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DOI

[10.1016/j.biocontrol.2017.10.005](https://doi.org/10.1016/j.biocontrol.2017.10.005)

Publication date

2017

Document Version

Final published version

Published in

Biological Control

License

Article 25fa Dutch Copyright Act

[Link to publication](#)

Citation for published version (APA):

Fonseca, M., Lima, E., Lemos, F., Venzon, M., & Janssen, A. (2017). Non-crop plant to attract and conserve an aphid predator (Coleoptera: Coccinellidae) in tomato. *Biological Control*, 115, 129-134. <https://doi.org/10.1016/j.biocontrol.2017.10.005>

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Non-crop plant to attract and conserve an aphid predator (Coleoptera: Coccinellidae) in tomato



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ARTICLE INFO

Keywords:

Agroecosystems
Ecosystem services
Plant diversity
Natural pest control
Aphids
Coccinellids

ABSTRACT

Pest control is an important ecosystem service that can be enhanced by increasing plant diversity. One of the simplest forms of plant diversification is making use of the occurring weeds that may benefit natural enemies of crop pests. We investigated the interaction between tomato plants, beggar-ticks (*Bidens pilosa*, Asteraceae), a common weed in Brazil and elsewhere, and the native ladybird beetle *Cycloneda sanguinea*, an important predator of aphids. The predators occurred on beggar-ticks in the field, independent of the presence of aphids, confirming that they obtained some benefit other than aphid prey from the plants. Predators were attracted to volatiles of clean, flowering beggar-ticks, and volatiles of flowering tomato plants plus flowering beggar-ticks were more attractive than volatiles of tomato plants alone. In the absence of aphids, *C. sanguinea* did not oviposit on tomato plants, beggar-ticks, or a combination of the two plants, but adult survival was higher on a combination of both plants than on tomato plants alone. These results show that the management of an abundant plant species in agricultural crops has potential for increasing pest control.

1. Introduction

The disturbance caused by agricultural production practices has induced dramatic changes in plant biodiversity and consequent deterioration of ecosystem services (Altieri and Letourneau, 1982; Tscharntke et al., 2005). One of the essential ecosystem services is natural pest control (Altieri and Letourneau, 1982; Myers, 1996; Van Emden, 1965). Approaches for restoring this ecosystem service form a continuum based on spatial scale (Gurr et al., 2017, 2003; Kremen and Miles, 2012; Landis et al., 2000; Tscharntke et al., 2005). The large-scale approach is diversification of the landscape, and this can indeed result in increased pest control (Bianchi et al., 2006; Gagic et al., 2011), although there are few studies on effects of landscape diversification on pest densities and crop damage (Chaplin-Kramer et al., 2011). At a smaller spatial scale, crops are combined with other plants that can benefit the natural enemies of pests and thus increase pest control (Altieri and Whitcomb, 1980; Landis et al., 2000). Plants are selected that may favor natural enemies by providing alternative prey or food such as pollen and nectar (Rezende et al., 2014; Wäckers et al., 2005), or that offer shelter or favorable microclimatic conditions (Diehl et al., 2012; Fiedler et al., 2008; Gurr et al., 2003). A meta-analysis showed that, overall, increasing plant diversity indeed resulted in increases of

natural enemy densities and decreases of herbivore densities and of plant damage (Letourneau et al., 2011). To develop plant diversification practices to enhance natural pest control, detailed knowledge of specific associations of natural enemies with non-crop plants is required (Amaral et al., 2016, 2013; Fiedler et al., 2008; Landis et al., 2000).

