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What lies beneath?

Linking litter and canopy food webs to protect ornamental crops

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General introduction

This thesis is on biological control, which is the use of live organisms to keep agricultural pests, diseases, and weeds at low levels (DeBach 1974). Since ancient times, humans have utilized natural enemies to control pests. Thousands of years ago, ants and spiders were used in China to protect tree crops from herbivore pests. Through history, there have been many successful programs of biological control worldwide (Van Driesche & Bellows 1996). Only after World War II, the use of chemical pesticides replaced natural and biological control (Bale et al. 2008). Thanks to the pressure of consumers for pesticide-free agricultural products, biological control has again become a key component for pest control (Calvo et al. 2015). Moreover, growers have actively chosen to use biological control because of the advent of pests resistant to chemical pesticides (Bolckmans 1999). Nowadays, biological control is a viable alternative to chemical pest control.

Currently, there is a wide range of biological control agents commercially available, such as parasitoids, entomopathogens and predators. Parasitoids are wasps and flies that deposit their eggs in or on their host. In the case of biological control, these hosts are insect pests. The developing parasitoid larva feeds on the haemolymph of the host, affecting the host's development and finally causing its death (Godfray 1994). Entomopathogens used in biological control are viruses, fungi, bacteria, and protozoa that cause diseases in insects and mites (Federici 1999). These pathogens infect arthropod pests, eventually killing them (Federici 1999). In this thesis I focus on arthropod natural enemies. Arthropod predators living on crop plants can be either specialist, attacking one or a few closely related pest species, or generalist, attacking a wider range of pests. In the past, biological pest control has focused on the use of one or a few specialist natural enemies for each pest species (Huffaker & Messenger 1976; Hokkanen & Pimentel 1984; van Lenteren & Woets 1988; Hoy 1994) because the use of generalist predators was judged to be more risky as they could also target non-pest species (van Lenteren et al. 2003). Moreover, they were considered inferior enemies to parasitoids because their dynamics would not be synchronized with the pest, and because they usually do not have a high potential for increase (Murdoch et al. 1985). Nevertheless, generalist predators are widely used in biological control nowadays (Symondson et al. 2002). These predators have the advantage of being able to feed on food sources different than the target pest. Thus, they are able to establish in the crop before pest invasions (Symondson et al. 2002). The introduction of different natural enemies (either gener-

alists, specialists, or both) results in artificial communities in the crops, and the members of those communities can interact in complex ways. Not only do natural enemies interact with the target pest, but interactions also occur among different pest species and among natural enemy species (Helle & Sabelis 1985; Minks & Harrewijn 1989; Sabelis 1992), and these interactions can affect biological control (Sih et al. 1985; Janssen et al. 1998; Prasad & Snyder 2004; Evans 2008). A lot of attention has been given to the effects of interactions among various species of natural enemies. Compared to the effect of each enemy species separately, the effect of such interactions can be negative, neutral or positive for biological control (Rosenheim et al. 1995; Losey & Denno 1998; Rosenheim 1998; Colfer & Rosenheim 2001; Snyder & Ives 2001; Venzon et al. 2001; Cardinale et al. 2003; Snyder & Ives 2003; Finke & Denno 2004; Cakmak et al. 2009).

Interactions among natural enemies

When multiple species of arthropod natural enemies are present in a crop, there can be negative effects on biological control. Especially generalist predators can interfere with other natural enemies not just through competition for prey or food, but also through hyperpredation or intraguild predation (Rosenheim et al. 1995; Rosenheim 1998; Snyder & Wise 2002). Intraguild predation takes place when two natural enemies that attack the same prey are also involved in predation (Polis & Holt 1992; Ferguson & Stiling 1996). Intraguild predation is common in food webs in crops and its effects can be strong, resulting in low survival of one or both natural enemies, disrupting biological control (Rosenheim et al. 1995; Rosenheim & Harmon 2006; Janssen et al. 2007; Vance-Chalcraft et al. 2007; but see Janssen et al. 2006).

