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What Lies Beneath? Linking Litter and Canopy Food Webs to Protect Ornamental Crops.

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Summary

Arthropod food webs associated with plants are commonly composed of several species of herbivores, the detritivore community, and specialist and generalist predators and parasitoids that feed on the first two groups and on each other. In the past, specialist natural enemies were preferably used for biological control because they are adapted to their prey. However, they cannot persist in a crop when these prey are scarce or absent. Thus, specialist natural enemies can only be successfully released after the pest has invaded the crop, or must be released repeatedly, which can be costly. In contrast, populations of generalist predators can persist in crops by feeding on different species of pests, plant-provided food sources such as honey and pollen, and on organisms of the detritivore community. Thus, generalist natural enemies mediate a number of direct and indirect interactions within and between arthropod communities associated with plants. These interactions can have positive or negative effects on biological control. For example, a prey species is often attacked by several species of natural enemies, which thus compete for this prey. As a consequence, different species of natural enemies can have additive effects on prey populations: their combined effects on a prey population equal the sum of the effects of the different natural enemy species, thereby increasing biological control. Multiple natural enemies can also disrupt biological control, for example because of interactions such as intraguild predation among natural enemies, or because the response of the prey to one species of natural enemy decreases the risk of being attacked by the other species. 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, or because the response of prey to one natural enemy species makes them more vulnerable to the other species. Thus, in biological control the effect of multiple natural enemies versus the effect of a single natural enemy varies and must be investigated before implementing biological control strategies in crops. Studies that show 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, in different seasons, or at different life stages. An aspect that has not received enough attention and I investigated in this thesis is the effect of the addition of alternative food for different generalist predators (on the canopy and in the litter) on biological control.

The effects of adding alternative food such as pollen to increase biological control by a generalist predator has been widely investigated. There can be positive effects of adding alternative food or prey on biological control because it results in an increase in predator densities in the long term, after one or a few predator generations. Alternative prey and food thus affect the density of a pest indirectly by changing the population densities of the generalist natural enemies. Adding alternative food or prey to a system of one predator and one pest species increases the density of the predator, and this numerical response leads to a decrease in pest densities. This is called ‘apparent competition’, because the effect of the alternative food on to the pest is reminiscent of competition for resources. These negative effects of alternative food or prey on the pest are a consequence of the numerical response of the predators, hence, become manifest after a few generations of the predator. In the short term, when the populations of predators have not reached dynamic equilibria, the natural enemy-mediated indirect interaction may cause the opposite effect: the addition of alternative prey or food can result in satiation of the predator population, which will decrease predation of the pest population. In this case, the pest benefits from the addition of alternative food (so-called ‘apparent mutualism’). Such effects may also occur repeatedly in predator-prey systems that show long-term persistent fluctuations. Hence, positive or negative consequences can be expected when using generalist predators for biological control. Studying the effects of the interactions of generalist predators with other members of the food

webs is therefore important to predict the effects of releasing these predators and supplying them with alternative food on pest control.

Generalist predators can also connect above-ground and below-ground food webs when they feed on prey and other food sources in both food webs. The effect of the connection of these food webs by generalist predators on pest control has not received much attention, especially in the case of ornamentals. Thus, the main research question of this thesis was how interactions between above-ground and litter food webs affect biological control. In the first chapter, I investigated the effect of a mixed diet of above-ground plant pests (spider mites, thrips, whiteflies) on life history traits of a generalist below-ground predator, *Balaustium leanderi*, which also forages on the canopy of crop plants. I recorded its life history traits (reproductive performance, survivorship and development) when fed on mixed diets of three pest species that inhabit above-ground plant parts. I showed that *B. leanderi* benefits from a mixed diet of two of the species that inhabit above-ground plant parts. The predators reproduce more and faster when feeding on this mixed diet than on single diets. In the second chapter, I investigated *Amblyseius swirskii,* another generalist predator that mainly inhabits the canopy. I show that it makes excursions to the litter layer to feed or disperse. From this chapter on, I focused on the control of the western flower thrips *Frankliniella occidetalis* because it is one of the most damaging pests in ornamentals. Like many other pests, this thrips spends its life cycle partly on above-ground plant parts and partly in the liter or soil. In the specific case of thrips, they move to the soil or litter to pupate. I show that by adding astigmatic mites (Acari: Astigmata) as alternative prey for the predators to the litter, the densities of *A. swirskii* were boosted, resulting in decreases of thrips densities (apparent competition) and decreases in plant damage. In the third chapter, I investigated the effect of predators that inhabit the litter of commercial rose production greenhouses on thrips control. I show that supplying astigmatic mites in the litter as alternative food for either a community of predators or for a single predator species, *Cosmoalelaps* n. sp., results in decreases in thrips densities (apparent competition) and plant damage.

