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Linking litter and canopy food webs to protect ornamental crops

Muñoz Cárdenas, K.A.

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Alternative food for litter-inhabiting predators decreases pest densities and above-ground plant damage

Karen Muñoz-Cárdenas, Diana Rueda-Ramirez, Firdevs Ersin, Farid Faraji & Arne Janssen

Biological control using generalist predators is successful in many crops. Such predators feed on pests and food or alternative prey that do not cause economic damage to the plants. Adding food for predators to a crop has a positive effect on their numerical response. Thus, more predators are available to potentially attack the pest, reducing their densities (apparent competition). However, in the short term, the addition of alternative food may decrease the attack of pests because the predators are satiated or because they preferentially feed on the alternative food (apparent mutualism). Such positive effects of alternative food on pest densities may occur repeatedly when populations of pests or of alternative food fluctuate. We investigated whether providing generalist litter-inhabiting predators with alternative prey in the litter can increase control of thrips, *Frankliniella occidentalis*. The larvae of this pest feed on above-ground plant parts, causing significant damage, but prepupae and pupae live in the litter layer. Densities of thrips and damage on above-ground plant parts were significantly reduced when supplying litter-inhabiting predators, predominantly *Cosmolaelaps* n. sp., with alternative food. Subsequently, *Cosmolaelaps* n. sp. was tested separately; this species alone also reduced thrips densities and damage significantly when it was supplied with alternative food. Concluding, litter-inhabiting predators can significantly reduce above-ground plant damage when supplied with alternative food in the litter layer.

Introduction

Generalist predators can efficiently control pest populations in crops (Fleschner 1959; Ramakers 1990; Symondson et al. 2002; van Rijn et al. 2002; Messelink et al. 2008, 2010). They can act as a link between above-ground and below-ground food webs (Scheu 2001; Muñoz-Cárdenas et al. 2014, 2017) when they feed on above-ground plant pests but also on below-ground prey such as herbivores and detritivores (Settle et al. 1996; Muñoz-Cárdenas et al. 2017). Alternative foods allow generalist predators to survive and reproduce when densities of the target pest are low (Settle et al. 1996; Wäckers et al. 2005; Liu et al. 2006), and they can also result in lower pest densities in the long term due to a negative indirect interaction between the pest and the alternative food. In short, this interaction works as follows: the addition of alternative food results in higher densities of the predators, resulting in lower densities of the pest (so-called apparent competition; Holt 1977). However, adding food for predators to the crop can also result in higher pest densities (so-called apparent mutualism; Holt 1977; Abrams & Matsuda 1996), and this is obviously detrimental for biological control (van Maanen et al. 2012). The mechanism behind this is that in the short term, predators might concentrate their attacks on the alternative prey or become satiated by feeding on this prey, freeing the target pest from attacks. Concluding, adding alternative food for predators may not always result in better pest control and this needs to be verified for each combination of predator and prey species and alternative food type.

Several studies in vegetable crops have demonstrated the benefits of additional herbivorous prey or supplementary food for plant-inhabiting predators on biological control of above-ground pests (Collyer 1964; Karban et al. 1994; van Rijn et al. 1999, 2002; Liu et al. 2006; Messelink et al. 2008). In contrast, biological control in ornamentals has been less successful because of the much lower damage thresholds. This could in theory be solved by adding more alternative food, resulting in higher predator populations. The obvious danger of adding more alternative food are that it may result in decreased pest suppression (apparent mutualism). Another problem could be that consumers might not be prepared to accept a product with alternative food or alternative prey on it, even when these do not damage the product. Thus, a solution would be supplying alternative food to increase populations of potential biological control agents away from the marketable part of the crop, for example in the litter or in the parts of the plant that are not sold.

A few studies have investigated the effect of adding alternative food below-ground to control pests on the above-ground plant parts. Some of these studies showed a positive effect on biological control, other studies showed negative effects, reminiscent of apparent mutualism (Settle et al. 1996; Birkhofer et al. 2008; Muñoz-Cárdenas et al. 2017). In a previous study, we show that a generalist predatory mite

[*Amblyseius swirskii* (Athias-Henriot)] can act as a link between above-ground and below-ground food webs by feeding on an above-ground plant pest [*Frankliniella occidentalis* (Pergande)] but making excursions to feed on alternative prey (astigmatic mites) below-ground (Muñoz-Cárdenas et al. 2017). Adding this alternative prey resulted in improved biological control of thrips and higher densities of predators on the above-ground plant parts. In some experiments, we observed that predators that naturally inhabit the litter also fed on the alternative prey and on pupae of *F. occidentalis* (western flower thrips), which occur in the litter (Muñoz-Cárdenas et al. 2017). In this paper, we investigate the suitability of these predators for biological control of thrips in roses.

