MORGANA MARIA FONSECA PORTO

STOP AND SMELL THE WEEDS: AN APPROACH TO ATTRACT AND CONSERVE PREDATORY COCCINELLIDS IN TOMATO

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae.*

VIÇOSA
MINAS GERAIS - BRASIL
2013

Ficha catalográfica preparada pela Seção de Catalogação e Classificação da Biblioteca Central da UFV

T

Porto, Morgana Maria Fonseca, 1983-

P853s
2013

Stop and smell the weeds : an approach to attract and conserve predatory coccinellids in tomato / Morgana Maria Fonseca Porto. – Viçosa, MG, 2013.

xii, 54 f. : il. ; 29 cm.

Texto em inglês.
Orientador: Eraldo Rodrigues de Lima.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Ervas daninhas - Controle. 2. Tomate - Erva daninha - Controle. 3. Habitat (Ecologia). 4. Inseto predador. I. Universidade Federal de Viçosa. Departamento de Entomologia. Programa de Pós-Graduação em Entomologia. II. Título.

CDD 22. ed. 632.5

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APROVADA: 24 de Julho de 2013.

Prof. Arnoldus Rudolf Maria Janssen

Dr. Lessando Moreira Gontijo

Prof. Eraldo Rodrigues de Lima
Orientador

A você mamãe, que sempre se doou inteira
para a realização dos meus sonhos,
me mostrando em todos os momentos
o mais divino dos sentimentos,
o amor incondicional, dedico essa conquista.

BEGINNING my studies, the first step pleased me so much,
The mere fact, consciousness - these forms - the power of motion,
The least insect or animal - the senses - eyesight;
The first step, I say, awed me and pleased me so much,
I have never gone, and never wished to go, any farther,
But stop and loiter all my life, to sing it in ecstatic songs.
Walt Whitman (1819-1892).

Agradecimentos

Agradeço em primeiro lugar, ao Deus criador da vida e seus desafios, pela saúde e possibilidades de atuação.

À minha mãe, inspiração elementar da minha vida, e aos meus irmãos, pelo amor e apoio constante a mim dedicado.

Ao professor Eraldo Lima, pela orientação, ensinamentos, conselhos e compreensão.

Ao professor e coorientador Arne Janssen, pelo conhecimento transmitido e por toda contribuição para a realização deste trabalho.

À professora e coorientadora Madelaine Venzon, pela colaboração e sugestões.

Ao pesquisador Lessando Gontijo, por participar da banca de defesa da minha dissertação e pelas sugestões que certamente serão proveitosas.

Aos amigos do Laboratório de Semioquímicos e Comportamento de Insetos, pelo companheirismo, momentos de descontração e por todo apoio.

Aos colegas do Laboratório de Acarologia (UFV) e do Laboratório de Entomologia da Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG), por toda ajuda e disponibilidade.

À Universidade Federal de Viçosa e ao Departamento de Entomologia, pela oportunidade de realizar o mestrado.

Ao CNPq pela concessão da bolsa de estudos.

A todos os que colaboraram de alguma forma para o êxito deste trabalho, o meu eterno agradecimento e estima.

Biografia

Morgana Maria Fonseca Porto, filha de Rousibel da Silva Fonseca e Rubens Raimundo Eustáquio, nasceu em 6 de outubro de 1983 na cidade de Patos de Minas - MG.

Em fevereiro de 2004 iniciou o curso de Ciências Biológicas no Centro Universitário de Patos de Minas. Em dezembro do mesmo ano, trancou o curso e mudou-se para a Inglaterra onde morou e trabalhou por dois anos. Retornou ao curso e graduou-se licenciada em dezembro de 2008 e bacharel em dezembro de 2009, em Ciências Biológicas. Durante a graduação, foi bolsista de iniciação científica e monitora no Laboratório de Citogenética e Mutagênese sob a orientação do Prof. Júlio César Nepomuceno.

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Em agosto de 2011, iniciou o curso de Mestrado em Entomologia, na Universidade Federal de Viçosa, sob orientação do Prof. Eraldo Lima e co-orientação de Arne Janssen e Madelaine Venzon, submetendo se à defesa da dissertação em julho de 2013.

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Resumo

PORTO, Morgana Maria Fonseca, M. Sc., Universidade Federal de Viçosa, julho de 2013. **Pare e cheire as plantas daninhas: uma abordagem para atrair e conservar coccinelídeos predadores em tomate**. Orientador: Eraldo Rodrigues de Lima. Coorientadores: Arnoldus Rudolf Maria Janssen e Madelaine Venzon.

O manejo de habitat, uma abordagem do controle biológico conservativo, tem como objetivo alterar habitats através da manipulação de recursos de origem vegetal na paisagem para melhorar a disponibilidade de recursos para os inimigos naturais. As plantas daninhas têm sido amplamente usadas para esse fim em agroecossistemas devido ao seu potencial de fornecer recursos alternativos para os inimigos naturais, mesmo quando as densidades de pragas são baixas. No entanto, há uma escassez de informações relativas aos recursos fornecidos por plantas daninhas e suas interações com os inimigos naturais. Para que o manejo de habitat seja uma prática funcional, é necessário o conhecimento detalhado do comportamento de forrageamento e da capacidade sensorial de inimigos naturais. A fim de contribuir para esse entendimento, estudei a atratividade e os efeitos de recursos fornecidos pela planta daninha *Bidens pilosa*, conhecida como picão-preto, utilizando plantas de tomate como a cultura principal, para o predador generalista *Cycloneda sanguinea*. As fêmeas de *C. sanguinea* são capazes de reconhecer os sinais químicos do picão-preto, mas elas não discriminam entre os estímulos do picão-preto ou das plantas de tomate. No campo, a ocorrência de *C. sanguinea* no picão-preto não depende da presença de pulgões e isso só é evolutivamente estável se a joaninha obtém vantagens da visita na planta. Os recursos alternativos fornecidos pelo picão-preto e pelas plantas de tomate, em conjunto ou não, não afetou a taxa de oviposição de *C. sanguinea,* tanto na presença quanto na ausência de pulgões. Entretanto, uma dieta com apenas os recursos fornecidos pelas plantas testadas aqui não é suficiente para promover a sua oviposição. Porém, estes recursos podem aumentar a sobrevivência de casais de joaninhas adultas de forma significativa. A sobrevivência de *C. sanguinea* foi significativamente maior na combinação picão-preto e plantas de tomate do que no tomate sozinho, mas não foi diferente do picão-preto somente. Concluindo, *C. sanguinea* pode usar pistas químicas do picão-preto durante o forrageamento e os recursos oferecidos pela planta podem permitir que este predador persista no campo quando os recursos-presa são escassos, o que pode levar a uma melhora na sua eficiência como agente de controle biológico.

Abstract

PORTO, Morgana Maria Fonseca, M. Sc., Universidade Federal de Viçosa, july of 2013. **Stop and smell the weeds: An approach to attract and conserve predatory coccinellids in tomato**. Adviser: Eraldo Rodrigues de Lima. Co-advisers: Arnoldus Rudolf Maria Janssen and Madelaine Venzon.

