RESEARCH REPORT

Antibiosis of tomato, *Solanum lycopersicum* (Solanaceae) plants to the Asopinae predator *Supputius cincticeps* (Heteroptera: Pentatomidae)

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Abstract

Plant feeding can improve development and reproduction of the stink bug *Supputius cincticeps* (Heteroptera: Pentatomidae), an important biological control agent in South American agro-forestry ecosystems. However, defensive compounds of plants may negatively impact this predator. The development, reproduction and survival of *S. cincticeps* fed on mealworm, *Tenebrio molitor* (Coleoptera: Tenebrionidae) pupae with bean (Fabaceae), cotton (Malvaceae), eucalyptus (Myrtaceae), soybean (Fabaceae), or tomato (Solanaceae) leaves were evaluated. Females and males were heavier and the number of nymphs produced per female, the oviposition period and the longevity of females of this predator were higher when fed on eucalyptus, soybean, bean, and cotton than with tomato leaves. Leaves of those plants improved biological parameters of *S. cincticeps*, while tomato leaves showed antibiosis with lower reproduction and survival of *S. cincticeps*, probably due to toxic compounds.

Key Words: antagonistic association; defense; development; natural enemy; reproduction

Introduction

Zoophytophagous stink bugs of the subfamily Asopinae, such as *Supputius cincticeps* (Heteroptera: Pentatomidae) are considered important biological control agents of numerous pests in South American agro-forestry ecosystems (Zanuncio *et al*., 2005, 2012, 2014). However, populations of Asopinae predators often only reach significant levels after pest population peaks (Münster-Swendsen and Berryman, 2005; Neves *et al*., 2009; De Menezes *et al*., 2013), especially in short cycle crops under conditions of intensive management, such as cotton (*Gossypium hirsutum*, Malvaceae), soybean (*Glycine max*, Fabaceae) and tomato (*Solanum lycopersicum*, Solanaceae) (Vivan *et al*., 2002; Malaquias *et al*., 2010; Zanuncio *et al*.,2012). The absence of suitable prey (particularly Lepidoptera) at the early crop stages could partially explain the asynchrony between population dynamics of pests and Asopinae predators (Júnior *et al*., 2004; Coelho *et al*., 2009). Furthermore, leaf hairs and plant secondary metabolites can affect the establishment and development not only of pests but also of the Asopinae predators (Holtz *et al*., 2006).

Predatory stink bugs are considered zoophytophagous or phytozoophagous depending on the importance of prey or plant for their development and reproduction (Coll and Guershon, 2002; Lemos *et al*., 2009a). Plant and animal food sources provide apparently amino acids and other nutrients to predators which cannot be obtained from each of the two food sources alone (Eubanks and Denno, 1999; Freitas *et al*., 2006). Reproductive and biological characteristics of predators can be positively affected by plant feeding (Eubanks and Denno, 2000; Robinson *et al*., 2008; Paleari, 2013), but plant secondary compounds can

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Table 1 Effect of feeding of different plants and *Tenebrio molitor* pupae on the duration (mean ± standard error) (days) of different nymphal stages of *Supputius cincticeps*

Instar	Treatments				
	Bean	Cotton	Eucalyptus	Soybean	Tomato
I	4.00 ± 0.00 a	4.00 ± 0.00 a	4.00 ± 0.00 a	4.00 ± 0.00 a	4.00 ± 0.00 a
II	4.94 ± 0.22 b	5.34 ± 0.16 a	3.40 ± 0.12 c	4.79 ± 0.14 b	5.49 ± 0.17 a
III	4.27 ± 0.17 b	5.10 ± 0.17 a	3.93 ± 0.08 b	4.10 ± 0.10 b	4.87 ± 0.12 a
IV	4.53 ± 0.09 a	4.72 ± 0.09 a	4.70 ± 0.13 a	4.19 ± 0.12 a	4.91 ± 0.58 a
V	6.35 ± 0.09 a	6.82 ± 0.16 a	6.39 ± 0.11 a	6.19 ± 0.15 a	6.77 ± 0.74 a
Total	24.09 ± 0.30 b	25.98 ± 0.34 a	22.43 ± 0.22 b	23.26 ± 0.35 b	26.05 ± 1.28 a