Some predatory mites from the soil and litter are known to play an important role in controlling insect pests with edaphic stages such as thrips (Wu et al. 2014), especially when they are released in combination with other biological control agents (Gillespie & Quiring 1990; Premachandra et al. 2003; Wu et al. 2016). In some cases, releases of commercially available soil-inhabiting predators have resulted in satisfactory reduction of thrips populations, but only when released in high numbers (Wiethoff et al. 2004). Such high densities of soil-inhabiting predators could also be obtained by adding alternative prey to the soil or litter, thus increasing predator populations. However, the effect of adding alternative prey on the population dynamics of litter-inhabiting predators and above-ground pests has not been studied. The goal of this study is to assess whether biological control of thrips can be increased by supplying litter-inhabiting predators with alternative prey. We collected litter with predatory mites from a commercial greenhouse and tested the two most common predatory mites for their capacity to feed on the alternative prey and on thrips. Subsequently, two experiments were done to assess the capacity of the predators to control thrips damage on rose plants; one experiment with multiple predatory mite species and one with the most promising species.

Materials and methods

The experimental system

We studied rose plants, which are often damaged by the western flower thrips (Park et al. 2002; Manners et al. 2013). Above-ground plant parts of many crops are affected by this thrips species, which spends part of its life cycle in the soil or litter (Tommasini & Maini 1995; Lewis 1997). The alternative prey used here was *Carpoglyphus lactis* (L.), an astigmatic mite commonly found in the litter of commercial rose crops in The Netherlands (Muñoz-Cárdenas et al. 2017). These mites are not considered a pest in roses and are used for mass-rearing of predatory mites (Ramakers & van Lieburg 1982; Bolckmans & van Houten 2006).

Cultures

Rose plantlets were bought when they were 4 weeks old and had 4-5 leaves (*Rosa* sp. var. *Avalanche*) (Olij Rozen Int. BV, De Kwakel, The Netherlands). Because these plants had been kept in a commercial greenhouse, there was a risk that they were contaminated with pests. In order to eliminate these, we removed the leaves and washed the stems and roots under running tap water. Subsequently, the remaining plant parts were dried and planted in clean peat. They were allowed to regrow for 4 weeks in a greenhouse compartment (22 °C, RH 70%, photoperiod L14:D10) inside insect-proof cages to avoid new contaminations. The regrown plants were inserted in rock wool strips (Grodan®Delta: 40 × 6 × 28), were watered twice a week, and macro- and micronutrients were applied dissolved in water once a week (0.5 g N-P-K and 0.5 g micronutrients mix/200-500 ml of water/plant). Before the first experiment, *P. persimilis* (Spidex®, Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands) was preventively released (20 per cage) to avoid contamination with spider mites.

Frankliniella occidentalis was taken from the stock colony of Koppert Biological Systems. They were reared (at 23 °C, RH 65%) using a method adapted from Loomans & Murai (1997). In short, thrips were reared on fresh bean pods inside plastic containers (8 × 8 × 12 cm) with openings covered with mite-proof mesh (30 µm) for ventilation. Around 200 adult thrips were introduced in a rearing unit and allowed to oviposit in two bean pods for 1 or 2 days to obtain cohorts to be used in the experiments. Before use, the pods were washed with soap, rinsed and dried to remove residues of pesticides. *Typha latifolia* pollen was provided as food for the thrips. This pollen was collected during spring from plants growing on the campus of the University of Amsterdam. *Carpoglyphus lactis* were provided by Koppert Biological Systems and were reared as explained in Muñoz-Cárdenas et al. (2017), inside cylindrical plastic containers (8 cm diameter, 12 cm high) to which 5 g of bran plus 5 g of yeast were added as food once per week. To facilitate the release of *C. lactis* in experiments, we counted *C. lactis* per mg of the mixture of bran and yeast from the rearing unit and added the appropriate weight of the mixture to the experimental units to end up with the desired numbers of *C. lactis* females per experimental unit.

Litter-inhabiting predators that benefit from alternative prey

In previous experiments, we observed that predators inhabiting the moss and litter in commercial greenhouses might play a role in controlling thrips when alternative food (*C. lactis*) was added to the litter (Muñoz-Cárdenas et al. 2017). For this reason, we did not collect the mite fauna directly from the samples taken in the commercial greenhouses, but we selected mites that could reproduce on *C. lactis*. To this end, we collected five samples of 1.5 l of various materials from different rose greenhouses in The Netherlands: 1) litter covering the soil in Amstelveen in October, 2011 and

2) in December, 2013; 3) litter from Stompwijk, July 2012; 4) moss growing on the surface of rock wool strips where plants were grown from Aalsmeer, January 2013; and 5) old, open flowers from Amstelveen, July 2013. These latter flowers are non-marketable, and their stems are bent as a common practice. When those flowers develop they can be found touching the litter layer, thus serving as bridges between the above-ground plant parts and the litter. Samples were placed on top of humid rock wool (Grodan®Delta: 28 × 6 × 28) in a plastic tray and spread c. 100 g of food (c. 4000 *C. lactis* females plus bran) on top of the samples. Each tray was placed inside a mite-proof cage (47.5 × 47.5 × 92 cm) in a greenhouse compartment. After 10 days, we collected each sample and placed it in a Berlese funnel for 5 days.