Non-crop vegetation that provides alternative resources enables natural enemies to persist in crops when primary hosts or prey are scarce, and this may prevent outbreaks after pest invasions (Ehler and Miller, 1978; Murdoch et al., 1985). The existing weed vegetation can also provide these critical resources for natural enemies (Altieri and Whitcomb, 1979; Gurr et al., 2003; Norris and Kogan, 2005, 2000). Nevertheless, because modern agriculture generally considers weeds as harmful and because of the negative connotation of the term “weed”, it is commonly thought that all weeds should be eliminated (Araj and Wratten, 2015; Chacon and Gliessman, 1982; Norris and Kogan, 2005). However, there are many instances in which weeds can be beneficial (Altieri and Koohafkan, 2004; Araj and Wratten, 2015). For example, some weeds can enhance soil fertility as well as prevent erosion by increasing moisture (Araj and Wratten, 2015). Associated to pest control, the presence of weed communities has been linked to an increase of natural enemy populations (Altieri and Whitcomb, 1979; Gurr et al., 2003; Nentwig, 1998; Norris and Kogan, 2005, 2000; Wyss, 1995).

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Therefore, the management of existing weeds in agricultural crops is perhaps the simplest means to improve natural pest control and other ecosystem services, requiring low investments by the farmers (Altieri and Koohafkan, 2004; Amaral et al., 2013; Nentwig, 1998).

In this paper, we study the attractiveness and fitness effects of a common weed on an aphidophagous coccinellid. The weed *Bidens pilosa* L. (Asteraceae) is a tropical and subtropical plant, native to America (Needham, 1948) and commonly known as ‘beggar-ticks’. This annual can flower continuously, and its flowers are visited by a rich diversity of insects, including predators (Needham, 1948). In Brazil, beggar-ticks is one of the most important species of weeds in annual and perennial crops (Santos and Cury, 2011). Although it has been mentioned as possible plant for diversification (Altieri and Whitcomb, 1980), it is not managed with the aim of improving natural control of pests.

One of the predators often encountered on beggar-ticks in Brazil is the native ladybird *Cycloneda sanguinea* L. (Amaral et al., 2013). It is one of the main coccinellid species in Brazil (Martins et al., 2009), feeds on various aphid species (Işıkber and Copland, 2002), and is considered a candidate for biological control of aphids on tomatoes (Oliveira et al., 2005; Sarmiento et al., 2007). Feeding on beggar-ticks flower resources resulted in increased survival of *C. sanguinea* (Amaral et al., 2013). Among other cues, *C. sanguinea* uses volatiles to find plants with prey (Sarmiento et al., 2007). It is repelled by the volatiles of clean tomato plants, but is highly attracted by volatiles from tomato plants with aphids (Sarmiento et al., 2008). It is also attracted to clean coriander plants (*Coriandrum sativum* L.), and feeding on coriander flower resources increased adult female survival, but not oviposition (Togni et al., 2016). Here, we systematically investigated its occurrence on beggar-ticks with or without aphids in the field. Subsequently, we investigated attractiveness of beggar-ticks volatiles, either alone or in combination with tomato volatiles. Lastly, we investigated oviposition and survivorship of adult *C. sanguinea* on beggar-ticks, tomato plants, and their combination, as first steps towards integration of beggar-ticks and ladybirds in diversified tomato production systems.

2. Materials and methods

2.1. Predator rearing

Cycloneda sanguinea was collected from non-crop vegetation and on horticultural crops in three experimental fields (Fruticultura, Vale da Agronomia and Pomar do Fundão) located on the campus of the Federal University of Viçosa, Minas Gerais, Brazil (20° 45′24″S and 42° 52′30″ W). Adults were taken to the laboratory and kept under controlled conditions (25 ± 2 °C, 70 ± 10% RH, 12:12 Light: Dark). They were placed in transparent plastic pots (500 ml) with an opening in the lid covered with mesh for ventilation. They were fed with aphids (*Myzus persicae* (Sulzer) and *M. euphorbiae* Thomas), and a solution of 10% honey water applied to a piece of cotton wool. *Myzus persicae* was reared in a greenhouse on cabbage plants (*Brassica oleracea* L. v. *capitata*), *M. euphorbiae* was collected from diverse weed plants in the field.

In each pot, three males and three females were confined together to produce eggs from which adults were obtained for all experiments. The eggs deposited in the pots were collected daily and transferred to other pots until egg hatching. The larvae were kept individually in transparent plastic pots (50 ml) and were fed with aphids until reaching adulthood.

