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Linking litter and canopy food webs to protect ornamental crops

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Single and combined predator releases with alternative food increases thrips control in an ornamental crop

Karen Muñoz-Cárdenas, Ada Leman, Marcus V. A. Duarte, Gerben J. Messelink & Arne Janssen

Many pest species spend part of their life cycle in the soil or litter and another part on the above-ground plant parts. Therefore, a viable strategy to control such pests may be to release a combination of canopy-dwelling predators and litter-inhabiting predators. However, when predators attack the same pest population, there will be competition at some point, even if they attack different stages and different parts of the population. This competition may be reduced when predators have alternative food sources. The effect of adding alternative food for predators can have positive or negative effects on pest control, depending on the time frame and fluctuations of prey and predator populations. We tested the effect of single or combined predator releases with alternative food on thrips control on cut roses in an experimental greenhouse. In a first experiment, we released thrips before the predators *Amblyseius swirskii* and the soil-dwelling predatory mites *Macrocheles robustulus* and *Stratiolaelaps scimitus*, using *Acarus siro* or pollen as alternative food. In a second experiment, we released *A. swirskii* and *M. robustulus* before the thrips and supplied *Typha* spp. pollen on the plants for *A. swirskii* and *A. siro* in the litter for *M. robustulus*. We found best thrips control when *A. swirskii* plus pollen were released, independently of the release of soil-dwelling predatory mites. Furthermore, better thrips control was achieved when predators were released before the thrips. Our results suggest that soil-dwelling predatory mites, which are present in the litter layer in many commercial greenhouses, do not affect thrips control by *A. swirskii*. Hence, growers can use this latter species independent of the presence of these soil-dwelling predators. Growers should preferably release *A. swirskii* plus pollen before thrips invade the crop.

Introduction

Prey are often attacked by several species of predators (Polis 1991; Polis & Strong 1996; Sih et al. 1998). Different species of natural enemies can have additive effects on prey populations, meaning that their combined effect equals the sum of the effects of the different natural enemy species (Sih et al. 1998; Casula et al. 2006). Multiple natural enemies can also cause further increases in prey densities, for example because of the occurrence of interactions such as intraguild predation among predators (Ferguson & Stiling 1996; Rosenheim et al. 1993, 2004; Rosenheim 2001; Snyder & Ives 2001), or because the response of the prey to a species of natural enemy decreases the risk of being attacked by the other species (Magalhães et al. 2002; Sih et al. 1998). Furthermore, the combined effect of several species of natural enemies can cause further decreases in prey densities than their additive effect, for example because they feed on different stages of the prey (Takagi & Hirose 1994), or because the response of prey to one natural enemy species makes them more vulnerable to the other species (Losey & Denno 1998, 1999).

In biological control, the effect of multiple natural enemies versus the effect of one natural enemy varies according to the crop and the species involved (Chang 1996; Ferguson & Stiling 1996; Sih et al. 1998). There are examples of disruption of biological control by multiple natural enemies (Finke & Denno 2004), of neutral effects, where the addition of other species of natural enemies does not result in further reduction of pest populations (Cardinale et al. 2003), and positive effects, which can be additive or synergistic, increasing pest control (Losey & Denno 1998). Studies showing interactions among predators that have a positive effect on pest control involve systems in which predators attack the pest at different locations or on different plant parts, different seasons, or at different life stages (Murdoch et al. 1984; Onzo et al. 2004). However, when predators attack the same pest population, they will compete in the end, even when they attack different stages or different parts of the population. Such competition may be reduced when the predators have alternative food (Onzo et al. 2005). Here, we investigated the effect of adding alternative food for a combination of predator species that attack different stages of a pest and at different locations (i.e. the canopy and the litter).

The effects of adding alternative food, such as pollen, to increase biological control by generalist predators has been widely investigated (McMurtry & Scriven 1966; van Rijn et al. 2002; Nomikou et al. 2002, 2010). There can be positive effects on biological control of adding alternative food, because the addition of food results in an increase in predator densities in the long term, after one or a few predator generations. These higher predator densities result in more attacks on pest individuals (apparent competition; Holt 1977), enhancing biological control. However, during the first few generations of the predator, biological control might also be negatively

affected by adding alternative food, because predators may feed on the alternative prey instead of feeding on the target pest, or because adding alternative food results in predator satiation (apparent mutualism; Holt 1977; Abrams & Matsuda 1996).

Several studies have demonstrated that adding pollen as food for predators to the plant canopy can indeed increase pest control (McMurtry & Scriven 1966; Kennett et al. 1979; van Rijn et al. 2002; Maoz et al. 2009; Nomikou et al. 2010; Adar et al. 2014; Leman & Messelink 2015; Duarte et al. 2015). Alternative prey for predators can also be added to the litter. In previous studies, we showed that litter-inhabiting predators that feed on litter-inhabiting stages of an important plant pest (western flower thrips) can benefit from alternative prey supplied in the litter, resulting in increased thrips control (Muñoz-Cárdenas et al. 2017; CHAPTER 3). So far, studies focusing on releases of combinations of predators on plants and in the litter or soil have not addressed the effect of alternative food sources for both predators on biological control. Thus, our question is whether a combination of predators on the plants and in the litter, each with their own alternative food, would increase biological control.