The predatory mites were collected in vials with alcohol 70% for taxonomic identification. Most predators were found in the litter samples; only few were found in the moss and open flowers, we therefore refer to them as litter-inhabiting predators. Predatory mites were mounted on glass slides with Hoyer's medium. Subsequently, they were observed under a phase contrast microscope and taxonomic keys were used for identification (Krantz & Ainscough 1990; Lindquist et al. 2009). Adult females were identified to species, based on the original and complementary descriptions. An extra sample (1.5 l of litter) was taken from the greenhouse in Amstelveen in December 2013 in order to extract live mites to set-up cultures of the most common predatory mites (*Cosmolaelaps* n. sp. and *Proctolaelaps pygmaeus*) in the laboratory (22 °C). Rearing units consisted of plastic containers (125 ml) with humid plaster of Paris mixed with coal at the bottom (Lesna et al. 2009). Peat mixed with autoclaved rose litter was added on top of the plaster. We introduced 50 adult females of *Cosmolaelaps* n. sp. or *P. pygmaeus* to each rearing unit. The plastic containers with the colonies were placed inside a tray with water to increase humidity, the tray was covered with another plastic tray to shield from direct light. A mix of bran with fresh yeast and *C. lactis* (30 g) were added to each container as food for the predators once per week. We collected around 10 individuals from the colonies, three times during this study for identification.

Predation of *Frankliniella occidentalis* and *Carpoglyphus lactis* by *Cosmolaelaps* n. sp. and *Proctolaelaps pygmaeus*

This experiment was performed to assess whether the litter-inhabiting predatory mites *Cosmolaelaps* n. sp. and *P. pygmaeus* feed on thrips and the alternative prey *C. lactis*. Twenty *P. pygmaeus* females and 30 *Cosmolaelaps* n. sp. females were taken from the rearing units and starved individually by placing each in a vial (3 cm diameter, 4 cm high) with a moistened bottom of plaster of Paris mixed with charcoal (Lesna et al. 2009). The next day, we added 10 protonymphs of *C. lactis* to the vials of one group of females of each species (10 females of *P. pygmaeus* and 15 females of *Cosmolaelaps*

n. sp.), and we added three thrips pre-pupae to the vials of second groups of predators (same numbers as above). We added pieces of dried leaves to simulate the structure of the litter. One day later, we scored how many individuals of each prey were eaten. This experiment was carried out at 25 °C, RH 60%, and photoperiod L16:D8.

Thrips control by litter-inhabiting predators

Litter was collected in plastic bags from a commercial greenhouse (Amstelveen, April, 2014) and was kept in a cold room (4 °C) until the beginning of this experiment in May, 2014. This litter harboured different predator species inhabiting the commercial greenhouse. In a greenhouse compartment at the University of Amsterdam, experimental units consisted of two rose plants in rock wool in a mite-proof cage (47.5 × 47.5 × 92 cm). During the first week of the experiment, 1 l of litter moistened with 100 ml of water was placed at the foot of the rose plants. Around 2 h later, c. 100 g of bran with alternative prey (c. 4000 *C. lactis* females) was dispersed on the litter of three of the experimental units; six other cages received bran without alternative prey. The three treatments (predators with or without alternative prey and the control with only thrips) were replicated three times (three cages). Subsequently, for the treatment with alternative prey, 30 adult females of *Cosmolaelaps* n. sp. were transferred from the colonies to plastic Petri dishes with bran and *C. lactis* with a fine brush. For the treatment without alternative prey, three Petri dishes were prepared with only bran and 30 *Cosmolaelaps*. For the control treatment, we removed all the visible predatory mites from the litter with an aspirator and we prepared Petri dishes with only bran. The content of the Petri dishes was subsequently dispersed on the litter inside the three cages with alternative prey and in six cages without alternative prey. In the second week, the rose plants were infested with 60 adult thrips/cage, which were collected from the colonies using an aspirator made of a disposable polypropylene pipette tip covered at the wide end with a piece of gauze (mesh 30 µm) (Muñoz-Cárdenas et al. 2017). This wide end was connected with a long, flexible piece of tubing to a pump. Thrips were sucked up through the tip, which was subsequently closed with Parafilm® (Sigma-Aldrich, The Netherlands). To release the thrips, we taped a piece of yarn to the pipette tip and suspended it from a branch of the plant. Subsequently, the Parafilm was removed and thrips were free to infest the plant.

