Effect of gossypol on survival and reproduction of the zoophytophagous stinkbug *Podisus nigrispinus* (Dallas)

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ABSTRACT. Effect of gossypol on survival and reproduction of the zoophytophagous stinkbug *Podisus nigrispinus* (Dallas). Gossypol is a sesquiterpene aldehyde found in cotton plants conferring resistance against herbivory. Although the effect of this sesquiterpenoid on insect pests of cotton is known, the interaction of this compound with zoophytophagous predators such as *Podisus nigrispinus* (Dallas) (Hemiptera, Pentatomidae) has not been studied so far. Thus, the objective of this study was to evaluate the effect of the purified gossypol on nymphs and adults of *P. nigrispinus*. Nymphs and adults of this predator were fed on *Tenebrio molitor* pupae and supplemented with solutions of gossypol at concentrations of 0.00, 0.05, 0.10, and 0.20% (w/v) during the nymphal and adult stages or, only during the adult stage of *P. nigrispinus*. The nymphal stage of the predator was, on average, two days longer when suplemented with gossypol. Emerged adults had lower fecundity and egg hatching, especially at the highest gossypol concentration (0.20%) ingested during the nymphal and adult stages. However, this predator was not affected when it ingested the compound only during the adult stage. *P. nigrispinus* can have delayed nymphal development and lower reproductive performance when ingesting the gossypol during the nymphal and adult stages, but only at higher concentrations of gossypol than that produced by cotton plants.

KEYWORDS. Asopinae; host plant resistance; omnivory; zoophytophagy.

RESUMO. Efeito do gossipol na sobrevivência e reprodução do percevejo zoofitófago *Podisus nigrispinus* (Dallas). O gossipol é um aldeído sesquiterpeno produzido pelo algodoeiro que confere resistência contra a herbivoria. A interação deste sesquiterpeno com predadores zoofitófagos, como *Podisus nigrispinus* (Dallas) (Hemiptera, Pentatomidae), é inexistente apesar do reconhecido efeito do gossipol sobre insetos pragas do algodoeiro. Assim, este estudo avaliou o efeito do extrato de gossipol sobre ninfas e adultos de *P. nigrispinus*. O predador foi alimentado com pupas de *Tenebrio molitor* L. (Coleoptera, Tenebrionidae) e suplementado com soluções do gossipol nas concentrações 0, 0,05, 0,10 e 0,20% (peso/volume) durante os estágios ninfal e adulto e somente durante o estágio adulto. A duração do estágio ninfal do predador foi em média dois dias mais longo quando suplementado com gossipol. Adultos oriundos de ninfas suplementadas com gossipol apresentaram menor fecundidade e viabilidade dos ovos, em especial na maior concentração (0,20%). Contudo, adultos não foram afetados quando suplementados com gossipol somente durante este estágio. Os resultados demonstram que a ingestão prolongada do gossipol ocasiona efeito no desenvolvimento e reprodução do predador *P. nigrispinus*, porém somente em concentração superior àquela produzida naturalmente pela planta de algodão.

PALAVRAS-CHAVE. Asopinae; onivoria; resistência de plantas; zoofitofagia.

The allelochemical gossypol is a sesquiterpenoid phenol aldehyde with variable concentrations in the leaves depending on the cotton [Gossypium hirsutum L. (Malvaceae)] variety and other cotton plant parts with glandular predisposition for this compound (Rudgers et al. 2004; Younis & Darrag 2007). The properties of gossypol include reduction of the digestibility in herbivores (Elsebae et al. 1981), representing a resistance factor by antibiosis to chewing and sucking cotton pests (Syed et al. 2003; Du et al. 2004). Cotton plants with high gossypol levels are resistant by antibiosis or non preference to Aphididae, Miridae, Tetranychidae, Thripidae, and caterpillars, especially Heliothis and Helicoverpa larvae (Noctuidae) (Gannaway 1994; Stipanovic et al. 2006). Furthermore, abundance of insect pests in cotton fields cultivated with varieties with gossypol shows that this compound acts as a defense mechanism against herbivory (Syed *et al.* 2003; Leghari *et al.* 2001).

