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Supplying high-quality alternative prey in the litter increases control of an above-ground plant pest by a generalist predator



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HIGHLIGHTS

- In biocontrol, alternative food for predators is normally supplied on the plants.
- We used the litter as source of alternative food for plant-inhabiting predators.
- The food in the litter was of superior quality than was the pest.
- Nevertheless, predators commuted between the litter and above-ground plant parts.
- Predators controlled thrips better with food in the litter than without it.

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ABSTRACT

Supplying predators with alternative food can have short-term positive effects on prey densities through predator satiation (functional response) and long-term negative effects through increases of predator populations (numerical response). In biological control, alternative food sources for predators are normally supplied on the crop plants; using the litter-inhabiting food web as a source of alternative food for plant-inhabiting predators has received less attention. We investigated the effect of supplying plant-inhabiting predatory mites with alternative prey (astigmatic mites) in the litter on pest control. Predator (*Amblyseius swirskii*) movement and population dynamics of the pest (western flower thrips) and predators were studied on rose plants in greenhouses. Predators commuted between the above-ground plant parts where they controlled thrips, and the litter, where they fed on alternative prey, although the latter were a superior diet. Predators controlled thrips better in the presence of the astigmatic mites than in their absence. We show that predatory mites can form a link between above-ground pests and the litter food web, and propose that adding alternative prey to the litter of ornamental greenhouses can result in higher predator densities and increased biological control.

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1. Introduction

Traditionally, above-ground and below-ground interactions involving the food web associated with plants were studied inde-

pendently, but it has become clear that these two food webs are connected (A'Bear et al., 2014; Bezemer and van Dam, 2005; Gange and Brown, 1989; van der Putten et al., 2001). Generalist predators can link above-ground and below-ground food webs by attacking prey in both habitats, thus shaping the composition and structure of the communities (Scheu, 2001; Wardle et al., 2004). Such links between spatially coupled food webs may affect the stability of prey dynamics in ecosystems (de Roos et al., 1998;

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¹ Maurice Sabelis sadly passed away. We miss him dearly.

McCann et al., 2005). Here, we investigate whether such predator-mediated links can be used to improve biological control.

Generalist predators are commonly used in biological control of crop pests (Symondson et al., 2002). They can feed on both the target pest and non-pest prey or other food sources (English-Loeb et al., 1993). Supplying alternative food to predators can affect biological control positively by increasing predator survival and reproduction when target pests are scarce (Eubanks and Denno, 2000). If populations of predators and prey do not exhibit sustained oscillations, adding extra food will result in an increase in the densities of predators in the longer term through the numerical response. This, in turn, will result in a decrease of the densities of both the pest and the alternative prey (apparent competition, Holt, 1977). However, the addition of alternative prey or food may initially decrease predation on target pests when predators concentrate feeding on the alternative food, or because predators become temporarily satiated (Abrams and Matsuda, 1996; Holt, 1977; van Baalen et al., 2001; van Maanen et al., 2012). These positive effects of adding alternative food on a prey are reminiscent of apparent mutualism (Holt, 1977; Abrams and Matsuda, 1996).

Whereas apparent mutualism is undesired in biological control, apparent competition is beneficial. For example, Liu et al. (2006) showed better control of spider mites on apple trees in the presence of alternative prey in the longer term (3.5 months), whereas there was no evidence of apparent mutualism in the shorter term. Messelink et al. (2008) found better control of one pest in the presence of another pest, both of which were attacked by the same predator species. Here too, there was no evidence of short-term apparent mutualism, but pest densities of the initial four weeks were lacking. A follow-up of this study indeed did show short-term apparent mutualism (van Maanen et al., 2012). Messelink et al. (2008) furthermore showed that the predators performed better on a mixed diet of two pest species, an effect that has not been included in the theory of apparent competition, but which results in even further reductions of prey densities.

Another strategy to improve biological control is to boost the populations of predators not with alternative prey, but with alternative food that does not damage the plant, such as pollen (Calvert and Huffaker, 1974; van Rijn et al., 2002; Janssen and Sabelis, 2015). However, the application of pollen to a crop can sometimes be risky because pests can also benefit from the presence of pollen (Chitturi et al., 2006; Leman and Messelink, 2015; Vangansbeke et al., 2016; but see van Rijn et al., 2002).

We studied a novel approach to improve biological control in ornamental greenhouses, which is supplying alternative prey for predators in the soil/litter layer. Plant-inhabiting predators can feed on alternative prey belonging to the decomposer community, which can feed and reproduce on the available organic material (Settle et al., 1996). The advantage of using the litter food web to supply alternative food is that it leaves no residues on the plant parts to be commercialized, which is desirable in ornamental crops. The risk is that the above-ground target pest and the alternative food are spatially separated, and predators may not commute sufficiently between the above-ground plant parts and the litter, thus either not benefitting fully from the alternative food, or reducing their attacks on the pest. This will even be more risky when the alternative food is of better quality for the predator than the plant-inhabiting pest.