From the third to the tenth week, five leaves were collected from each of three plant strata (higher, medium and lower) and thrips larvae and adults were counted using a stereo-microscope. The total number of leaves and the number of leaves with thrips damage were also recorded. As soon as the plants produced flowers (after 4 weeks), these were collected once every 2 weeks, until the tenth week, placed in plastic containers with alcohol (70%), washed with 70% alcohol on a mesh (100 µm) and the thrips remaining on the mesh were counted under a stereo-microscope. Flowers were also

checked for damage under the stereo-microscope. We recorded a flower as damaged when it had more than five scars on petals and sepals (each scar of around 2 mm diameter). We selected this number and size of scars because previous studies showed that this area of damage is not visible to the naked eye (Muñoz-Cárdenas et al. 2017). The presence of astigmatic mites and predators in the litter was confirmed by checking 50 ml of humid litter with bran from each cage under a stereo-microscope every 2 weeks (from the fourth to the tenth week), but mites were not counted. On the tenth week we identified up to 10 predatory mite adults from the litter samples per cage.

The average numbers of thrips per leaf were $\log(x+0.1)$ transformed and analysed with a linear mixed effects model (package LME of R; Pinheiro et al. 2014; R Development Core Team 2015) with replicate (cage) as random factor and time and treatment as fixed factors. The significance of factors and their interaction was determined by comparing models with and without them with the anova function of R. Contrasts between treatments were assessed with a general linear hypothesis test (glht function of the package lsmeans of R; Lenth 2016) with the Tukey method for correction of multiple comparisons. The proportions of damaged flowers and the average numbers of thrips per flower were \sqrt{x} transformed. The proportions of damaged leaves were analysed using a similar model as above on untransformed proportions.

Thrips control by *Cosmolaelaps* n. sp.

For this experiment, we excluded predators from the litter (from a commercial greenhouse in Amstelveen, September 2014) by sterilizing it (108 °C, ± 1 bar pressure, 20 min), thus avoiding possible negative effects of competition among predator species on biological control due to competition or intraguild predation among predator species (Rosenheim et al. 1995; Messelink & van Holstein-Saj 2011). We used *Cosmolaelaps* n. sp. as litter predator because it inhabits the litter in greenhouses and it feeds on prepupae of thrips. Moreover other species of this genus have also shown potential for thrips control (Furtado et al. 2015). This experiment was performed from September to November 2014 (22 °C, RH 85%, photoperiod L16:D8) at the University of Amsterdam. There were three treatments: *Cosmolaelaps* n. sp. with alternative prey (*C. lactis* + bran in sterilized litter), *Cosmolaelaps* n. sp. without alternative prey (only bran in sterilized litter), and a control with only thrips (60/cage) with bran in sterilized litter. Each treatment was replicated three times (cages).

Besides the sterilization of the litter, the experimental set-up and the samplings were similar to those in the experiment above. The alternative prey and the predators were released as above, for the treatment with alternative food (c. 100 g of bran + 4000 *C. lactis* females + 30 *Cosmolaelaps* n. sp.) and for the treatment without alternative food we used bran without *C. lactis*; thrips were released as above (second week, 60 thrips/cage). Sampling was similar as above, but we sampled nine leaves

per week per cage, three leaves per stratum (higher, medium and lower plant parts). As soon as the plants produced flowers (week 4), these were sampled every week. Here, we identified and counted predators per 50 ml of litter sample every week. We checked for the presence of *C. lactis* but we did not count the mites.

The average numbers of thrips and damage on leaves and flowers were analysed as above. The numbers of predators per sample were $\log(x+1)$ transformed and analysed as above for thrips.

Results

Litter-inhabiting predators that benefit from alternative prey

We found two species of thrips predators benefiting from the alternative prey added to the greenhouse litter. *Cosmolaelaps* n. sp. naturally occurs in the litter layer in rose greenhouses and was found in high percentages in all samples (TABLE 3.1). *Stratiolaelaps scimitus* was found in low numbers in two samples (TABLE 3.1), this predator is commercially available in The Netherlands, possibly, it was present because of previous releases by the grower (K. Muñoz-Cárdenas, pers. comm.). The other species encountered are not known to feed on thrips but on fungi, nematodes, collembolans, mites, insects other than thrips, or different combinations of these groups (TABLE 3.1).

Predation of *Frankliniella occidentalis* and *Carpoglyphus lactis* by *Cosmolaelaps* n. sp. and *Proctolaelaps pygmaeus*

Cosmolaelaps n. sp. fed on *C. lactis* immatures (average \pm s.e.: 8.2 ± 0.4 per day) and *F. occidentalis* pre-pupae (1.3 ± 0.2 per day). *Proctolaelaps pygmaeus* did not feed on *F. occidentalis* pre-pupae but it fed on *C. lactis* immatures (3.5 ± 0.5 per day).