2.2. Plant material

In a greenhouse, beggar-ticks and tomato seeds (*Solanum lycopersicum* L., var. Aguamiel, Vilmorin®) were sown in polystyrene trays (8 × 16 cells), using a commercial plant substrate (Bioplant®, Bioplant Misturadora Agrícola LTDA). After 20 days, the plants were transplanted to plastic pots (500 ml) containing the same substrate. The plants were kept inside cages (1.20 × 1.20 × 1.20 m) covered with a

fine mesh (90 µm) to prevent insect and mite infestation. The plants were watered daily and were fertilized with a solution of 10 g of N-P-K (4-14-8) and 20 g of superphosphate simple in 20 l of water every two weeks. For the experiments, we selected plants at the reproductive stage, with similar numbers of flowers. We verified that tomato pollen became available from the flowers upon slight vibration, which could easily be achieved by coccinellids.

2.3. Field sampling

To assess the probability of co-occurrence of ladybirds with aphids on beggar-ticks, sampling was conducted at irregular intervals, between 08:00 and 12:00 h, from 14 March to 13 June 2013, at randomly selected sites surrounding orchards and horticultural crops in the experimental fields mentioned above. All fields contained a mixture of weed vegetation including beggar-ticks, but coccinellids were mainly found on beggar-ticks. During each visit to each area, forty randomly selected beggar-ticks plants were sampled *in situ* for the presence of adults of *C. sanguinea*, of aphids and both together on the plants. The first field (Fruticultura), consisting of an orchard with *Plinia cauliflora* (DC.) Kausel (jaboticaba) and *Psidium guajava* L. (guava) trees, was sampled 15 times; the second field (Vale de Agronomia), containing mainly potatoes (*Solanum tuberosum* L.), pumpkin (*Cucurbita maxima* Duchesne) and cassava (*Manihot esculenta* Crantz), was sampled 14 times and the third field (Pomar), containing cabbage and a citrus (*Citrus* spp. L.) orchard, six times, resulting in a total of 1400 sampled plants. The probability of co-occurrence was calculated following Griffith et al. (2016), assuming a hypergeometric distribution:

$$P_j = \frac{\binom{N_1}{j} \times \binom{N-N_1}{N_2-j}}{\binom{N}{N_2}}$$

with N_i the number of plants with species i ($= 1, 2$) and N the total number of plants sampled, and j ranging from 1 to N_1 (Griffith et al., 2016). This probability shows whether two species are positively, negatively or randomly associated. A positive association would be the result of attraction and/or arrestment of *C. sanguinea* to plants with aphids, the absence of a positive or negative association would show that the predators are not arrested or attracted to plants with aphids, suggesting that they receive some benefit from visiting plants without aphids.

2.4. Olfactometer

To study the attraction of adult females of *C. sanguinea* by volatiles of beggar-ticks and beggar-ticks plus tomato plants, two-choice tests were done in a Y-tube olfactometer (Janssen, 1999; Sabelis and van de Baan, 1983). The olfactometer consists of a Y-shaped glass tube (27 cm in length × 3.5 cm in diameter), with a black Y-shaped metal wire in the middle to guide the predator, with the base of the tube connected to a pump that causes an airflow from the arms of the tube to the base (Janssen, 1999). Each arm was connected to a glass container (50 × 36 × 43 cm) where pots containing beggar-ticks and/or tomato plants were placed. The wind speed in each arm of the Y-tube was measured with a hot-wire anemometer and calibrated to 0.45 m/s, which is the best wind speed to assess the foraging behavior of *C. sanguinea* in a Y-tube olfactometer (Sarmiento et al., 2007). When wind speeds in both arms are equal, the air coming from the containers form two separated fields in the base of the Y-tube (Sabelis and van de Baan, 1983).

Prior to the experiments, mated adult females of *C. sanguinea*, judged by the production of eggs, were starved for 24 h, because starved females need to find suitable food and oviposition sites (Obrycki and Kring, 1998). They were tested in the olfactometer by introducing

them one at a time by disconnecting the pump and putting the female on the metal wire at the base of the Y-tube. After reconnecting the pump, the female started moving upwind to the junction of the wire, where she had to choose for one of the two arms. Each female was observed from the time that it was introduced until it reached the end of one of the arms or for a maximum of 5 min and was subsequently removed, after which the next female was introduced.