Links between the above-ground and below-ground food webs through generalist predators have been observed in different systems (Moore et al., 2003), such as crops in the field (Settle et al., 1996), forests (Miyashita et al., 2003), grasslands (Hunt et al., 1987; Wardle et al., 2005) and organic farms (Birkhofer et al., 2008). However there are only a few examples of applications of such links between above-ground and below-ground food webs for biological control (Birkhofer et al., 2008; Halaj and Wise,

2002; Settle et al., 1996). Settle et al. (1996) added organic matter in rice fields, thus boosting populations of decomposers and plankton feeders and significantly increasing the abundance of predators and enhancing pest control. In contrast, Birkhofer et al. (2008) showed that increasing decomposer prey densities in wheat fields resulted in increases of populations of herbivores above-ground, and concluded that the predators switched from feeding on herbivores to decomposers (apparent mutualism, Holt, 1977).

Hence, contrasting effects have been found of adding alternative prey on biological control. We therefore tested the effect of adding alternative prey to the litter on densities of plant-inhabiting predators and an above-ground plant pest. The study system consisted of rose plants, the pest species *Frankliniella occidentalis* (Pergande), which cause economic damage in many different crops (Loomans and Murai, 1997), the predatory mite species *Amblyseius swirskii* Athias-Henriot, a predatory mite used to control thrips and whiteflies (Buitenhuis et al., 2015; Calvo et al., 2015; Messelink et al., 2006; Nomikou et al., 2001; Pijnakker and Ramakers, 2008) and several species of soil-inhabiting predators. We assessed whether predators commuted between the above-ground plant parts and the litter layer with alternative prey (astigmatic mites). Subsequently, we tested whether the alternative prey is of superior or inferior quality compared to the pest. Finally, we carried out experiments in the laboratory and greenhouse to test whether control of thrips was improved by supplying alternative prey for their predators in the litter.

2. Materials and methods

2.1. Rearing methods

Rose plants for cut flower production were purchased when they were four weeks old and kept in acclimatized rooms or in a greenhouse. To avoid contamination with arthropods, we removed all leaves and washed the stems with running tap water. Subsequently, the stems and roots were allowed to regrow in an acclimatized room (25 °C, RH 60%, photoperiod 16:8, Sylvania GRO-LUX F58W/GRO 5FT T8 58W) or a greenhouse compartment (22 °C, RH 70%, photoperiod 14:10) inside cages. They were either planted in pots (diam. 26 cm, height 25 cm) with peat as substrate (50% coco peat, 15% white peat, 35% frozen black peat, Jongkind grond BV, Aalsmeer) or in a rockwool strip (Grodan® Delta) inside a plastic tray (42 × 8 × 30). Plants were watered twice a week, and macro- and micronutrients (0.5 g N-P-K and 0.5 g micronutrients mix/200–500 ml of water/plant) were applied once a week.

Frankliniella occidentalis came from the stock colony of Koppert Biological Systems, where they had been reared on runner bean pods *Phaseolus vulgaris* L. plus *Typha latifolia* L. pollen for more than 10 years. The thrips were reared in the laboratory (T 23 °C, RH 65%) in plastic containers (8 × 8 × 12 cm), with openings covered with mite-proof mesh (30 µm) for ventilation (adapted from Loomans and Murai, 1997). Around 200 adult thrips were introduced into each container with four half bean pods, in which the females laid eggs for one day. Subsequently, the pods were replaced with fresh ones for further egg laying. The egg-infested pods were transferred to clean rearing containers, giving rise to individuals of the same age. Young first-instar thrips were taken from these containers and used for experiments on food quality.

Amblyseius swirskii used for laboratory experiments were originally collected from cotton in Redavim, Israel (Nomikou et al., 2001). They were reared on plastic arenas (8 × 15 cm), placed on a wet sponge in a plastic tray containing water, following Overmeer (1985). Strips of wet tissue were placed along the periphery of the arena to provide water. A tent-shaped piece of plastic sheet (1–2 cm²) was placed on each arena and functioned

as a shelter for the mites. A few cotton wool threads were put underneath the shelter as oviposition substrates. Cultures were fed with *Typha latifolia* pollen. To produce cohorts of predators of the same age, the threads were transferred to a new rearing arena every one to two days. Ten days later, adults from these arenas were used for experiments. For greenhouse experiments, commercially available predators were used (Swirski-mite[®], Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands).