Thrips control by litter-inhabiting predators

Thrips densities on leaves differed significantly through time among treatments (FIGURE 3.1a; LME: interaction of treatment with time: $\chi^2 = 25.5$, d.f. = 2, $P < 0.0001$). This interaction was caused by the numbers of thrips increasing through time without alternative food and in the control and remaining low when predators were supplied with alternative food. Overall, the two treatments without alternative prey differed significantly from the treatment with alternative prey (FIGURE 3.1a; contrasts after LME). Thrips densities in the flowers did not differ significantly among treatments (FIGURE 3.1b; LME: $\chi^2 = 4.8$, d.f. = 2, $P = 0.09$). There was no significant effect of the interaction of treatment with time (LME: $\chi^2 = 1.97$, d.f. = 2, $P = 0.37$).

The proportion of damaged leaves varied significantly through time (LME: $\chi^2 = 5.70$, d.f. = 2, $P = 0.17$), but there was no significant effect of the interaction of treatment and time (LME: $\chi^2 = 2.22$, d.f. = 2, $P = 0.33$; FIGURE 3.1c). The proportions of damaged leaves differed significantly among treatments (LME: $\chi^2 = 26.7$, d.f. = 2,

TABLE 3.1. Relative abundance and number of predatory mite species found in litter, old flowers and moss of a rose greenhouse, after offering astigmatic mites as food for 10 days.

| Habitat/ Sample ^a | Species | % ^b | Feeding habits (reference) ^c | |
|---------------------------------|----------------------------------|----------------------------------|---|-------------------|
| Litter/A | <i>Benoiyssus</i> sp. | 9.3 | Fungi / Yeast (1) | |
| | <i>Cosmolaelaps</i> n. sp. | 14.8 | Collembolans / Insects: Thysanoptera / Mites Nematodes (2) | |
| | <i>Gaeolaelaps queenslandica</i> | 8.6 | Nematodes (3) | |
| | <i>Gamasellodes</i> sp. | 1.9 | Collembolans / Mites / Nematodes (4) | |
| | <i>Lasioseius subterraneus</i> | 29.0 | Collembolans / Insects: Hemiptera and Diptera / Mites / Nematodes (5) | |
| | <i>Proctolaelaps pygmaeus</i> | 32.7 | Fungi / Mites / Nematodes (5) | |
| | <i>Robustocheles mucronata</i> | 3.7 | No info found | |
| | Total (N) | 162 | | |
| | Litter/B | <i>Ameroseius pseudoplumosus</i> | 6.7 | Fungi / Mites (6) |
| | | <i>Cosmolaelaps</i> n. sp. | 40.0 | |
| <i>Lasioseius floridensis</i> | | 6.7 | Fungi / Mites (5,7) | |
| <i>Proctolaelaps pygmaeus</i> | | 6.7 | | |
| <i>Stratiolaelaps scimitus</i> | | 40.0 | Collembolans / Insects: Thysanoptera, Diptera, Lepidoptera / Mites / Nematodes (2,8) | |
| Total (N) | 15 | | | |
| Litter/C | <i>Benoiyssus</i> sp. | 1.2 | | |
| | <i>Cosmolaelaps</i> n. sp. | 50.9 | | |
| | <i>Lasioseius subterraneus</i> | 9.0 | | |
| | <i>Proctolaelaps pygmaeus</i> | 38.3 | | |
| | <i>Robustocheles mucronata</i> | 0.6 | | |
| | Total (N) | 167 | | |
| Moss/D | <i>Cosmolaelaps</i> n. sp. | 100.0 | | |
| | Total (N) | 7 | | |
| Flowers/E | <i>Cosmolaelaps</i> n. sp. | 55.6 | | |
| | <i>Stratiolaelaps scimitus</i> | 33.3 | | |
| | <i>Proctolaelaps pygmaeus</i> | 5.6 | | |
| | <i>Ameroseius pseudoplumosus</i> | 5.6 | | |
| | Total (N) | 18 | | |

^a Plant material collected in commercial greenhouses in The Netherlands (A: Litter, Amstelveen, October 2011; B: Litter, Stompwijk, July 2012; C: Litter, Amstelveen, December 2013; D: Moss, Aalsmeer, January 2013. E: Old flowers, Amstelveen, July 2013).

^b Relative abundance (%) calculated as the proportion of each species in each sample, based on the total (N) given for each sample.

^c References for feeding habits for each genus: (1) Abou-Awad et al. 2008, (2) Furtado & de Moraes 2015, (3) Salehi et al. 2014, (4) Evans 1987, (5) de Moraes et al. 2015, (6) Flechtmann 1985, (7) Britto et al. 2012, (8) Wu et al. 2014.

$P < 0.0001$). The proportions of damaged leaves were lower in the treatment with alternative prey than in the two other treatments (FIGURE 3.1c; contrasts after LME).