In commercial crops, canopy-dwelling predators (such as *A. swirskii*) are commonly released to control pests, and these may interact with the litter-inhabiting predators that are already present (such as *Macrocheles robustulus, Stratiolaelaps scimitus* and *Cosmolaelaps* n. sp.), and this might affect biological control. For this reason, I investigated control of thrips by the combination of the canopy-dwelling predator *A. swirskii* and litter-inhabiting predatory mite species such as *M. robustulus* and *S. scimitus* in Chapter four. Because pests such as thrips inhabit above-ground plant parts and the litter or soil, attempts have been made to increase thrips control by combining canopy-dwelling predators and soil-inhabiting predators. The novelty here is that I investigated whether biological control can be enhanced by supplying different alternative foods for canopy-dwelling and litter-inhabiting predators (pollen and astigmatic mites respectively). Moreover I assessed whether the presence of thrips before predator releases would affect biological control and whether the frequency of addition of pollen for canopy-dwelling predators would affect thrips control. I conclude that adding pollen on the plants for canopy-dwelling predators resulted in the best thrips control (as in apparent competition), either with or without litter-dwelling predators, and these latter predators did not interfere with thrips control. In this experiment, litter was placed on the soil, under the tables on which the plants are grown, as is customary in commercial rose production. Because the litter predators were released in that litter, the distance from the canopy was rather large. Further studies could therefore include treatments in which litter-dwelling predators with alternative food are added at the base of the plant, just below the canopy. This would create a tighter link between the food webs above-ground and in the litter. The study of these litter-dwelling predators to control other pests deserves further study because they are well adapted to the crop and their populations can be boosted with alternative food (Chapter 3). The release of predators after thrips was introduced proved detrimental for biological control, with high plant damage in all the treatments. In contrast, plants were protected from thrips damage when the predators were released with pollen before introducing the thrips. Furthermore, I found no differences in thrips densities or thrips damage either by adding pollen weekly or when interrupting the addition of pollen. However, there were significantly more predators on plants that received pollen weekly. Concluding, in chapter four I show that in order to decrease flower damage by thrips in ornamentals such as roses, canopy-dwelling predators should be released before thrips invasions. Also, pollen should be added on a weekly basis. I suggest that more studies on the frequency and quantity of supplemented alternative food should be conducted. Moreover, the role of litter-dwelling predators in control of thrips and other pests in crops with higher damage thresholds as in ornamentals deserves further study.

Thus, in this thesis I present different aspects that can be used by biological control practitioners. I also demonstrate that greenhouse experiments can help to test ecological theories: I show that adding alternative food for generalist predators mainly results in apparent competition, apparent mutualism was found only in few occasions for short periods of time, when the pest was present before the predators were released. Based on this thesis I recommend two factors that deserve further theoretical exploration. The first is that the effect of mixed diets on apparent competition should be further investigated. The second is the effect of the frequency of supplying alternative food on the dynamics of the pest and natural enemy. I also show that the interactions between above-ground and below-ground food webs affect pest densities. In this regard, I recommend that theoretical approaches could be directed to study the impact of multiple generalist predators and food sources in above-ground and below-ground plant parts on pest control.

Summarizing, I conclude that litter and canopy food webs can be linked and this can result in increased biological control in an ornamental crop and that greenhouse experiments evaluating the population dynamics of multiple predators with multiple food sources are crucial for the development of new biological control strategies. At the same time, such experiments are excellent test cases for ecological theories.