Toxic effects of *Nerium oleander* on the reproduction of the desert locust *Schistocerca gregaria* (Forskål 1775, Orthoptera, Acrididae)

Efectos tóxicos de *Nerium oleander* en la reproducción de la langosta del desierto *Schistocerca gregaria* (Forskål 1775, Orthoptera, Acrididae)

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Palabras clave: *Nerium oleander*, *Schistocerca gregaria*, supervivencia, inhibición ovárica.

ABSTRACT

The desert locust *Schistocerca gregaria* is an economically dangerous pest invading several countries along its distribution area from North Africa to West Asia. The present study aims at assessing the effect of the toxic effects of *Nerium oleander* (Apocynaceae) leaves used as staple food on survival and ovarian development of this pest. The experiment was carried out under laboratory conditions by feeding a group of young desert locust females on fresh leaves of *Brassica oleracea* (control treatment) and another group on *N. oleander*. Ovarian development was analyzed by performing dissections and measurements on the ovarioles and terminal oocytes from both *N. oleander* fed and control females during the experiment. The results showed a cumulative mortality rate of females fed with *N. oleander* leaves of over 50% on the 6th day, while total mortality was reached on the 25th day. However, in control females, the mortality at these dates was 3% and 17%, respectively. The size of ovarioles and terminal oocytes were highly reduced and remained at previtellogenesis stage in *N. oleander* fed females compared to the control treatment. The ovaries of *N. olender* fed females showed no significant development and female reproductive apparatus remained at the juvenile stage. The leaves of *N. oleander* exhibited an inhibitory effect on the ovarian development of *S. gregaria*.

RESUMEN

La langosta del desierto *Schistocerca gregaria* es una plaga económicamente peligrosa que invade diversos países a lo largo de su área de distribución desde el norte de África hasta Asia occidental. El presente estudio tiene como objetivo evaluar los efectos tóxico de las hojas de *Nerium oleander* (Apocynaceae) usadas como alimento principal sobre la supervivencia y el desarrollo ovárico de esta plaga. El experimento se llevó a cabo en condiciones de laboratorio alimentando a un grupo de hembras jóvenes de langosta del desierto con hojas frescas de *Brassica oleracea* (tratamiento control) y otro grupo de hembras con *N. oleander*. El desarrollo ovárico fue analizado mediante la realización de disecciones y medidas de las ovariolas y oocitos terminales de hembras control y hembras alimentadas con *N. oleander* durante el experimento. Los resultados mostraron una tasa de mortalidad acumulada de más del 50% en el sexto día y una mortalidad total en el día 25 en las hembras alimentadas con hojas de *N. oleander*. Sin embargo, en las hembras control la mortalidad en esos mismos días fue de 3% y 17%, respectivamente. El tamaño de las ovariolas y de los oocitos terminales tenían un tamaño mucho más reducido y permanecieron en estado de previtelogénesis en las hembras alimentadas con *N. oleander* comparadas con los de las hembras del tratamiento control. Los ovarios de las hembras alimentadas con *N. oleander* no mostraron un desarrollo significativo y el aparato reproductor de las hembras permaneció en el estado juvenil. Las hojas de *N. oleander* tuvieron un efecto inhibidor sobre el desarrollo ovárico de *S. gregaria*.

INTRODUCTION

The desert locust *Schistocerca gregaria* is a polyphagous pest that feeds on many plant species of which no aboveground part escapes its voracity by devouring stems, bark, flowers, fruits and seeds. Its capacity of migration enables it to adapt to different ecological situations (Popov, 1958; Uvarov, 1977; Lecoq, 2005). Damage caused by the desert locust is a consequence of its polyphagous behavior, high population density, and aggregation to form swarms. However, it was observed that the desert locust refuses completely or partially to eat some plants species (Rao & Mehrotra, 1976; Ghaout, 1990; Latchininsky & Launois-Luong, 1997; Woldewahid, 2003).