Females that did not make a choice within 5 min were scored as having made no choice and were excluded from further analysis. Three replicates were done per combination of volatile sources, each with a new set of plants and a new group of predators. Each replicate was terminated after 20 females had responded to either of the volatile sources. To correct for any unforeseen asymmetry in the experimental set-up, volatile sources were switched to the opposite arm of the olfactometer after each 5 females tested. The following choices were offered: (i) beggar-ticks vs. clean air; (ii) beggar-ticks vs. tomato plants; (iii) beggar-ticks vs. tomato plants plus beggar-ticks plants (each in a separate pot) and (iv) tomato plants vs. tomato plants plus beggar-ticks plants (again in a separate pot).

We first assessed whether the choice of the predators differed significantly among replicates, using a satiated log-linear model for contingency tables with Generalized Linear Models (GLM) using a Poisson error distribution (log link) (Crawley, 2013) with volatile source, replicate and their interaction as factors. A significant interaction between the volatile and replicate would indicate that the preference of the predators varied significantly among replicates, and a significant effect of replicate on the preference would indicate that the overall preference was more strongly determined by some replicates. This was never the case. The significance of the preference was subsequently assessed with a simple binomial test with an expected proportion of predators choosing each volatile of 0.5. This statistical analysis was done using R (R Development Core Team, 2014).

2.5. Oviposition

This experiment was conducted to verify whether beggar-ticks combined with tomato plants supply sufficient resources for egg production by *C. sanguinea*. Adult ladybird beetles were placed with flowering beggar-ticks and tomato plants in cages (1 × w × h = 0.60 × 0.60 × 1.20 m) made of PVC tubes covered with mesh, outside the laboratory. Only pairs of females and males that previously produced eggs on a diet of aphids and water in plastic pots (500 ml) in the laboratory were used. Three pairs were released in each cage. There were four replicates of three treatments: (i) one beggar-ticks plant; (ii) one beggar-ticks plus one tomato plant; and (iii) one tomato plant. The twelve cages were placed alternately in the sequence as above. Oviposition rates were assessed daily by checking the entire plant plus the cage during five days, and the plants were replaced daily to facilitate the counting of eggs. After five days, the females had stopped ovipositing. We subsequently added ample amounts of aphids to each cage in a Petri dish. This Petri dish was placed inside a larger Petri dish containing wet cotton wool. This cotton wool served as barrier to prevent the wingless aphids from going to the plants, yet allowing access of flying predators to the aphids. The oviposition rate was then evaluated for five more days. Oviposition data in the absence and in the presence of aphids were analyzed separately using linear mixed-effects models (LME, package nlme of R, Pinheiro et al., 2017) with plant species, time and their interaction as fixed factors and replicate as a random factor. Numbers of eggs were log(x + 1) transformed, and the distribution of the residuals was checked for normality and heteroscedasticity. Non-significant interactions and factors were removed until a minimal adequate model was reached (Crawley, 2013).

2.6. Survivorship

We evaluated the survival of adults of *C. sanguinea* with flowering

beggar-ticks, flowering tomato plants, and a combination of these two as food source. Newly-emerged adults were fed in the laboratory with aphids and water for 6 days to reduce mortality due to starvation. Subsequently, pairs of adult females and males were released in cages (as above) under a roof outside the laboratory. There were four treatments, each with four replicates: (i) a cage with one beggar-ticks; (ii) a cage with one beggar-ticks plus one tomato plant; (iii) a cage with one tomato plant and (iv) a control, i.e. an empty cage. The sixteen cages were placed alternately in the sequence mentioned above. Survival was assessed daily until most individuals had died.

Survival data were analyzed with a Cox mixed effects proportional hazards model (package Coxme in R, Therneau, 2015) with plant species as fixed factor and replicate as random factor. Contrasts were obtained through general linear hypothesis testing (package lsmeans of R, Lenth, 2016). The Kaplan–Meier estimator, which takes censored data into account, was used to produce estimates of the survival through time.

