Bulletin of Insectology ***69*** *(2): 271-276, 2016*
ISSN 1721-8861

Geocoris punctipes nymphs and adults easily prey on leaf-mining larvae of *Tuta absoluta* on tomato

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Abstract

The tomato borer *Tuta absoluta* (Meyrick) is quickly developing into a serious, worldwide pest of tomato. Its larvae penetrate to the mesophyll, resulting in mines in the leaves. Larvae also can attack the stem and fruits, and, thus, tomato yields can be completely lost if no control methods are used. Rapid development of resistance to frequently applied pesticides necessitates a search for alternative control methods, such as biological control. Here we present quantitative results of predation of larvae of *T. absoluta* by nymphs and adults of *Geocoris punctipes* (Say). All five nymphal instars of the predator *G. punctipes* detect, attack and consume 1st larval instars of *T. absoluta*. The 1st nymphal instar of the predator consumes on average 4 prey larvae, while the 5th nymphal instar consumes more than 10 prey larvae per day. Male and female adult predators are able to detect and attack all four larval instars of the pest, and on average 2 (4th larval instar) to 13 (1st larval instar) can be attacked per day. Females kill more prey than males. These predation results are promising, because they show that *G. punctipes* nymphs and adults consume large numbers of larvae and can contribute to a considerable reduction of larval pest populations Thus, this predator might be a potential candidate for augmentative biological control of *T. absoluta*.

Key words: generalist predator, predation rate, augmentative biological control, tomato borer.

Introduction

The tomato borer *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), native to South America, invaded Europe in 2006, followed by Africa, the Near East and Middle East, and Asia (EPPO, 2015). It causes major damage to tomato crops wherever it occurs (Guedes and Picanço, 2012; Tropea *et al.*, 2012). Currently, *T. absoluta* is present in more than 65 countries throughout Central and South America, Africa, Europe and Asia (CABI, 2015). In Brazil this pest has been a problem since its introduction in the 1980s (Guedes and Picanço, 2012).

After hatching from an egg, a *T. absoluta* larva scrapes a leaf surface for 20-30 minutes with its mouth parts before entering the mesophyll; to fully penetrate the leaf takes an hour or more (Coelho and França, 1987; Cuthbertson *et al.*, 2013). The four larval instars usually feed on the leaf and develop in leaf mines between the upper and lower epidermis, but they may also be found inside tomato fruit and stems (Cuthbertson *et al.*, 2013). Once larvae have entered the mesophyll, applications of insecticides are relatively ineffective, and larvae can only be controlled by frequent applications of insecticides (Guedes and Picanço, 2012), resulting in resistance of the pest to different active ingredients (Siqueira *et al.*, 2000) and in severe population reductions of its natural enemies (Bueno *et al.*, 2013).

Both in Latin America and in Europe, many natural enemies of *T. absoluta* have been found, and some of these have been evaluated for augmentative biological control (e.g. van Lenteren, 2012; Bueno *et al.*, 2013; Zappala *et al.*, 2013 for recent overviews). In Europe, the mirid predator *Nesidiocoris tenuis* (Reuter), which was already used for control of several pests in greenhouses, appeared also to efficiently reduce *T. absoluta* (e.g. Calvo *et al.*, 2012a; 2012b). Several egg and larval parasitoids were found in Latin America: *Trichogramma pretiosum* Riley (Hymenoptera Trichogrammatidae) (Garcia Roa, 1989; Haji *et al.*, 2002; Parra and Zucchi, 2004; Parra and Consoli, 2009), *Pseudoapanteles dignus* Muesebeck (Hymenoptera Braconidae), *Dineulophus phythorimaeae* De Santis (Hymenoptera Eulophidae) (Sanches *et al.*, 2009; Luna *et al.*, 2010), and *Apanteles gelechiidivoris* Marsh (Hymenoptera Braconidae) (Bajonero *et al.*, 2008). However, even if these parasitoids are capable of controlling *T. absoluta*, various other pests (other lepidopterans, whiteflies, aphids, thrips, dipteran leaf miners and mites) still need to be controlled by pesticides, which will interfere with the use of parasitoids. This made us decide to study generalist predators that might be used in augmentative biological control programmes against co-occurring pest species, resulting in strongly reduced or no pesticide use. We have previously reported the first promising results obtained with three mirid predators, *Macrolophus basicornis* (Stal), *Engytatus varians* (Distant) and *Campyloneuropsis infumatus* (Carvalho) (Hemiptera Miridae), which appear to be able to establish populations on tomato and consume large numbers of *T. absoluta* eggs (Bueno *et al.*, 2013). We are currently comparing the biology and predation capacity of these three mirids, and two other native Brazilian generalist species of heteropteran predators present on tomato infested with *T. absoluta*: *Orius insidiosus* (Say) (Hemiptera Anthocoridae) and *Geocoris punctipes* (Say) (Hemiptera Geocoridae).