We studied the control of Western flower thrips (*Frankliniella occidentalis*) in greenhouse cut roses. In the particular case of this pest, adding pollen as alternative food can be risky, because pollen is also a high-quality food source for thrips (van Rijn et al. 2002; Chitturi et al. 2006; Leman & Messelink 2015; Vangansbeke et al. 2016). There are only few studies on the effect of adding pollen for predatory mites on thrips control in ornamentals (Delisle et al. 2015; Leman & Messelink 2015). In one of these studies, potted chrysanthemum plants received more damage when the predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae) was released together with pollen than without pollen (Delisle et al. 2015). However, this experiment lasted for 4 weeks (Delisle et al. 2015), so the evaluation period may have been too short to observe the long term positive effect of adding pollen for predators on thrips control. The study of Leman & Messelink (2015) on chrysanthemum lasted for 8 weeks and shows enhanced control of thrips when predatory mites are provided with pollen, but plant damage was not assessed. Another study, in rose plants, shows increases in densities of *A. swirskii* and other phytoseiid predators when adding pollen, but thrips densities and plant damage were not assessed (Pijnakker et al. 2016). Because thrips spend part of their life cycle in the litter or soil, attempts have been made to increase control of thrips by using canopy-dwelling predators that attack thrips larvae together with soil-inhabiting predators that attack prepupae and pupae (Wiethoff et al. 2004; Thoeming & Poehling 2006; Manners et al. 2013; Pozzebon et al. 2015). These studies did not find a significant increase in thrips control using such combinations of predators. However, they did not supply alternative food for the predators. We therefore conducted two experiments. In the first experiment, we supplied one type of alternative prey in the litter for a combination of predators. Previous studies

(Muñoz-Cárdenas et al. 2017; CHAPTER 3) show that both the soil-inhabiting and the canopy-dwelling predators do use this alternative food when supplied to the litter. Here, we assessed the combined effects of these predators with alternative food on thrips control. In the second experiment, we supplied each predator with its own alternative food; alternative prey was again added to the litter, but we also added pollen to the above-ground plant parts.

Materials and methods

The experimental system

Plants were grown in rockwool (Grodan®) and nutrients were applied in the irrigation system. Rose plants in rockwool slabs were placed on top of gutters (JBHydroponics®) at around 60 cm from the ground. In the Netherlands, cut rose plants are grown in this way for 5-10 years, resulting in the accumulation of litter on the greenhouse floor. Some plant branches touch this litter layer, forming a connection between the above-ground and below-ground habitats. In this study we simulated these conditions in an experimental greenhouse under conditions resembling those of commercial crop production systems.

The western flower thrips *Frankliniella occidentalis* (Pergande) causes important economic damage in many different crops, including roses (Park et al. 2002; Manners et al. 2013). The predators used in this study were *A. swirskii*, which is commonly released to control thrips and whiteflies in various crops (Nomikou et al. 2001, 2002; Messelink et al. 2008), and the soil-dwelling predatory mites *Macrocheles robustulus* (Berlese) and *Stratiolaelaps scimitus* (Womersley), which can also control thrips (Berndt et al. 2004; Messelink & van Holstein-Saj 2011) and sciarids (Grosman et al. 2011). We used *Typha latifolia* L. or *Typha angustifolia* L. pollen as alternative food for *A. swirskii*. Both predators feed on the alternative prey *Acarus siro* (L.), which was released in the litter.

Arthropod cultures and pollen

Western flower thrips (*F. occidentalis*) were reared on flowering chrysanthemum plants (*Dendranthema grandiflora* Tzelev, var. Miramar) in a greenhouse compartment. The flour mite *A. siro* was reared on wheat bran (Ramakers & van Lieburg 1982). *Amblyseius swirskii* (Swirski-mite®), *S. scimitus* (Entomite M®) and *M. robustulus* (Macro-mite®) were obtained from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). For the first experiment, we used *T. latifolia* pollen, collected from plants in the surroundings of the experimental station (Bleiswijk, The Netherlands). It was dried and stored at -20 °C. For the second experiment, we used *T. angustifolia* pollen (Nutrimite®) provided by Biobest (Westerlo, Belgium).

Study area and plant material

The experiments were performed in a greenhouse compartment at Wageningen UR Greenhouse Horticulture in Bleiswijk, The Netherlands. The compartment was 96 m², the average temperature was 22.2 °C, RH 80%, photoperiod L13:D11. Artificial light was 10.000 lux, and was switched on when natural light in the greenhouse was less than 150 Watt/m². The windows of the greenhouse were provided with insect gauze (0.40 × 0.45 mm) to prevent arthropod invasions. Twenty cages, consisting of a plastic frame (1 × 1.5 × 2 m) covered with insect-proof mesh (mesh size 0.22 × 0.31 mm), were placed inside this compartment. Cages were located about 50 cm from each other. Each cage had two zippers at the front for easy access. In March 2014, 10 rose plants (1 year old, var. Avalanche ++; Leo Ammerlaan, Bleiswijk) rooted in rock wool were placed in each cage on top of two gutters (JBHydroponics®) (5 plants/gutter). The plant density (6 plants/m²) is characteristic of Dutch commercial roses. Litter from a commercial greenhouse (Royal Roses, Stompwijk, The Netherlands) was sterilized (120 °C, 20 min) and placed below the gutters of the cages. To start the experiment with plants that were free of pests and diseases, we treated all plants prior to the experiment with a mix of pyridylethylamide (Luna privilege, Bayer) against powdery mildew and lufenuron (Match, Syngenta), abamectin (Vertimec gold, Syngenta) and pyridalyl (Nocturn, Nufarm) against western flower thrips. To prevent powdery mildew infection, we used a Sulphur evaporator until the week before the start of the experiment. Because the cages had no bottom, we built a barrier of sand (10 cm wide, 10 cm high) on the floor against the cage walls on the inside and outside of all the cages to prevent escapes of litter-inhabiting mites. During both experiments, a standard nutrient solution was provided to the plants with a drip irrigation system. Roses were harvested once per week, stems were bent and buds from these stems were removed according to commercial practice. As a preventive measurement, each cage was weekly supplied with *Encarsia formosa* Gahan (150 individuals/cage, En-strip®, Koppert) against whiteflies (*Trialetrodes vaporariorum* Westwood) and *Phytoseiulus persimilis* Athias-Henriot (200 individuals/cage, Spidex®, Koppert) against spider mites (*Tetranychus urticae* Koch).