3. Results

3.1. Field sampling

In all three fields, most beggar-ticks did not harbor aphids or ladybirds (Fig. 1). The observed number of plants with both aphids and ladybirds did not differ significantly from expected assuming that they distributed themselves independently over the plants (P values above bars in Fig. 1). This implies that the ladybirds often occurred on plants without aphids, perhaps because they encountered other rewards on these plants (Amaral et al., 2013).

3.2. Olfactometer experiments

In the olfactometer, *C. sanguinea* females showed a significant preference for volatiles from beggar-ticks when ambient air was given as alternative (Fig. 2, top bar). When given a choice between volatiles from beggar-ticks and volatiles from tomato plants, *C. sanguinea* showed no preference (Fig. 2, 2nd bar). Volatiles from beggar-ticks and volatiles from tomato plants plus beggar-ticks were equally attractive (Fig. 2, 3rd bar), but tomato plants plus beggar-ticks were somewhat

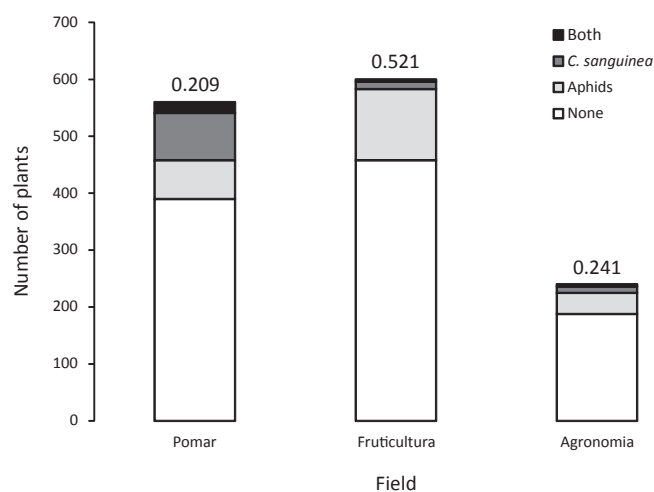


Fig. 1. Co-occurrence of *C. sanguinea* with aphids on beggar-ticks in 3 fields. Shown are frequencies of occurrence of plants without aphids or *C. sanguinea* (Empty, white bars), plants with aphids (light grey bars), plants with *C. sanguinea* (dark grey bars), and plants with both (black bars). Fields were sampled 14 (Pomar), 15 (Fruticultura) and 6 (Agronomia) times, 40 plants were inspected for each sample (1400 plants in total). The probability of finding the observed proportion of plants with both aphids and *C. sanguinea* or more extreme proportions was assessed assuming a hypergeometric distribution (Griffith et al., 2016), probabilities are given above the bars.