The proportion of damaged flowers differed significantly among treatments (LME: $\chi^2 = 13.7$, d.f. = 2, $P = 0.0011$). The proportion of flowers with thrips damage was

lower in the treatment with alternative prey than in the control treatments (FIGURE 3.1d; contrasts after LME). The proportion did not vary significantly through time (LME: $\chi^2 = 1.54$, d.f. = 2, $P = 0.21$; FIGURE 3.1d) and there was no significant effect of the interaction of treatment and time on flower damage (LME: $\chi^2 = 2.38$, d.f. = 2, $P = 0.30$).

In week 2, we observed low numbers of the astigmatic mite *Tyrophagus putrescentiae* in all treatments, this mite can also serve as alternative prey for predators. After 8 weeks, we found unidentified predatory mites in the control (without predators), but these were not encountered in the tenth week. From the samples of predatory mites taken in the last (tenth) week (maximum 10 individuals), we found mainly *Cosmolaelaps n. sp.* and *P. pygmaeus* in the treatment with alternative food (average \pm s.e.: 6 ± 1.15 and 3 ± 0.58 , respectively) and in the treatment without alternative food (1.33 ± 0.33 and 0.66 ± 0.66). The numbers of other predatory mite species were lower; these were not identified.

Thrips control by *Cosmolaelaps n. sp.*

The results with *Cosmolaelaps n. sp.* as the only predator were comparable to those described in the previous experiment. The effect of treatment on the average num-

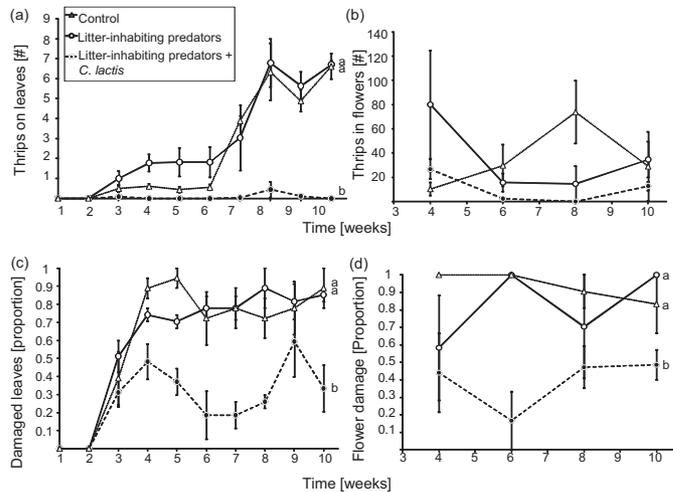


FIGURE 3.1. Effect of addition of *Carpoglyphus lactis* as alternative prey for litter-inhabiting predators on (a) the average numbers of thrips on leaves (\pm s.e.); (b) the average numbers of thrips in the flowers (\pm s.e.); (c) the average proportion of damaged leaves (\pm s.e.) and (d) the average proportion of damaged flowers per week (\pm s.e.). Predators were released in the first week, thrips were released in the second week, leaf sampling started in the third week and flower sampling in the fourth week. Different letters indicate significant differences among treatments (contrasts with general linear hypothesis testing after LME, $P < 0.05$).

bers of thrips per leaf varied significantly through time (FIGURE 3.2a; LME: interaction of treatment with time: $\chi^2 = 13.3$, d.f. = 2, $P < 0.0013$). This interaction occurred because the densities of thrips remained low in the treatment with alternative food but increased in the other treatments, which differed significantly from the former (FIGURE 3.2a). The effect of treatments on the average numbers of thrips in the flow-