The effect of gossypol on herbivorous species of cotton is well-known; however, the interaction of gossypol with natural enemies of herbivorous is poorly known. Gossypol can have direct and indirect effects on these natural enemies. Direct contact of zoophytophagous predatory species with gossypol might take place when predators feed on plants. Predatory stinkbugs, such as *Podisus nigrispinus* (Dallas) (Hemiptera, Pentatomidae) usually feed on host plants of their prey independent of the satiation level (Evangelista Junior *et al.* 2004; Coelho *et al.* 2008). On cotton plants this predatory stinkbug feeds on apoplastic spaces and xylem (Torres *et al.* 2010) and ingests considerable amount of plant material which corresponds to approximately 28% and 30% of their body weight

(Coelho *et al.* 2009). Indirect contact with gossypol produced by plants might also occur when predators consume contaminated herbivore prey fed on cotton with high levels of gossypol. Gossypol had negative effect on *Campoletis sonorensis* (Cameron) (Hymenoptera, Ichneumonidae) parasitizing *Heliothis virescens* (Lepidoptera, Noctuidae) reared on cotton cultivars with high levels of gossypol (Gunasena *et al.* 1989). On the other hand, the biological traits of *Propylaea japonica* (Thunberg) (Coleoptera, Coccinellidae) were similar when preying on *Aphis gossypii* Glover (Hemiptera, Aphididiae) fed on the cotton variety M9101 with high gossypol levels in relation to ZMZ13 and HZ401 with low and medium gossypol levels, respectively (Du *et al.* 2004).

The combination of plant resistance and biological control measures is essential for the success of any integrated pest management program. A series of studies after Campbell & Duffey (1979), however, has demonstrated that secondary compounds conferring resistance against herbivores sometimes result in negative effects on their natural enemies (Bottrell et al. 1998; Coley et al. 2006). Furthermore, herbivores have coevolved with host plant defense mediated by the detoxification of the secondary compounds becoming specialized and, hence, using of the secondary compounds as a second hand defense against their own predators and parasitoids (Nishida 2002; Coley et al. 2006). However, specialized plant defense has a larger impact on generalist predators when interacting with their herbivore prey living on plants expressing secondary compounds for resistance (Traugott & Stamp 1997; Francis et al. 2000; Vivan et al. 2003). The predatory stinkbug P. nigrispinus preys on a large variety of defoliating insects (Torres et al. 2006). Moreover, this predator, also displays plant feeding behavior, thus creating direct exposure pathways of interaction with possible poisonous effects of the gossypol directly by feeding on plants and indirectly by preying on contaminated insects that ingested the gossypol from cotton plants. In fact, plant feeding by P. nigrispinus implies direct contact with toxicants in cotton plant vessels (Torres et al. 2003; Torres & Ruberson 2004; Torres et al. 2010). Thus, in this study we investigated the hypothesis that the gossypol, a compound offerring cotton plant resistance against herbivores through reducing digestibility, affects the development and reproduction of zoophytophagous predators. To ascertain about this hypothesis the effect of direct ingestion of the gossypol for long periods by P. nigrispinus were performed. The experiments were set up to allow the continuous ingestion of gossypol by nymphs and adults or only through the exposure during the adult stage.

MATERIAL AND METHODS

The effect of the ingestion of gossypol on the development, survival and reproduction of the predator *P. nigrispinus* was investigated in two experiments: long-term ingestion during the nymphal and adult stages (i); and only during the adult stage (ii). The purified gossypol was obtained from Embrapa Algodão, Campina Grande, in the State of Paraíba, Brazil.