The use of multiple predators can also result in positive effects on biological control (Losey & Denno 1998). A predator with a certain foraging behaviour can cause behavioural changes in a particular prey, making it more available to other predator species (Sih et al. 1998). For example, Losey & Denno (1998) show that better biological control of aphids is achieved with two predators instead of either one separately. The mechanism for this positive effect is that a canopy-dwelling predator induced 'dropping' behaviour in the aphids, which makes them available to a predator on the soil. Yet other studies show that the effect of the presence of multiple predators on pest control can be neutral, meaning that the multiple predator effects on the pest population correspond to the sum of the single-species effects (Gillespie & Quiring 1990; Sokol-Hessner & Schmitz 2002; Wiethoff et al. 2004), which would still result in better biological control.

Summarizing, the indirect interactions among arthropods in food webs with generalist arthropod predators are complex and need more study. To make adequate use of generalist predators for biological control, it is crucial to study their interactions

with all pests and predators present in a crop. In this thesis, I studied the combined effect of multiple predator species on the control of one pest species.

Interactions among pest organisms

Herbivorous prey might compete among each other for plant resources, but this only occurs at high pest densities, which is undesirable in agriculture because it would certainly result in exceeding the economic damage threshold. For this reason, I will not further discuss resource competition among herbivores in this thesis. Herbivores can also affect each other indirectly by inducing plant defence responses: the attack of an herbivore triggers a plant defensive response that does not only affect the inducing herbivore, but also other herbivore species on the same plant (Karban & Carey 1984). Plants have direct defences against herbivores, for example, they might produce toxins or anti-feeding compounds, resulting in reduced survival, fecundity or developmental rate of the herbivore (Kessler & Baldwin 2002). The structure and composition of herbivore communities are often shaped by plant-mediated interactions between herbivores due to induction of plant defences (Karban & Baldwin 1997; Kessler & Halitschke 2007). For example, resistance against leaf miners increases when tomato and cucumber plants are previously attacked by whiteflies (Inbar et al. 1999; Zhang et al. 2005). In contrast, susceptibility to aphids increases when tomato plants were previously attacked by whiteflies (Nombela et al. 2009). Plant defences can also be down-regulated, the spider mite *Tetranychus evansi* suppresses plant defences (Sarmiento et al. 2011a), which enhances the mite's performance, as well as that of the closely related spider mite *Tetranychus urticae* (Sarmiento et al. 2011b).

Plant defences can also be indirect by affecting the action of the natural enemies of the herbivores (see Sabelis et al. 1999 for a review). They can do this by providing food or shelter to the natural enemies, thus arresting the natural enemies on the plant, and increasing their survival or reproduction. Plants are also known to produce specific blends of volatiles upon attack by herbivores, and these volatiles are attractive to natural enemies (Turlings et al. 1990; Dicke & Sabelis 1988) and herbivores can thus also affect each other through the induction of plant volatiles. For example, Shiojiri et al. (2002) show lower parasitism of *P. xylostella* on cabbage plants co-infested with another herbivore (*Pieris rapae*) than on plants infested only with *P. xylostella*, because the parasitoids of *P. xylostella* are not attracted to the volatile blends produced by plants that are attacked by both herbivores. The opposite effect is recorded on cabbage plants with the parasitic wasp of *P. rapae*, which attacked more hosts on plants attacked by both herbivores (Shiojiri et al. 2002).

Herbivores can also affect each other through structural changes of the environment. For example, several species of spider mites cover the leaf area on which they feed with a dense web, which is thought to serve as protection against predators

(Sabelis & Bakker 1992), but this web can also serve as refuge for other herbivores (Pallini et al. 1998; Magalhães et al. 2007), but may exclude yet other herbivores (Sarmiento et al. 2011b). Concluding, interactions among herbivores might affect biological pest control in crops.