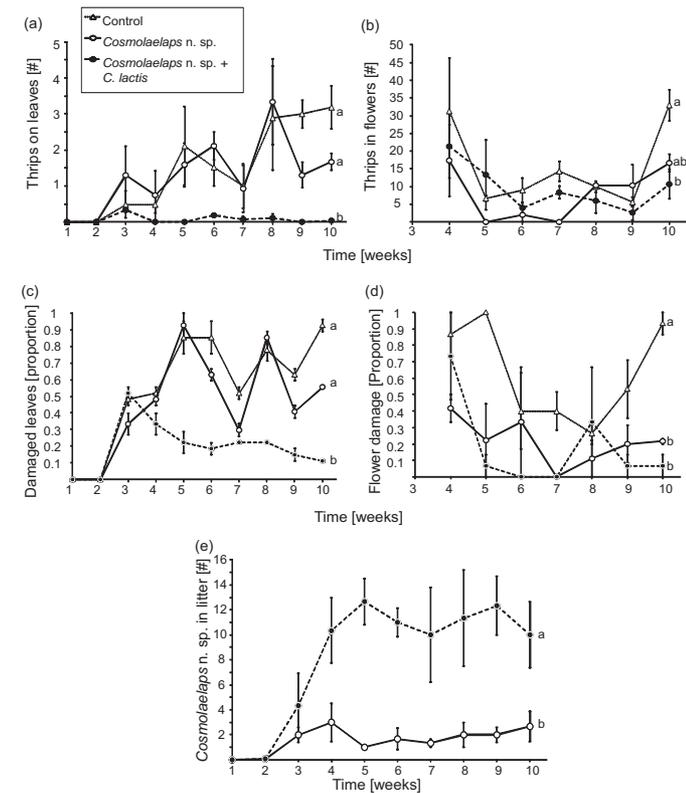


FIGURE 3.2. Effect of *Cosmolaelaps n. sp.* with or without alternative prey (*Carpoglyphus lactis*) on (a) the average (\pm s.e.) number of thrips on leaves; (\pm s.e.); (b) the average numbers of thrips in the flowers (\pm s.e.); (c) the average proportion of damaged leaves (\pm s.e.); (d) the average proportion of damaged flowers per week (\pm s.e.) and (e) the average number of *Cosmolaelaps n. sp.* adults in litter samples (\pm s.e.). Predators were released in the first week, thrips were released in the second week, leaf sampling started in the third week and flower sampling in the fourth week. Different letters indicate significant differences among treatments (contrasts with general linear hypothesis testing after LME, $P < 0.05$).

ers varied significantly through time (FIGURE 3.2b; LME: interaction of treatment with time: $\chi^2 = 7.4$, d.f. = 2, $P < 0.02$). This interaction occurred because the densities of thrips remained low in the treatments with *Cosmolaelaps* n. sp. but increased significantly in the treatment without predators (FIGURE 3.2b).

The proportions of damaged leaves varied differently through time among treatments (FIGURE 3.2c; LME: interaction of treatment with time: $\chi^2 = 19.9$, d.f. = 2, $P < 0.0001$). It was significantly lower in the treatment with alternative food than in the two other treatments (FIGURE 3.2c). There was also a significant effect of treatments on flower damage (FIGURE 3.2d; LME: $\chi^2 = 14.0$, $P < 0.001$). Releasing *Cosmolaelaps* n. sp. independently of the addition of alternative prey resulted in flowers with less thrips damage. The proportion of damaged flowers varied significantly through time (LME: $\chi^2 = 4.26$, d.f. = 2, $P = 0.039$; FIGURE 3.2d), and there was no significant effect of the interaction between treatment and time ($\chi^2 = 0.49$, d.f. = 2, $P = 0.78$).

The addition of alternative prey significantly increased the densities of predators (FIGURE 3.2e; LME: $\chi^2 = 20.5$, d.f. = 1, $P < 0.0001$), which did not vary significantly through time ($\chi^2 = 1.57$, d.f. = 1, $P = 0.21$) and there was no significant effect of the interaction of treatment with time ($\chi^2 = 0.74$, d.f. = 1, $P = 0.39$). We did not find other species of predators in these samples. We found *C. lactis* in all replicates in which it was released.

Discussion

Rose is a prime example of an ornamental that must be damage-free to be marketable (Parrella et al. 1999). Introducing generalist predators has been a successful method of biological control (Symondson et al. 2002), mainly in vegetable crops. One way of improving biological control to meet the standards for ornamentals is to boost the densities of predators in the crop before pest invasion. Nowadays, growers add food to above-ground plant parts to increase the densities of various generalist predators (Vangansbeke et al. 2014). Studies have shown that adding food or prey can enhance biological control (van Rijn et al. 2002; Nomikou et al. 2002, 2010; Janssen & Sabelis 2015; Kumar et al. 2015). These studies, however, concerned above-ground food webs. Only few studies show that biological control can be improved by linking food webs inhabiting the litter to above-ground food webs (Muñoz-Cárdenas et al. 2017). Here, we show that adding food for predators in the litter reduces pest damage on above-ground plant parts.

We found different species of predators in the litter samples collected in commercial greenhouses after adding alternative prey (TABLE 3.1). The dominating species was *Cosmolaelaps* n. sp. (TABLE 3.1), from a genus that is known to occur in litter of natural forests (Furtado & de Moraes 2015). Another species that was abundant in four of the five samples was *P. pygmaeus* (TABLE 3.1), which has been reported from

soil in general and in association with plants, mammals, bark beetles and their galleries, birds, insects, rotting fruits, stored products and bird and mammal nests (de Moraes et al. 2015). It is possible that the different predatory mites in the litter of the greenhouse came from the soil or were carried by insects invading the crop. In the litter, these predatory mites might feed on other arthropods and fungi that are commonly associated with the decomposition of litter (Walter & Proctor 2013). We found that both species fed on the alternative prey *C. lactis* but only *Cosmolaelaps* n. sp. fed on western flower thrips. This coincides with findings of other authors (de Moraes et al. 2015).