Ns = Not significant; Means (± standard error) followed by the same letter in a row are not significantly different by the Scott-Knott's test at 5 %. Number of insects = 375.

also have negative effects on natural enemies (De Clercq *et al*., 2000; Holtz *et al*., 2010). Phytophagy is commonly beneficial to Asopinae predators (Holtz *et al*., 2009; Lemos *et al*., 2009b; Malaquias *et al*., 2010), mainly during prey shortages (Perdikis *et al*., 2007; Holtz *et al*., 2009, 2010) or during periods of low nutritional prey (Vivan *et al*., 2003; Lemos *et al*., 2009b), and it has been shown to reduce cannibalism (Laycock *et al*., 2006; Leon-Beck and Coll, 2007; Frank *et al*., 2010).

The zoophytophagous predator *S. cincticeps* occurs on bean (*Phaseolus vulgaris*, Fabaceae), cotton and soybean crops in Brazil (Zanuncio *et al*., 2003, 2012; de Castro *et al*., 2013a) preying mainly on species of Diptera, Coleoptera, Hemiptera, and Lepidoptera (Zanuncio *et al*., 2005; Lemos *et al*., 2009b; da Silva *et al*., 2012). Presence of this stink bug can reduce insecticide sprays (Zanuncio *et al*., 1998, 2003; Tavares et al., 2009) and it seems to be compatible with certain products (Zanuncio *et al*., 2013; de Castro *et al*., 2013a; Malaquias *et al*., 2014). Development and reproduction parameters of *S. cincticeps* are highest when fed on a diet composed of both, plant and prey, although negative effects have been observed when feeding on certain plant species (Zanuncio *et al*., 2004, 2005; Lemos *et al*., 2009b).

Therefore, this study aimed to investigate the effects of different food plants on *S. cincticeps* by comparing biological aspects of the predator when fed on mealworm, *Tenebrio molitor* (Coleoptera: Tenebrionidae) pupae combined with bean, cotton, eucalyptus (*Eucalyptus cloeziana*, Myrtaceae), soybean, or tomato leaves.

Material and Methods

Seeds

Seeds of bean variety majestoso, eucalyptus, soybean variety UFV 16, and tomato variety Santa Clara were obtained from the Federal University of Viçosa (UFV) in Viçosa, Minas Gerais State, Brazil and those of cotton variety BRS aroeira from the germplasm bank of the Brazilian Agricultural Research Corporation (EMBRAPA Algodão) in Campina Grande, Paraíba State, Brazil. Plant species were chosen due to their economic importance for grain, fruit, wood production, and their numerous potential pest species, mainly caterpillars, which can be preyed by *S. cincticeps* (Zanuncio *et al*., 2004; Lemos *et al*., 2009b). Plants were grown in 500 mL plastic pots with a mixture of soil and humus from earthworms, *Eisenia fetida* (Haplotaxida: Lumbricidae) and *Eudrilus eugeniae* (Haplotaxida: Eudrilidae) in 4:1 ratio. Plants were cultivated in a greenhouse, watered as needed and pests controlled manually. No chemical fertilizers were applied.

Supputius cincticeps

Nymphs of *S. cincticeps* were obtained from the mass rearing of the Laboratory of Biological Control of Insects (LCBI) of the Institute of Biotechnology Applied to Agriculture (BIOAGRO) at the UFV.

Experiments

All experiments were conducted at 25 ± 2 °C, 60 ± 10 % relative humidity and a 12:12 light:dark photoperiod in a Biochemical Oxygen Demand (BOD). Seventy-five early second instar nymphs of *S. cincticeps* were transferred to 15 plastic pots (500 mL) (five nymphs per pot) per treatment. Two pupae of *T. molitor* were introduced per pot three to four times a week. Two cylindrical tubes (2.5 mL), one with distilled water and one with leaves of different plants, were inserted in the pots through the cover. Plants were replaced after loss of turgidity. Nymphs were fed on one of the following diets: T1 (bean leaves + *T. molitor* + water), T2 (cotton leaves + *T. molitor* + water), T3 (eucalyptus