Habitat management is a conservation biological control approach that aims to alter habitats through manipulating plant-based resources in the landscape to increase the availability of resources for natural enemies. Weed communities have been adopted for habitat management in agroecosystems due to their potential to supply food resources to natural enemies, even when pest densities are low. However, there is a paucity of information pertaining to the resources provided by non-crop weeds and their interactions with natural enemies. To make the management of non-crop weeds a functional practice, detailed knowledge of the behavior and sensory ability of natural enemies is necessary. In order to contribute to such understanding, I studied the attractiveness and the effects of resources provided by the weed hairy beggarticks (non-crop), using tomato plant as the main crop, on the generalist predator *Cycloneda sanguinea*. I found that *C. sanguinea* females are able to recognize cues from hairy beggarticks but they do not discriminate between cues from hairy beggarticks or tomato plants. In the field, the occurrence of *C. sanguinea* on hairy beggarticks plants does not depend on the presence of aphids and it is only evolutionary stable if the ladybird gains advantage from visiting the plant. The alternative resources provided by the hairy beggarticks and tomato plants, either together or separate, did not affect the oviposition rate of *C. sanguinea*, both in the presence and absence of aphid prey. Hence, a diet with only the resources provided by the plants is not enough to promote their oviposition. Nevertheless, these resources were found to increase adult survivorship significantly. Survival of *C. sanguinea* was significantly higher on the combination of tomato plants plus hairy beggarticks than on tomato plants alone but was not different from hairy beggarticks alone. Concluding, *C. sanguinea* can use cues from hairy beggarticks when foraging and the resources offered by plants may allow them to persist in the field when prey resources are scarce which might improve its efficiency as biological control agent.

General Introduction

Many studies have shown that plant community diversity has positive effects on organisms and processes across trophic levels (Balvanera *et al.*, 2006; Cardinale *et al.*, 2006), including important ecosystem services (Myers, 1996), such as suppression of pest populations in crops by natural enemies. The loss of biodiversity caused by agricultural production practices has resulted in dramatic changes in agricultural landscapes and consequent deterioration of these ecosystem functions (Robinson & Sutherland, 2002; Bianchi *et al.*, 2006). Ecosystem services such as biological control depend on maintenance or enhancement of biodiversity, resulting in suitable ecological infrastructure within the agricultural landscape (Altieri, 1994; Landis *et al.*, 2000).

Habitat management is a conservation biological control approach that aims to alter habitats through manipulating plant-based resources in the landscape to improve the availability of resources for natural enemies (Bugg & Pickett, 1998; Landis *et al.*, 2005). This is accomplished by selecting and establishing plants within the managed system, which may favor natural enemies by providing food such as pollen, nectar and alternative prey and that offer shelter or a favorable microclimate (Gurr *et al.*, 2003; Fiedler *et al.*, 2008). The existing weed community can also provide these critical resources for natural enemies and this is perhaps the simplest means of increasing biological control (Landis *et al.*, 2005) with a low investment of the farmers (Amaral *et al.*, 2012).

There are several examples of weeds that positively affect the survivorship of parasitoids and predators when primary hosts or prey are not available (Van Emden, 1963, 1965; De Bach, 1991; Menalled *et al.*, 1999). Weeds serve as food for herbivores, and these, in turn, can serve as a food for predators and parasitoids, and thus weeds can indirectly serve as a resource for such natural enemies (Narajo & Stimac, 1987; Norris & Kogan, 2005). Many natural enemies also feed directly on plant resources such as pollen, floral and extrafloral nectar, foliage and plant sap (Landis *et al.*, 2005; Wäckers *et al.*, 2005; Lundgren, 2009).

In particular, the resources provided by flowers of weeds attract and maintain a diverse community of arthropod predators (Amaral *et al.*, 2012). Needham (1948) observed a community of insect living in association with flowers of the weed *Bidens pilosa* L. (Asteraceae), wherein the predatory members were the most diverse species and some predators had lifelong associations with the plant. *Bidens pilosa* is a pantropical weed, native of South America and commonly known as "Hairy beggarticks" (Geissberger & Séquin, 1991; Brandao *et al.*, 1997). In Brazil, hairy beggarticks constitutes one of the most important weeds in annual and perennial crops (Santos & Cury, 2011), nevertheless, it is not managed in order to improve natural control of pests.

To make the management of a non-crop plant a functional practice, detailed knowledge of the trophic relationships among non-crop plants, herbivores and natural enemies is necessary (Burgio *et al.*, 2006; Fiedler *et al.*, 2008). Individual natural enemy species may use fairly specific resources at different temporal and spatial scales, hence, not all attempts to manipulate habitat diversity are effective (Fiedler *et al.*, 2008; Landis *et al.*, 2005). Predatory species of Coccinellidae are good models for studying these effects due to their wide use as biological control agents (Obrycki & Kring, 1998). They feed on a large number of prey including aphids and phytophagous mites (Obrycki & Kring, 1998; Isikber, 1999), and if given the chance, they will feed on pollen and extrafloral nectaries (Lundgren, 2009).

Cycloneda sanguinea (Coleoptera: Coccinellidae) is an aphidophagous predator native to Central and South America (Isikber, 1999) and one of the most abundant Coccinellids in Brazil (Sujii *et al.*, 2007; Martins *et al.*, 2009). This ladybird has been reported as an important natural enemy in different cultures (Isikber, 1999) and is considered one of the promising biological control agents of aphids on tomatoes (Oliveira *et al.*, 2005; Sarmento *et al.*, 2007). Adult females of *C. sanguinea* must search for suitable patches for feeding and reproduction (Evans, 2003; Sarmento *et al.*, 2007). Sarmento *et al.* (2007) demonstrated that mated females of *C. sanguinea* use a hierarchy of olfactory cues when choosing foraging patches.

Semiochemical messages from the herbivore, from its host plant, or from interactions between these sources can be expected to contribute to habitat/patch attraction or arrestment of polyphagous coccinellids (Hodek *et al.*, 2012). The message from plants would carry information either from their constitutive volatiles or caused by the presence of herbivores (Vet & Dicke, 1992). Coccinellids searching for food can combine information from both trophic levels, and to be successful, this searching strategy presupposes a capacity to perceive and process a broad set of information on different food sources and adapt to them (Lundgren, 2009; Hodek *et al.*, 2012).

Patch choice can also be associated with the presence of plants that provide alternative prey, nectar and pollen or other resources. A diet of pollen mixed with aphid prey may help to promote reproduction (Hemptinne & Desprets, 1986; Michaud, 2000; Omkar, 2006; Berkvens *et al.*, 2008) and the sugars found in nectars can considerably increase survival of coccinellids in the absence of such prey (Matsuka *et al.*, 1982; Dreyer *et al.*, 1997). Ultimately, surrounding vegetation that provides alternative resources may facilitate the selection of suitable habitats and seems to have a direct effect on the density of some coccinellids, modifying their immigration and emigration patterns (Grez & Prado, 2000) and predation rate (Harmon *et al.*, 2000).

Although understanding the foraging behavior of predators is crucial for the successful development of biological control, only few studies consider the role of non-crop vegetation on habitat selection by coccinellid predators (Isikber, 1999; Sloggett, 2005). To maximize their use in biological control it is also important to analyze the behavior and sensory ability which operate during searching activities of these predators (Ferran & Dixon, 1993).

In order to contribute to such understanding, I studied the attractiveness and the effects of resources provided by the weed hairy beggarticks (non-crop), using tomato plant as the main crop, on the generalist predator *C. sanguinea*. In the first chapter, I investigate if adult females of *C. sanguinea* are able to recognize volatile cues from tomato plants and hairy beggarticks. I also assessed the presence of *C. sanguinea*, of aphids and both together on hairy beggarticks plants in the field. In the second chapter, I investigated whether the oviposition rate and survivorship of adults of *C. sanguinea* are affected by the resources provided by these plants.