Our first results with adults of *G. punctipes* were not very favourable as they showed very poor predation of *T. absoluta* eggs (0.5 eggs per day), while other heteropteran predators we tested showed egg predation rates of up to 100 eggs per day (Bueno *et al*., 2013). However, *G. punctipes* is also reported to attack larvae of *T. absoluta*, *Helicoverpa armigera* (Hubner), *Helicoverpa* (=*Heliothis*) *zea* (Boddie) and *Heliothis virescens* (F.) (Lepidoptera Noctuidae), nymphs of *Bemisia tabaci* (Gennadius) (Hemiptera Aleyrodidae), *Aphis gossypii* Glover, *Myzus persicae* (Sulzer) (Hemiptera Aphididae) and *Frankliniella occidentalis* (Pergande) (Thysanoptera Thripidae) (Lingren *et al*., 1968; Joseph and Braman, 2009; Oida and Kadono, 2012; Rondon *et al*., 2004; Torres *et al*., 2004; Velasco-Hernández *et al*., 2013). Only limited quantitative data exist for predation by *G. punctipes* (Chiravathanapong and Pitre, 1980; Cohen and Byrne, 1992), and as information about daily predation of *T. absoluta* larvae by this predator is not yet available, we decided to study this topic.

The aim of this study was to evaluate whether all nymphal stages and adults of *G. punctipes* are able to detect and prey on *T. absoluta* larvae, and to quantify this predation. Together with life history data, which we are also collecting, these predation data of *G. punctipes* will allow us to determine the daily prey kill rate of the predator (Tommasini *et al*., 2004), which is a helpful characteristic to compare predation capacity of various candidates that are currently evaluated for control of *T. absoluta*.

Materials and methods

Insect rearing

Adult *G. punctipes* were collected on pigweed plants (*Amaranthus viridis* L.) in a field of the municipality of Lavras, Minas Gerais, Brazil, located at 21°14'S 45°00'W and 918 m altitude. They were placed in glass jars (1.7 l) containing shredded paper towel, pigweed inflorescences placed in a glass tube (10 ml) with water, and eggs of *Ephestia kuehniella* (Zeller) (Lepidoptera Pyralidae) as food. Paper towel and pigweed inflorescences are used as oviposition substrate by *G. punctipes*. Twice a week, the oviposition substrates were transferred to Petri dishes (20 cm diameter) containing moistened cotton and eggs of *E. kuehniella.* Daily, newly-emerged adults were removed from the Petri dishes and placed in glass jars (1.7 l) at a density of 50 individuals/jar. This procedure provided a maintenance rearing of *G. punctipes*, based on the one previously described by Bueno *et al*. (2006) for *O. insidiosus*. The rearing was kept at 25 ± 2 °C, RH 70 ± 10% and 14L:10D photoperiod. The nymphal instars and adults of *G. punctipes* used in the experiments were obtained from this maintenance rearing. To obtain newly emerged nymphs of a certain instar, the oviposition substrate containing eggs was placed in a Petri dish (20 cm diameter) and observed daily until they developed to the right instar (Calixto *et al*., 2014). Nymphal instars can be distinguished by the presence of exuviae resulting from moulting and on the basis of certain distinct characteristics like size and colour as described by Sweet and Slater (1961) and Herring and Ashlock (1971). Male and female adults can be distinguished by their genitals and the size of the abdomen (Calixto *et al*., 2014).

Eggs, larvae and pupae of *T. absoluta* were both collected in tomato crops on the campus of the Federal University of Lavras (UFLA) and in commercial tomato fields. After *T. absoluta* adults emerged, a rearing colony was started on potted tomato plants (cv Santa Clara) kept in an acrylic cage (150 × 150 × 180 cm) maintained inside a climate room at 25 ± 2 °C, RH 70 ± 10% and 12L:12D photoperiod. In order to obtain larvae of the four different instars of *T. absoluta*, we carefully opened the mines, took out the larvae and placed them in a Petri dish and measured their cephalic capsules under a stereomicroscope with a graduated ocular scale (10 mm/100). Based on the size of the cephalic capsules, the larval stages can be determined with the information provided in Bogorni and Carvalho (2006).