Ingestion of gossypol during nymphal and adult stages. The experiment was carried out at the Laboratory of Biological Control of Insects of the Universidade Federal Rural de Pernambuco (UFRPE) in Recife, state of Pernambuco, Brazil. Sixty nymphs of the predator, at the beginning of second instar (< 24 hours) since the first instar does not feed on prey, were separated in groups of six per Petri dish (15 cm diameter and 1.2 cm height) at $25 \pm 1^{\circ}$ C, $71 \pm 10\%$ RH and photoperiod of 12 hours. These nymphs were continuously exposed to the gossypol through ingestion during the nymphal and adult stages by offering solutions of gossypol at concentrations of 0.05, 0.10 or 0.20%, and 0%. The solutions were offered to the nymphs in 1.5 cm³ plastic tubes fastened to the superior internal part of the Petri dish covers used to rear the nymphs. Later these tubes were fixed to the cover of the 500 mL plastic containers used to rear the adults of P. nigrispinus. Predators in all treatments (gossypol concentrations and water control) were fed with Tenebrio molitor L. (Coleoptera, Tenebrionidae) pupae. The duration and mortality of nymphs and emergence and mortality of adults P. nigrispinus were monitored.

Adults of *P. nigrispinus* were separated by sex and maintained individually during three days during the pre-reproductive period (Carvalho *et al.* 1995). After this period, predators were paired in 50 mL plastic containers with 10 pairs per treatment and each pair represented a replication. The gossypol solution and *T. molitor* pupae were substituted every two days during the adult stage. During food replacement, the egg masses were collected and the mortality of females was also recorded. The duration and survival of the nymphal period, the longevity of females and egg and nymph production of this predator were obtained.

Ingestion of gossypol during adult stage. In the second experiment the gossypol solution was offered only during the adult stage of *P. nigrispinus* to exclude the possible effect of the gossypol on the developmental stage. Newly emerged adults of *P. nigrispinus* were obtained from the rearing facility of the Laboratory of Biological Control of UFRPE. The adults were weighed to select females between 50 and 70 mg and males between 30 and 50 mg, which were randomly assigned to receive one of the following treatments: control (water) or the gossypol concentrations of 0.05, 0.10 and 0.20%. The solutions of gossypol were continuously offered to the predator and the replacement of the solution was every other day, as done in the previous experiment. Egg masses were collected and maintained in Petri dishes with moistened cotton pad to evaluate egg hatching.

Statistical analysis. To determine whether the predator responded positively or negatively to the ingestion of different gossypol concentrations compared to the water as the control treatment, the results were subjected to analysis of regression. The analysy was conducted using the Proc REG of SAS (SAS Institute 2001) considering the duration and the viability of the nymphal stage, pre-oviposition period, number of eggs, and the proportion of egg hatching as the dependent variables (y) as a function of gossypol concentrations as the independent variables (x). The fitted models were

selected based on significance of the coefficients (P < 0.05) and their contribution to the best biological representation. The proportions of live females along the adult stage, starting from 10 females per treatment (control and gossypol concentrations) were used to estimate the survival curves of predator fed gossypol solution and the control using the Kaplan-Meier method through Proc LIFETEST of the SAS and the test of Long-Rank to compare survival means (SAS Institute 2001).

RESULTS AND DISCUSSION

The nymphs of P. nigrispinus supplemented with gossypol experienced significant delay in the development, which ranged from 20.3 to 20.7 days compared to nymphs from control treatment (0% gossypol, 18.2 ± 0.37 days) disregarded the gossypol concentrations (Fig. 1). Delayed nymphal development of P. nigrispinus fed on gossypol concentrations (0.05, 0.10 and 0.20%) indicates negative effect of this sesquiterpenoid on this predator and that these effects do not seem to depend on the amount of product ingested. The effect of gossypol ingestion was not related with the concentrations used because nymphal development of the predator was similar among the concentrations from 0.05 to 0.20%. Since gossypol is, in general, a reducer of digestibility (Meisner et al. 1978; Elsebae et al. 1981; Stipanovic et al. 2006), the effect may not depend on the concentration used and the common result is related to lower development, weight and fecundity.