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Attractiveness of the weed *Bidens pilosa* to the predatory ladybird *Cycloneda sanguinea*

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Abstract

In the process of searching for hosts or prey, natural enemies base their foraging decisions on chemical cues emitted by herbivores and their originary hosts, or from interactions between these entities. The message from plants would carry information either from their constitutive volatiles or caused by the presence of herbivores. The response of predators to constitutive plant volatiles is only evolutionary stable if the predators gain advantage from visiting the plant. In an olfactometer, I investigated the responses of the predatory ladybird *Cycloneda sanguinea* to chemical cues emitted by the weed hairy beggarticks, whether intercropping with tomato plants. I also assessed the presence of the ladybird, of aphids and both together on hairy beggarticks plants in the field. The females were able to recognize cues from the weed hairy beggarticks but they did not discriminate between cues from hairy beggarticks or tomato plants. In the field, the occurrence of *C. sanguinea* on hairy beggarticks plants does not depend upon presence of aphids. Since once attracted, the ladybird stays on the plants even in the absence of aphids, it is inferred that this predator benefits from alternative resources provided by the plants. As result of such attraction, *C. sanguinea* may persist in the field when prey are scarce which might improve its efficiency as biological control agent.

1 Introduction

Predators and parasitoids of insect herbivores are sensitive to chemical aspects of both allelochemicals (interspecific) and pheromones (intraspecific), alone or in association, particularly with regard to host habitat location (Lewis & Martin Jr, 1990; Poppy, 1997; Venzon *et al.*, 1999). Thus, the physiology and behavior of natural enemies are influenced by elements from other trophic levels, such as their herbivore victim and its plant food (Price *et al.*, 1980; Vet & Dicke, 1992). In the first steps of searching for hosts or prey, natural enemies base their foraging decisions on chemical cues emitted by plants, especially at longer distances, while the meaning of herbivore derived chemicals increases with decreasing distance from the victim (Tumlinson *et al.*, 1992; Vet & Dicke, 1992).

The how of this searching process has been reviewed extensively for parasitoids, which contrasts to the relatively limited information available for predators (Dicke *et al.*, 1990; Sengonca *et al.*, 2002). However various studies have shown that olfactory stimuli cause targeted searching behaviour not only in parasitoids but also in generalist predators, such as polyphagous coccinellids, which are the most important biological control agents for aphid pests (McEwen *et al.*, 1994; Seagraves, 2009). Therefore knowledge of these semiochemicals and how they govern the behavior of foraging predators is a key consideration to enhance their effectiveness in biological control programs (Lewis & Martin Jr, 1990).

The foraging behaviour of predatory coccinellids involves navigation through a complex landscape in which suitable, high quality food sources are found and exploited using multiple cues, especially olfaction and vision (Harmon *et al.*, 1998; Pettersson *et al.*, 2005). Both the presence and quality of food have a very strong effect on retention of adult coccinellids in a habitat and on their reproductive output (Seagraves, 2009). Aphids are the main food on the ladybirds' menu, but if other food sources such as pollen are more easily available, they do not necessarily eat aphids and so it can be expected that their foraging behavior is adaptive and complex (Majerus, 1994; Ninkovic *et al.*, 2001).

During foraging, coccinellids can respond to semiochemicals from aphids such as alarm pheromone (Majerus, 1994), but the use of herbivore-derived stimuli is often limited by low detectability, especially at longer distances (Dicke *et al.*, 1990). More commonly, chemicals that are released by plants as a direct result of herbivore feeding activity have been shown to be essential cues because they are usually more readily available due to the plants' relatively larger biomass (Vet & Dicke, 1992). In many cases, coccinellid predators have been shown to prefer volatiles emitted from herbivore-attacked plants to unifested plants (Obata, 1997; Zhu & Park, 2005; Bahlai *et al.*, 2008). The herbivore-induced volatiles are highly specific and natural enemies can discriminate between different plant-herbivore combinations (Sabelis & Dicke, 1985; Turlings *et al.*, 1991). Sarmento *et al.* (2007) demonstrated that mated females of the ladybird *Cycloneda sanguinea* choose between patches based on prey quality, preferentially moving toward volatiles of tomato infested with essential prey, the aphid *Macrosiphum euphorbiae*, versus non-essential prey, the mite *Tetranychus evansi*. Besides these semiochemicals derived of herbivores and of plants by herbivore damage, the constitutive plant volatiles can also attract or recruit coccinellids before plants are attacked by herbivores (Schmid, 1992), however, there is lack of research on the olfactory attractiveness of these volatiles to such predators (Sengonca *et al.*, 2002).

The response of predators to constitutive plant volatiles is only evolutionary stable if the predators gain advantage from visiting the plant, such as nectar and pollen, alternative prey and hosts, and a favourable microclimate, which could improve their performance (Altieri & Whitcomb, 1979;

Price *et al.*, 1980). A study by Schmid (1992) on plant discrimination in the field by coccinellids with 73 plant species, most of which were common agricultural weeds, at least 20 were highly attractive to coccinellid predators. Other studies have shown that resources provide by weeds promote the abundance and survival of coccinellids in agricultural systems (Hodek *et al.*, 2012; Amaral *et al.*, 2012). Thus, the use of constitutive plant volatiles by generalist predators is assumed to enhance their searching efficiency and fitness, and consequently may improve the natural control of their prey pests (Vet & Dicke, 1992; Ninkovic *et al.*, 2001). Therefore, better methods to attract and maintain generalist predators populations may result from a better understanding of their olfactory ability (Schaller & Nentwig, 2000).

To elucidate the relation between constitutive plant volatiles and foraging behavior of generalist predators, I investigated in this study the responses of the ladybird *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae) to chemical cues emitted by the weed *Bidens pilosa* L. (Asteraceae), known as hairy beggarticks (non-crop), whether intercropping with tomato plants (main crop). I also assessed the presence of *C. sanguinea*, of aphids and both together on hairy beggarticks plants in the field.

2 Materials and methods

2.1 Predator rearing

Cycloneda sanguinea was collected on 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, Viçosa, Minas Gerais, Brazil (20° 45' 24" S and 42° 52' 30" W). Individuals were taken to the laboratory and kept under controlled temperature (25 ± 2°C), humidity (70 ± 10% RH) and photoperiod (12:12 L:D). They were placed in transparent plastic pots (500 ml) with an opening in the lid covered with mesh. They were fed with aphids (*Myzus persicae* and *Macrosiphum euphorbiae*), honey and water. *Myzus persicae* was reared in a greenhouse on cabbage plants (*Brassica oleracea* v. capitata L.), *M. euphorbiae* was collected in the field.

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

2.2 Plant material

In a greenhouse, hairy beggarticks (*Bidens pilosa* L.) and tomato plants (*Solanum lycopersicum*, variety Aguamiel, Vilmorin®) were sown in polystyrene trays (8 × 16 cells), using a commercial plant substrate (Bioplant®, Bioplant Misturadora Agrícola LTDA) composed of vermiculite plus organic fertilizer. 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 gauze (90 μm) to avoid infestation with herbivores. The plants were watered and fertilized with NPK (4-14-8) and superphosphate according to need. For the experiments, we used plants in the reproductive stage, with similar numbers of flowers.

2.3 Olfactometer experiments

To study the behavioural attraction and/or arrestment of adult females of *C. sanguinea* in response to odour sources, two-choice tests was performed in a Y-tube olfactometer (Sabelis & Baan, 1983; Janssen, 1999). 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 plastic vessels containing hairy beggarticks and/or tomato plants were placed. The wind speed in each arm of the Y-tube was measured with two hot-wire anemometers and calibrated to 0.45m/s, which is the best wind speed to assess the foraging behaviour of *C. sanguinea* in a Y-tube olfactometer (Sarmento *et al.*, 2007). When wind speeds in both arms are equal, the air coming from the containers forms two separated fields in the base of the Y-tube (Sabelis & Baan, 1983).