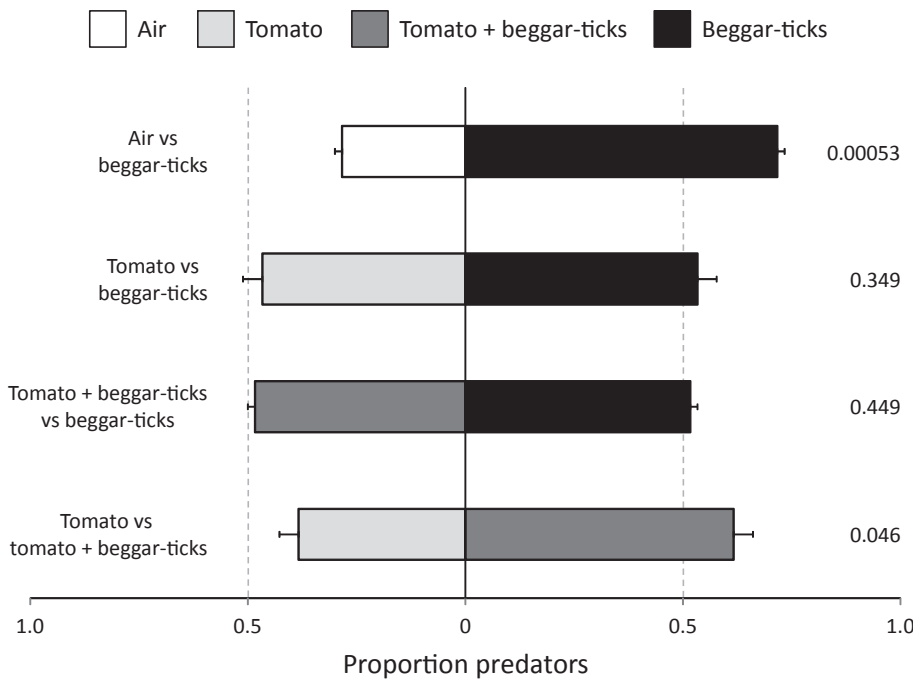


Fig. 2. The response of *C. sanguinea* to plant volatiles in an olfactometer. Each combined horizontal bar is the average response (+ s.e.) of 3 replicates. Ladybeetles were given the choice between volatiles of beggar-ticks (black bars), tomato (light grey bars), tomato plus beggar-ticks (dark grey bars) or ambient air (white bars). The significance of the preference is given at the right-hand side of the bars (P-values of binomial test).

more attractive than tomato plants alone (Fig. 2, 4th bar).

3.3. Oviposition

Oviposition of *C. sanguinea* did not differ significantly among plants, neither in the absence (Fig. 3, day 1–5, LME: $\text{Chi}^2 = 0.15$, d.f. = 2, $P = 0.56$) nor in the presence of aphids (Fig. 3, day 6–10, LME: $\text{Chi}^2 = 0.07$, d.f. = 2, $P = 0.96$). In the absence of aphids, ladybird oviposition decreased over time and stopped completely after 3 days. Oviposition observed during the first 3 days was likely due to the previous diet consisting of aphids. The females resumed oviposition only after they were supplied with aphids (Fig. 3, days 6–10), showing that they could still reproduce. Thus, the plant resources alone were not sufficient for oviposition of the ladybirds. Most oviposition occurred on the cage walls.

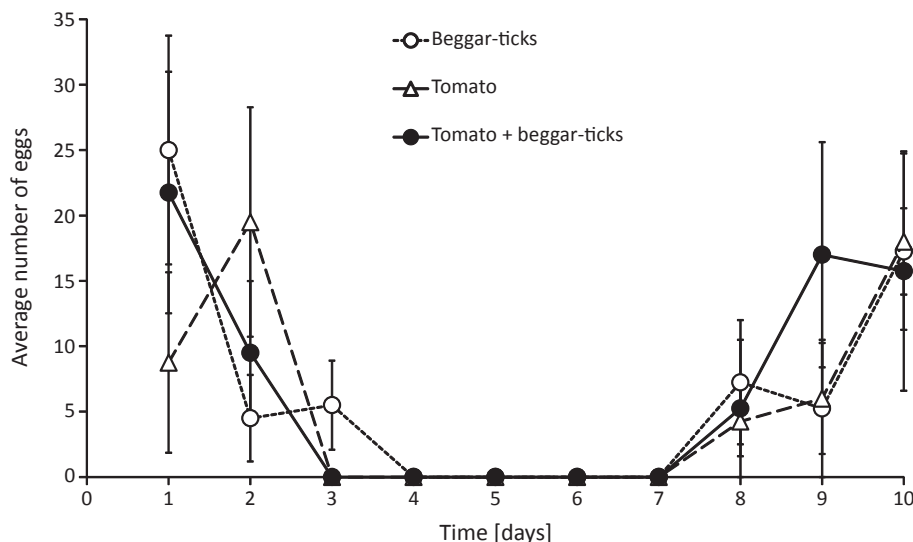


Fig. 3. Average oviposition (\pm s.e.) of *C. sanguinea* on tomato plants (open triangles), beggar-ticks (open circles) and on a combination of beggar-ticks and tomato plants (closed circles). During the first 5 days, the ladybirds were offered clean plants, aphids were added as food during the last 5 days.