Experiments

In previous studies (Muñoz-Cárdenas et al. 2017; CHAPTER 3) we found that the positive effect of adding alternative prey on biological control of thrips in roses is achieved only when the predator populations are established before pest invasion (also known as the predator-in-first approach; Ramakers 1990; Kutuk & Yigit 2011; Kumar et al. 2015). However, in the case of ornamentals, there are no studies comparing the effect of predator pre-establishment with releases of predators after pest invasions on biological control. For this reason, we carried out the first experiment by releasing predators with alternative food after thrips. For the second experiment,

predator populations were allowed to establish by releasing them with their alternative food before releasing the pest.

Thrips control with two predators and one alternative food source

This experiment was carried out for 19 weeks from June to October of 2014. *Frankliniella occidentalis* adults were released during the first 3 weeks of the experiment to simulate a thrips invasion (see TABLE 4.1 for numbers). Thrips adults were collected from the colony in 10 ml pipette points with a vacuum pump. The tips were closed with cotton wool and transferred to the greenhouse for release of thrips inside the cages. In the fifth week, the cages received one of five treatments, each with four replicates (cages): 1) no predators, 2) *A. swirskii*, 3) *A. swirskii* + pollen, 4) *M. robustulus* + *S. scimitus* + *A. siro*, or 5) *M. robustulus* + *S. scimitus* + *A. siro* + *A. swirskii*. Females of *A. swirskii* were taken from the bottles of the commercial product using a fine brush and placed on sweet pepper leaf discs (*Capsicum annuum* L.). Subsequently the discs were placed on the rose plants in the cages. These predators were released in week 5 and week 12 (TABLE 4.1). As alternative food source for *A. swirskii*, *T. latifolia* pollen (1 g/cage) was evenly distributed with a fine brush on the plants in the cages according to the treatment (TABLE 4.1).

Food and substrate for the alternative prey *A. siro* consisted of sterilized wheat bran, coarse vermiculite, peat, water and yeast. Subsequently *A. siro* were added to this mix. Individuals of the soil-dwelling predatory mites *S. scimitus* and *M. robustulus* were added to this mix of food and alternative prey. The release of *A. siro* as alternative prey was repeated in the twelfth week (TABLE 4.1).

Cages were sampled every 2 weeks (from weeks 7 to 19), by haphazardly collecting twenty leaves from the top and lower parts of the plants per cage. The thrips (larvae and adults) and predatory mites (larvae, nymphs and adults) were counted on each leaf under a stereo-microscope in the laboratory and the predatory mites were mounted on slides for identification. The number of damaged leaves per cage was also recorded.

For sampling litter-inhabiting predators, we took 250 ml of litter from each cage two times during the experiment (weeks 10 and 17) and incubated it in Tullgren funnels during 1 week. Subsequently, the samples were sieved, predatory mites and alternative prey were counted and the predatory mites found were mounted on slides for identification. Mature flowers were also sampled; five open flowers per cage were collected in plastic bags every week (from weeks 9 to 19), and the presence of scars on the sepals and on the petals of the flowers was recorded. Flowers were considered as damaged if they had any deformations or scars on the petals. Flowers were subsequently washed with 70% alcohol on a mesh (100 μ m) and the thrips and predators remaining on the mesh were counted under a stereo-microscope.

Average numbers of thrips per flower and per leaf were $\log(x+1)$ transformed, the average numbers of thrips per leaf and the average number of *A. swirskii* per leaf and per flower were $\log(x+0.01)$ transformed. Numbers of *M. robustulus* and *S. scimitus* were $\log(x+1)$ transformed before analysis. Because almost no *A. swirskii* were encountered in the flowers during the first 14 weeks of the experiment, only data from week 15 onwards were evaluated for this species. All data were analyzed with linear mixed effects models (LME of the nlme package of R, Pinheiro et al. 2014) with experimental unit (cage) as random factor and time and treatment and their interaction as fixed factors. Contrasts among treatments were assessed with the glht function with Tukey HSD (package lsmeans of R; Lenth 2016). We found *A. siro* individuals in the litter only in week 17, not in week 10. The numbers per sample of these mites were therefore compared using generalized lineal models (GLM instead of LME) with treatment as factor and a quasi-Poisson error distribution. All statistical analyses were done using R (R Development Core Team 2015). Leaf sampling started in week 7, flower sampling in week 9 when the first flowers could be harvested.