Prior to the experiments, mated adult females of *C. sanguinea* were starved for 24 hours, because in these conditions they are responsible for finding suitable food and oviposition sites for the development of their offspring (Kindlmanni & Dixon, 1993; Obrycki & Kring, 1998; Evans, 2003). They were tested individually 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 it had to choose for one of the two arms. Each female was observed from the time that it left the tube until it reached the end of one of the arms or for a maximum of 5 and was subsequently removed.

The female that did not make a choice within 5 minutes was scored as having made no choice and was excluded from further analysis. Three replicates were done per treatment and individuals were tested until 20 females had responded to either of the odour sources in each replicate. To correct for any unforeseen asymmetry in the experimental set-up, odour sources were switched to the opposite arm of the olfactometer after each 5 females tested.

The following two-choice experiments were tested: (i) hairy beggarticks vs. clean air; (ii) hairy beggarticks vs. tomato plants; (iii) hairy beggarticks vs. tomato plus hairy beggarticks plants and (iv) tomato plants vs. tomato plus hairy beggarticks plants. Different set of plants and group of females were used for each replicate.

The data of each two-choice olfactometer experiment were analyzed with a log-linear model for contingency tables with Generalized Linear Models (GLM) using a Poisson error distribution (Crawley, 2007). This statistical analysis was done using R (R Development Core Team, 2013) following the method of Crawley (2005).

2.4 Field sampling

Field research was undertaken in three experimental fields ("Fruticultura", "Vale da Agronomia" and "Pomar do Fundão"), located on the campus of the Federal University of Viçosa, Viçosa, Minas Gerais, Brazil (20° 45’ 24” S and 42° 52’ 30” W). Sampling was conducted on irregular intervals, between 08:00 and 12:00 h, from 14 March to 13 June 2013, in randomly selected sites surrounding orchards and horticultural crops in the experimental fields. Hairy beggarticks plants were sampled randomly in each area and we assessed the presence of *C. sanguinea*, of aphids and both together on the plants.

The data were analyzed using a co-occurrence analysis and the distribution of values with a binomial probability test.

3 Results

3.1 Olfactometer experiments

In the olfactometer, *C. sanguinea* females showed a significant preference to odours from hairy beggarticks volatiles when clean air was given as alternative (GLM: Dev = 11.7, d.f. = 1, P = 0.0006) (Figure 1). The preference was homogeneous among the three replicates (GLM: Dev = 0.17, df = 2, P = 0.9202). There was no significant difference between the number of *C. sanguinea* that has moved to the right side or the left side of the olfactometer in all replicates (GLM: Dev = 0.40, d.f. = 1, P = 0.53), showing that the experiment was not affected by factors other than volatiles.

When given a choice between volatiles from hairy beggarticks and volatiles from tomato plants, *C. sanguinea* showed no preference to any of these odor sources (GLM: Dev = 0.27, d.f. = 1, P = 0.61) (Figure 2). The choices were homogeneous among the three replicates (GLM: Dev = 0.94, df = 2, P = 0.6252). There was no significant difference between the number of *C. sanguinea* that had moved to the right side or the left side of the olfactometer in all replicates (GLM: Dev = 0.00, d.f. = 1, P = 1.0), showing that the experiment was not affected by factors other than volatiles.

When *C. sanguinea* was offered a choice between volatiles from hairy beggarticks and volatiles from tomato plants plus hairy beggarticks, there was no preference to any of these odor sources (GLM: Dev = 0.07, d.f. = 1, P = 0.80) (Figure 3). The choices were homogeneous among the three replicates (GLM: Dev = 0.13, df = 2, P = 0.94). There was no significant difference between the number of *C. sanguinea* that had moved to the right side or the left side of the olfactometer in all replicates (GLM: Dev = 0.0007, d.f. = 1, P = 0.98), showing that the experiment was not affected by factors other than volatiles.

Cycloneda sanguinea also did not show preference between the volatiles from tomato plants and volatiles from tomato plants plus hairy beggarticks (GLM: Dev = 3.30, d.f. = 1, P = 0.07) (Figure 4). The choices were homogeneous among the three replicates (GLM: Dev = 1.00, df = 2, P = 0.6065). There was no significant difference between the number of *C. sanguinea* that has moved to the right side or the left side of the olfactometer in all replicates (GLM: Dev = 0.0067, d.f. = 1, P = 0.93), showing that the experiment was not affected by factors other than volatiles.

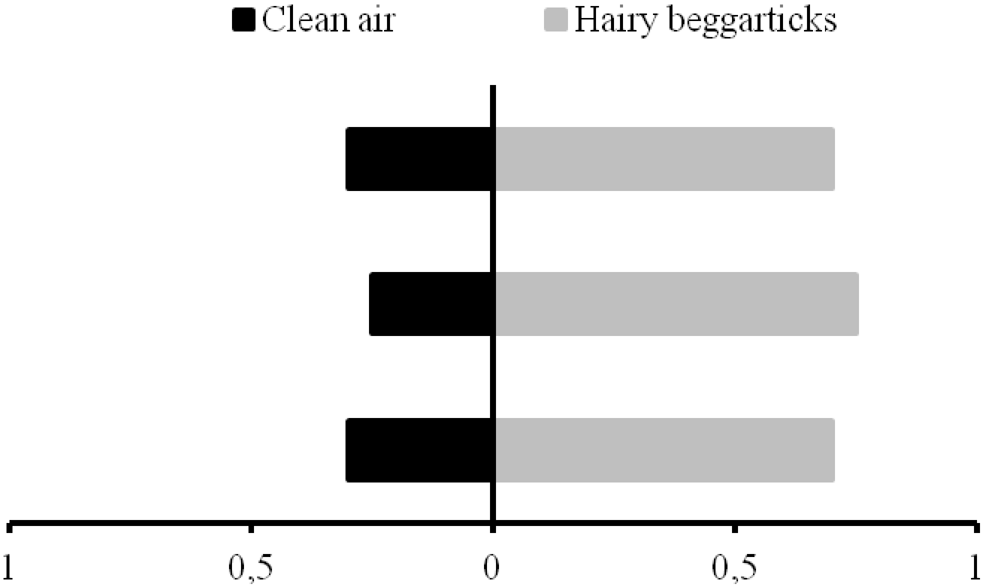

Figure 1: Choice of *Cycloneda sanguinea* females when offered odours of clean air (black bars) vs. hairy beggarticks (gray bars). Each bar represents the result of one replicate, in which 20 ladybirds were tested.

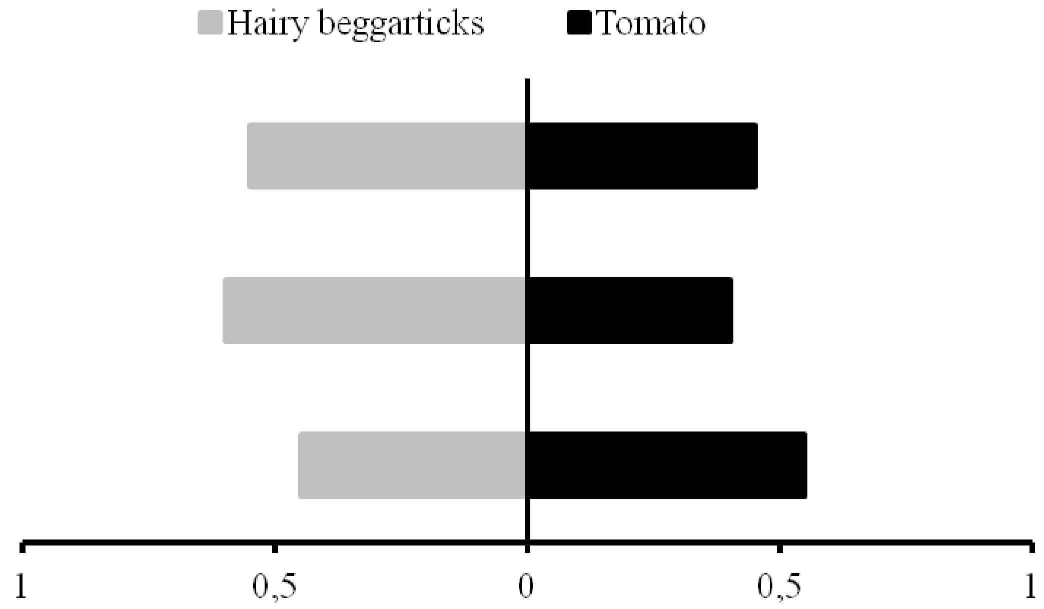

Figure 2: Choice of *Cycloneda sanguinea* females when offered odours of hairy beggarticks (gray bars) vs. tomato plants (black bars). Each bar represents the result of one replicate, in which 20 ladybirds were tested.