Different prey species can also affect each other indirectly through a population of generalist predators and this is one of the main themes of this thesis. For example, when a generalist predator feeds on a target pest and on an alternative prey, the alternative prey can indirectly affect the densities of the pest (Holt 1977). The presence or addition of alternative food or prey to a population of generalist predators can result in positive effects on the pest species (apparent mutualism; Holt 1977). For example, the predator can direct its attacks to the alternative food or prey and thus become satiated, resulting in fewer attacks of the pest (apparent mutualism; Holt 1977), negatively affecting biological control. However, after one or a few generations, the increased availability of food will boost the densities of the predators, resulting in increased predation of both the target pest and the supplied food (apparent competition; Holt 1977), thus biological control is increased. When populations of natural enemies and pests show fluctuations, periods of positive effects of the two prey on each other will alternate with periods of negative effects (Abrams & Matsuda 1996). Whereas apparent mutualism is undesired when supplying alternative food, apparent competition is beneficial for biological control (van Rijn et al. 2002). The occurrence of apparent competition in biological control systems has been widely studied (Collyer 1964; Karban et al. 1994; Hougén-Eitzman & Karban 1995; Müller & Godfray 1997; Liu et al. 2006; Messelink et al. 2008). For example, Karban et al. (1994) shows that releasing an economically unimportant herbivore together with predatory mites increases the biological control of Pacific spider mites, a pest of grapevines. Hence, apparent competition between herbivores and between a pest population and alternative food can improve biological control. In this thesis, I present several examples of this.

An important aspect that has not been incorporated in the theory of apparent competition and apparent mutualism is the effect of a mixed predator diet. Depending on the quality of the prey or food source, the performance of generalist predators can be affected by feeding on a mixed diet (Uetz et al. 1992; Toft & Wise 1999; Oelbermann & Scheu 2002; Messelink et al. 2008; Marques et al. 2015). For example, the fecundity of the predatory mite *Homeopronematus anconai* (Baker) is significantly increased when it feeds on its prey plus pollen (Hessein & Perring 1988). Messelink et al. (2008) found a shorter immature development of the predatory mite *Amblyseius swirskii* (Athias-Henriot) when feeding on two prey (thrips and whiteflies) compared to predators that feed on either of the two prey separately. Other studies show that a mixed diet can have positive or negative effects on performance of generalist predators, depending on the combinations (Toft & Wise 1999; Oelbermann & Scheu 2002).

A meta-analysis performed by Lefcheck et al. (2013) shows that animals that feed on mixed diets have higher fitness than animals feeding on single diets.

A question that arises is why a mixed diet affects performance of generalist predators. There are two possible reasons. Firstly, different prey may provide the predators with different essential nutrients. With certain mixed diets, predators can acquire the nutrients needed to reproduce more or develop faster compared with a single food or another mixed diet (Uetz et al. 1992; Lefcheck et al. 2013). Another reason is that, by mixing different prey or foods, predators can avoid ingesting harmful quantities of poisonous or growth-reducing substances from each food or prey separately (Coll & Guerson 2002; Lefcheck et al. 2013). In order to design a food web that enhances pest control, it is crucial to assess the effects of mixed diets on the performance of predators. In this thesis, I studied the effects of mixed diets on the performance of generalist predatory mites used for biological control.

Pollen as alternative food

Many species of plants produce pollen that are edible for arthropods, including predators and parasitoids. Thus, plants invoke a kind of apparent competition between the pollen and the pests attacked by these natural enemies. For some natural enemies, pollen is a highly nutritious food. It contains proteins, lipids, carbohydrates, and minerals (Lundgren 2009). The presence of edible pollen can result in the persistence of populations of arthropod predators in the absence of their prey. Currently, the pollen of some plant species, such as *Typha* spp., are being used in Europe as an alternative food for generalist predators in greenhouse crops (Vangansbeke et al. 2014; Pijnakker et al. 2016a). A risk of adding pollen to crops is that insect pests such as thrips can benefit from it (Chitturi et al. 2006; Leman & Messelink 2015; Vangansbeke et al. 2016). However, studies have shown that pollen can help boosting the populations of generalist predators, increasing biological control of thrips and herbivorous mites (van Rijn et al. 1999; Nomikou et al. 2002; Duarte et al. 2015). For example, van Rijn et al. (2002) added pollen as alternative food for phytoseiid mites and found increased control of thrips on cucumber plants compared with treatments in which pollen was not added.