Predation rate of *Geocoris punctipes*

Nymphs and adult predators were starved for 24 h in a tube (8 cm × 5 cm) with moistened cotton before the experiment.

The predation rates of each nymphal instar of the predator were determined on 1st instar larvae of the prey. A tomato leaflet was inserted into an Eppendorf tube (2 ml) filled with distilled water and kept in a Petri dish (9 cm diameter) closed by a transparent acrylic cup (6.5 cm, 8 cm in diameter). Twenty 1st instar *T. absoluta* larvae were put on the tomato leaflet two hours before the nymphs of *G. punctipes* were introduced. This time period was enough for most of the 1st larvae instar to fully penetrate into the leaf. Next, a nymph of *G. punctipes* was introduced in the Petri dish for 24 h, after which the number of *T. absoluta* larvae eaten, characterized by their dead, transparent and shrivelled bodies, was recorded.

To determine the predation rates of adult predators, two-day-old males or females were individually released for 24 h in a Petri dish containing either 5, 10 or 20 *T. absoluta* larvae of one of the four instars. After 24 h the number of larvae eaten was recorded.

Ten nymphs of each instar, and twenty adult males and females of *G. punctipes* were tested. As control we determined prey mortality in the absence of predators on the same tomato cultivar: twenty replicates, each with 20 prey larvae, were checked daily until pupation.

Data analysis

Numbers of *T. absoluta* larvae consumed by *G. punctipes* were found to be normally distributed (Shapiro-Wilk test, $P \geq 0.05$), so the untransformed predation data could be subjected to a One-way analysis of variance (ANOVA) and a Tukey test at 5%. Numbers of larvae consumed by the adults were subjected to a Two-way analysis of variance (ANOVA) and a Tukey test at 5% (Sigmaplot 11.0, Systat Software Inc.) with *T. absoluta* larval instar and sex of the predator as factors.

Results

Mortality of *T. absoluta* larvae on tomato CV Santa Clara in the absence of predators was very low. All 400 1st instar larvae developed into second instar larvae. Two 2nd instar larvae, four 3rd instar larvae and two 4th instar larvae died during the control experiment, resulting in 97.5% larval survival.

Predation rates of *G. punctipes* nymphs on 1st instar *T. absoluta* larvae were similar for the 2nd and 3rd nymphal instars, but significantly different between 1st, 2nd + 3rd, 4th and 5th nymphal instars ($F_{4,45} = 0.216$; $P < 0.001$). The 5th instar consumed significantly more prey than the other instars, and the 1st instar consumed significantly less. Predation increased with nymphal instars from about 4 prey per 1st nymphal instar to about 11 prey per 5th nymphal instar per 24 h, though predation by the 4th instar was somewhat, but significantly lower than that of the 2nd, 3rd and 5th instar (figure 1).

The predation rates of males and females were similar at a prey density of 5 *T. absoluta* larvae per dish at a prey density of 5 larvae per dish, predator adults consumed more 1st and 2nd larval instars than 3rd and 4th larval instars of the prey ($F_{3,152} = 2.30$; $P < 0.001$; figure 2A). At a prey density of 10 larvae per dish, females consumed significantly more 1st larval instars than males did ($F_{3,152} = 3.78$; $P = 0.023$), but the predation rate on 2nd, 3rd and 4th larval instars was similar for females and males (figure 2B). The predation rate was inversely correlated with prey size. At a prey density of 20 larvae per dish, females consumed significantly more 1st, 2nd and 3rd larval instars than males did ($F_{3,152} = 7.42$; $P = 0.023$), but predation rates were similar when 4th larval instars were offered (figure 2C); the predation rate again was inversely correlated with larval size ($F_{3,152} = 5.18$; $P < 0.001$)

The number of prey consumed was positively correlated with prey density, and this effect was stronger for the smaller prey larvae than for the older ones.