We investigated the effect of *Cosmolaelaps* n. sp. plus alternative food on thrips populations because we previously observed that these predators benefit from the alternative prey *C. lactis* and we suspected that they might play a role in thrips control (Muñoz-Cárdenas et al. 2017). Another reason for investigating *Cosmolaelaps* n. sp. is that plants that were left in the greenhouse outside cages and that harbored *Cosmolaelaps* n. sp. predators were less likely to become contaminated by thrips (K. Muñoz-Cárdenas, pers. obs.).

The various predator species present in the litter in the experiment ‘*Thrips control by litter-inhabiting predators*’ could have engaged in negative predator-predator interactions such as competition or intraguild predation, which could have affected biological control (Rosenheim et al. 1995; Messelink & van Holstein-Saj 2011; but see Janssen et al. 2006). However, thrips densities on leaves were lower when multiple predators plus alternative prey were present than in the controls without predators or without alternative food (FIGURE 3.1). As was found here, several studies show that the effect of the presence of multiple predators on pest control can be neutral or positive (Gillespie & Quiring 1990; Losey & Denno 1998; Sokol-Hessner & Schmitz 2002; Wiethoff et al. 2004; Thoeming & Poehling 2006; Snyder et al. 2008; Wu et al. 2016); however, none of these publications used alternative food. Yet, other studies show negative effects of the presence of multiple predators on pest control (Rosenheim et al. 1993, 2004; Rosenheim 2001; Schausberger & Walzer 2001). In another study, we also studied the effect of multiple predators on pest control, showing that releasing the predatory mites *A. swirskii* on the plants and *M. robustulus* in the litter, each with their own alternative food, also resulted in a positive or neutral effect on thrips control (CHAPTER 4).

Because the experiments of population dynamics of thrips with several predator species and with *Cosmolaelaps* n. sp. alone were carried out at different times for logistical reasons, assessing the effect of single or multiple predators on thrips control is not straightforward. To nevertheless compare thrips control with multiple and single predator species, we calculated the proportional decrease of thrips densities by predators with alternative food relative to the treatment without predators for both

experiments. Thus, we compared two time series with relative changes of the thrips populations. The two time series did not differ significantly for thrips found in the flowers (glm with Gaussian error distribution: $F_{1,9} = 0.007$, $P = 0.93$) or for the thrips on leaves ($F_{1,14} = 0.79$, $P = 0.38$), suggesting that *Cosmolaelaps* n. sp. alone was as efficient in reducing thrips densities as it was together with the other predator species. Further research is needed to assess the effects of interactions among soil predators on biological control.

In both experiments reported here, thrips densities decreased when adding food to a single predator or to a community of predators in the litter. Leaf damage was also reduced compared with the control and a treatment without alternative prey (FIGURE 3.2). We did not observe short-term increases of thrips densities (as in apparent mutualism), perhaps because predators were released before the thrips. In another study, where thrips were released before the predators, we found a short-term negative effect when adding alternative food for thrips, as in apparent mutualism (CHAPTER 4).

In the current experiment, there were high densities of thrips in the flowers causing damage in all treatments with *Cosmolaelaps* n. sp., and this is not acceptable for commercial growers. Hence, further studies are needed to investigate the possibilities of optimizing control methods with this predator species. Moreover, it is worthwhile to investigate the potential of adding alternative food for *Cosmolaelaps* n. sp. to control thrips in crops with higher damage tolerance, but also for the control of other pests with stages living in the soil. It is estimated that around 75% of all insect pests inhabit the litter or soil at some stage of their lives (Wahab 2010) and having high densities of *Cosmolaelaps* n. sp. as a result of adding alternative prey could increase pest control.

Another avenue to increase control of thrips in roses would be to combine *Cosmolaelaps* n. sp. with canopy-dwelling predators plus alternative food. In the case of the plant-dwelling predator *A. swirskii*, there can be negative interactions with *Cosmolaelaps* n. sp., such as competition or intraguild predation that could affect thrips biological control. This topic deserves further study; however, we expect that the simultaneous use of these two species would not affect thrips control based on a study we performed in which we released *A. swirskii* together with another species of litter-inhabiting predator (CHAPTER 4).

Summarizing, we showed that adding alternative food in the litter increased the control of an important pest species by litter-inhabiting predators. Most studies of food webs associated with plants focus on above-ground and below-ground communities that are linked via the plant (Scheu 2001), for example, how below-ground herbivores or mycorrhizae modify plant quality, thus affecting the performance of above-ground herbivores (Masters et al. 1993; Gange & West 1994; Brussard 1998;

Mortimer et al. 1999; A'Bear et al. 2014). Less attention has been given to herbivores with stages that feed on above-ground plant parts and other stages that occur below-ground (Johnson et al. 2016). Here, we show that such herbivores can form a direct link between above-ground and below-ground food webs. We suggest that adding alternative prey for litter-inhabiting predators could also increase biological control of other pests that inhabit the litter or soil at some stage of their lives, also in other crops.

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