Contrasting results have also been found. Delisle et al. (2015) show that by adding pollen as alternative food for predatory mites, thrips cause more damage than when pollen has not been added. However, the duration of the experiment may have been too short to observe a positive effect of adding pollen for predators on thrips control (i.e. the authors observed short-term apparent mutualism, but no longer-term apparent competition between the pollen and the pest). Although the addition of pollen and other alternative foods to the above-ground parts of a crop often does seem to result in better pest control, the disadvantage is that these alternative foods may contam-

inate the marketable parts of the crop. This is especially the case for ornamentals. I therefore investigate the possibilities of adding alternative food for predators to the litter instead of to the plant canopy. This requires investigating the connections between food webs occurring in the litter and the above-ground plant parts.

Links between above-ground and litter food webs

One clear distinction between the food web occurring above-ground and that occurring in the litter is the presence of detritivores. These organisms usually do not cause damage to the plants, but have an important role in recycling nutrients and minerals from the litter (Seastedt 1984). Coincidentally, several detritivore species are used as food for mass production of natural enemies, hence, there is potential for using the litter food web as a source of alternative food for predators. Although the two food webs were often studied in isolation, it is now clear that the above-ground and below-ground communities associated with plants are strongly interlinked (Scheu 2001; van der Putten et al. 2001, 2009; Miyashita et al. 2003; Moore et al. 2003; Wardle et al. 2004). For example, some generalist predators can switch from feeding on detritivores below-ground to herbivores in the canopy, thus forming a direct link between the two (Scheu 2001). There are a few examples of biological control systems in which the link of above-ground and below-ground food webs is investigated (Settle et al. 1996; Halaj & Wise 2002; Birkhofer et al. 2008; Von Berg et al. 2009). Settle et al. (1996) increase organic matter in rice fields, thus enhancing populations of decomposers and plankton feeders, resulting in a significant increase in the abundance of spiders and insect predators and a decrease of above-ground herbivores. Contrasting results are reported by Birkhofer et al. (2008), who show that an increase in decomposer prey densities in wheat fields results in an increase of pest populations above-ground 1 month later. The authors conclude that increasing the densities of decomposers results in shifts in the foraging of beetles and spiders, predators that typically have long generation times, reducing predation of the pest herbivores (reminiscent of apparent mutualism; Holt 1977, Abrams & Matsuda 1996). Another study shows that generalist predators feed on organisms from the above-ground and below-ground food webs, having an effect on above-ground pest densities (Von Berg et al. 2009). Although most of these studies show that the below-ground food web and the herbivore food web on the above-ground plant parts are connected through generalist predators, many of them did not study population dynamics of predators and pests and the impact on plant damage and thus on biological control. In this thesis, I therefore investigate interactions among and between food webs on above-ground plant parts and the litter and how these interactions affect biological pest control in a rose crop (Box 1). Food web interactions in such a system can be very complex (FIGURE 0.1), and the effect of these interactions are likely to affect biological control. Studying these interactions is impor-

tant for two reasons: first, it can help to design food webs that allow growers to improve biological control programs, and second, it can help to test ecological theories. In this thesis, I specifically study the effects of apparent competition and apparent mutualism and the interactions between above-ground and below-ground food webs on pest densities.