Plants preferred by the locusts are generally those that provide the necessary nutritional compounds for its better development and reproduction. The quest for plants depends on both the capacity of the locust, the characteristics of the plant and the environmental conditions (Duranton *et al.*, 1982). Phytophagous insects have evolved to recognize plants with toxic defensive compounds (Blum, 1983; Rembold, 1994). Several plants species are not consumed by a large number of insects due to the toxic or repellent secondary substances contained in these plants (Bruneton, 1996). Over 2000 species of plants are known that possess some insecticidal activity (Jacobson, 1989).

The use of chemical pesticides is the main insect controlling approach against insect pests during the recent decades but it is not without significant drawbacks, such as the development of strain resistance to insecticides (Mallet, 1989; Haubruge & Amichot, 1998; Garriga & Caballero, 2011), handling hazards, increased costs, concerns about insecticide residues, great threats to non-target fauna, and both human and environmental health (Van der Valk, 1990; Everts & Ba, 1997; Bagari *et al.*, 2010). Therefore, alternative methods to chemical pesticides for controlling *S. gregaria* could have considerable value.

Plant control agents are biodegradable and harmless to the environment. They are generally pest-specific and relatively harmless to non-target organisms including man (Rembold, 1994). The plants studied in the context of the research for new insecticidal substances were classified as plants with deterrent or repellent effects on desert locust (Despland & Simpson, 1999; Abbassi *et al.*, 2003a; Abbassi *et al.*, 2004). The plant species classified as plants with deterrent or lethal effect on desert locust affect differentially its fertility, development, behavior and survival. More than 200 insect species were reported to be controlled by the pesticides derived from the neem tree *Azadirachta indica* (Hamilton, 1992).

The use of plants as a mean of the locust control without side effect on the environment can be an alternative way to overcome the adverse effects of pesticides spraying against pests. Indeed, several studies of the effect of plant-derived substances on desert locust gave satisfactory results, thus encouraging further research to implement an alternative method to chemical control against locust pest (Nasseh *et al.*, 1993; Wilps & Diop, 1997; Abbassi *et al.*, 2003a).

It was reported that all parts of *Nerium oleander* (Apocynaceae) are toxic to man and animals including some insects (Langford & Boor, 1996; Adome *et al.*, 2003; Barbosa *et al.*, 2008). This plant is unpalatable for locust. The diet based on *N. oleander* leaves halted the development of the fourth instar larvae of the desert locust *S. gregaria* and caused weight loss due to low food intake related to the repellent and anti-palatable effect of this plant (Bagari *et al.*, 2013).

In this study, the effects of *N. oleander* leaves on the ovarian development and survival of the desert locust *S. gregaria* were studied under laboratory conditions using *Brassica oleracea* (which is well consumed by the desert locust) as a control plant.

MATERIALS AND METHODS

Insect culture

Gregarious locusts used in this study were obtained from the mass rearing facility of the National Center of Locust Control (Ait-melloul, Agadir). Locusts were reared in aluminum cages of 37 × 37 × 50 cm and 100 × 50 × 54 cm size with Plexiglas sides. The front top of the cages was equipped with an opening clamshell to allow the introduction of food, aeration, cleaning and handling of individuals. Two or three perches were placed vertically inside each cage to allow the larvae to moult. The cages were maintained in a room at 32 ± 2°C temperature. The lighting of cages was provided by incandescent bulbs of 40 watts for 12/12 hours photoperiod and 65 ± 3% relative humidity. The room was equipped with a ventilation system to remove odors secreted by locusts.

Plant material

During reproduction, the locusts were reared with a diet of fresh leaves of several plants such as cabbage (*Brassica oleracea*), alfalfa (*Medicago sativa*), lettuce (*Lactuca sativa*) and other seasonal species such as *Diplotaxis harrae*. Wheat bran was added to this diet.

