What lies beneath?

Linking litter and canopy food webs to protect ornamental crops

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General discussion

Biological control of pests is an important component in crop management (Bale et al. 2008). Usually, crops are attacked by various pest species, therefore, generalist predators have been considered as a solution for pest control (Symondson et al. 2002). Contrary to specialist predators, generalist predators can feed on different prey species and on plant-provided foods (Symondson et al. 2002). For a long time, there was scepticism regarding the use of generalists for pest control: their ability to feed on different sources was sometimes considered a disadvantage for biological control because it was interpreted as generalist predators not being well adapted to the pest (Huffaker et al. 1969). However, since the 1950s, numerous studies have shown that the presence of alternative food for generalist predators on the plant did not have negative effects on biological control, but rather improved it (Huffaker & Kennett 1956; Collyer 1964; van Rijn et al. 2002). In theory, two prey populations can affect each other's densities indirectly when they are attacked by the same population of natural enemies (Holt 1977). The fact that generalist predators feed on different prey or other foods could negatively affect biological control because they might feed on the alternative food or prey, thus releasing the target pest from attacks, this short-term effect is called apparent mutualism (Murdoch 1969; Abrams & Matsuda 1996). This positive effect of adding alternative prey or food on pest densities is obviously detrimental for biological control. In the long-term, however, the densities of prey may decrease in response to increases of predator populations, increasing biological control (Collyer 1964; Karban et al. 1994; Müller & Godfray 1997). Hence, the effect of the alternative food or prey on each pest densities can be positive (apparent mutualism) or negative (apparent competition). When population densities do not reach equilibria, but show cycles, apparent mutualism can occur also in the long-term, resulting in repeated satiation of the shared predators and repeated reduced predation on the other prey, thus affecting biological control negatively (Abrams et al. 1998). Moreover, the use of generalist predators might be also detrimental for biological control because they can compete for prey or food with other natural enemies and they can also engage in negative interactions such as intraguild predation (Rosenheim et al. 1995). However, the use of combinations of species of generalist predators or combinations with other natural enemies do not always result in negative effects on biological control (Cardinale et al. 2003; Losey & Denno 1998). Summarizing, generalist predators can mediate interactions between prey (apparent mutualism, apparent competition; Holt et al. 1977) and can also engage in positive

or negative interactions with other natural enemies. Thus, the outcome of using generalist predators for biological control can best be predicted when studying the different interactions among predators and prey.

Because generalist predators interact with several species, they increase connectivity within and among food webs. In the past, above-ground and below-ground food webs were studied independently. However, it has become clear that these two food webs are connected, which affects the composition and structure of the communities in both habitats (Gange & Brown 1989; van der Putten et al. 2001; Bezemer & van Dam 2005; A'Bear et al. 2014). Generalist predators can form direct links between above-ground and below-ground food webs when they feed on pests present on above-ground plant parts and on pest or alternative prey from the decomposer community below-ground (Settle et al. 1996; Scheu 2001). As a result, there are complex food web interactions in crops due to the presence of generalist predators, pests, other natural enemies and alternative prey not only on above-ground plant parts but also in the below-ground plant system. In CHAPTER 1, I show an example of a generalist predator that lives in the soil or litter layer and also preys on pests on the plant. This predator's life history inspired me to investigate the possibilities of connecting above-ground and litter food webs. Therefore, the question addressed in the rest of the dissertation was how connecting above-ground and below-ground plant systems can be used to improve biological control by generalist predators. Furthermore, I study how supplying natural enemies with alternative prey or food can improve biological control. In CHAPTERS 2 and 3, I show how alternative prey added to the litter increases the biological control of thrips, a pest that causes damage on above-ground plant parts and spends part of its life cycle in the litter or soil. In CHAPTER 4, I show how a combination of generalist predator species and alternative foods in the litter and on above-ground plant parts affects the biological control of thrips.