We used two species of astigmatic mites as alternative prey; *Tyrophagus putrescentiae* (Shrank), the most abundant astigmatic species in the litter of commercial rose crops in greenhouses in the Netherlands (K. Muñoz-Cárdenas pers. obs.), and *Carpoglyphus lactis* L., also commonly occurring in rose litter (K. Muñoz-Cárdenas pers. obs.) and used for mass rearings of *A. swirskii* (Bolckmans and van Houten, 2006). Astigmatic mites were provided by Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands) and were reared in cylindrical plastic containers (diameter 8 cm, height 12 cm). For *T. putrescentiae* 10 g of bran (De Halm[®], Heeswijk, The Netherlands) was added as food; *C. lactis* cultures received 5 g of bran and 5 g of yeast (De Halm[®], Heeswijk, The Netherlands), all once per week. The containers were kept in the laboratory inside styrofoam boxes at 21 °C with wet tissue paper at the bottom to increase humidity.

2.2. Movement of *Amblyseius swirskii*

Because *A. swirskii* is mainly known to occur on above-ground plant parts, we tested whether they moved to the litter to feed on alternative prey. In a greenhouse compartment at the University of Amsterdam, four-week-old rose plants (var. Avalanche, Olij Rozen Int., de Kwakel, The Netherlands) with 3–4 leaves (c. 15 cm high) planted in rock wool were placed inside small insect-proof cages (30 × 30 × 30 cm). Small Petri dishes (2.5 cm) with c. 100 adult females of *T. putrescentiae* mixed with bran were placed on the rock wool under each plant. There were four treatments: a control without thrips and three treatments with 5, 10 or 25 first-instar thrips larvae on plant leaves. Immediately after releasing the thrips (at 21:00 h), we released five *A. swirskii* females (10–12 days old) per plant on the leaves. Thrips and predators were transferred to the plants using a fine brush. There were two blocks (October 3 and October 24, 2012), with three replicates of each treatment per block. Predatory mites in the Petri dishes and on the rock wool were counted 10 h later using a stereo-microscope.

The numbers of predators found under the plant per cage were ($\log + 1$) transformed to stabilize variance, and the transformed data were compared among treatments using a linear mixed effects model (LME, package nlme of R, Pinheiro, 2014) with the number of thrips as fixed factor and block as random factor. Residuals were analysed to check the suitability of the models (Crawley, 2013). All statistical analyses were done using R (R Development Core Team, 2013).

2.3. Effect of alternative prey on thrips densities

Two ten-week-old rose plants (var. White Naomi, Olij Rozen Int, c. 70 cm high) in pots with peat as substrate were placed in mite-proof cages (47.5 × 47.5 × 92 cm) in an acclimatized room at the University of Amsterdam (25 °C, RH 60%, photoperiod 16:8). Fallen, dried leaves were kept in the pots and flower buds were removed; both are common growers' practices during the early stages of plants development (Yong, 2004). There were two treatments, cages to which *A. swirskii* was added and cages with *A. swirskii* plus alternative prey (*T. putrescentiae*) added. The experiment was done in two blocks (May and August, 2012), with three replicates (cages) of each treatment per block. Thrips were collected from the rearing unit with a disposable polypropylene pipette tip covered at the

wide end with a piece of gauze (mesh 30 µm) and connected to a flexible plastic tube, which was either connected to a pump or used as mouth piece. Air carrying thrips or predators was sucked through the tip, and the tip was subsequently closed at both sides with Parafilm[®]. A small piece of yarn was taped to the pipette tip to suspend it from a branch of a rose plant. After removing the Parafilm, the thrips could move onto the plants. In the first week, 40 adult thrips were released per cage. During the first, second and third week, 50 adult female *T. putrescentiae*, mixed with 2 g of bran serving as food, were dispersed on the substrate under the plants of the respective treatment. In the third and fifth week, 40 female *A. swirskii* (10–12 days old) were released onto the leaves with a fine brush.

In the second week, ten leaves/cage were collected, five leaves from the upper part and five from the lower part of the plants to confirm establishment of the thrips. This was repeated in the fourth week, one week after the first predator release. The numbers of thrips and the proportion of leaves with thrips damage were scored using a stereo microscope. The plants did not produce any flowers during the experiment. Because most leaves were already damaged since the first sampling, the proportions of damaged leaves were not analysed. We checked for the presence and identity of *A. swirskii* in all the cages. After six weeks, all leaves were collected from each cage and the average numbers of thrips per leaf were scored. These numbers were $\log(x + 0.1)$ transformed and analysed with a linear mixed effects model (LME) with treatment as fixed factor and block as random factor. Residuals were checked as above.

2.4. Food quality of pest and alternative prey

The quality of astigmatic mites and thrips larvae as food for the predators was assessed by measuring juvenile survival and development and oviposition of *A. swirskii* in the laboratory at the University of Amsterdam. Cohorts of *C. lactis* were prepared by allowing 50–60 females to oviposit on a plastic arena (similar to those used for *A. swirskii*, see Section 2.1) with one gram of solid yeast during 24 h (25 °C, 70 RH). Five days later, larvae were taken from these arenas. One day old thrips larvae were taken from the thrips colony.