During the experiments, fresh leaves of *Brassica oleraceae* (control diet) or *N. oleander* were provided as the staple food to newly-emerged adult female of desert locust, depending on the treatment assigned to each female (see below). The leaves used to feed locusts were collected from early flowering plants in Ait Melloul-Agadir area. The *N. oleander* leaves provided as diet for the tested individuals were only fresh apical leaves, to avoid the limited edibility of old leaves caused by the hardness of their epidermis.

Experimental design

Fifth instar larvae of the desert locust, *S. gregaria* were selected for synchronization of fledging. Newly-emerged adult females were fasted for 12 hours to empty their digestive tracts and then placed in cages of 37 × 37 × 50 cm of size. Two groups up to 30 females each were used for the experiment. Three cages of 10 females each were used for each treatment (*Nerium oleander* diet vs control *Brassica oleracea* diet). Other females were used for dissections. After fasting for 12 hours, 5 mature males were introduced into each cage to stimulate the ovarian development. According to several authors, males usually mature before females initiate sexual maturation of their congeners (Norris, 1954) and the terminal oocytes in the ovarioles develop much more rapidly than the terminal oocytes of females reared without males and copulation results in the discharge of material from the neurosecretory system (Highnam & Lusis, 1962). In many species of insects and other animals, females are choosy about their mates (Andersson, 1994). Desert locust females generally copulate several times during their lifetime, both before and after oviposition, and mating competition has been observed.

The cages were placed in a room at a temperature of 32 ± 2°C. The lighting of cages was provided by incandescent bulbs of 40 watts, linked to a timer to control for a 12/12 hours photoperiod. The mortality rate of females fed on *N. oleander* compared with that of *B. oleracea* and the ovarian development were followed during the experiment for 25 days.

Dissection of females

Ovarian development of females subjected to diets based on *N. oleander* leaves compared to the control treatment, fed with *B. oleracea* leaves, was followed by performing dissections on *S. gregaria* females. Three dissections at regular intervals of seven days (12, 19 and 26 days) were completed for each diet during the experiment using three females at each time. Sexual maturity of a female is reflected by the state of its ovaries which plays an important role in the reproductive potential of locusts. A longitudinal abdominal incision was made on the dorsal part of the insect to prevent damage to the ovaries. These were impregnated in a physiological fluid of Ringer [Nacl (7.5 g) + KCl (0.35 g) + $CaCl_2$ (0.21 g) + 1 liter of distilled H_2O] (Ephrussi & Beadle, 1936). Both ovaries were separated and ovarioles were thoroughly isolated from each other. Ovarian development was estimated based on the size (length) of the oocytes and ovarioles. Measurements were performed under a binocular microscope equipped with a micrometer. The presence of vitellus, fat body, and resorption bodies (resorbed oocytes) was recorded.

Statistical analysis

The analysis of ovarian development using ovariole and oocyte size was carried out by means of an analysis of variance (ANOVA) since data were normally distributed. The significance level was set at 5% using the SPSS statistical software IBM SPSS Statistics 21.

RESULTS

Effect on the female survival

The results on the evolution of the mortality of females fed with *N. oleander* leaves have shown that the first dead individuals were recorded on the 4th day and a cumulative mortality rate of over 50% was obtained on the 6th day, while total mortality was attained on the 25th day. However, in control females fed with fresh cabbage leaves the mortality rate was 3% and 17% in the 6th and 25th days, respectively (fig. 1).

N. oleander leaves affected the development of locust females and reduced their physical activity. No mating activity was observed during the experimental period in *N. oleander* fed females. Pink feces were excreted by these females, and this could be due to digestive disorders caused by their diet. Control females, fed with *B. oleracea*, presented a normal activity during their development and started mating from the 24th day during the experimental period.