In CHAPTER 1 I investigated how the generalist predator *Balaustium leanderi*, which inhabits the below-ground plant system and forages on above-ground plant parts, was affected by feeding on a mixed diet of different species of important crop pests that affect above-ground plant parts. Several generalist predators have been shown to reproduce better on mixtures of prey species than on each prey species alone (Bilde & Toft 1994; Toft & Wise 1999; Messelink et al. 2008; Lefcheck et al. 2013, Marques et al. 2015). A special characteristic of *B. leanderi* is that it exhibits big-bang reproduction (semelparous reproduction), which means that females lay all their eggs at once and die soon after ovipositing. I show that *B. leanderi* females reproduce earlier and lay more eggs on a mixed diet of whitefly eggs and spider mite eggs. Predator females that reproduce early consequently have higher population growth rates than late reproducers (CHAPTER 1). The effect of a mixed diet on *B. leanderi* is

important for biological control because the mixed diet of whiteflies with spider mites boosts its population densities, possibly increasing the biological control of the three prey species (see Messelink et al. 2008 for an example). Further experiments should be carried out to confirm whether apparent competition mediated by *B. leanderi* occurs between the pests under cropping conditions.

In CHAPTER 2, I further investigated how connecting above-ground and below-ground food webs can serve to improve biocontrol with the predatory mite *Amblyseius swirskii*, which was known as an above-ground predator. I studied how the indirect interaction between the thrips and an alternative prey affected thrips control. Astigmatic mites (*Carpoglyphus lactis* or *Tyrophagus putrescetiae*) were used as alternative prey and were released in the litter, because during the litter decomposition process, astigmatic mites can feed on fungi and other organisms, ensuring adequate conditions for the alternative prey to establish. I found that this predator developed faster when feeding on *C. lactis* either alone or in combination with the canopy-inhabiting thrips larvae. Hence, *C. lactis* was of higher nutritional value for *A. swirskii* than the pest. Adding a high-quality alternative prey may result in the predators concentrating their attacks on the alternative prey, resulting in a temporal release of thrips from predation (short-term apparent mutualism; Holt 1977; Abrams & Matsuda 1996). However, I found no evidence for this effect when performing population dynamics experiments in the greenhouse: when astigmatic mites were present as alternative prey for *A. swirskii*, the population densities of thrips decreased and predator densities increased (CHAPTER 2). Hence, there was a predator-mediated negative interaction between prey (apparent competition; Holt 1977). *Amblyseius swirskii* were initially released in the litter together with the alternative prey and were subsequently found on the above-ground plant parts, showing that it commutes between the above-ground and below-ground food web. To conclude, the predatory mite *A. swirskii* acts as a link between the above-ground and litter food webs and mediates a negative indirect interaction between prey, enhancing thrips control.

During the experiments performed in CHAPTER 2, I observed that litter-inhabiting predatory mites found in commercial greenhouses (i.e. other species than *A. swirskii*) can also feed on thrips pupae and pre-pupae that inhabit the litter and on the alternative prey in the litter. Therefore, the next question was whether the negative indirect interaction among thrips and astigmatic mites could also be mediated by these litter-inhabiting predators. In CHAPTER 3, I therefore selected a predatory mite species, *Cosmolaelaps* n. sp. from the community of predators found in the litter in commercial rose crops. This predator benefits from an alternative prey added to the litter, the astigmatic mite *C. lactis*, and it also feeds on thrips. I studied the population dynamics of this predator and the pest, thrips. Similar to results in CHAPTER 2, I showed better thrips control by either the community of litter-inhabiting predator species or by

Cosmolaelaps n. sp. alone when astigmatic mites were added as alternative prey to the litter. I found that another species of predatory mite, *Proctolaelaps pygmaeus*, was abundant when the alternative prey was added to the community of predators, and that this predator feeds on the alternative prey *C. lactis* but not on thrips. It is not known to which extent the presence of predators like *P. pygmeus* can affect thrips control by species such as *Cosmolaelaps* n. sp. Predator-predator interactions such as competition for food or intraguild predation among these litter-inhabiting predators should be addressed in future studies. Thus, in CHAPTER 3, I showed that litter-inhabiting predators can also mediate a negative interaction between prey, resulting in increased biological control of thrips.