Newly hatched predator larva were transferred each to a separate leaf disc (var. Avalanche) with either eight *C. lactis* immatures, four young first-instar thrips or four *C. lactis* immatures plus two thrips. A surplus of prey was offered, based on reported consumption rates of *A. swirskii* (Bolckmans and van Houten, 2006; Messelink et al., 2008). Every day, the juvenile predatory mites were transferred to a new leaf disc with the same food. There were two blocks in time, with between 14 and 15 predators (replicates) per treatment in the first block and six in the second block. Survival and the stage of the predator were recorded daily until all mites had reached adulthood or died. Juvenile development and survival were analysed using time-to-event analysis (Cox proportional hazards, R package coxme, Therneau, 2015), with diet as fixed factor and block as random factor. Contrasts among treatments were assessed through general linear hypothesis testing (glht of the lsmeans package with the "tukey" adjustment of p values, Lenth, 2016).

The oviposition of adult *A. swirskii* was measured during ten days on the three diets mentioned above. To obtain adult females, rose leaves on pieces of wet cotton wool in Petri dishes were supplemented with around 50 predator eggs. When the larvae hatched, we daily added around 100 *C. lactis* and/or thrips larvae according to the treatment until copulations of adult predators were observed (after c. seven days). Twelve females per diet were transferred each to a separate leaf disc with a cotton thread (0.5 cm) as oviposition substrate. They were supplied with either

20 *C. lactis* immatures, eight first instar thrips larvae or ten *C. lactis* plus four thrips larvae per day. The cotton thread was replaced daily during ten days and predator eggs were counted. The ($\log + 1$) transformed numbers of eggs produced per female per day were analysed with an LME with individual as random factor and the age of the predator and the treatment as fixed factors.

2.5. Thrips control by *Amblyseius swirskii* with alternative prey

Because soil-inhabiting predators were encountered in the experiment above (Section 2.3), another experiment was done to specifically study the effect of *A. swirskii* with alternative food on thrips control. We therefore thoroughly washed roots of rose plantlets with running tap water to remove soil mites. Plants (var. Avalanche, 4 weeks old) were planted in clean peat before placing them inside cages in a greenhouse compartment at the University of Amsterdam, where two plants were allowed to grow for four weeks, having 10–12 leaves and an approximate height of 30 cm. Litter collected from a commercial greenhouse was sterilized (108 °C, 1 bar, 20 min) to kill mites, moistened (100 ml water/l L) and placed at the base of the plants.

There were four treatments, each replicated three times: thrips with bran; thrips, *A. swirskii* with bran; thrips with c. 4000 adult female *C. lactis* mixed with all other stages; thrips, *A. swirskii* with bran and female *C. lactis* (same quantities). *Carpoglyphus lactis* was reared on bran, and was released on the litter with c. 100 g of bran for practical reasons. The same quantity of sterilized bran was added to the control treatments. Forty predators (*Swirskimite*[®]) were released on the litter of each cage with a mix of bran with or without *C. lactis*. One week later, each cage received 60 adult thrips using pipette tips (Section 2.3). From the third to the twelfth week, we counted thrips, thrips damage and predators on six leaves (two from the top part, two from the middle and two from the lower leaves). All flowers were collected in plastic containers with alcohol (70%), washed with 70% alcohol on a mesh (100 μ) and the thrips and mites on the mesh were counted under a stereo-microscope. Once per week, we checked 50 ml of litter and bran from each cage for the presence of astigmatic mites and predatory mites under a stereo-microscope. Each week, three of the adult female predators found were identified (Chant and McMurtry, 2007; Demite et al., 2014). Predatory mites from the flowers and the litter were identified by Farid Faraji (Mitox Consultants/Eurofins).

The densities of thrips on leaves and in flowers and predators were $\log(x + 0.1)$ transformed, the proportions of damaged leaves (judged by the presence of feeding scars) were not transformed, and all were analysed with linear mixed effects models (LME) with the experimental unit (cage) as random factor and time (week) and treatment as fixed factors. The proportion of flowers with heavy thrips damage (>5 feeding scars/flower) were analysed with a generalized linear model (GLM) with treatment as factor and a quasi-binomial error distribution. Contrasts among treatments and checking of the error distribution were done as above.

3. Results

A pilot experiment showed that high densities of *A. swirskii* controlled thrips and decreased the thrips damage of flowers after four weeks (Supplementary material). We therefore investigated whether adding alternative food to the litter could boost densities of this predator to sufficiently high levels for thrips control.