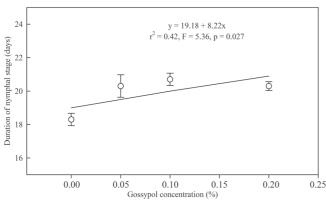


Fig. 1. Duration of nymphal stage for *Podisus nigrispinus* fed *Tenebrio molitor* pupae and supplemented with different concentrations of gossypol.

Females of *P. nigrispinus* from nymphs fed on *T. molitor* pupae and receiving continuous gossypol during the nymphal and adult stages exhibited similar pre-oviposition period ($F_{df=1,42} = 0.29$, P = 0.594) with values from 6.4 to 7.2 days. However, egg production was significantly affected according to the concentration of gossypol offered to the female ($F_{df=1,42} = 9.94$, P = 0.003) (Fig. 2A). Females from control treatment (0% gossypol) produced, on average, 452 eggs, whereas those supplemented with the concentrations of 0.05,

0.10 and 0.20% gossypol produced, on average, 423, 305 and 244 eggs, respectively. Egg hatching was also reduced ($F_{df=3,42} = 11.73$, P = 0.001), for those females fed on the highest gossypol concentration (i.e., 51.4% versus 75%) (Fig. 2B). However, females exposed to gossypol only during the adult stage exhibited similar pre-oviposition periods ($F_{df=1,39} = 0.01$, P = 0.971), mean number of eggs per female ($F_{df=1,39} = 0.11$, P = 0.199) and egg hatching proportion ($F_{df=1,39} = 0.11$, P = 0.962). The pre-oviposition period and the number of eggs per female varied from 4.2 to 5.4 days and from 248.5 to 369.9 eggs, and egg hatching from 68 to 75%, respectively (Fig. 2B).

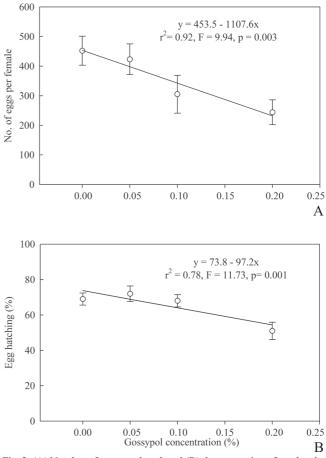


Fig. 2. (A) Number of eggs produced, and (B) the proportion of egg hatching for *Podisus nigrispinus* fed *Tenebrio molitor* pupae and supplemented or not (0%) with different concentrations of gossypol during the nymphal and adult stage or only during the adult stage. Symbols stand for mean \pm standard error.

Nymphal survivorship of *P. nigrispinus* supplemented continuously with gossypol under different concentrations was similar ($F_{df=1,42} = 2.91$, P = 0.095) including the control and, with values from 86.1 to 96.6% survival. However, females fed gossypol since nymphal stage exhibited survival values variable among treatments in the adult stage (Test of Log-Rank, df = 3, $\chi^2 = 10.92$, P = 0.0122) (Fig. 3B) with

mean longevity ranging from 26.0 to 49.7 days, and higher values for females exposed to the highest concentration of gossypol. Female *P. nigrispinus* fed on gossypol only during the adult stage had similar survival (Test of Log-Rank, df = 3, $\chi^2 = 0.74$, P = 0.8631) (Fig. 3A), with similar longevity ranging from 39.2 to 48.5 days.

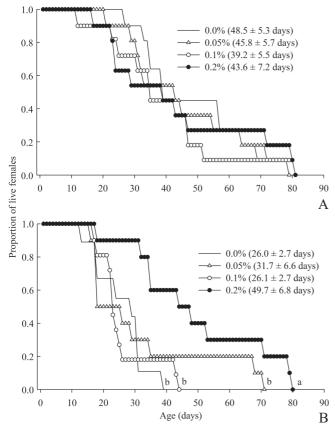


Fig. 3. Age-specific survivorship for *Podisus nigrispinus* females fed *Tenebrio molitor* pupae and supplemented or not (0%) with gossypol in different concentrations during the adult stage (a) or continually in the nymphal and adult stages (A). Different letters in B stand for pairwise comparisons of the survival curves for concentrations by Log Rank Test at 0.05% level of significance. Values between parentheses stand for means of longevity \pm standard error.