Thrips control with two predators and two alternative food sources

This experiment was performed using the same cages with the same plants as in the previous experiment. To remove arthropods and mildew, we sprayed with a solution containing the insecticides flonicamid (Teppeki®, Belchim) and abamectin (Vertimec gold®, Syngenta), the fungicide dodemorf (Meltatox®, BASF) against powdery mildew, and heptamethyltrisiloxane (Silwet gold®, Certis Europe) as wetting agent. Furthermore, the plants were pruned, the stems that had flowered were bent, all colored buds were removed, and the litter from the bottom of the cages was removed for sterilization and placed back under the gutters in the cages. After allowing the plants to regrow, an experiment was done from April to July of 2015. There were five treatments with four repetitions (cages): 1) untreated (no predators), 2) *M. robustulus* + *A. siro*, 3) *A. swirskii* + pollen weekly, 4) *M. robustulus* + *A. siro* + *A. swirskii* + pollen weekly, or 5) *A. swirskii* + pollen (interrupted). We released only *M. robustulus* as litter predators in this experiment because they were the dominant species in the previous experiment. To test whether the frequency of adding pollen had an effect on thrips densities, pollen was added weekly in two of the treatments, and in one other treatment, the pollen supply was interrupted (TABLE 4.2). Thrips, alternative prey and predators were released as in the previous experiment, timing of their release can be found in TABLE 4.2. Leaves, flowers and litter were sampled as in the previous experiment. For data analysis, average numbers of thrips per flower were $\log(x+1)$ transformed, thrips per leaf were $\log(x+0.01)$ transformed. The densities of *A. swirskii* in flowers were very low during the first 9 weeks of the experiment; these data were therefore excluded from the analysis. The remaining densities were $\log(x+0.1)$ trans-

formed, as were the densities of this predator per leaf. Densities of *M. robustulus* and *A. siro* were $\log(x+1)$ transformed. Proportions of damaged leaves and flowers were $\arcsin \sqrt{x}$ transformed. All transformed data were compared using LME as in the previous experiment.

Results

Thrips control with combined predators and one alternative food source

The average numbers of thrips per flower differed significantly among treatments through time (FIGURE 4.1a; LME, interaction of treatment with time: d.f. = 4, $\chi^2 = 74.5$, $P < 0.0001$). This was because the average thrips densities increased in most treatments, but decreased in the treatment with *A. swirskii* plus pollen. Thrips densities were on average highest in the control and with *A. swirskii* without pollen, and lowest with *A. swirskii* plus pollen (FIGURE 4.1a). Overall, thrips densities in the flowers were high, with unsatisfactory control, except in the treatment with *A. swirskii* plus pollen during the last 3 weeks of the experiment (FIGURE 4.1a; contrasts with glht function of package lsmeans).

The average numbers of thrips per leaf also differed significantly among treatments through time (FIGURE 4.1b; LME, interaction of treatment with time: d.f. = 4, $\chi^2 = 17.1$, $P = 0.0018$). This may have been because the densities of thrips dropped in the treatment with *A. swirskii* plus pollen during the last few weeks, as it did in the flowers. However, none of the contrasts among treatments was significant (FIGURE 4.1b; contrasts).

Amblyseius swirskii was practically absent in the flowers during the first 14 weeks of the experiment (FIGURE 4.1c). Analysis of the data from week 15 onwards showed a significant difference among treatments through time (LME: d.f. = 2, $\chi^2 = 6.91$, $P = 0.032$), caused by the higher numbers of *A. swirskii* in the presence of pollen during the last 4 weeks than in the other treatments (FIGURE 4.1c). The average density of *A. swirskii* per leaf also differed significantly among treatments through time (FIGURE 4.1d; LME, interaction: d.f. = 2, $\chi^2 = 10.8$, $P = 0.0044$), likely caused by the high numbers of predators towards the end of the experiment in the treatment with *A. swirskii* plus pollen, but not in the other treatments (FIGURE 4.1d; contrasts).

By releasing the thrips before the predators and the alternative food, all the flowers had thrips damage on the petals, independently of the treatment (K. Muñoz-Cárdenas, pers. obs.). Moreover, the proportion of leaves damaged by thrips was high in all treatments (FIGURE 4.1e), but differed significantly among treatments through time (LME, interaction: d.f. = 4, $\chi^2 = 13.3$, $P = 0.01$). This was because the proportion of damaged leaves in the treatment with *A. swirskii* plus pollen was the highest at the start of the experiment and lowest at the end of the experiment. Nevertheless, the differences among treatments through time were not significant (FIGURE 4.1e; contrasts).