3.4. Survival

Survival of adult ladybird beetles differed significantly among plants (Fig. 4, Cox proportional hazards, $\text{Chi}^2 = 25.0$, d.f. = 3, $P < 0.001$). Cumulative survival was highest with the combination of tomato plants plus beggar-ticks, somewhat lower with beggar-ticks, and lowest with tomato plants and without plants.

4. Discussion

There is a plethora of publications showing that predators and parasites are attracted by plant volatiles induced by herbivore feeding, but much less on the attraction by volatiles constitutively produced by plants that are not under attack by herbivores (Elzen et al., 1983; Salamanca et al., 2015; Takabayashi et al., 1991; Togni et al., 2016). Here we add another case, that of beggar-ticks that attract *C. sanguinea*. Predators were mainly found on beggar-ticks in the field and were hardly encountered on other plants. On beggar-ticks, they were not

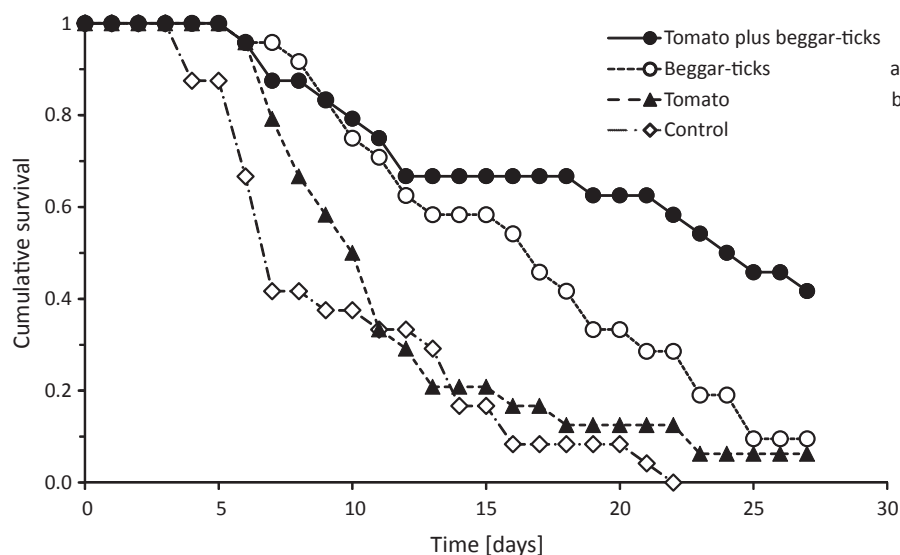


Fig. 4. Cumulative survival of adult *C. sanguinea* on tomato plants (closed triangles), beggar-ticks (open circles), tomato plus beggar-ticks (closed circles) and without plants (control, open diamonds). Treatments with different letters in the legend are significantly different (contrasts after a mixed effects Cox proportional hazards model). Standard errors are not shown for reasons of clarity.

significantly associated with aphids, suggesting that they did not specifically search for aphids on these plants. Although we could not rule out that the beggar-ticks in the field had been attacked by aphids or other herbivores before we sampled them, hence, that the ladybirds were attracted to herbivore-induced plant volatiles, the olfactometer experiments clearly showed that undamaged beggar-ticks were attractive. The response of predators to plant volatiles can only be preserved over evolutionary time if the predators benefit from visiting the plant (van Baalen and Jansen, 2003). Coccinellids frequently use plant resources to complement their diet, hence, there may be selection to respond to volatiles associated with these resources (Giorgi et al., 2009; Lundgren, 2009). Thus, the attraction of *C. sanguinea* to beggar-ticks can be understood because this plant offers resources that can increase adult survival (this study and Amaral et al., 2013). Our field results confirm earlier findings of coccinellids visiting plants without prey and feeding on non-prey foods (Amaral et al., 2013; Lundgren, 2009).