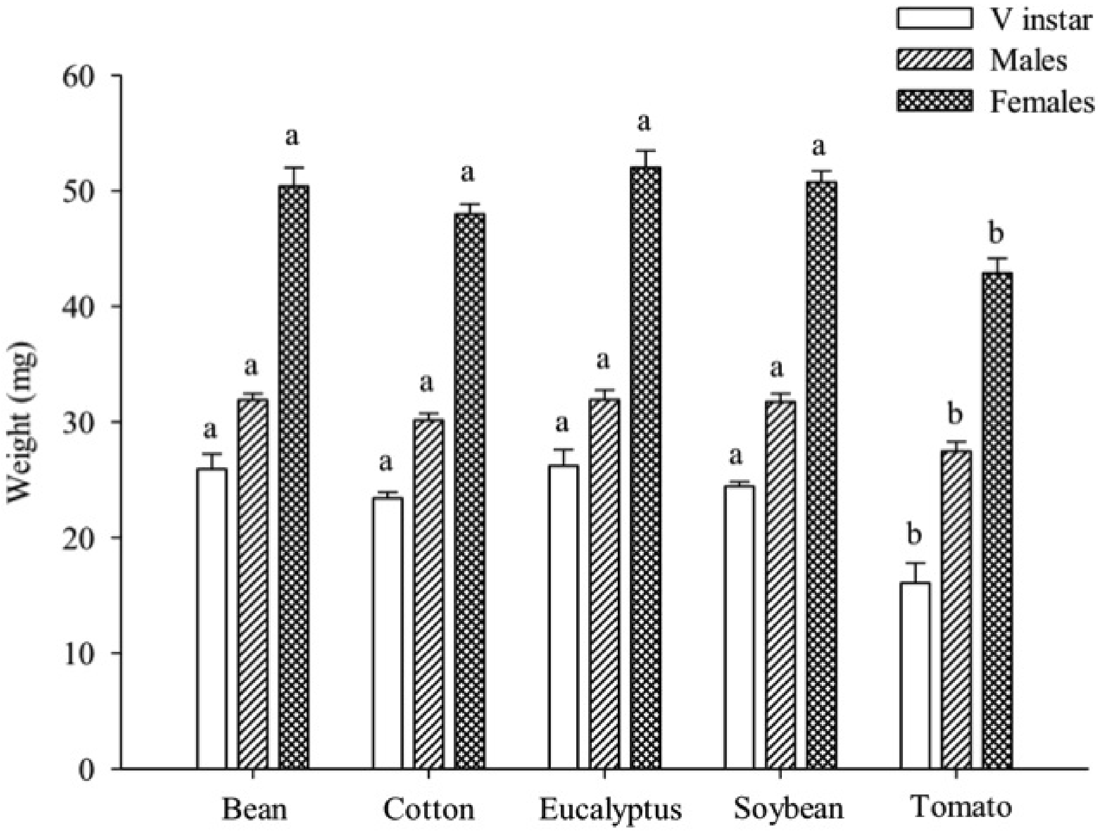

Fig. 1 Effect of feeding of different plants and *Tenebrio molitor* pupae on the weight (mg) of fifth instar nymphs and adults of *Supputius cincticeps*. Bars with the same letters do not differ significantly by the Scott-Knott's test at 5 %. Comparison was made within the same developmental stage feeding on different plants. Number of insects = 210.

leaves + *T. molitor* + water), T4 (soybean leaves + *T. molitor* + water), and T5 (tomato leaves + *T. molitor* + water). Adults of *S. cincticeps* were sexed by the appearance of the external genitalia (De Castro *et al*., 2013b) and weighed after emergence (< 24 h). Duration (days) and survival per instar (%) and of the total nymph stage (%), weight of fifth instar nymphs (mg) and of male and female adults (mg) were recorded. Three days after emergence, adults of *S. cincticeps* were mated placing each one couple into one plastic container (twenty pairs per treatment) (Zanuncio *et al*., 2004). Couples of *S. cincticeps* received water daily and two *T. molitor* pupae three to four times a week. Adults were fed on the same combinations of *T. molitor* as prey and plant species as nymphs. Males of *S. cincticeps*, which died during the experiment, were replaced by others of similar age and reared with the same conditions and treatments. Egg masses of *S. cincticeps* were collected daily and placed in Petri dishes with a moistened cotton ball and the nymphs counted 48 h after hatching. The number of eggs and nymphs per female and egg mass, respectively, and of egg masses; period of pre-oviposition, oviposition and post-oviposition, and of incubation (days); female longevity (days), and egg viability (%) of *S. cincticeps* were measured.