Effect on ovarian development

Each one of the two panoistic ovaries of the desert locust consists of ovarioles, arranged in line and opening into the lateral paired oviducts. The

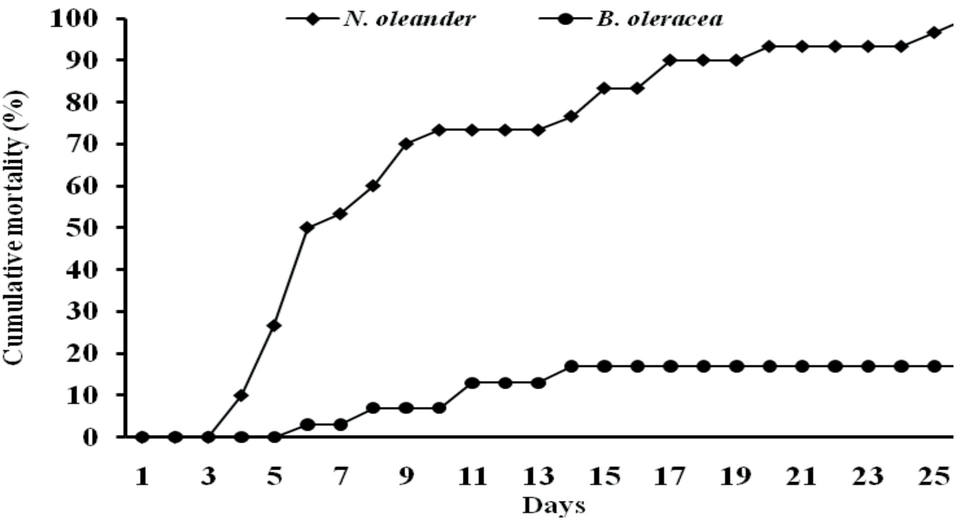

Fig. 1.—Cumulative mortality rate (%) of desert locust females fed on *Nerium oleander* and *Brassica oleracea* leaves.

Fig. 1.—Tasa de mortalidad acumulada (%) de hembras de la langosta del desierto alimentadas con hojas de *Nerium oleander* y *Brassica oleracea.*

mean number of ovarioles of control females was 48 ± 0.52 ovarioles/ovary, ranging from 46 to 49 ovarioles.

The ovarian development of females fed with *N. oleander* was studied by dissections of the female reproductive tract (fig. 2A). The ovariole size depends on the development of the primary oocytes. The mean size of ovarioles from the first to the third dissections were 4.49 ± 0.08 mm, 5.16 ± 0.07 mm and 5.17 ± 0.07 mm after 12, 19 and 26 days, respectively. The statistical analysis showed a significant difference in ovariole size between 12 and 19 days ($F = 38.63$, $p < 0,001$, d.f. = 19) and 12 and 26 days ($F = 40.72$, $p < 0,001$, d.f. = 19) but there were no differences between 19 and 26 days ($F = 0.007$, $p = 0.93$, d.f. = 19). The ovarioles of *N. oleander* fed females were still blocked in previtellogenesis stage and showed a whitish aspect. The development of the fatty body was very low.

For the females fed on *B. oleracea*, the ovarioles developed normally (fig. 2B) and their mean size developed from the 12th to the 26th days as follows: 6.65 ± 0.25 mm, 8.71 ± 0.15 mm and 12.19 ± 0.18 mm. The difference between the three dissections was significant ($F = 222.10$, $p < 0.001$, d.f. = 19). The growth was more than doubled compared to *N. oleander* fed females at the third dissection (fig. 3). The fat body was well developed in control females and resorption bodies were observed at a rate of 3.33% during the third dissection, but no track of egg laying was noted.