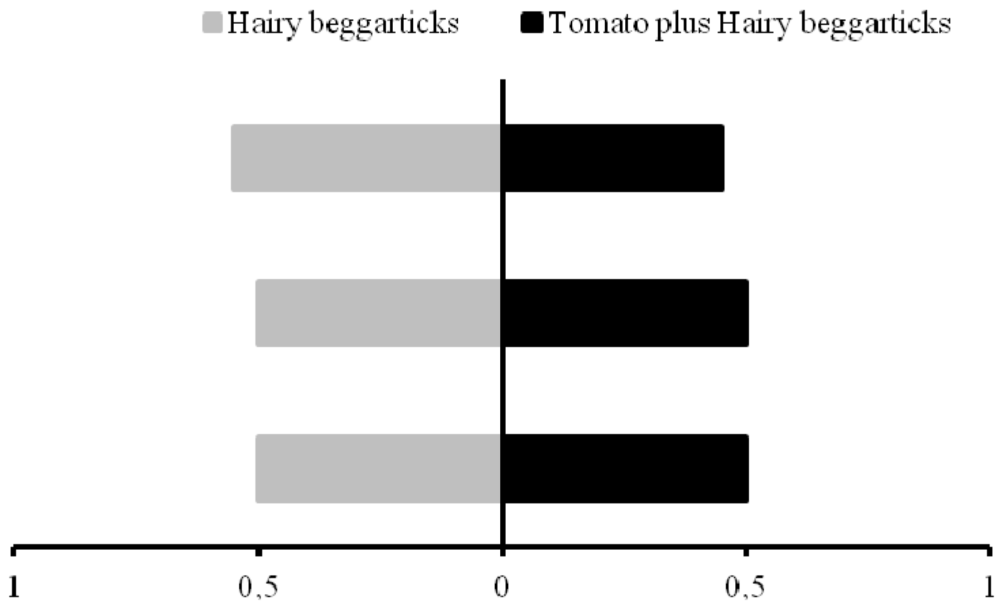

Figure 3: Choice of *Cycloneda sanguinea* females when offered odours of hairy beggarticks (gray bars) vs. tomato plants plus hairy beggarticks (black bars). Each bar represents the result of one replicate, in which 20 ladybirds were tested.

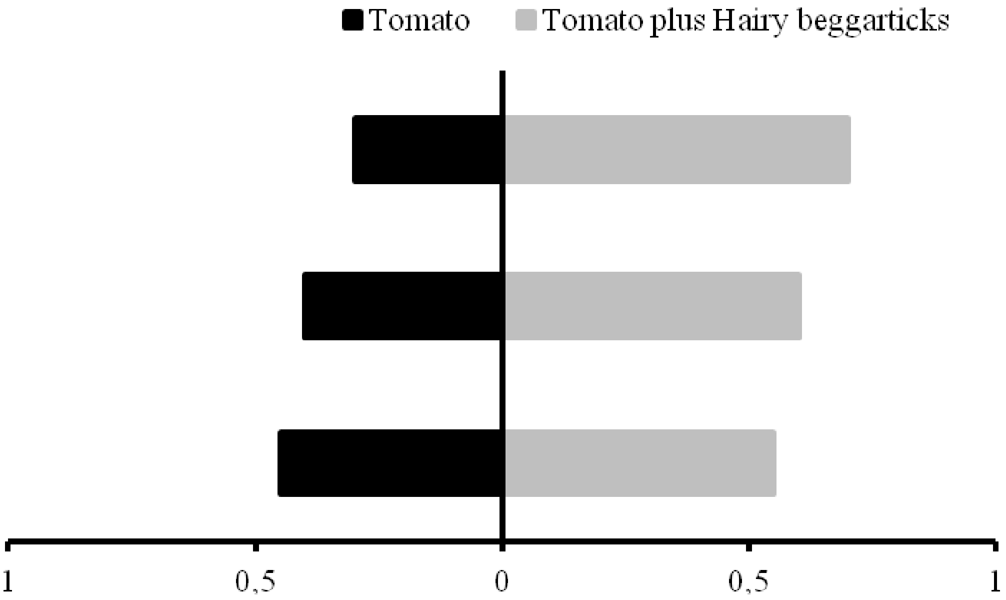

Figure 4: Choice of *Cycloneda sanguinea* females when offered odours of tomato plants (black bars) vs. tomato plants plus hairy beggarticks (gray bars). Each bar represents the result of one replicate, in which 20 ladybirds were tested.

3.2 Field sampling

To assess if the occurrence of *C. sanguinea* in hairy beggarticks plants depended on the presence of aphids, we sampled a total of 1400 plants in three experimental fields. The observed number of plants with both aphids and ladybirds were not significantly different than the expected number in all three areas: “Pomar do Fundão” (Binomial test: P=0,82), “Fruticultura” (Binomial test: P=0,70) and “Vale da Agronomia” (Binomial test: P=0,80).

4 Discussion

The volatiles that plants synthesize in the absence of attacks by phytophagues are known as constitutive volatiles and some natural enemies can use these volatiles emitted by undamaged plants to locate the habitats of herbivores (Elzen *et al.*, 1983; Benrey *et al.*, 1997; Takabayashi *et al.*, 1998). However, attraction by constitutive volatiles among predatory species is poorly known (Vet & Dicke, 1992) and there are only few reports suggesting that volatiles from specific plants can be attractive to coccinellids.

Our olfactory choice experiments showed that females of *C. sanguinea* were attracted to volatiles of the weed hairy beggarticks when clean air was given as alternative. The response of predators to constitutive plant volatiles is only evolutionary stable if the predators gain advantage from visiting the plant (Altieri & Whitcomb, 1979; Price *et al.*, 1980). Accordingly, *C. sanguinea* attraction may be due to the fact that hairy beggarticks provides alternative resources that increase survival of adults and larvae of *C. sanguinea*, as revealed by Amaral *et al.* (2012). Our experiments on the second chapter also show that hairy beggarticks can significantly increase survival of adults of *C. sanguinea.* Ninkovic & Pettersson (2003) demonstrated that the ladybird *Coccinella septempuctata* was attracted to odour sources from two common weeds (*Cirsium arvense* and *Elytrigia repens*). Another study with the same ladybird testing ethanol extracts from 22 plant species showed that most plants were neutral in terms of olfactory attraction, some repelled, while only volatiles produced by the weeds *Berberis vulgares* and *Tripleurospermum inodoratum* were attractive to *C. septempuctata* (Schaller & Nentwig, 2000). All plants that were attractive to this coccinellid in both studies are also used as alternative resource by *C. septempuctata* (Schmid, 1992).