Statistics

The experimental design was completely randomized (CRD). The data were submitted to univariate variance analysis (ANOVA) and the means compared with the Scott-Knott post hoc test at 5 % probability using the software SAS version 9.0 (Statistical Analysis System, 2002) (Supplier: UFV). Homogeneity of variance and normality of errors were checked using Q-Q plots (Wilk and Gnanadesikan, 1968) and data were transformed when necessary.

Results

Supputius cincticeps fed on a mealworm pupae diet supplemented with leaf material of different plant species showed marked difference in their life history parameters according to the plant species.

The duration of the total *S. cincticeps* nymph stage was significantly influenced by the plant food source (Table 1). It was shorter with eucalyptus, soybean or bean leaves than with cotton or tomato leaves (Table 1). Duration of the first, fourth and fifth nymph instars were unaffected by the diet, whereas the second instar was significantly shorter on eucalyptus leaves compared to the other plant food sources (Table 1). The third instar was significantly

Table 2 Effect of feeding of different plants and *Tenebrio molitor* pupae on the survival (mean ± standard error) (days) of different nymphal stages of *Supputius cincticeps*

Instar	Treatments				
	Bean	Cotton	Eucalyptus	Soybean	Tomato
II	85.33 ± 3.63 a	86.67 ± 5.11 a	93.33 ± 3.19 a	92.00 ± 3.27 a	66.67 ± 5.40 b
III	80.00 ± 3.38 a	78.67 ± 4.56 a	88.00 ± 4.28 a	86.67 ± 5.04 a	62.67 ± 4.31 b
IV	73.33 ± 4.22 a	68.00 ± 5.79 a	82.66 ± 5.11 a	82.67 ± 5.12 a	51.33 ± 4.87 b
V	70.67 ± 3.84 a	65.33 ± 6.01 a	80.00 ± 5.16 a	76.00 ± 5.59 a	44.67 ± 4.24 b
Total	70.66 ± 3.83 a	65.33 ± 6.00 a	82.67 ± 4.31 a	76.00 ± 5.58 a	44.66 ± 4.23 b

Means (± standard error) followed by the same letter in a row are not significantly different by the Scott-Knott's test at 5 %.

prolonged with cotton or tomato leaves as food source (Table 1).

Weight of *S. cincticeps* was also significantly affected by the plant species fed (Fig. 1). Fifth instar nymphs were significantly lighter when fed with tomato leaves, compared to all other plants. This effect was visible in both sexes (Fig. 1).

Overall survival of *S. cincticeps* nymphs, as well as stage-specific survival of second, third, fourth, and fifth instar nymphs was influenced by the plant species fed (Table 2). Survival was significantly higher with eucalyptus, soybean, bean, or cotton than with tomato leaves (Table 2).

The longevity of *S. cincticeps* females was significantly longer with eucalyptus, soybean, bean, and cotton leaves than with tomato leaves (Table 3). While the total number of eggs per female and egg mass and the number of egg masses were similar among treatments (Fig. 2), the pre-oviposition period of *S. cincticeps* was significantly longer with tomato leaves and the oviposition period significantly shorter. The post-oviposition period was similar between treatments (Table 3).

The number of emerging nymphs per egg mass was significantly higher with eucalyptus or cotton leaves than with soybean, bean or tomato leaves (Table 3). Egg viability of *S. cincticeps* was significantly lower with tomato leaves and higher with eucalyptus leaves, while the incubation period was similar between treatments (Table 3). The number of surviving nymphs per female was significantly higher with eucalyptus, soybean, bean, or cotton leaves than with tomato leaves (Table 3).