The lowest fecundity and egg viability results for *P. nigrispinus* females reared continuously supplemented with gossypol at 0.2% confirms the hypothesis that this compound offers resistance against herbivores through reducing digestibility and has potential to affect a predator ingesting it. Thus, the accumulative effect reduces development of insects and, consequently, reproduction (Elsebae *et al.* 1981). However, the similar fecundity and egg hatching for females of this predator exposed to gossypol only in the adult stage indicate a negative effect of this compound only if ingested during the nymphal stage. The direct relation between lower fecundity (Fig. 2A) and higher survival (Fig. 3B) for females continuously exposed to 0.2% of gossypol indicates an effect of this compound at higher concentration through phagodeterrence (Meisner *et al.* 1977). In addition, the prey ingested results in lower assimilation of food. The use of prey might have been lower, because this compound affects the digestibility, resulting in a situation of reduced food assimilation (Meisner *et al.* 1977; Legaspi & O'Neil 1994). The trade-off between higher survival and lower fecundity is a common finding for *P. nigrispinus* (Molina-Rugama *et al.* 1997; Oliveira *et al.* 2002), and for other predators under prey scarcity (Torres *et al.* 2004). Gossypol at the higher concentrations might reduce food absorption thereby limiting nutrients and causes the predator to relocate energy from reproduction to survival.

Gossypol reduced the development and, hence, delayed the period for *P. nigrispinus* to complete its nymphal stage and reproduction, but with minimum or no effect on survival. This result is typical of digestibility reducers on Asopinae predators (Ashouri *et al.* 1998; Bell *et al.* 2003). Digestibility reducing compounds usually cause sublethal effects by interferring with the development and reproduction of these organisms, similar to what was found for the development and reproduction of *P. nigrispinus*.

The adverse effects found on the development of P. nigrispinus nymphs characterize impact of continuous ingestion of gossypol. Conversely, the indirect exposure of this predator through the prey Alabama argillacea (Hüebner) (Lepidoptera, Noctuidae) reared on cotton cultivar with high levels of gossypol, demonstrated the absence of the effect on this predator (Santos & Boica-Junior 2002). Furthermore, caging P. nigrispinus on the cotton genotype "XG 15" producing high levels of gossypol showed no negative effect on the predator development and reproduction (W.S.E. Jr. unpublished data). Thus, despite the sublethal effect of gossypol on this zoophytophagous insect as evidenced in this study, the negative interaction of cotton varieties expressing gossypol can be minimized by the plant feeding habit of P. nigrispinus. This predator feeds on apoplastic spaces and xylem structures of the plant and, likely, avoinding the gossypol producing glands (Torres et al. 2010). The adverse effects of gossypol on development and reproduction of P. nigrispinus found in this study characterize the worst possible scenario of contamination. In the field, feeding on prey or directly on the plant, P. nigrispinus is likely to be exposed to negligible concentrations of gossypol. This agrees with the results found in this study when offering gossypol at lower concentrations or when the predators were exposed to the gossypol only during the adult stage only.

Resistance of cotton plants based on gossypol levels is promising against generalist herbivore species, but do not provide a full control (Stipanovic *et al.* 2006). Furthermore, specialized cotton pest species as the leaf feeding caterpillars are not affected by the level of gossypol naturally produced in commercial cotton due to co-evolvotion with the host plant defense (Nishida 2002). Therefore, the additional mortality caused by natural enemies such as *P. nigrispinus* are important within the pest management approach of cotton pests.

ACKNOWLEDGEMENTS

This research was sponsored by CAPES, CNPq, and FACEPE.

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Received 1/9/2010; accepted 18/4/2011 Editor: Sonia Maria Noemberg Lázzari

Revista Brasileira de Entomologia 55(2): 267-271, junho, 2011