Adding alternative food for predators does not always result in better pest control: some studies have shown that offering two prey to a generalist predator did result in increases in numbers of predators and decreases in the pest number, but not in decreases of plant damage or yield loss (Delisle et al. 2015; Jaworski et al. 2015). In CHAPTERS 2 and 3, I show that releasing *A. swirskii* or litter-inhabiting predators together with alternative prey in the litter results in decreases in thrips damage compared to treatments in which alternative prey was not added. However, damage to flowers, the marketable part of the crop, is more effective when the canopy-dwelling predator *A. swirskii* was released with alternative food (CHAPTER 2) than litter-inhabiting predators or *Cosmolaelaps* n. sp. with alternative prey (CHAPTER 3). Thus, the combination canopy-dwelling predators and litter-inhabiting predators with alternative prey might lead to lower damage of flowers.

Therefore, the question that I addressed in CHAPTER 4 was whether it would be possible to further decrease thrips damage when using different kinds of alternative food and a combination of canopy-dwelling and litter-inhabiting predators. I also tested thrips control when releasing predators preventively or only after thrips had established, which has shown to affect thrips control in other crops (Ramakers 1990; Kutuk & Yigit 2011; Kumar et al. 2015).

Previous experiments (CHAPTERS 2 and 3) were done with litter added to the base of the plants, but the litter in commercial Dutch greenhouses is not found at the base of the plants, but further down, under the tables on which the plants are grown. In CHAPTER 4, I therefore tested the effects of addition of food under more realistic conditions, including the presence of a common soil predator that might improve or interfere with control. Thus, the distance between the litter and the plants was larger than in the previous chapters.

In the first experiment in CHAPTER 4, the question was whether adding alternative food either in the litter (*Acarus siro*) or on the plant (pollen) for a canopy-dwelling predator (*A. swirskii*) and litter-inhabiting predators would increase thrips control. In this experiment, thrips were released before the predators with alternative prey or

pollen, and as a result, damage was too high to find differences among treatments. Decreases in thrips numbers were observed only during the last 3 weeks of the experiment, and only in the treatment with *A. swirskii* plus pollen (CHAPTER 4). All the leaves and flowers were damaged by thrips and I observed higher densities of thrips and higher plant damage during the first weeks on plants to which pollen was added as alternative food. This could have been an effect of apparent mutualism, of thrips feeding on the pollen, or of both. These results are similar to those obtained by Delisle et al. (2015), whom found more thrips damage on plants on which pollen was added than on plants without pollen. As explained above, apparent mutualism can occur when the shared predator becomes satiated or switches to feed on the alternative prey or food decreasing the attacks to the alternative prey (Murdoch 1969; Abrams & Matsuda 1996). This effect occurs in the short-term but can also occur in the long term when population densities fluctuate. Curiously, I did not observe apparent mutualism-like phenomena in CHAPTERS 2 and 3. One obvious difference between the experiment described in CHAPTER 4 and those of the previous chapters was the distance between the litter and the above-ground plant parts. Possibly, *A. swirskii* did not commute as much between the litter and the canopy because of this increased distance, and instead concentrated their attacks initially on the alternative prey in the litter (apparent mutualism; Holt 1977; Abrams & Matsuda 1996). Holt (1984) studied models of prey that occurred in different habitats, but were attacked by the same predators. He predicted that negative effects of prey species on each other's densities decrease when migration by the shared predator is slow, because it decouples the dynamics of the predators in the two habitats. This may have occurred in my experiments as well, which may explain the less effective control of thrips. Additionally, thrips perhaps did not only pupate in the litter under the tables with plants, but also on the tables at the base of the plant, where they would experience less predation by the litter predators. Summarizing, this experiment shows that the distance between the sites where alternative food or prey is supplied and the part of the crop where the pest occurs may be critical for efficient pest control. It also shows that by releasing thrips before predators, plant damage is too high in all treatments with or without predators and alternative food.