Discussion

In the present study we could show that almost all life history characteristics of *S. cincticeps* were negatively affected when they were fed with tomato leaves, and some parameters were also inferior when the nymphs fed on cotton leaves compared to the other plant food sources. These differences could result from differences in food accessibility, the content of secondary plant defense compounds and/or differences in nutritional quality of these plants (Júnior *et al*., 2004; Holtz *et al*., 2009; Malaquias *et al*., 2010).

Morphological and chemical properties of plants may influence their attractiveness for herbivores as well as the biological characteristics of herbivores (Agrawal, 2000; Hagenbucher *et al*., 2013; Eaton and Karban, 2014) and Asopinae predators (Hilker and Meiners, 2002; Degenhardt *et al*., 2003). While Asopinae predators often benefit from additional plant feeding by enhanced growth and reproduction (Holtz *et al*., 2009; Lemos *et al*., 2009b; Malaquias *et al*., 2010), morphological characteristics, *e.g.,* trichomes and chemical characteristics, such as secondary plant compounds, may have negative effects on the predator. Thereby influences on the life cycle may vary among plant species, as well as among stink bug species feeding on the same plant (Júnior *et al*., 2004; Lemos *et al*., 2009b; Malaquias *et al*., 2010).

Similar studies have reported shortened durations of the nymph stage and higher fecundity of *P. nigrispinus* fed on cotton or whiteweed, *Ageratum conyzoides* (Asteraceae) without prey (Júnior *et al*., 2004); fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on cotton cultivars (de Jesus *et al*., 2014), and cotton leafworm, *Alabama argillacea* (Lepidoptera: Noctuidae) with cotton or fennel, *Foeniculum vulgare* (Apiaceae) (Malaquias *et al*., 2014). However, the longer duration of the second and third instar, and of the total nymph stage as well as reduced longevity of *S. cincticeps* with cotton or tomato leaves in our study suggest negative effects, as were found for the longer duration of the nymph stage of *Brontocoris tabidus* (Heteroptera: Pentatomidade) with cotton (Coelho *et al*., 2009; Torres *et al*., 2010). Like tomato plants, cotton

Table 3 Effect of feeding of different plants and *Tenebrio molitor* pupae on the reproductive parameters and longevity of *Supputius cincticeps*

Reproductive parameters	Treatments				
	Bean	Cotton	Eucalyptus	Soybean	Tomato
Number of eggs/female	157.11 ± 20.03 a	125.76 ± 20.77 a	163.28 ± 18.94 a	165.73 ± 25.25 a	121.67 ± 18.05 a
Number of nymphs/female	120.38 ± 16.02 a	101.28 ± 17.42 a	142.00 ± 17.36 a	125.80 ± 21.64 a	59.78 ± 8.23 b
Pre-oviposition period (days)	8.81 ± 0.38 b	8.72 ± 0.51 b	9.39 ± 0.16 b	8.07 ± 0.73 b	10.78 ± 0.79 a
Oviposition period (days)	31.81 ± 3.44 a	25.36 ± 2.76 a	29.83 ± 3.17 a	28.00 ± 3.92 a	17.11 ± 2.25 b
Post-oviposition (days)	4.12 ± 0.68 a	3.80 ± 0.73 a	2.22 ± 0.42 a	5.47 ± 1.23 a	3.78 ± 0.62 a
Longevity (days)	45.42 ± 3.49 a	37.40 ± 3.12 a	43.50 ± 2.98 a	41.53 ± 4.18 a	28.22 ± 2.01 b
Egg viability (%)	74.11 ± 3.25 b	77.64 ± 2.25 b	86.06 ± 1.45 a	72.48 ± 3.57 b	53.30 ± 3.74 c
Incubation period (days)	5.91 ± 0.04 a	5.84 ± 0.07 a	5.81 ± 0.03 a	5.85 ± 0.08 a	5.85 ± 0.07 a
Number of eggs/egg mass	10.55 ± 0.49 a	11.30 ± 0.72 a	11.49 ± 0.46 a	11.95 ± 0.79 a	11.81 ± 0.64 a
Number of nymphs/egg mass	7.24 ± 0.55 b	8.97 ± 0.71 a	9.89 ± 0.44 a	7.83 ± 0.78 b	6.67 ± 0.52 b
Number of egg masses	14.69 ± 1.74 a	11.04 ± 1.66 a	14.28 ± 1.57 a	14.13 ± 2.01 a	10.89 ± 1.70 a