3.1. Movement of *Amblyseius swirskii*

Of the five mites released per plant on the above-ground parts, we recaptured on average 37.5% (s.e. 7.2%). The majority of these

(1.4 mites/replicate) were found in the Petri dishes with alternative prey; the others were found on the plants. Most probably, the rest of the mites were inside the rock wool, which was not sampled because of its complex structure. If they were indeed there, this would mean that they also moved down. The densities of thrips on the plants had no effect on the movement of predatory mites (Fig. 1, LME: d.f. = 3, $\text{Chi}^2 = 6.34$, $P = 0.10$). These results confirm observations of *A. swirskii* individuals in the litter in commercial rose greenhouses in which they had been released on the plants (K. Muñoz-Cárdenas, pers. obs.).

3.2. Effect of alternative prey on thrips densities

There were no significant differences in the average numbers of thrips per leaf before releasing the predators in the second week (Fig. 2, LME: d.f. = 1, $\text{Chi}^2 = 0.17$, $P = 0.67$) or after predator release in the fourth week of the experiment (Fig. 2, LME: d.f. = 1, $\text{Chi}^2 = 0.05$, $P = 0.83$). Destructive sampling in the sixth week showed significantly fewer thrips per leaf in treatments with *A. swirskii* plus alternative prey than with *A. swirskii* alone (Fig. 2, LME: d.f. = 1, $\text{Chi}^2 = 6.75$, $P = 0.009$). Besides *A. swirskii*, similar densities of litter-inhabiting thrips predators from the family Laelapidae (genera *Cosmolaelaps* and *Stratiolaelaps*) were found in the litter in both treatments. Similar results were obtained in a larger scale experiment in the greenhouse (Supplementary material).

3.3. Food quality of pest and alternative prey

The rate of juvenile development was affected by diet (Fig. 3a, mixed-effects Cox model: d.f. = 2, $\text{Chi}^2 = 25.1$, $P < 0.001$); it was similar on diets of *C. lactis* alone or combined with thrips and lower on a diet of only thrips (Fig. 3a). Survival was higher in the treatments with *C. lactis* alone (90%) or combined with thrips (80%) than in the treatment with thrips alone (77%), but these differences were not significant (Fig. 3a, d.f. = 2, $\text{Chi}^2 = 1.18$, $P = 0.55$).

The average oviposition through time of *A. swirskii* on a diet of *C. lactis* immatures, first instar thrips larvae or on a mixed diet did not differ significantly (Fig. 3b, LME: $\text{Chi}^2 = 3.03$, $P = 0.22$).

3.4. Thrips control by *Amblyseius swirskii* with alternative prey

There was a significant effect of the interaction between treatment and time on the densities of thrips on leaves (Fig. 4a, LME: d.f. = 3, $\text{Chi}^2 = 222.7$, $P < 0.0001$). This was caused by the densities

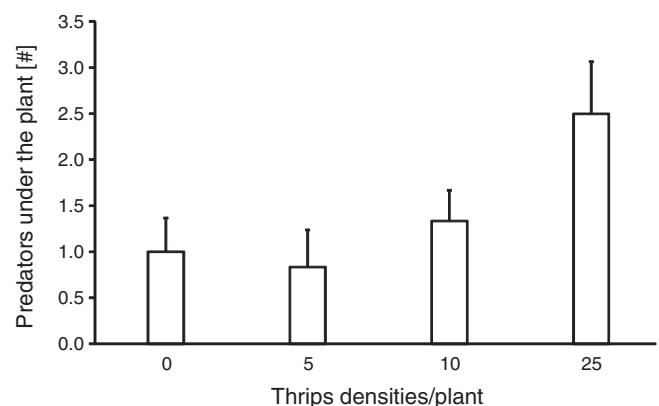


Fig. 1. Effect of the density of first instar larvae of thrips (horizontal axis) on leaves of rose plants on the average number (\pm s.e.) of *A. swirskii* moving down from the leaves to Petri dishes with astigmatic mites on the substrate under the plant. There was no significant effect of the number of thrips larvae on predator movement (LME, $P > 0.05$).

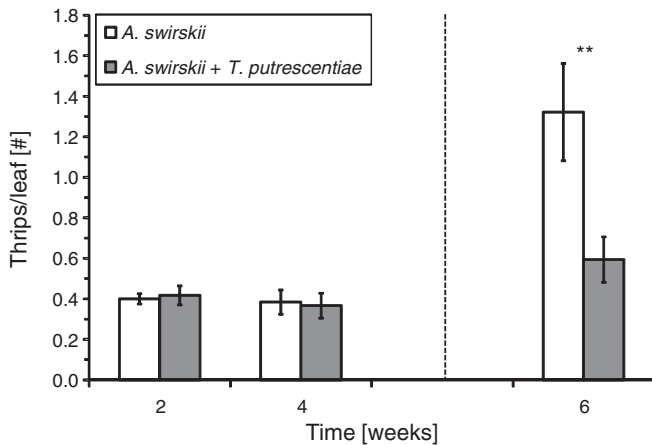


Fig. 2. Effect of addition of astigmatic mites (*T. putrescentiae*) as alternative prey in the litter layer under laboratory conditions on average numbers of thrips/leaf (\pm s.e.). Data of the second and fourth weeks correspond to samplings of ten leaves per cage; data of the sixth week correspond to destructive sampling in which the number of thrips were scored on all leaves of each cage. The asterisks indicate a significant difference between treatments (LME, $P < 0.01$).