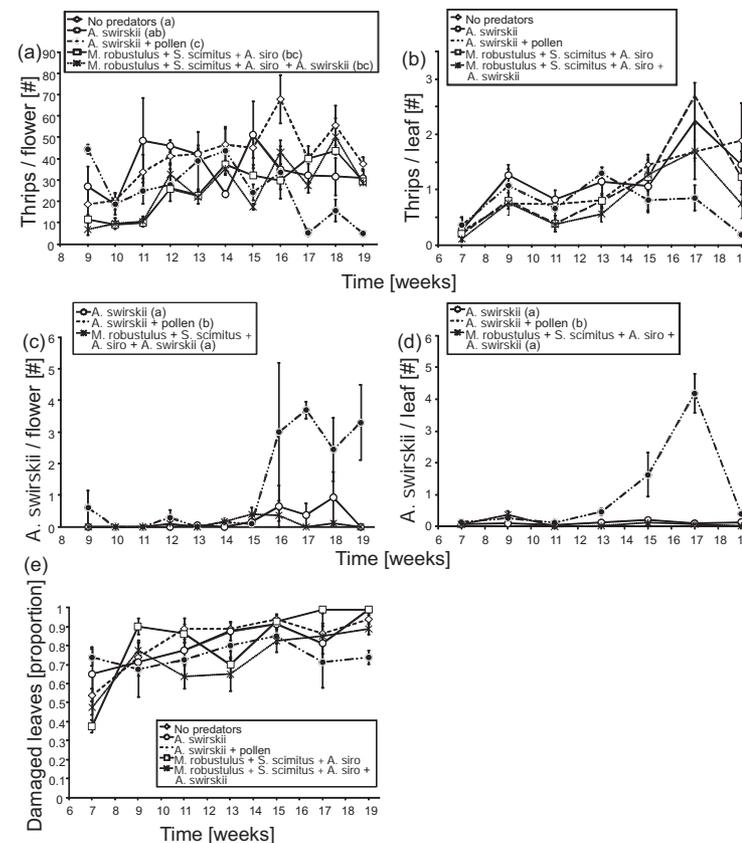


FIGURE 4.1. Effect of addition two predators and one alternative food source on thrips densities, predator densities and proportion of damaged leaves on rose plants. In all the treatments thrips were released before predators plus alternative food (TABLE 4.1): 1) no predators; 2) *Amblyseius swirskii*, without alternative food; 3) *A. swirskii* + pollen on leaves; 4) *Macrocheles robustulus* + *Stratiolaelaps scimitus* + *Acarus siro* in the litter; or 5) *M. robustulus* + *S. scimitus* + *A. swirskii* + *A. siro*. Shown are average numbers (\pm s.e.) of (a) thrips/flower, (b) thrips/leaf, (c) *A. swirskii*/flower, (d) *A. swirskii*/leaf, and (e) proportion of damaged leaves. Different letters in the legends represent significant differences among treatments through time.

The numbers of *M. robustulus* in litter samples differed significantly among treatments through time (LME, interaction: d.f. = 1, $\chi^2 = 9.7$, $P = 0.0018$). This was because the numbers of this predator did not differ between treatments in the tenth week of the experiment, whereas the numbers were significantly higher in the treatment without *A. swirskii* at 17 weeks (FIGURE 4.2a). The densities of *S. scimitus* in the litter samples did not differ significantly among treatments through time (LME, interaction: d.f. = 1, $\chi^2 = 3.5$, $P = 0.061$), and there was no significant effect of treatment (FIGURE 4.2b; LME: d.f. = 1, $\chi^2 = 0.0036$, $P = 0.95$). There were significantly more *S. scimitus* present in the litter after 17 weeks than after 10 weeks (FIGURE 4.2b; LME: d.f. = 1, $\chi^2 = 10.8$, $P = 0.001$). Besides the species of litter predators released, we found high densities of *Lasioseius fimetorum* (Acari: Podocinidae) (average \pm s.e. = 68.1 ± 37.3) in the treatments with soil dwelling predators in week 10. Probably they came from the soil in the greenhouse and their populations increased as a result of the alternative prey added (*A. siro*). After 17 weeks, we found high densities of *Ameroseius* sp. (Acari: Ameroseiidae) (112.3 ± 54.9) in the treatments without releases of soil dwelling predators. At the same time, we found low numbers of *Neoseiulus barkeri* (Acari: Phytoseiidae) (6 ± 3.5) and *Geolaelaps aculeifer* (Acari: Laelapidae) (5.3 ± 4) in the litter samples of all treatments.

Acarus siro, the alternative prey added to the litter, was not encountered after 10 weeks and was therefore added another time in week 12 (TABLE 4.1). This resulted in their presence in the litter after 17 weeks, and their numbers did not differ significantly between treatments [*M. robustulus* + *A. siro*: (average \pm s.e.) 847.5 ± 465.1 , *M. robustulus* + *A. siro* + *A. swirskii*: 535 ± 185.7 ; GLM: d.f. = 1, $F_{1,6} = 0.45$, $P = 0.53$].

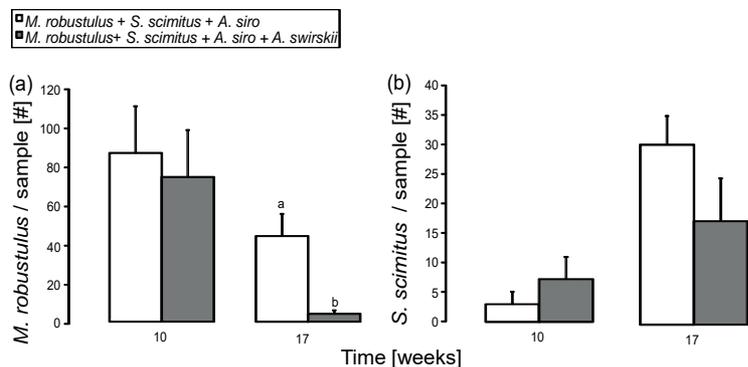


FIGURE 4.2. Average numbers (\pm s.e.) of mites found in 250 ml of litter samplings after 10 and 17 weeks in the treatments in which *Macrocheles robustulus* + *Stratiolaelaps scimitus* were released with the alternative prey *Acarus siro*. (a) *M. robustulus*/litter sample, (b) *S. scimitus*/litter sample. Different letters above the bars in week 17 indicate a significant difference between treatments.

