Controls	37.85 ± 2.57	—	35.33 ± 1.84	—
Lufenuron	1000.0	39.57 ± 3.14 a	4.49	38.26 ± 1.79 a	9.06
	62.5	38.26 ± 2.50 a	10.50	36.75 ± 2.77 a	3.96
	Controls	37.85 ± 2.57	—	35.33 ± 1.84	—

Conc.: concentration; mean ± SD followed with the letter (a): is not significantly different ($P > 0.05$), (b): significantly different ($P < 0.05$), and (d): very highly significantly different ($P < 0.001$).

=: adults died.

content at either age. Lufenuron had no effect on fat body carbohydrate at either concentration, and individuals survived to 4-d.

DISCUSSION

Some authors have reported elevated carbohydrate contents in some insect species as a response to the action of different insect growth regulators (IGRs), while others reported opposite results. These contradictory findings may be due to differences in species sensitivity, the potency of the IGRs, or the developmental stage (Ghoneim et al. 2003).

In general, no certain trend of metabolic effects of the present IGRs was detected. Pyriproxyfen continuously prohibited the nymphs from gaining normal carbohydrate content in hemolymph, but tebufenozide caused statistically significant increases, or non-significant changes in carbohydrate content throughout the nymphal life span. Lufenuron showed variable effects on the hemolymph carbohydrates in that slightly decreased content was measured for the early-aged nymphs, but considerably increased content was recorded for older nymphs. In addition, a stimulatory action of all 3 IGRs on fat body carbohydrates of nymphs of all ages was detected with few exceptions.

Decreasing carbohydrate content in some tissues of the developmental stages of different insect species as a response to some insecticides has been reported (Shakoori et al. 1988; Mandal & Chaudhuri 1992; Radwan & Shaurub 1995; El-Bokl et al. 1998). Various juvenoids (JHAs), and IGRs in general, suppressed carbohydrate content in some insects, e.g., *Spodoptera littoralis* Boisduval (Noctuidae) by the JHA, isopropyl 3,7,11-triethyl-2,4-dodecadiote (Ismail 1980); *S. gregaria* by fenoxycarb (El-Gammal et al. 1989); L. (Diptera: Muscidae) by methoprene (Abou El-Ela et al. 1990), and by lufenuron and diofenolan (Ghoneim et al. 2006); *Synthesomyia nudiset* Van Der Wulp (Diptera: Muscidae) by some IGRs (Abou El-Ela et al. 1993); and the newly formed and late-aged pupae of *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae) by lufenuron and diofenolan (Ghoneim et al. 2003).

As shown in the present study on *S. gregaria*, tebufenozide caused the treated last instar nymphs to gain more carbohydrate in the hemolymph throughout this entire stadium, while lufenuron exhibited a similar inducing effect only on the mid- and late-aged nymphs. Moreover, all IGRs stimulated the nymphs of all ages to accumulate excess carbohydrates in their fat bodies. However, the Increased carbohydrate content occurred in several other insect species after treatment with different IGRs, e.g., kinoprene significantly elevated the carbohydrate content in the last instar larvae of *S. littoralis* (Fouda & Amer 1990); chlorfluazuron and mevalonic acid (separately or combined) induced last instar larvae and pupae of *S. littoralis* to gain various increments of carbohydrate in hemolymph and fat body (Ghoneim 1994); increasing carbohydrate content of *S. gregaria* was triggered by chlorfluazuron (El-Gammal et al. 1993); pupae or adult females of *Tenebrio* molitor Linné (Coleoptera: Tenebrionidae) treated with diflubenzuron had excessive carbohydrate (Soltani et al. 1987; Soltani-Mazouni et al. 1999); mid-aged pupae of *R. ferrugineus* were induced to accumulate excess carbohydrates after treatment of prepupae with lufenuron and diofenolan (Ghoneim et al. 2003); topical application of lufenuron or diofenolan of late last (3rd) instar larvae of *M. domestica* led to increased carbohydrates throughout the pupal period with few exceptions (Ghoneim et al. 2006); novaluron-treated 4th instar larvae of the mosquito *Culiseta longiareolata* Macquart (Diptera: Culicidae) attained

increased carbohydrate content starting from the d-5 post-treatment (Bouaziz et al. 2011).

The varied effects of pyriproxyfen, tebufenozide and lufenuron on the carbohydrate content in hemolymph or fat bodies of nymphs, in the present study on *S. gregaria*, may be caused by interference of these IGRs with hormonal actions on carbohydrate metabolism (Orr 1964; Price 1973; Imboden & Luscher 1976). Also, the production or utilization of the main body metabolites, such as carbohydrates, which are under the control of JH (or IGRs, in general), was suggested by several authors (Slama 1965; Slama & Hodkova 1975; Gade 2004; Sugumaran 2010).

In addition, the disturbance in carbohydrate content of *S. gregaria* nymphs, as we clearly recorded after treatment with pyriproxyfen, tebufenozide or lufenuron, can be understood in the light of their ability to modify the synthesis of certain metabolites and disrupt the functionality of the organism (Rodriguez-Ortega et al. 2003). Other studies show that the carbohydrate reserves with the different developmental stages of the insect. They increase during the rest periods, like metamorphosis, and decrease during the growth periods, like the stages of maturation of the gonads in insects (Bouaziz et al. 2011). Decreased content of carbohydrates after treatment with IGRs may be attributed to their anti-feeding action (Salem 1994), to a decrease in the trehalase activity (El-Shiekh 2002), or to their effects on the carboxylase activity (Mukherjee & Sharma 1996).

In the present work, pyriproxyfen drastically affected the hemolymph carbohydrate content of 1-d-old adults but a carbohydrate increase was determined for 4-d-old adults (at 62.5 ppm). Tebufenozide exhibited an inducing action on hemolymph carbohydrate content (at 62.5 ppm) and lufenuron at both concentrations exhibited a similar effect, regardless of the age of the adult. With regard to fat bodies of adults, pyriproxyfen treatment of last instar nymphs resulted in reduced carbohydrates in 1-d-old adults. In contrast, carbohydrates slightly increased in fat bodies of adults of both ages as a response to the action of tebufenozide and lufenuron at both concentrations. However, elevating or reducing effects of some IGRs on the carbohydrate content of adults belonging to various insects species were reported, e.g., IGR-increased carbohydrate contents in adults of *Chrysocoris stolli* Wolf (Hemiptera: Pentatomidae) (Saha et al. 1986) and *S. littoralis* (Abdel-Hafez et al. 1988). In addition, Ezz & Fahmy (2009) found increased carbohydrate content of the adult striped mealybug, *Ferrisia virgata* (Cockerell) (Hemiptera: Pseudococcidae) at d 4 and significantly decreased carbohydrate content 10 d post-treatment. The reducing or inducing effects of pyriproxyfen, tebufenozide or lufenuron on the carbohydrate content of adult *S. gregaria*,

in the present study, may be due to the extended action of each (Anwar & Abdel-Mageed, 2005).

In conclusion, the results obtained with pyriproxyfen, tebufenozide and lufenuron in the present study show that they disrupt the metabolism of the essential energy source, carbohydrates, in nymphs and adults of the desert locust, *S. gregaria*. This finding provides appreciable evidence that these IGRs have considerable promise for effective use as environmentally-friendly alternatives to synthetic chemical insecticides against this destructive pest. However, more research is needed for elucidating the mode of action of each IGR, including ascertaining what receptors are involved.

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