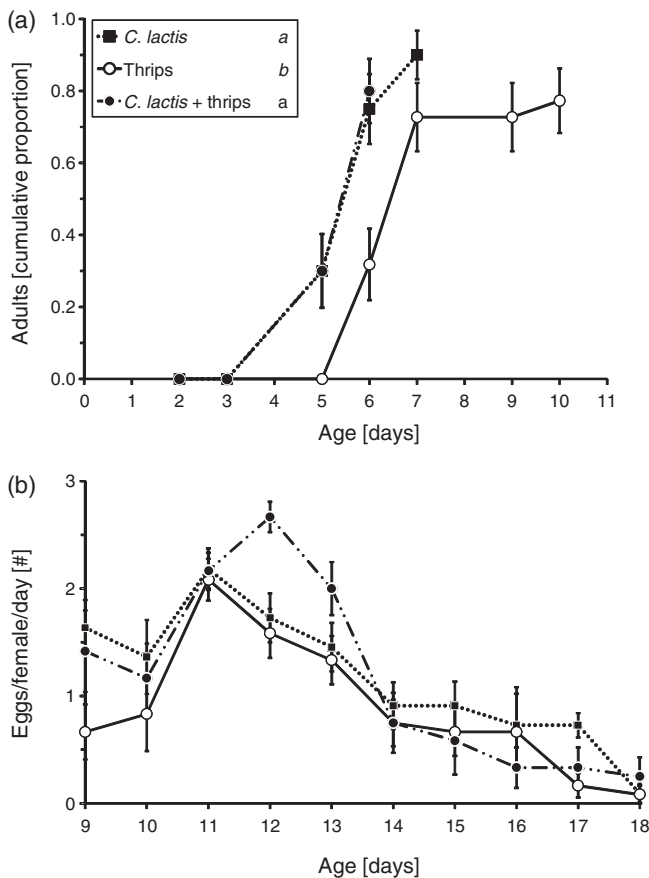


Fig. 3. (a) Development of juveniles of the predatory mite *A. swirskii* on a diet of either *C. lactis*, thrips, or *C. lactis* plus thrips. Shown are the cumulative proportions of juveniles that developed into adults (\pm s.e.). Different letters in the legend represent significant differences in developmental rate among treatments (contrasts with general linear hypothesis testing after Cox proportional hazards, $P < 0.05$). Differences in survival until adulthood were not significant ($P > 0.05$). (b) Average numbers of eggs per female per day (\pm s.e.) of young female *A. swirskii* during 10 days on a diet of *C. lactis*, thrips or *C. lactis* plus thrips. There was no significant effect of diet on oviposition (LME, $P > 0.05$).

of thrips remaining low in the treatment with *A. swirskii* plus alternative food and increasing in the other treatments (Fig. 4a). Thrips densities on leaves were significantly lower in the treatments with

A. swirskii than in the control (Fig. 4a). The numbers of thrips in the flowers differed significantly among treatments (Fig. 4b, d.f. = 3, $\text{Chi}^2 = 9.26$, $P = 0.026$) and with time (d.f. = 1, $\text{Chi}^2 = 31.4$, $P < 0.0001$). The numbers of thrips in flowers were significantly lower with *A. swirskii* plus alternative food than in the control (Fig. 4b). The interaction between treatment and time had no significant effect (d.f. = 3, $\text{Chi}^2 = 7.66$, $P = 0.054$). Alternative prey significantly increased densities of predators (Fig. 4c, LME: d.f. = 1, $\text{Chi}^2 = 11.8$, $P < 0.001$). We found *A. swirskii* in the litter throughout the experiment when it was released together with alternative prey.

The proportion of damaged leaves was significantly affected by the interaction between treatment and time (Fig. 4d, d.f. = 3, $\text{Chi}^2 = 12.6$, $P = 0.0057$). Initially the proportion of damaged leaves was similar in all treatments, but overall, damage levels were significantly lower when *A. swirskii* was released than in the other two treatments (Fig. 4d).

The proportion of flowers with heavy thrips damage varied significantly with treatment (GLM, $F_{3,8} = 5.11$, $P = 0.029$). The treatment with *A. swirskii* with alternative food ($12 \pm 8.5\%$ flowers damaged) differed significantly from the control ($73 \pm 11.6\%$). The treatments with *A. swirskii* alone ($32 \pm 13.4\%$) and with alternative food alone ($61 \pm 14.6\%$) did not differ significantly from the other treatments. No litter-inhabiting predators were found in this experiment, confirming that sterilizing the litter and washing the roots of the plants before the experiment had resulted in their exclusion.