TABLE 4.1. Thrips control with combined predator species and one alternative food source. The timing of releases of the western flower thrips *Frankliniella occidentalis*, predatory mites (*Amblyseius swirskii* and *Macrocheles robustulus*) and alternative prey (*Acarus siro*) or food (pollen) on rose plants or in the litter.

Week	1	2	3	5	12	14	16
<i>F. occidentalis</i> ^a	15	15	15				
<i>A. swirskii</i> ^a				100	200		
Pollen ^b				1	1	1	0.5
<i>M. robustulus</i> ^a				200			
<i>S. scimitus</i> ^a				200			
<i>A. siro</i> ^c				90000	15000		
Food in the litter ^d				1.75	0.35		

^a Number of adults released per week per cage.

^b Grams added per cage.

^c Number of immatures and adults.

^d Liters of food and substrate for alternative prey containing 1 l of sterilized wheat bran + 200 ml of coarse vermiculite + 300 ml of peat + 250 ml of water + 25 g of dried baker's yeast.

Thrips control with two predators and two alternative food sources

The average numbers of thrips per flower differed significantly among treatments through time (FIGURE 4.3a; LME, interaction: d.f. = 4, $\chi^2 = 16.1$, $P = 0.0029$). Whereas thrips densities did not differ during the first few weeks, they subsequently increased in the treatments without *A. swirskii* plus pollen, whereas they remained low in all treatments with *A. swirskii* plus pollen (FIGURE 4.3a).

Densities of thrips per leaf did not vary significantly through time (FIGURE 4.3b; LME: d.f. = 4, $\chi^2 = 0.35$, $P = 0.56$), nor was there a significant interaction of treatment with time (d.f. = 4, $\chi^2 = 8.61$, $P = 0.072$). There was a significant effect of treatments (d.f. = 4, $\chi^2 = 11.6$, $P = 0.021$), but contrasts among treatments did not reveal any significant differences (FIGURE 4.3b).

The densities of *A. swirskii* per flower were very low during the first 9 weeks of the experiment (FIGURE 4.3c), and did not differ significantly among treatments from week 10 onwards (LME: d.f. = 2, $\chi^2 = 1.32$, $P = 0.52$). There was no significant effect of time (d.f. = 2, $\chi^2 = 0.87$, $P = 0.35$) or of the interaction of treatment with time (d.f. = 2, $\chi^2 = 1.97$, $P = 0.37$). Densities of *A. swirskii* on the leaves varied significantly among treatments (FIGURE 4.3d; LME: d.f. = 2, $\chi^2 = 25.5$, $P < 0.0001$), and there was no significant effect of time (d.f. = 2, $\chi^2 = 0.045$, $P = 0.83$) or of the interaction of treatment with time (d.f. = 2, $\chi^2 = 3.65$, $P = 0.16$). Densities of *A. swirskii* on leaves were much lower when pollen supply was interrupted (FIGURE 4.3d).

The proportion of damaged flowers varied significantly through time among treatments (FIGURE 4.3e; LME, interaction of treatment with time: d.f. = 4, $\chi^2 = 40.1$, $P < 0.0001$). Initially, there were few damaged flowers in all treatments, but this subsequently increased in the treatments without *A. swirskii* plus pollen (FIGURE 4.3e). The average proportion of damaged leaves varied significantly among treatments