For terminal oocytes, the results showed a low level of development in *N. oleander* fed females. Their mean size slightly increased from 0.64 ± 0.04

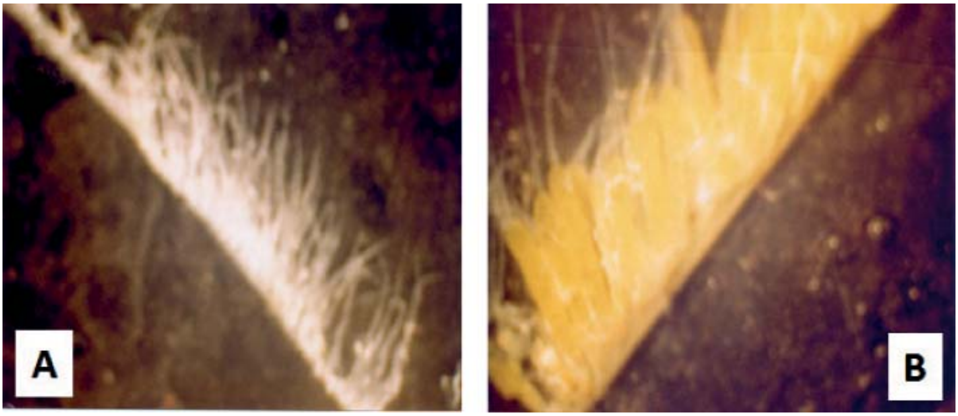

Fig. 2.—Female ovary of *Schistocerca gregaria* fed on *Nerium oleander* (A) and *Brassica oleracea* (B) leaves.

Fig. 2.—Ovario de hembra de *Schistocerca gregaria* alimentada con hojas de *Nerium oleander* (A) y *Brassica oleracea* (B).

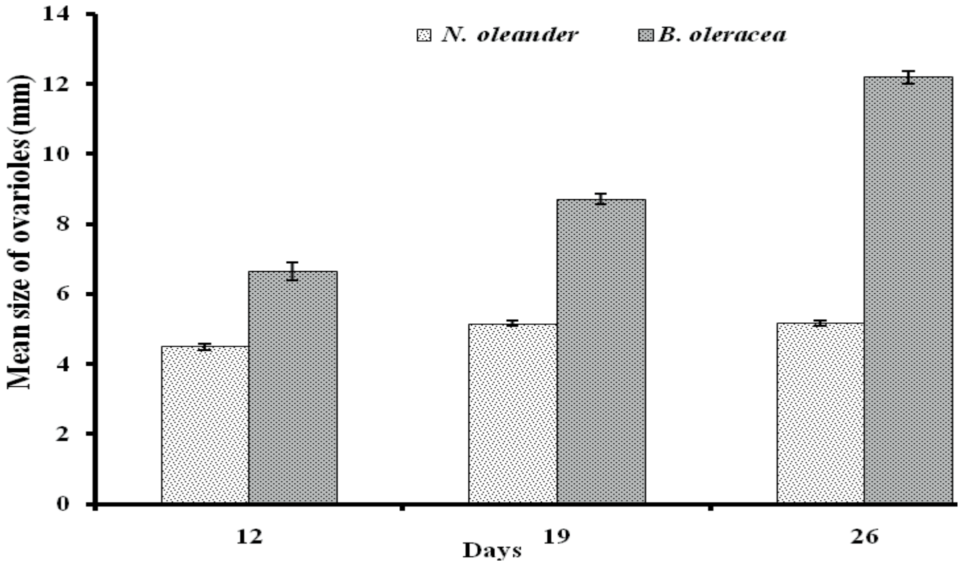

Fig. 3.—Mean size (± S.E.) of ovarioles of *Schistocerca gregaria* females fed on *Nerium oleander* and *Brassica oleracea* leaves.
Fig. 3.—Tamaño medio (± E.E.) de las ovariolas de hembras de *Schistocerca gregaria* alimentadas con hojas de *Nerium oleander* y *Brassica oleracea*.

mm to 0.77 ± 0.03 mm from 12 to 19 days and 1.11 ± 0.02 mm after 26 days. The difference between the three times was significant ($F = 93.21$, $p < 0.001$, d.f. = 19). Growth of terminal oocytes was limited to juvenile stage, without production of vitellus reflecting the maturation of females.