4. Discussion

The use of generalist predators for biological pest control has become a commonplace (Janssen and Sabelis, 2015; Symondson et al., 2002). Generalists have the advantage that their populations can be maintained in a crop when no pests are present. To date, this was mainly achieved by supplying alternative food on the above-ground plant parts (Adar et al., 2014; Delisle et al., 2015; Duarte et al., 2015; Kumar et al., 2015; Leman and Messelink, 2015; Liu et al., 2006; Messelink et al., 2008; Nomikou et al., 2010, 2002; Pijnakker et al., in press; van Rijn et al., 2002). The current study capitalized on the use of soil or litter-inhabiting arthropods as food for predators. For this strategy to be effective, generalist predators need to forage in both habitats, which was confirmed here for *A. swirskii*. This resulted in better biological control of thrips, an above-ground pest which passes part of its life cycle in the litter.

A risk of supplying generalist predators with alternative prey is the occurrence of positive effects on pest densities (apparent mutualism, Holt, 1977), for which we did not find evidence. Supplementary food or prey can hamper biological control in the short term (Koss and Snyder, 2005; Prasad and Snyder, 2006), but the presence or addition of alternative food or prey can also lead to high densities of predators (Nomikou et al., 2010). Supplying alternative food in the litter has two advantages. First, no alternative prey or food needs to be added to the above-ground crop parts, which is the marketable part in roses. Second, no pollen needs to be dusted on the plants, which can be risky because thrips can also feed on pollen (Chitturi et al., 2006; van Rijn et al., 2002; Vangansbeke et al., 2016).

Some studies show that the presence of alternative food on plants did not result in yield loss or decrease of plant damage, even if there were decreases in pest numbers and increases in predator numbers (Delisle et al., 2015; Jaworski et al., 2015). In contrast, we found that adding alternative prey for *A. swirskii* to the litter resulted in lower damage of leaves and flowers. When *A. swirskii* and alternative prey were released before thrips infestations, a sig-