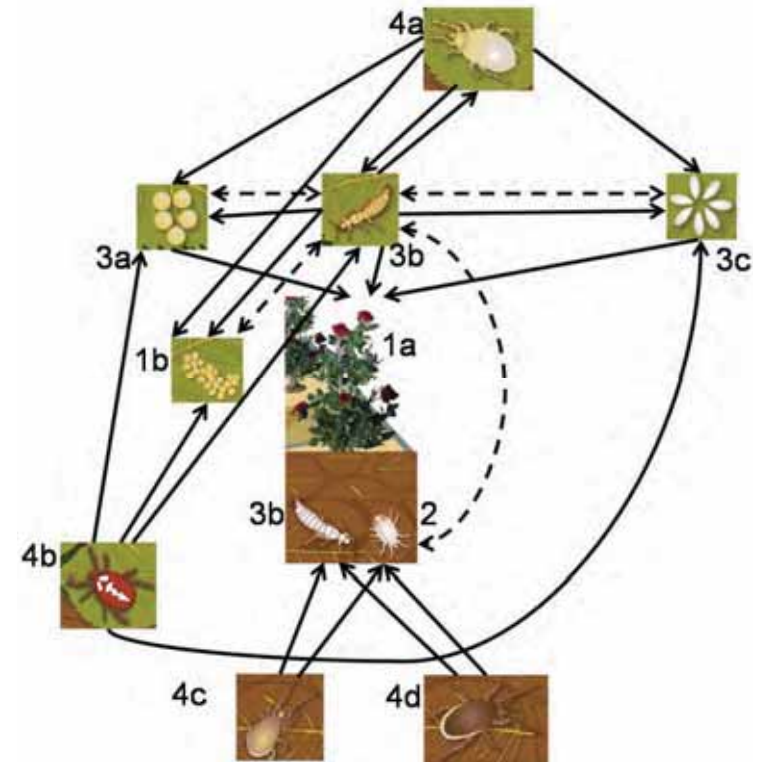


FIGURE 0.1. A food web associated with roses in a greenhouse. (1) Plant resources: (1a) rose plants; (1b) pollen, which serves as food for some pests and predators. (2) Detritivores in the litter can be used as alternative prey for predators. (3) Pest species: (3a) spider mite eggs; (3b) thrips, which cause damage on above-ground plant parts and spend part of their life cycle as pre-pupae and pupae in the litter or soil; (3c) whitefly eggs. Notice that I have depicted eggs of spider mites and whiteflies, which do not feed on plants, but the other stages of these pest species do, hence the solid arrows. (4) Generalist predators, which connect above-ground and litter or soil food webs by feeding on pests, and by feeding on herbivores and alternative prey in the litter or soil: (4a) *Amblyseius swirskii*; (4b) *Balaustium leanderi*; (4c) *Cosmolaelaps n. sp.*; (4d) *Macrocheles robustulus*.

Box 1: Cut-rose production

Biological control strategies commonly used for vegetable crops do not always work in ornamentals (Parrella et al. 1999). This is because damage thresholds are much lower for ornamentals than for vegetable crops: for example, the presence of thrips or thrips damage is unacceptable for cut-flower commercialization. Thus, growers of ornamental crops often spray chemical pesticides and fungicides regularly and year-round (Parrella et al. 1999). In order to use biological control as a feasible alternative to chemical pesticides, natural enemies must therefore be efficient in maintaining ornamentals free from pests.

Cut-rose production is important worldwide, it provides thousands of jobs in many countries (Parrella et al. 1999). In some countries, like The Netherlands, roses are grown using a technique developed in Japan, known as arching (Ohkawa & Suematsu 1999). Growers buy budded stock plants from propagator companies. The substrate used is rockwool; fertilizers dissolved in water are provided through the irrigation system. Under these conditions, the rose plants can last for around 10 years (Parrella et al. 1999). During this time, rose plants produce a large amount of litter (FIGURE 0.2a) For practical reasons, this is disposed below the gutters, a special kind of benches where the plants on the rockwool are growing (FIGURE 0.2b). From each rose plant, a few stems are selected to produce marketable roses, the other stems are bent, but remain attached to the plant (Ohkawa & Suematsu 1999). The bent stems connect the litter layer to the foliage of the plants (FIGURE 0.2a). In rose crops, the food web within the litter or soil layer has not been studied before, nor the interactions among the organisms belonging to this food web, and with the food web on the above-ground plant parts.

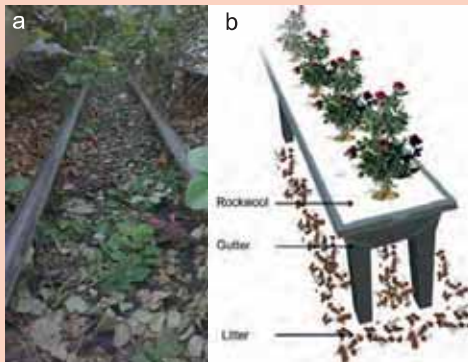


FIGURE 0.2. Characteristics of commercial rose crops in The Netherlands. (a) Litter in a commercial rose greenhouse. (b) Diagram of a commercial rose production system.