The measurements obtained in oocytes of control females were 2.75 ± 0.07 mm, 6.6 ± 0.08 mm and 7.49 ± 0.06 mm, for 12th, 19th and 26th days, respectively (fig. 4). The differences between these three times was significant ($F = 77.24$, $p < 0.001$, d.f. = 19).

The difference between the mean size of oocytes of *N. oleander* fed and control females was highly significant ($F = 9334.23$, $p < 0.001$, d.f. = 19).

DISCUSSION

The anatomical study of the ovaries of the desert locust showed that *N. oleander* caused toxic effect on the females provoking a decrease of their biological activities, low food intake and inhibiting the process of vitellogenesis and therefore, halted the ovarian development. The *N. oleander* diet impacted survival of locusts and the total mortality rate was obtained after 25 days during the experiment. The development of the ovarioles which depends

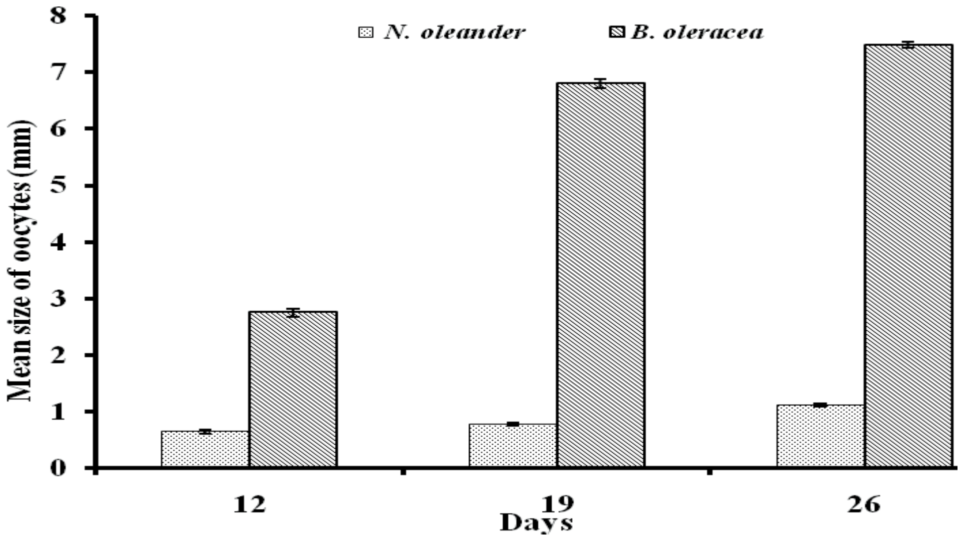

Fig. 4.—Mean size (± S.E.) of oocytes of *Schistocerca gregaria* females fed on *Nerium oleander* and *Brassica oleracea* leaves.
Fig. 4.—Tamaño medio (± E.E.) de los oocitos de hembras de *Schistocerca gregaria* alimentadas con hojas de *Nerium oleander* y *Brassica oleracea*.

on the growth of the terminal oocytes was blocked in the previtellogenesis stage as the vitellus was not yet formed. The development of the fat body was very low. Females subjected to a monospecific diet of *N. oleander* leaves have retained the characteristic pink color of immatures until the end of the experiments. The ovarian development which is controlled by the neurosecretory system of the female with the presence of males (Highnam & Lusis, 1962) and the activity of follicular cells involved in the synthesis of yolk could be disturbed by the *N. oleander* diet. During vitellogenesis, the follicular cells play an active part in the synthesis of yolk in terminal oocytes of the desert locust (Lusis, 1963).