The field sampling present here, showed that the occurrence of *C. sanguinea* on hairy beggarticks plants does not depend on presence of aphids. The use of alternative resources from hairy beggarticks by *C. sanguinea* is possible the reason why this predator once attracted remains on these plants even in the absence of aphids. Schmid (1992) in a field survey of the abundance of coccinellids in herbaceous plants found 40% of the coccinellids on plants without aphids and also concluded that the use of alternative resources by coccinellids may account for the ladybirds visiting uninfested plants. For most predaceous coccinellids, non-prey foods are an integral component on their diet and feeding preferences vary widely (Giorgi *et al.*, 2009). Coccinellids polyphagy served as an evolutionary stepping stone for primarily predaceous groups to adopt new feeding habits (Giorgi *et al.*, 2009; Magro *et al.*, 2010). Aphidophagy evolved before non-prey feeding habits, but in some instance they recognized these abundant resources as food, and become to respond behaviorally to its availability within a habitat (Giorgi *et al.*, 2009; Lundgren, 2009). Thus, the presence of plants that provide alternative resources may be an indicator of habitat quality to predatory coccinellids that evolved the ability of assessing this information (Ninkovic & Pettersson, 2003; Giorgi *et al.*, 2009).

Although *C. sanguinea* were attracted to hairy beggarticks when clean air was given as alternative, in our experiments the ladybird did not show preference when offered a choice between volatiles from hairy beggarticks vs. volatiles from tomato plants. Sarmento *et al.* (2008) also using a Y-tube olfactometer, showed that *C. sanguinea* preferred clean air over tomato plants and concluded that tomato plants do not produce odors that are attractive to such predator. However, the tomato plants that these authors used were on the vegetative stage, without flowers, and therefore with no alternative resources to offer to the predator, which may be the reason why *C. sanguinea* preferred clean air. In our experiment *C. sanguinea* did not distinguish the volatiles of hairy beggarticks than tomato plants, which may be due to the ability of this predator to recognize different compounds from both plants or even the same compound can be released by these plants, for example volatiles from flowers. Additionally, the volatile blend from different plants have different chemical compositions and therefore are not equal in terms of food quality for coccinellids and so a preference for certain plants is likely to develop (Smith, 1961; Vet & Dicke, 1992).

When we tested hairy beggarticks and tomato plants with the intercropping hairy beggarticks plus tomato plants, *C. sanguinea* also did not show any preference. Isolated plants may not be sources of infochemicals for predators but may contribute to the mixture of compounds emitted by other plants and then be attractive or repellent to predators (Ninkovic & Pettersson, 2003). In our results the intercropping had no effect on *C. sanguinea* differing from the finding by Togni (unpublished data), where intercropping of the herb *Coriandrum sativum* plus tomato plants was significantly more attractive to this ladybird than the tomato or the herb isolated. Ninkovic & Pettersson (2003) also showed a significantly more positive response by the ladybird *C. septempunctata* to mixed odours of barley intercropped with two weed species than to barley alone. In both studies cited above no aphids or pollen resources were present on the plants, suggesting that cues from plant-plant communication may also play role in the attraction of predators towards prey habitat. Moreover, increased botanical diversity has frequently been discovered in connection with mixed cropping and positive effects on natural enemies (Norris & Kogan, 2005; Pettersson *et al.*, 2008).

In conclusion, our results suggest that hairy beggarticks constitutive volatiles can be an important chemical stimulus on the foraging behavior of *C. sanguinea* since the plant provides alternative resources that may contribute to the persistence of this predator in the field when prey are not available, which might affect positively their efficiency as biological control agent.

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Effects of the weed *Bidens pilosa* on oviposition and survival of the predatory ladybird *Cycloneda sanguinea*

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Abstract

There is a range of habitat management approaches that can provide non-prey resources to generalist predators with broader feeding habits and habitat requirements. The conservation of weed community has extensively adopted for habitat management, resulting in an increase of many predator and parasitoid populations in agroecosystems. Alternative resources provided by weeds include pollen, nectar and plant sap, sites for oviposition or protection against other unfavorable conditions. Such resources are often required for predatory coccinellids reproduction and survival, hence, affect their effect on plant pests. I studied the effects of the weed hairy beggarticks (non-crop) whether intercropping with tomato plants (main crop), on the oviposition rate and survival of the generalist predator *Cycloneda sanguinea*. The alternative resources provided by the hairy beggarticks and tomato plants, either together or not, did not affect the oviposition rate of *C. sanguinea*, both in the presence and absence of aphid prey. However, a diet with only the resources provided by the plants tested here is not enough to promote their oviposition. Nevertheless these resources can increase adult survivorship significantly. Survival of *C. sanguinea* was significantly higher on the combination of tomato plants plus hairy beggarticks than on tomato plants only but was not different from the hairy beggarticks alone. Therefore, hairy beggarticks can perform a vital role in the diet of *C. sanguinea*, allowing them to persist when prey resources are scarce which could be essential for their ability to respond quickly to aphids once they colonize the crops, improving the natural control of such pests.

1 Introduction

The main biotic cause determining the numbers and fluctuations of insect herbivore populations in agricultural ecosystems is the mortality caused by predators, parasitoids and pathogens (Rosenheim *et al.*, 1999; Symondson *et al.*, 2002). This has led to an increasing use of these natural enemies in insect pest management programs and special attention has been devoted to the role of generalist predators as biological control agents (Wiedenmann & Smith, 1997; Riudavets & Castane, 1998; Rosenheim *et al.*, 1999). In contrast to specialist species, generalist predators do not engage in density dependent predator-prey dynamics with one single prey species (Hassell & May, 1986; Hajek, 2004) and they can act as intraguild predators, occasionally limiting their effectiveness at controlling herbivore populations (Rosenheim *et al.*, 1993; Polis & Strong, 1996; Snyder & Ives, 2001). On the other hand, the ability of generalist predators to explore non-prey resources enables them to persist in crops even in the absence of pests, thus preventing outbreaks after pest invasions (Wiedenmann & Smith, 1997; Eubanks & Denno, 2000; van Rijn *et al.*, 2002).

There is a range of habitat management approaches that can provide non-prey resources to generalist predators with broader feeding habits and habitat requirements (Rosenheim *et al.*, 1999; Wäckers *et al.*, 2005; Sloggett *et al.*, 2008). Among these approaches, the conservation of the weed community has been extensively adopted for habitat management, resulting in an increase of many predator and parasitoid populations in agroecosystems (Altieri & Whitcomb, 1979; Nentwig, 1998; Gurr *et al.*, 2003; Norris & Kogan, 2005; Amaral *et al.*, 2012). Alternative food resources provided by weeds include pollen, nectar and plant sap, which can attract and arrest a diverse community of arthropod predators such as ladybirds, which are coccinellid predators, widely used as biological control agents for many pests, mainly aphids (Nentwig, 1998; Obrycki & Kring, 1998; Landis *et al.*, 2000; Burgio *et al.*, 2006).

Coccinellids are true polyphagous opportunists that use a wide range of food sources. When prey are scarce or of low quality, pollen and nectar are believed to be the most important foods (Benton & Crump, 1979; Hemptinne & Desprets, 1986; Triltsch, 1999; Lundgren, 2009). At least 39 coccinellid species have been recorded consuming more than 88 species of pollen (Lundgren, 2009) and 41 species were found feeding at extrafloral nectaries of plants from 15 families (Pemberton & Vandenberg, 1993). In addition to providing alternative food, several weed species also provide excellent sites for oviposition or protection against other unfavorable conditions (Landis *et al.*, 2000). The resources provided by weed seem to have direct effects on the density of some coccinellids and weeds are often required for coccinellid reproduction and survival, hence, affect their effect on plant pests (Norris & Kogan, 2005; Bianchi & Wäckers, 2008).