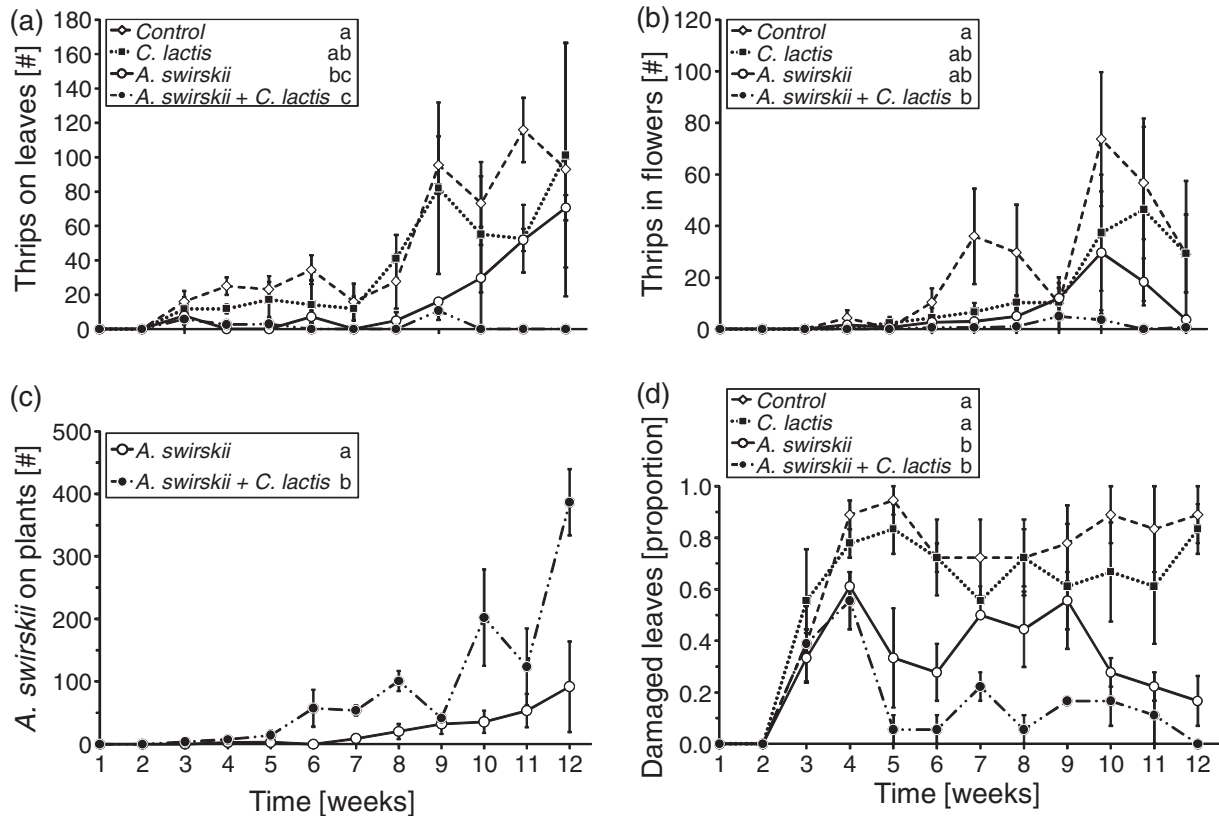


Fig. 4. Effect of addition of *C. lactis* to a sterilized litter layer as alternative prey for *A. swirskii* on thrips control under greenhouse conditions. (a) The average number (\pm s.e.) of thrips per leaf on rose plants inside cages. Thrips were released in the second week and larvae and adult thrips were sampled from the third week on. (b) The average number of thrips (\pm s.e.) in flowers inside the same cages as (a). (c) The average number of *A. swirskii* (\pm s.e., all stages). (d) The average proportion of damaged leaves (\pm s.e.) per week. Different letters in the legend represent significant differences among treatments through time (contrasts with general linear hypothesis testing after LME, $P < 0.05$).

nificant reduction of pest damage was observed (Fig. 4c, Supplementary Fig. 1). We therefore suggest that predators and alternative food should be added to the crop before pest invasion, which will decrease plant damage by thrips. Furthermore, instead of the common practice of putting the litter under the benches with plants, growers could add some humid litter (humidity is essential for survival and development of the alternative prey) at the base of the plants and provide alternative prey in this litter to increase pest control.

A possible disadvantage of adding alternative prey to the litter is that predators will have to commute between the litter and the above-ground plant parts where pests reside. In the case of western flower thrips, this is not a disadvantage because thrips prepupae and pupae live mainly in the litter and *A. swirskii* can attack these stages (K. Muñoz-Cárdenas & Marcus Duarte, pers. obs.). Another disadvantage of adding alternative prey is that predators may refrain from attacking the pest when the alternative prey in the litter is of superior quality, as was the case here (Fig. 3). Nevertheless, we found better thrips control with alternative prey in the litter (Fig. 4a). Moreover, there were four times more predators on the above-ground plant parts in the treatment with alternative prey in the litter (Fig. 4b). This suggests that the predators commuted from the litter to the plants and fed on both prey rather than concentrating their attacks on the superior prey in the litter. However, the alternative prey was added at the beginning of the experiments, and their densities may have been reduced towards the end of the experiment, resulting in hungry predators attacking thrips. Clearly, the dynamics and the timing of release of the alternative prey deserve further study, because adding high-quality alternative prey may result in a temporal release of thrips from

predation (short-term apparent mutualism, Holt, 1977; Abrams and Matsuda, 1996).

Another mechanism by which predatory mite populations can increase when feeding on two different prey is through diet supplementation (Marques et al., 2015; Messelink et al., 2008). We did not find evidence for better performance of *A. swirskii* on a mixed diet of thrips and the alternative prey *C. lactis* than on *C. lactis* only (Fig. 3). Instead, the juvenile survival and developmental rate was highest on diets containing *C. lactis*, irrespective of the addition of thrips (Fig. 3a). In agreement with this, we found the highest densities of predators when this alternative prey was present (Fig. 4b). This confirms that *C. lactis* is a better food source for *A. swirskii* than are thrips larvae.

It is not obvious that plant-inhabiting predators such as *A. swirskii* move down to the litter to feed on alternative prey. Buitenhuis et al. (2010) reported that *A. swirskii* moved down to the soil to disperse; we found that they move to this habitat provided there are astigmatic mites in the litter on which they can feed (Fig. 1). Possibly, the presence of alternative prey in the litter caused *A. swirskii* to forage more there, also attacking thrips pre-pupae and pupae (K. Muñoz-Cárdenas & M.V.A. Duarte, pers. obs.). Other litter-inhabiting predatory mites can also feed on these thrips stages and on the alternative prey in the litter. Therefore, further experiments should assess the effect of these litter-inhabiting predators on pest populations and their interactions with plant-inhabiting predatory mites, especially because it has been shown that intra-guild predation between plant-inhabiting and litter-inhabiting predators can occur (Messelink and van Holstein-Saj, 2011) and might disrupt biological control (Vance-Chalcraft et al., 2007; Rosenheim et al., 1995; but see Janssen et al., 2006).

In conclusion, our results demonstrate that links can be established between above-ground plant pests and the litter food web and that such links can benefit plant-inhabiting predators, resulting in an increase of predator densities and enhanced biological control. This confirms the importance of considering connections between above-ground and below-ground food webs associated with plants (A'Bear et al., 2014; van der Putten et al., 2001), also for applied purposes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2016.11.004>.

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