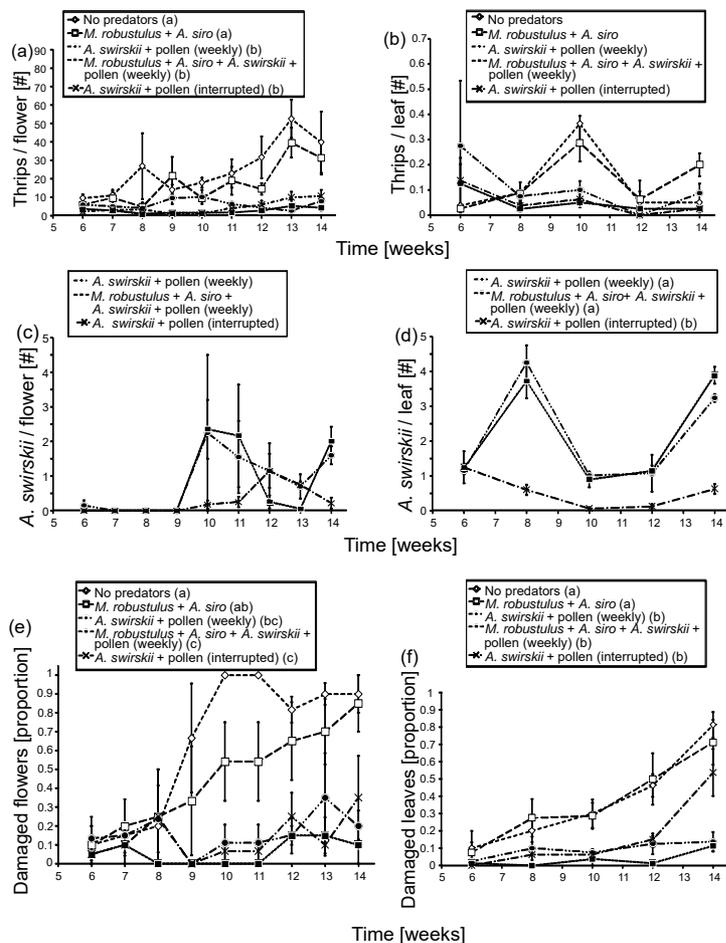


FIGURE 4.3. Effect of addition two predators and two alternative food sources on thrips densities, predator densities and proportions of damaged rose leaves and flowers. Predators plus alternative food were allowed to establish before thrips releases (TABLE 4.2). Treatments were: 1) No predators; 2) *Macrocheles robustulus* + *Acarus siro* in the litter; 3) *Amblyseius swirskii* + pollen weekly applied on leaves; 4) *M. robustulus* + *A. siro* + *A. swirskii* + pollen weekly; or 5) *A. swirskii* + pollen (interrupted); pollen was added four times during the experiment (TABLE 4.2). Predators and alternative food were released before thrips (TABLE 4.2). Shown are average numbers (\pm s.e.) of (a) thrips/flower, (b) thrips/leaf, (c) *A. swirskii*/flower, (d) *A. swirskii*/leaf, (e) proportion of damaged flowers, and (f) proportion of damaged leaves. Different letters in the legends represent significant differences among treatments through time.

TABLE 4.2. Thrips control with two predators and two alternative food sources. The timing of releases of the western flower thrips *Frankliniella occidentalis*, predatory mites (*Amblyseius swirskii* and *Macrocheles robustulus*) and alternative prey (*Acarus siro*) or food (pollen) on rose plants. Pollen was either added weekly or interrupted.

Week	1	2	3	5	7	9	10	11	12	13
<i>F. occidentalis</i> ^a				15	15	15				
<i>A. swirskii</i> ^a	100	100	100							
Pollen (interrupted) ^b	0.2	0.2	0.2							
Pollen (weekly)	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
<i>M. robustulus</i> ^a	400									
<i>A. siro</i> ^c	90000									
Food in the litter ^d	1.75									

^a Number of adults released per week per cage.

^b Grams added per cage

^c Number of immatures and adults.

^d Liters of food and substrate for alternative prey containing 1 L of sterilized wheat bran + 200 ml of coarse vermiculite + 300 ml of peat + 250 ml of water + 25 g of baker's yeast.

through time (FIGURE 4.3f; LME, interaction: d.f. = 4, $\chi^2 = 30.8$, $P < 0.0001$): the proportion of damaged leaves was initially low in all treatments, but increased considerably in the treatments without *A. swirskii* plus pollen (FIGURE 4.3f). It is noteworthy that the proportion of damaged leaves increased considerably in the last week when the addition of pollen to *A. swirskii* was interrupted (FIGURE 4.3f).

There was no statistically significant effect of the treatments on the numbers of *M. robustulus* in the litter (FIGURE 4.4; LME: d.f. = 1, $\chi^2 = 0.10$, $P = 0.75$), the numbers varied significantly with time (d.f. = 1, $\chi^2 = 4.20$, $P = 0.041$), but the interaction

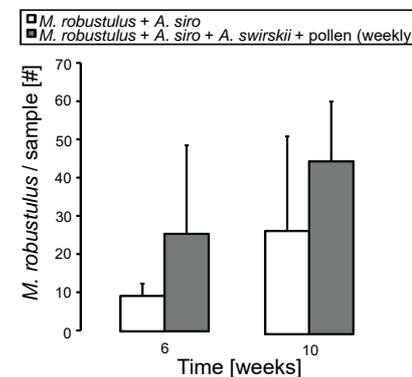


FIGURE 4.4. Average numbers (\pm s.e.) of mites found in 250 ml of litter samplings in the treatments in which *Macrocheles robustulus* was released with the alternative prey *Acarus siro*.

between treatment and time was not significant (d.f. = 1, $\chi^2 = 0.92$, $P = 0.34$). The densities of the alternative prey *A. siro* did not differ between treatments (LME: d.f. = 1, $\chi^2 = 0.25$, $P = 0.61$), but varied significantly with time (d.f. = 1, $\chi^2 = 35.8$, $P < 0.0001$; interaction treatment and time: d.f. = 1, $\chi^2 = 0.84$, $P = 0.36$). The averages of *A. siro* in week 6 were higher than in week 10 (week 6: *M. robustulus* + *A. siro*: (average \pm s.e.) 1787 ± 477 ; *M. robustulus* + *A. siro* + *A. swirskii* + pollen: 2225 ± 607 ; week 10: *M. robustulus* + *A. siro*: 10 ± 6 ; *M. robustulus* + *A. siro* + *A. swirskii* + pollen: 5 ± 5). Again, we found predatory mites of other families in all treatments (probably Phytoseiidae, Ameroseiidae and Laelapidae) (39.7 ± 21).

Summarizing both experiments, independent of the presence of *M. robustulus* and *A. siro*, releasing *A. swirskii* and adding pollen as alternative food resulted in the largest decrease in thrips densities, the largest increase in *A. swirskii* densities and the lowest plant damage, compared to the rest of the treatments.

Discussion

Combining predators does not increase or hampers thrips control

In the experiment with combined predators and one type of alternative food, we found lower thrips densities in the flowers of plants with *A. siro* and *M. robustulus* in the litter than in the treatment without predators. However, these densities did not differ significantly from those in other treatments with predators (FIGURE 4.1a). At the end of this experiment, we found significantly fewer *M. robustulus* when it was released in combination with *A. swirskii* and *S. scimitus* than when it was released with *S. scimitus* only (FIGURE 4.2a). This may have been caused by negative predator-predator interactions, such as competition for food or intraguild predation. This topic deserves further study, as well as the role of the other litter-inhabiting mites encountered in biological pest control.