Synopsis

The main research question of this thesis is how interactions between above-ground and below-ground food webs affect biological control. In CHAPTER 1, I investigated the effect of a mixed diet of above-ground plant pests on life history traits of a generalist below-ground predator, *Balaustium leanderi*, which also forages on the above-ground plant parts (Box 2). Females of *B. leanderi* lay one batch of eggs in 1 to 2 days at the end of their lives, exhibiting big-bang reproduction and their life cycle last c. 2 months. I recorded life history traits such as reproductive performance, survivorship and development when fed on mixed diets of three pest species that inhabit above-ground plant parts (Box 3).

In CHAPTER 2, I further investigated generalist predators that link above-ground and litter food webs. The canopy-dwelling predator *A. swirskii* mainly inhabits the above-ground plant parts but makes excursions to the litter layer (Box 2). I tested whether the addition of astigmatic mites (Box 4) as alternative prey in the litter would boost predator densities, resulting in better pest control (apparent mutualism or apparent competition, Holt 1977). I addressed the following questions. 1) Do predators move from the canopy to the litter to feed on an alternative prey? 2) Do predators still control the pest even if the quality of the alternative prey in the litter is higher than the pest? 3) Do pest densities and plant damage decrease when providing alternative prey in the litter?

Subsequently, I investigated the effect of litter-inhabiting predators (Box 2) present in commercial rose production greenhouses on thrips control (CHAPTER 3). Many pest species, including thrips, spend part of their life cycle in the litter or soil (Wahab 2010), so litter-inhabiting predators may contribute to thrips control. I specifically tested whether supplying food for these predators helps to increase biological control of thrips.

Growers commonly release canopy-dwelling predators to control pests (Branigan 1915; DeBach 1974; Gerson & Weintraub 2007), and these may interact with litter-inhabiting predators, which may affect pest control. Thus, in CHAPTER 4 I investigated the combination of species of canopy-dwelling and litter-inhabiting predator species. Combining natural enemies sometimes results in increased biological control compared with single releases of either of the natural enemy species separately (Losey & Denno 1998, 1999; Sih et al. 1998; Casula et al. 2006). For this reason, and 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 (Wiethoff et al. 2004; Thoeming & Poehling 2006; Manners et al. 2013; Pozzebon et al. 2015). The novelty of my study is that I investigated whether biological control can be enhanced by supplying different alternative food sources for canopy-dwelling and litter-inhabiting predators (pollen or astigmatic mites).

Box 2: Predators

One of the most successful groups of arthropods used to control pests in greenhouses are predatory mites (Gerson & Weintraub 2007). After being released, they can rapidly establish in the crops; they oviposit on different parts of the plants, including the lower stratum of the canopy. This is



important because not all predatory mites are removed when harvesting flowers. The main predatory mite species studied in this thesis are *Balaustium leanderi* (Haitlinger) (Actinotrichida: Erythraeidae), *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae), *Cosmolaelaps* n. sp. (Acari: Laelapidae) and *Macrocheles robustulus* (Berlese) (Acari: Macrochelidae). These predatory mites are chosen because they either occur in rose greenhouses or are released commercially in rose crops.

Balaustium leanderi (FIGURE 0.3a) is a generalist predator which is naturally found in Mexico and Colombia (Getiva & Acosta 2004; Fuentes et al. 2014). It inhabits the soil or litter layer in roses and other crops, where the applications

FIGURE 0.3. Generalist predators in greenhouse crops. (a) *Balaustium leanderi* adult; (b) *Amblyseius swirskii* adult feeding on a thrips larva; (c) *Cosmolaelaps* n. sp. adult. Photographs J. van Arkel.

of chemical pesticides are not frequent (Muñoz-Cárdenas et al. 2015). Some species of the genus *Balaustium* have been studied in regard to their potential use in biological control of agricultural pests (Cadogan & Laing 1977; Makol et al. 2012; CHAPTER 1). Due to difficulties rearing these predatory mites, biological control studies are scarce. However, studying the potential for pest control of these predatory mites is important because they are well adapted to crop conditions and they are found attacking different pest species in America and Europe (Muñoz-Cárdenas et al. 2015).