Means (± standard error) followed by the same letter in a row are not significantly different by the Scott-Knott's test at 5 %. Twenty couples per treatment.

contains secondary plant metabolites, *e.g*., the terpenoid gossypol that is active against leaf feeding insects (Hagenbucher *et al*., 2013). *Supputius cincticeps* is a generalist predator that may utilize prey and leaf material of different plants species (Lemos *et al*., 2009b) and thus it might not be adapted to metabolize tomato and cotton plant allelochemicals very efficiently. In contrast to generalist species that often possess enzymes to metabolize a broad range of defense substances to certain extend (Krieger *et al*., 1971; Li *et al*., 2004), specialist herbivores are able to detoxify the specific defense substances from their few host plants highly efficiently (Mao *et al*., 2006; Lampert *et al*., 2011).

Effects of plant feeding on life-history characteristics of predators can be negative, as with tomato plants, for *S. cincticeps* or in the case of *Podisus maculiventris* (Heteroptera: Pentatomidade) where feeding on a vegetable diet (bean) negatively affected the development, weight gain and growth of nymphs compared to individuals fed only on *T. molitor* pupae (Crum *et al*., 1998; Weiser and Stamp, 1998). However plant feeding can also have positive effects on *S. cincticeps,* when nymph stages are shortened, lifetime prolonged and reproduction is enhanced (Zanuncio *et al*., 2004, 2012). Shortened nymph stages of *S. cincticeps* would allow this predator to reach adulthood and reproduce faster (Zanuncio *et al*., 2004, 2005; Holtz *et al*., 2006).

Adult weight, mainly of females may indicate the reproductive success of predatory stink bugs, with heavier ones presenting greater longevity and reproduction (Legaspi and Legaspi, 2005; Oliveira *et al*., 2005; Lemos *et al*., 2009b). Likewise the lower weight of *S. cincticeps* females with tomato leaves resulted also in reduced longevity, oviposition period, number of nymphs produced per female and egg mass, and egg viability of this predator. In contrast, these parameters were enhanced with eucalyptus, soybean, bean, and cotton leaves, suggesting a positive effect of these plants, as found for the reproduction of *P. nigrispinus* with eucalyptus (Holtz *et al*., 2009, 2011; Torres *et al*., 2010). The favorable effect on development and reproduction of *S. cincticeps* was similar to other Asopinae fed on plant diets (Holtz *et al*., 2009, 2011; Lemos *et al*., 2009a).

As secondary plant defense compounds tomato plants contain chlorogenic acid (the ester of caffeic acid and (-) -quinic acid) and tomatine, a glycoalkaloid (Lambert, 2007; Inbar and Gerling, 2008; Tian *et al*., 2012) that can inhibit acetylcholinesterase and thus interrupt the transmission of nerve impulses (Friedman, 2002).