However, the effects of weed communities on predators and parasitoids have been variable (Heimpel & Jervis, 2005). Some studies report positive effects on pest control (Wyss, 1996; Nicholls *et al.*, 2001; Sengonca *et al.*, 2002), others found no effects (Hausammann, 1996) or negative effects (Baggen & Gurr, 1998; Cottrell & Yeargan, 1998). Therefore, knowledge of the key processes that drive the interactions between plants, pests and their natural enemies are important for managing habitats in order to increase essential ecosystem services such as natural pest control (Burgio *et al.*, 2006; Bianchi & Wäckers, 2008).

In order to better understand the ecological role of non-crop plants on generalist predators, I studied the effects of the weed *Bidens pilosa* L. (Asteraceae), known as hairy beggarticks, on the generalist predator *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae). My goal was to determine whether intercropping hairy beggarticks (non-crop) with tomato plants (main crop) increases the oviposition rate and survival of *C. sanguinea*.

2 Materials and methods

2.1 Predator rearing

Cycloneda sanguinea was collected on 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, Viçosa, Minas Gerais, Brazil (20° 45' 24" S and 42° 52' 30" W). Individuals were taken to the laboratory and kept under controlled temperature (25 ± 2 °C), humidity (70 ± 10% RH) and photoperiod (12:12 L:D). They were placed in transparent plastic pots (500 ml) with an opening in the lid covered with mesh. They were fed with aphids (*Myzus persicae* and *Macrosiphum euphorbiae*), honey and water. *Myzus persicae* was reared in a greenhouse on cabbage plants (*Brassica oleracea* v. capitata L.), *M. euphorbiae* was collected in the field.

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

2.2 Plant material

In a greenhouse, hairy beggarticks (*Bidens pilosa* L.) and tomato plants (*Solanum lycopersicum*, variety Aguamiel, Vilmorin®) were sown in polystyrene trays (8 × 16 cells), using a commercial plant substrate (Bioplant®, Bioplant Misturadora Agrícola LTDA) composed of vermiculite plus organic fertilizer. 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 gauze (90 μm) to avoid infestation with herbivores. The plants were watered and fertilized with NPK (20-05-20) and superphosphate according to need. For the experiments, we used plants in the reproductive stage, with similar numbers of flowers.

2.3 Oviposition experiment

This experiment was conducted to verify the role of the hairy beggarticks, intercropped with tomato plants, as alternative food source for egg production by *C. sanguinea.* The tests consisted in the exposure of adult ladybirds to hairy beggarticks and to tomato plants, placed in cages (1.20 × 0.60 m) made of PVC tubes covered with mesh, outside the laboratory. Only *C. sanguinea* couples that produced eggs on a diet of aphids and water in plastic pots (500 ml) in the laboratory were used.

Three couples of which the females were ovipositing were released in each cage. There were four replicates of the following treatments: (i) a cage with one hairy beggarticks; (ii) a cage with one hairy beggarticks plus one tomato plant and (iii) a cage with one tomato plant. The twelve cages were placed alternately in the same sequence above. The oviposition rate was assessed daily during 5 days, and the plants were replaced daily to facilitate the counting of eggs. After 5 days, the females had stopped ovipositing, and we subsequently placed aphids inside the cages to verify whether this would restore oviposition. Ample amounts of aphids were offered confined in a Petri dish to avoid infestation of the plants. The oviposition rate was evaluated for 5 more days in the presence of aphids. The data from oviposition in the absence and in the presence of aphids were analysed using a linear mixed-effects model (LME). Numbers of eggs were log-transformed to stabilize variance.

2.4 Survivorship analysis

We evaluated the survival of adults of *C. sanguinea* using hairy beggarticks, 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, adult couples were released in cages (1.20 × 0.60 m) made of PVC tubes covered with mesh containing the plants placed outside the laboratory. There were four treatments, each with four replicates: (i) a cage with one hairy beggarticks; (ii) a cage with one hairy beggarticks plus one tomato plant; (iii) a cage with one tomato plant and (iv) control. Control treatments consisted of the empty cage only. The sixteen cages were placed alternately in the same sequence as above. Survival was assessed daily until most individuals had died.

Survival data were analyzed with a Cox proportional hazards model (CPH). The Kaplan-Meier estimator, which uses algorithms taking into account censored data, was used to produce estimates of survival.

All statistical analyses were done using R (R Development Core Team, 2013) following the method of Crawley (2005).

3 Results

3.1 Oviposition experiment

The oviposition of *C. sanguinea* was not significantly affected by the plants in both the presence (LME: L-ratio = 0.67; df=2; P= 0.71) and absence of aphids (LME: L-ratio = 1.15; df=2; P= 0.56). In the absence of aphids, ladybird oviposition decreased over time and stopped completely after 3 days (LME: df= 2; P= 0.0001), (Figure 5, days 1 to 5). Because the ladybirds were reared on a diet with aphids prior to the experiments, the oviposition observed in the first 3 days was possibly due to this previous diet. The females started the oviposition again only after they were supplied with aphids (LME: df= 2; P= 0.0001), (Figure 5, days 6 to 10). We conclude that plant resources alone are not sufficient for oviposition of the ladybirds.

3.2 Survivorship analysis

Survivorship of adult couples of *C. sanguinea* was significantly affected by the treatments (CPH: L-ratio = 32.37; df= 3; P=0.0001). Cumulative survival was significantly higher on the combination of tomato plants plus hairy beggarticks (CPH: df=3; P=0.001) than on tomato plants and on the control. Survival on tomato plants plus hairy beggarticks did not differ from that on hairy beggarticks alone. Survivorship on hairy beggarticks was significantly higher than in the control (CPH: df= 3; P= 0.001), but not different from that on tomato plants. Tomato plants were not different from the control (CPH: df=3; P= 0.12) (Figure 6).

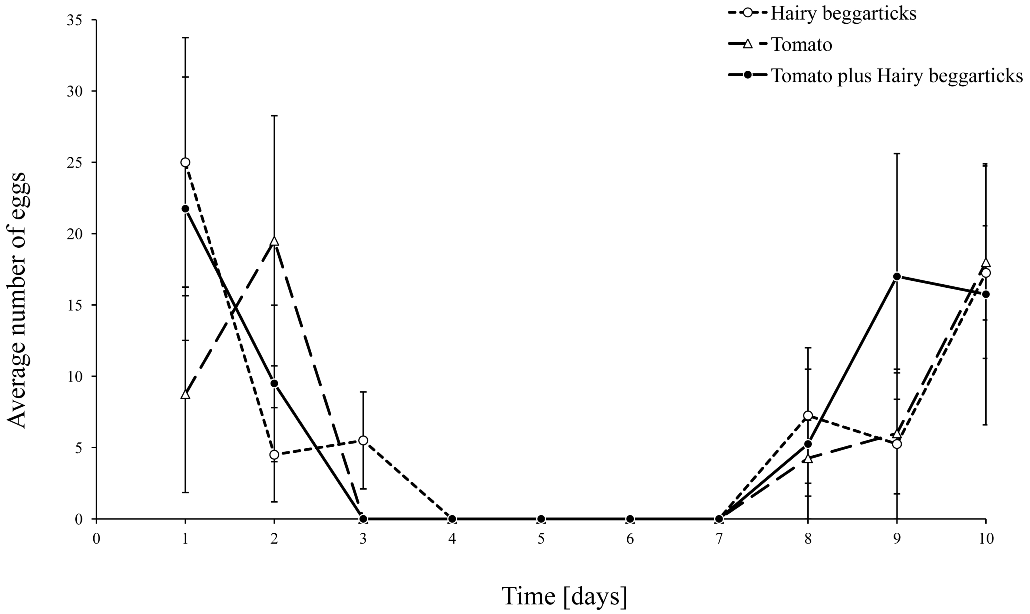

Figure 5: Oviposition (± SEM) of *C. sanguinea* on hairy beggarticks plants, hairy beggarticks plus tomato plants and tomato plants, both in the absence (days 1 to 5) and presence of aphids (days 6 to 10).