We observed low numbers of *S. scimitus* when they were released together with *M. robustulus*. Elsewhere (Berndt et al. 2004), this species (synonym *Hypoaspis miles*) was shown to be an effective predator of thrips in the litter. In their experiments, the plants were confined to small tubes and the thrips mainly pupated in the soil where *S. scimitus* and *M. robustulus* were released. In our experiments, thrips had more options for pupation, for example at the base of the plants or in the flowers, thus they may have escaped from predation by these litter-inhabiting predators. This may have caused the low effect of the litter-inhabiting predators on thrips control.

The combined release of the predatory mites *A. swirskii* with pollen as alternative food on the plant canopy and *M. robustulus* with *A. siro* in the litter resulted in increased biological control compared to the release of *M. robustulus* with *A. siro* as

alternative prey. However, the combined release did not result in better control than releases of only *A. swirskii* with pollen. Similar effects of combined releases of other species of canopy-dwelling and soil-inhabiting predators on thrips control were found by Wiethoff et al. (2004) and Thoeming & Poehling (2006), but these authors did not supply the predators with alternative food. Our results show that single releases of *A. swirskii* combined with pollen resulted in increased thrips control (FIGURES 4.1 and 4.3). There was no synergistic effect of the two predators (facilitation), as has been found in another system with canopy-dwelling and soil-dwelling predators (Losey & Denno 1998, 1999). However, we also did not find evidence that the soil predator hampered pest control by the canopy-dwelling predator, in contrast to a study in another system (Messelink & van Holstein-Saj 2011).

Many arthropod plant pests spend part of their life cycles in the litter or soil (Wahab 2010). This means that biological control could be directed to the pest in both habitats by releasing predators in the plant canopy and in the litter or soil. In the experiment with two predators and two alternative food sources, we did not find a significant effect of *M. robustulus* on thrips populations in the flowers, whereas Messelink & van Holstein-Saj (2008) show that this predator can substantially reduce thrips populations. In a previous study (CHAPTER 3), we found that another litter-inhabiting predatory mite, *Cosmolaelaps* n.sp., can control thrips in rose plants when released with alternative food in the litter at the foot of the plant. In the present study, we released the predators in the litter layer under the gutters on which rose plants were located, thus the predators were not in direct contact with the plants. Again, it is possible that some thrips pupated at the base of the plants, thus escaping from predation by *M. robustulus*. Further studies could therefore include treatments in which litter-inhabiting predators with alternative food are added at the foot of the plant, just below the canopy.

Supplying pollen to *Amblyseius swirskii* increases thrips control

Our results confirm that adding alternative food for predators can increase biological control even if the pest can also benefit from the alternative food (van Rijn et al. 2002). At the start of the experiment with one type of alternative food, however, we found the largest numbers of thrips in the flowers and a larger proportion of damaged leaves in the presence of *A. swirskii* and pollen (FIGURE 4.1a,e). This could have been caused by a direct short-term positive effect of pollen on thrips densities, by apparent mutualism (i.e. an indirect short-term positive effect mediated by the predators, Holt 1977), or both.

In the experiment with two types of alternative food, we found that adding pollen on plants weekly or interrupted (4 times in 14 weeks) caused decreases of thrips densities and plant damage (FIGURE 4.3). There were no significant differences in

thrips densities or plant damage between the treatments with weekly or interrupted pollen supply (FIGURE 4.3e,f), but there were significantly lower numbers of *A. swirskii* with interrupted pollen supply (FIGURE 4.3d) and an increase in damaged leaves in this treatment (FIGURE 4.3f). This suggests that it is not a good idea to interrupt pollen supply when thrips invade the crop. To our knowledge, there are no studies that investigate the most adequate frequency of food supply to predators; further studies should be devoted to this topic. The commercial recommendation for growers is to add pollen to the crop every 2 weeks (Pijnakker et al. 2016), according to our results, growers could add pollen weekly, which results in more predators on the leaves compared with an interrupted pollen supply (FIGURE 3d).

We found no negative effect of *M. robustulus* on thrips control by *A. swirskii*. This suggests that growers can preventively release *A. swirskii* and add pollen on the plants for control of *F. occidentalis* in roses even when these predators are in the litter.

Pre-establishment of predators is necessary for thrips control

Because the two experiments reported here were carried out at different times for logistical reasons, assessing the effect of releasing predators before or after releasing thrips is not straightforward. To nevertheless compare thrips control in the two experiments, we calculated the proportional decrease of thrips densities inside flowers, the marketable plant part, and on the leaves. Specifically, we calculated this decrease in the treatments with *A. swirskii* with pollen relative to the control (without predators and alternative food) for both experiments. This yielded two time series with relative changes of the thrips populations in the flowers, and two time series for the leaves. The average proportional thrips density in the flowers was 0.74 (s.e. 0.18) when thrips were released first and 0.34 (s.e. 0.078) when the predators were released first. Overall, this difference was significant (GLM with Gaussian error distribution: $F_{1,18} = 6.41$, $P = 0.021$). For the leaves, we did not find a significant difference in thrips densities (GLM with gamma error distribution: $F_{1,10} = 2.56$, $P = 0.14$). These comparisons suggest that pre-establishment of *A. swirskii* with pollen results in better control of thrips in rose flowers, confirming the findings of Muñoz-Cárdenas et al. (2017) and the results of other authors in vegetable crops regarding the importance of pre-establishment of predators for thrips control (Ramakers 1990; Kutuk & Yigit 2011; Kumar et al. 2015).

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