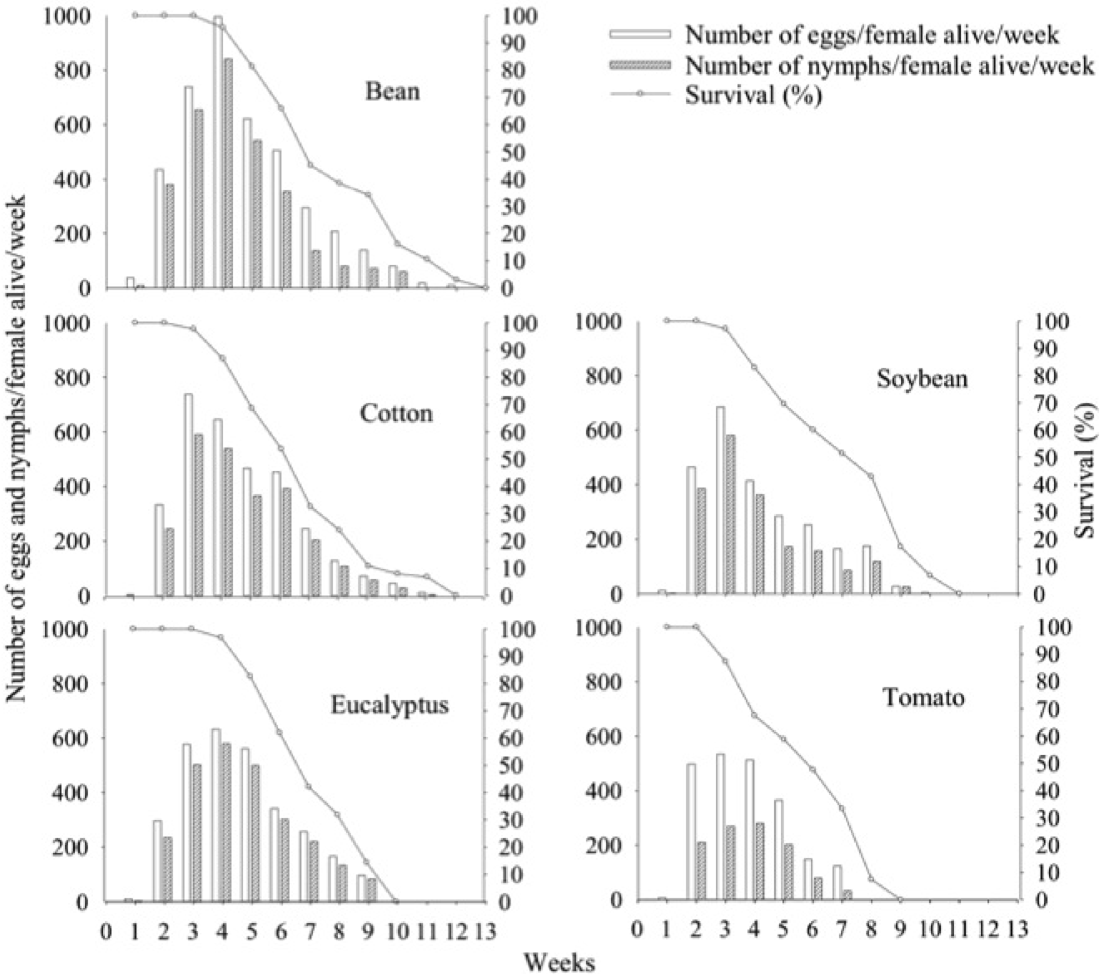

Fig. 2 Effect of feeding of different plants and *Tenebrio molitor* pupae on the number of eggs and nymphs produced per week and survival of *Supputius cincticeps*. Bars representing same letters do not differ significantly by the Scott-Knott's test at 5 %. Comparison was made within the same developmental stage feeding on different plants.

Nymphs of *P. maculiventris* and *P. nigrispinus* that were reared with prey (Lepidoptera) fed on chlorogenic acid, gossypol and tomatine of tomato plants developed slower and had other negative effects on development and reproduction (Traugott and Stamp, 1997; Kaplan and Thaler, 2010; Evangelista *et al*., 2011).

Plant secretions (enzymes) and trichomes may interfere with searching behavior of natural enemies and thus reduce their foraging efficiency (Gruenhagen and Perring, 2001; Bjorkman and Ahrne, 2005; Rodriguez-Lopes *et al*., 2011). Cotton trichomes inhibited searching behavior of natural enemies (mainly Hymenoptera) on insect-herbivores (Hagenbucher *et al*., 2013). Especially glandular trichomes that excrete enzymes such as gossypol can be a major problem for herbivores and beneficials alike (Evangelista *et al*., 2011). The glandular trichomes of the tomato variety Heinz, for example, excrete exudates and other substances that stuck to the legs of *P. maculiventris* nymphs, which hamper its movement and feeding (De Clercq *et al*., 2000; Lambert, 2007; Kaplan and Thaler, 2010). To assess directly whether the presence of trichomes has interfered with food accessibility for *S. cincticeps* behavioral bioassays would have been necessary.

In summary bean, cotton, eucalyptus, and soybean improved biological features of *S. cincticeps*, an important source of biological control. However, tomato had a negative impact on reproduction and survival of *S. cincticeps*, which may be due to toxic compounds acting by antibiosis on this predator.

Acknowledgments

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