Sarmiento et al. (2008) found that *C. sanguinea* was repelled by volatiles of clean tomato plants, which led us to expect that the volatiles of beggar-ticks would be preferred over those of tomato plants. However, this was not the case (Fig. 2). Contrary to the present study, Sarmiento et al. (2008) used plants in the vegetative stage. Hence, the flowering tomato plants used here may have been less repellent than plants without flowers. Another reason for the difference in attractiveness may be the different tomato varieties used here and by Sarmiento et al. (2008). This remains to be tested.

We found that a mixture of volatiles of beggar-ticks and tomato plants was somewhat more attractive than volatiles of tomato plants (Fig. 2), suggesting that combining these two plants will attract more ladybird beetles, which may increase natural control of aphids. In the olfactometer experiments, we offered *C. sanguinea* the choice between volatiles of one tomato plant vs. one tomato plant plus one beggar-ticks. Arguably, the volatiles of the combination were more attractive because there were more plants present. The experimental design of this kind of experiments is a difficult issue, because it is not clear how to compare the quantity of plants of different species, and should arguably be based on numbers, biomass, or on leaf area. We chose to add a beggar-ticks plant to a tomato plant because this is what growers could do: they will not voluntarily replace a tomato plant with a beggar-ticks, but they can opt to leave some beggar-ticks in their tomato field instead of weeding them.

There is one other example of a combination of a weed and a crop plant being more attractive than crop plants alone (Ninkovic and Petterson, 2003). Moreover, several studies have shown an increase in coccinellid densities in the field as a result of plant diversification with

weeds (Burgio et al., 2006; Cottrell and Yeargan, 1998; Harmon et al., 2000; Sengonca et al., 2002; Wyss, 1995). There are also examples of increased control of pests as a result of such increase in plant diversity. For instance, the presence of three weed species in lettuce cultures increased the density of three species of ladybirds, which resulted in a reduction of infestation by aphids (Sengonca et al., 2002). Also, increased densities of the weed *Taraxacum officinalis* (dandelion) in alfalfa fields resulted in higher ladybird densities, which in turn was associated with lower aphid densities (Harmon et al., 2000). Hence, there is potential for using weeds to promote the control of pests by natural enemies.

Because the beggar-ticks associated with tomato plants studied here did not result in increased reproduction of *C. sanguinea*, but only in increased survival, the densities of coccinellids in the field will not necessarily increase when beggar-ticks are allowed in or around tomato fields. This can be gleaned from simple models of predator-prey dynamics. For example, the Lotka-Volterra predator-prey model shows that reduced predator mortality does not result in increased equilibrium predator densities (Volterra, 1928), and the Rosenzweig-McArthur model (Rosenzweig and MacArthur, 1963) can show increases or decreases of predator densities with decreasing predator mortality. Indeed, there are several examples where increased predator survival due to increased plant biodiversity did not result in increased predator densities in the field (Bianchi et al., 2006; Letourneau et al., 2011). However, the increased survival will result in increased persistence of coccinellid populations in the field in times of prey scarcity, and will form a buffer against new pest invasions. Because beggar-ticks are a common weed at the borders and within field crops, this increase in persistence is gained at low costs: it only requires adequate management of this weed.

In conclusion, we show that beggar-ticks can play an important role in conservation of *C. sanguinea* in tomato crops. Field experiments should be done to investigate the effects of combining tomato plants with beggar-ticks on aphid dynamics and damage on tomato. Like other studies, our results suggest that the management of specific species of weeds may favour the conservation of natural enemies (Altieri and Whitcomb, 1979; Amaral et al., 2016, 2013; Landis et al., 2005).

Acknowledgments

We thank Daniel Griffith of the Oregon State University, USA for his clear and fast advice on the co-occurrence data analysis. Aline Francéz, Sandra Gomes and Manuel Ferreira are acknowledged for their assistance with the practical work. We thank two anonymous reviewers for

constructive comments. MF received a scholarship from the National Council of Scientific and Technological Development (CNPq, Brazil), MV and EL from CNPq, and FL from NWO (the Netherlands, TOP Project 854.11.005). The authors declare no conflict of interest.

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