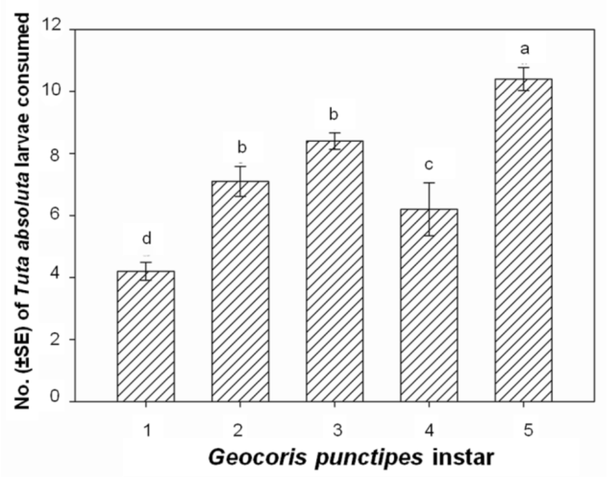

Figure 1. Number (± SE) of 1st instar larvae of *T. absoluta* consumed by nymphs of each instar of *G. punctipes*. Different letters indicate a significant difference in predation rate for the different instars of the predator (Tukey test; P < 0.05).

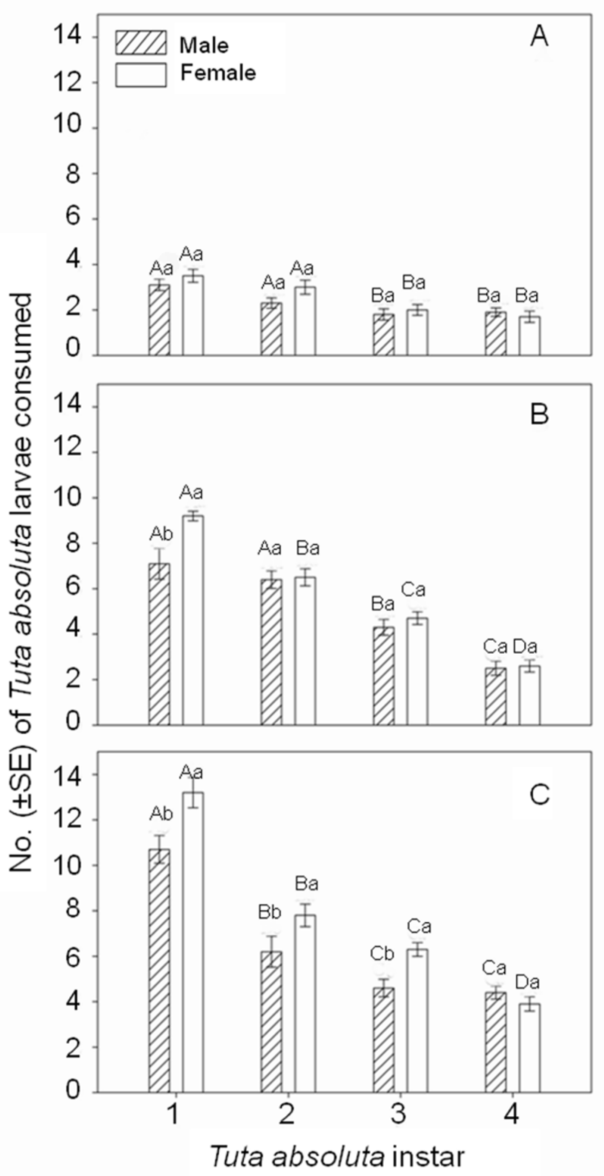

Figure 2. Number (± SE) of larvae of *T. absoluta* consumed by male and female adults of *G. punctipes* at three prey densities (A- 5 prey; B- 10 prey; C- 20 prey per dish). Different capital letters indicate a significant difference in predation rate between prey densities for the same larval instar; different lower case letters indicate a significant difference in predation rate between sexes at the same prey density (Tukey test; P < 0.05).

Discussion

Predation capacities of generalist insect predators such as *G. punctipes* have important consequences for predator-prey dynamics. We found that *G. punctipes* nymphs and adults successfully detected and consumed larvae of the tomato borer, *T. absoluta*. All five nymphal instars of *G. punctipes* were able to consume 1st instar *T. absoluta* larvae in the leaf mines. The predation rates were similar to those reported for *G. punctipes* nymphs preying on *Spodoptera frugiperda* (J. E. Smith) larvae (Lepidoptera Noctuidae) (Joseph and Braman, 2009), but lower than values found on *H. virescens* 1st instar larvae (Chiravathanapong and Pitre, 1980). Interestingly, Lawrence and Watson (1979) found that 1st instar nymphs of *G. punctipes* are primarily egg predators when exposed to eggs and larvae of *H. virescens*, but that the older nymphal stages consume both eggs and larvae.