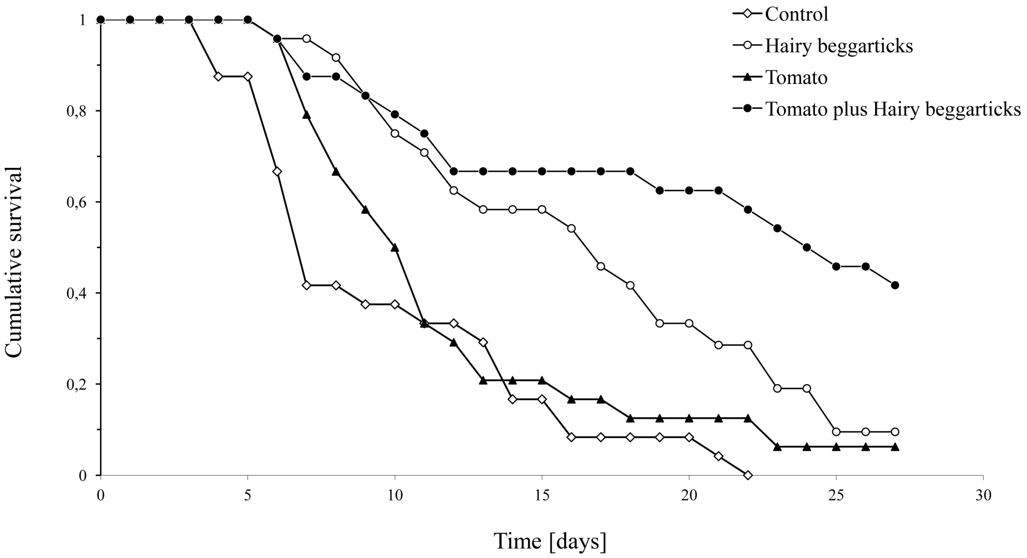

Figure 6: Survivorship of adult couples of *C. sanguinea* through time on hairy beggarticks, tomato plants, tomato plants plus hairy beggarticks and on the control.

4 Discussion

The alternative resources provided by the hairy beggarticks and tomato plants, either together or alone, did not affect the oviposition rate of *Cicloneda sanguinea*, both in the presence and absence of aphid prey. Michaud (2000) demonstrated that a mixed diet with pollen from a noxious weed of the ice plant family and citrus aphids (*Toxoptera citricida*) also do not improve oviposition of *C. sanguinea* females. However, many other coccinellids species such as *Harmonia axyridis* and *Hippodamia tredecimpunctata* do show an increase in oviposition with a diet containing plant resources and aphid prey (Cottrell & Yeargan, 1998; Lundgren *et al.*, 2004).

In our study, the oviposition of *C. sanguinea* decreased until it stopped completely when fed on a diet consisting only of the resources provided by the plants. However, when aphid prey were added to the diet, *C. sanguinea* oviposited again, showing that the females were capable of producing eggs. In the absence of high quality food (aphids), some coccinellids initiate a physiological shift in nutritional resources from reproduction to fat storage, inducing reproductive diapauses to use the energy to increase survival (Reznik & Vaghina, 2006). Other studies with generalist predatory ladybirds have also reported that plant resources alone do not allow egg production (Hemptinne & Desprets, 1986; Lundgren, 2009), with the species *Coleoegilla maculata* being an exception (Lundgren & Wiedenmann, 2004). Thus, our results suggest that a diet with only the resources provided by the plants tested here is not enough to promote the oviposition of *C. sanguinea*. Additionally, we observed that *C. sanguinea* preferred (93%) to oviposit on the walls of the cage rather than on the plants. This may be further evidence that these plants do not affect oviposition.

It is important to note that the consumption of nectar and pollen undoubtedly varies among coccinellids species and developmental stage (Lundgren, 2009; Amaral *et al.*, 2012). Also, the nutritional value of such resources to coccinellids can vary significantly among plant species (Lundgren & Wiedenmann, 2004; Lundgren, 2009). Understanding such variation in food requirements among natural enemies species is critical to determine the importance of different non-crop plants on the development of an effective habitat management for sustainable pest control (Bianchi & Wäckers, 2008; Amaral *et al.*, 2012).

Although the resources provided by hairy beggarticks and tomato plants did not improve the oviposition of *C. sanguinea*, the research presented here revealed that such resources can increase adult survivorship significantly. Survival of *C. sanguinea* was significantly higher on the combination of tomato plants plus hairy beggarticks than on tomato plants only but was not different from the hairy beggarticks alone. These results support previous findings by Amaral *et al.* (2012) that non-crop plant can increase survival of adults and larvae of *C. sanguinea*. Even though the consumption of nectar and pollen rarely supports reproduction in coccinellids on its own, it may contribute to flight energy (Nedvěd *et al.*, 2001), to fuel migrations and providing limited nutrients and energy that can dramatically increase survival in the absence of prey (Matsuka *et al.*, 1982; Dreyer *et al.*, 1997; Hodek *et al.*, 2012).

In conclusion, our survivorship analysis demonstrated that hairy beggarticks can perform a vital role in the diet of *C. sanguinea*, allowing them to persist when prey resources are scarce. In the context of biological control, the persistence of *C. sanguinea* in the absence aphids could be essential for their ability to respond quickly to aphids once they colonize the crops. Therefore, this study provides an important framework for pest managers on the utilization of hairy beggarticks to manipulate the abundance of *C. sanguinea* and ecological services provided by them as biological control agents. Finally, it suggests that the management of specific weed species might offer a favorable approach for the conservation of natural enemies that exploit alternative resources from plants.

5 References

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General Conclusions

Females of *Cycloneda sanguinea* are able to recognize cues from the weed hairy beggarticks but they do not discriminate between cues from hairy beggarticks or tomato plants. These predatory ladybirds do not show preference when offered hairy beggarticks or tomato plants with the combination hairy beggarticks plus tomato plants. In the field, the occurrence of *C. sanguinea* on hairy beggarticks plants does not depend upon presence of aphids. These results suggest that *C. sanguinea* can use constitutive volatile cues from hairy beggarticks to forage, since they gain advantage from visiting the plant, such as nectar and pollen, alternative prey and hosts, and favourable microclimate.

The alternative resources provided by the hairy beggarticks and tomato plants, either together or not, did not affect the oviposition rate of *C. sanguinea*, both in the presence and absence of aphid prey. Oviposition decreased until it stopped completely when fed on a diet consisting only of the resources provided by the plants. However, when aphid prey were added to the diet, *C. sanguinea* started to oviposit again, showing that the females were capable of producing eggs. Thus, these results suggest that a diet with only the resources provided by the plants tested here is not enough to promote the oviposition of *C. sanguinea*.

Although the resources provided by hairy beggarticks and tomato plants did not improve the oviposition of *C. sanguinea*, these resources can increase adult survivorship significantly. Survival of *C. sanguinea* was significantly higher on the combination of tomato plants plus hairy beggarticks than on tomato plants only but was not different from the hairy beggarticks alone. This demonstrates that hairy beggarticks can perform a vital role in the diet of *C. sanguinea*, allowing them to persist when prey resources are scarce.

Finally, our results suggest that constitutive volatiles of hairy beggarticks can be an important chemical stimulus on the foraging behavior of *C. sanguinea*, since the plant provides alternative resources that may contribute to the persistence of this predator in the field. In the context of biological control, the persistence of *C. sanguinea* in the absence of aphids could be essential for their ability to respond quickly to aphids once they colonize the crops which might improve its efficiency as biological control agent.