In a second experiment in CHAPTER 4, I tested the effect of the combination of predators (*A. swirskii* and litter-inhabiting predators) and two alternative foods (*A. siro* and pollen) on thrips control. The differences with the previous experiment were that a combination of predators and their own alternative food or prey were added simultaneously on the plant and in the litter, and that predators with alternative food were released before the thrips. Moreover, we included two frequencies of addition of pollen. The results of this experiment show that adding pollen to the plants for the plant-inhabiting predator *A. swirskii* leads to high predator densities and decreases

in thrips densities and their damage (CHAPTER 4). Adding litter-inhabiting predators plus *A. siro* did not result in better thrips control than releases of only *A. swirskii* plus pollen. In fact, the presence of litter-inhabiting predators plus alternative prey did not have any effect on thrips densities. This is in contrast with the findings of CHAPTER 3 when releasing another litter-inhabiting predator, *Cosmolaelaps* n. sp. plus alternative prey in the litter resulted in a decrease in thrips numbers and thrips plant damage (CHAPTER 3). A possible reason for litter-inhabiting predators not contributing substantially to the control thrips is that the litter-inhabiting predators were far removed from the above-ground plant parts in CHAPTER 4. However, the presence of litter-inhabiting predators plus the alternative prey did not have negative effects on thrips control by *A. swirskii* (CHAPTER 4). Future experiments should investigate whether placing some litter with litter-inhabiting predators plus alternative prey at the base of the rose plants would result in better control. Many pest species spend part of their life cycles in the litter or soil (Wahab 2010), others drop to the soil when threatened (Losey & Denno 1998). Thus, having high quantities of litter or soil-inhabiting predators could contribute to the control of various pest species in many crops.

Another aspect that should receive more attention in future studies is the timing at which alternative food should be added to the crop. Many studies have shown that adding alternative food can improve biological 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; Duarte et al. 2015), but none have investigated the amounts and supply frequencies on biological control. In the second experiment presented in CHAPTER 4, two frequencies of pollen addition were tested. In one treatment, pollen was added during 4 weeks out of the 14 weeks of the experiment. In other treatments pollen for *A. swirskii* was added weekly. There were no differences among treatments concerning thrips numbers or thrips plant damage. However, there were differences in the number of *A. swirskii*. Leaves of plants to which pollen was added every week harboured significantly more predators than plants with the interrupted feeding treatment. Future studies should further explore 'optimal' frequencies of addition of alternative food on crop protection.

Summarizing, in this thesis, I present experiments that contribute to the test of food web theory. I studied aspects such as apparent competition, apparent mutualism, effects of combined releases of predators on prey on above-ground and below-ground plant systems. The results in this thesis contribute to the understanding of the dynamics of above-ground and below-ground food webs and they are first steps in the development of a new biological control strategy in ornamentals, which is the addition of alternative food for predators in the litter. Comparing experimental results and existing theory of population dynamics can be challenging because of differences in time scale. Experiments are usually short, but most theory is based on long-

term equilibrium dynamics (Briggs & Borer 2005). The experiments performed in this thesis were long enough to record positive and negative effects of the addition of alternative food or prey on pest populations and on plant damage, hence they succeed in assessing whether such effects as apparent competition and apparent mutualism do occur. Moreover, they reveal connections between above-ground and below-ground food webs through the foraging of generalist predators. A question that arises at this point is how these findings can help growers to enhance biological control. In CHAPTER 2, I proposed a novel way to enhance pest control in ornamental crops by supplying alternative food in the litter. Adding alternative prey in the litter at the base of the plant, far from the commercial plant parts may be an important contribution to sustainable production of ornamentals. It has the advantage that no residues of alternative food will be left on the marketable plant parts (CHAPTERS 2 and 3). As a conclusion, links can be established between above-ground plant pests and the litter food web and such links can benefit above-ground and below-ground predators, resulting in an increase of predator densities and enhanced biological control. Thus, connections between above-ground and below-ground food webs associated with plants may play a key role not only in natural communities (van der Putten et al. 2001; A'Bear et al. 2014), but also in agricultural systems. They should therefore receive more attention when designing biological control programs.

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