The inhibitory effect of the oocyte development could be due to the toxic compounds contained in *N. oleander* leaves after they were ingested. Thus, the effect of *N. oleander* manifested by reduced consumption in locusts limited the production of the fatty body, which leads to blocking the synthesis of vitellogenin and consequently the stopping of vitellogenesis. The vitellogenin synthesized by the fatty body pass into the hemolymph before being absorbed by the ovary. Inhibition of vitellogenesis may be due to blocking of the synthesis of the juvenile hormone (JH) secreted by the *corpora allata*. Juvenile hormone plays a decisive role in regulating a multitude of physiological processes in desert locusts and affects different aspects of behaviour, including phase behaviour (Wiesel *et al.*, 1996), sexual behavior (Amerashinge, 1978) and spontaneous locomotor activity (Odhiambo, 1966).

The diet based on *N. oleander* leaves is known to affect the development of the desert locust, and previous results have shown that development of *S. gregaria* larvae and weight loss of treated individuals was due to the low food intake closely related to the toxic effect of this plant (Bagari *et al.*, 2013). The food intake of desert locust generally depends on secondary substances perceived through the olfactory and gustatory organs (Le Gall, 1989) , according to physico-chemical properties that characterize the quality of the food and may also be influenced by the temperature, physical and phase status of the insect.

It has been reported that undernourishment or ingestion of inappropriate host plant profoundly affects the basic systems of the body, including the reproductive system of insects. The importance of food intake of *S. gregaria* and *Locusta migratoria* appears to be related to the nutritional value of the food (Sinoir, 1968), the requirements of insects, their capacity to detect food and habitat conditions (Despland & Simpson, 1999), and may also be influenced by temperature and ethological and physical (solitary vs. gregary) state of the insect. *N. oleander* cuttings used to control the white grub larvae of *Rhizotrogini* beetles has a deterrent effect on these insects and limited the damage to cereals crops (Madaci *et al.*, 2008). Also, *N. oleander* extracts tested on *Lymantria dispar* larvae, showed insecticidal properties (Kerris *et al.*, 2008) and contained active compounds that are able to eliminate mosquito by affecting their reproduction (Lokesh *et al.*, 2010). According to Haddy (2006), the decomposition of *N. oleander* leaves leads to an important deoxygenation of aquatic receptors having a toxic effect on the freshwater snails *Melanopsis preamorsa*. The combined ethanolic extract of *Nyctanthes arbortristis* and *N. oleander* exhibited significant antibacterial activity (Ravi Kumar & Yadav, 2013).

Many studies have been achieved for the investigation on different plants to obtain natural compounds that may have the toxic effect or repellent, anti-feedant and anti-hormonal characteristics (Thomas & Callaghan, 1999). Secondary substances produced by plants such as alkaloids are known to interfere with the metabolic activities of insects and reduce the digestibility (Lebreton, 1982). Several plants or their extracts have given encouraging results to control the desert locust.

In addition to *N. oleander* other plants have exhibited insecticidal activity against the desert locust *S. gregaria*. Thus, *Calotropis procera* (Abbassi *et al.*, 2004) and *C. gigantea* (Rao & Mehrotra, 1976; Pari *et al.*, 1998), *Peganum harmala* (Idrissi-Hassani, 2000; Abbassi *et al.*, 2003b), *Azadirachta indica*, *Melia volkensii* (Schmutterer, 1990; Hamilton, 1992; Langwald *et al.*, 1995;

Rembold, 1997; Ould El Hadj *et al.*, 2006, Hamadah *et al.*, 2013), *Cestrum parqui* (Barbouche *et al.*, 2001) and *Cleome arabica* (Kemassi *et al.*, 2012) were classified as plants with deterrent or lethal effect on desert locusts. They affect differentially its fertility, development, behavior and survival.

CONCLUSION

The *N. oleander* leaves diet has been shown lethal to females and inhibited ovarian development of the desert locust and therefore delayed maturation. In this perspective, the direct use of *N. oleander* or preparations extracted from its organs could be valued for application against desert locusts in the context of integrated pest control in remission areas. However, it will be necessary to refine the prior knowledge on the functional properties of this plant and to determine the conditions of application in respect of ecosystems and human health.

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