The relatively low predation rate of the 1st nymphal instar of the predator may be due to the large prey size relative to the size of this instar, which has an impact on successful attack by generalist predators (Lafferty and Kuris, 2002). In older and larger nymphal stages, predation rates increase, while the highest rates were obtained by adult *G. punctipes*. Morphological characteristics of 1st instar nymphs of *G. punctipes*, such as a shorter rostrum than in older nymphs (Jaworski *et al*., 2013), may also help explain their low predation of *T. absoluta* larvae, as the young nymphs might not be able to reach *T. absoluta* larvae hidden inside mines in tomato leaves. A third explanation for the low predation rates might be satiation of the small nymphs. Behavioural observations are needed to determine which of the three explanations (difficulty in reaching prey larvae, lower attack success or satiation) plays the main role. The predation rate of the 4th nymphal stage was significantly lower than that of the 2nd, 3rd and 5th nymphal stage and we have no obvious explanation for this.

Adult predators are able to successfully consume all larval instars of *T. absoluta*. At the lowest prey density of 5 larvae per dish, female and male predation rates were equal. A similar result was reported by Urbaneja *et al*. (2009), when *T. absoluta* larvae were offered to the mirid predators *M. pygmaeus* and *N. tenuis*. However, in our study, *G. punctipes* females consumed significantly more larvae than males at the highest prey density of 20 larvae of *T. absoluta*. Female *G. punctipes* also consumed more larvae than males when *S. frugiperda* larvae were offered as prey (Joseph and Braman, 2009). Higher predation rates by females are not unexpected, because females have higher nutritional requirements than males, due to ovigenesis. Larval predation by adults decreased when older larvae of *T. absoluta* were offered, which is not surprising as older larvae offer a larger amount of food per prey item to the predator. Urbaneja *et al*. (2009) found similar results when offering *T. absoluta* larvae to *M. pygmaeus* and *N. tenuis*, though the number of *T. absoluta* larvae consumed by *G. punctipes* in our study was higher than the numbers attacked by the mirid predators (Urbaneja *et al*., 2009).

Our findings that *G. punctipes* nymphs are able to detect and to prey on 1st instar *T. absoluta* larvae and that adults of this predator are also able to detect and consume even the largest larvae of *T. absoluta*, suggest that this predator could play a role in controlling this pest in augmentative biological control programmes. *T. absoluta* is most susceptible to control strategies in the egg stage and when the larvae have not yet entered the mesophyll (Cuthbertson *et al*., 2013), and our research shows that all predatory stages of *G. punctipes* consume significant numbers of 1st instar prey larvae. Thus, *G. punctipes* can contribute to an early reduction of pest populations on tomato in South America when released around the egg laying period of *T. absoluta* and in combination with another predator [e.g. one of the following mirids: *M. basicornis*, *E. varians* and *C infumatus* (Bueno *et al*., 2013)] or a parasitoid [e.g *Trichogramma pretiosum* (Riley) (Haji *et al*., 2002)] which consume and parasitize large numbers of eggs. In addition, *G. punctipes* is able to kill considerable amounts of older larvae of the prey present in the leaf mines, thus further contributing to pest reduction.

Mass reared *G. punctipes* have been successfully applied in inoculative releases in cotton crops (Lingren *et al*., 1968) and in open field strawberries in the USA to obtain early establishment of predator populations in young crops (Wood, 1998). As in other zoophytophagous predators, *G. punctipes* feeds on plants to obtain additional resources (Bueno and van Lenteren, 2012). Torres *et al*. (2010) suggest that this phytophagous behaviour increases the possibility of this predator surviving in the field when prey items are scarce. The above mentioned earlier successes obtained with *G. punctipes* and its phytophagous behaviour are both positive indicators for its use in augmentative biological control of *T. absoluta*.

The current predation data about larval consumption will be used together with previously obtained egg predation data of adults and data on egg predation by nymphs which we still need to determine, to estimate the daily prey kill rate of *G. punctipes* (Tommasini *et al*., 2004). The following step in our research will be to compare the daily kill rates of the five species of predators of *T. absoluta*, in order to speculate which species might be the most promising natural enemy for practical use. Next, we will test the predators in experimental greenhouses with a *T. absoluta* infested tomato crop, similar to what Calvo *et al*. (2012b; 2016) have done for European and Mexican mirid predators. Finally, the best performing species will be tested at commercial tomato production situations in greenhouses and open field.

Acknowledgements

We thank Russell Messing (University of Hawaii, USA) for improving the manuscript, the Coordination for the Improvement of Higher Education Personnel (CAPES), the National Council for Scientific and Technology Research (CNPq) and the Foundation for Support of Research of Minas Gerais (FAPEMIG) for financial support.

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Received March 12, 2016. Accepted June 14, 2016.