Amblyseius swirskii (FIGURE 0.3b) is a predator from the Mediterranean region (Swirskii et al. 1967; Nomikou et al. 2001). This predator is widely used in Europe and North America to control pests in vegetable and ornamental crops like roses (Pijnakker & Ramakers 2008; Buitenhuis et al. 2015; Calvo et al. 2015). In vegetable crops, *A. swirskii* successfully controls whiteflies and thrips (Nomikou et al. 2002; Messelink et al. 2008; Nomikou et al. 2010), but it can also control herbivorous mites (van Maanen et al. 2010) and feeds on other alternative food sources and pest species (Hoogerbrugge et al. 2008; Calvo et al. 2015; Janssen & Sabelis 2015; Vangansbeke et al. 2016). This predator inhabits the plant canopy and moves to the litter or soil to disperse (Buitenhuis et al. 2010) or to feed on alternative prey (CHAPTER 2).

Cosmolaelaps n. sp. (FIGURE 0.3c) inhabits the litter layer in rose greenhouses in The Netherlands (CHAPTER 3). Individuals of this genus feed on nematodes, astigmatic mites, and thrips (de Moraes et al. 2015). A species of this genus found in Brazil, *Cosmolaelaps jaboticabalensis*, is considered to have potential to control thrips (Furtado & de Moraes 2015).

Macrocheles robustulus is a generalist predator that also inhabits the soil in greenhouses in The Netherlands. It feeds on astigmatic mites and it is commercially released in greenhouses to control insect pests like thrips (Messelink & van Holstein-Saj 2008).

Box 3: Target pests

The following pest species were studied in my thesis because they are cosmopolitan and represent some of the most important pest species in crops in the field and in greenhouses: the western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (FIGURE 0.4a); the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) (FIGURE 0.4b) and the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) (FIGURE 0.4b).

The two-spotted spider mite is known to attack over 1100 plant species (Migeon & Dorkeld 2016). It causes leaf decoloration by feeding on chlorophyll. Spider mites punc-

ture plant cells feeding on their contents (Helle & Sabelis 1985). Spider mite females produce silk webs, their populations can reach very high densities, killing the plant in a few weeks (Brødsgaard & Albajes 1999). However, successful biological control of spider mites can be achieved in many crops by using predatory mites such as *Phytoseiulus* spp. (Bravenboer & Dosse 1962; Hussey & Bravenboer 1971). These predatory mites are specialist predators of spider mites because they can penetrate the spider-mite web, which other predators cannot (Sabelis & Bakker 1992).

The greenhouse whitefly attacks more than 850 plant species (<http://www.cabi.org>). It feeds on the phloem of the plant, causing leaf deformation, discoloration and defoliation. Owing to the honeydew production by whiteflies, different parts of the plant can become fully covered by fungi growing on the honeydew, which blocks the light and reduces photosynthesis. The greenhouse whitefly also causes plant damage by transmitting plant viruses (Inbar & Gerling 2008). Successful biological control of this whitefly can be achieved in different crops by releasing the parasitoids *Encarsia formosa* Gahan, *Eretmocerus mundus* Mercet and *Eretmocerus eremicus* Rose & Zolnerowich and the predator *Macrolophus pygmaeus* (Rambur), but recently, phytoseiid mites have been

used more frequently (Speyer 1927; van Lenteren & Woets 1988; Nomikou et al. 2001, 2002; Perdakis & Lykouressis 2002; Pijnakker et al. 2016b).

The western flower thrips is another important pest, feeding on plant leaves, flowers, pollen or fruits of more than 250 plant species (<http://www.cabi.org>). It is the main pest organism studied in this thesis. They cause damage to plant parts by

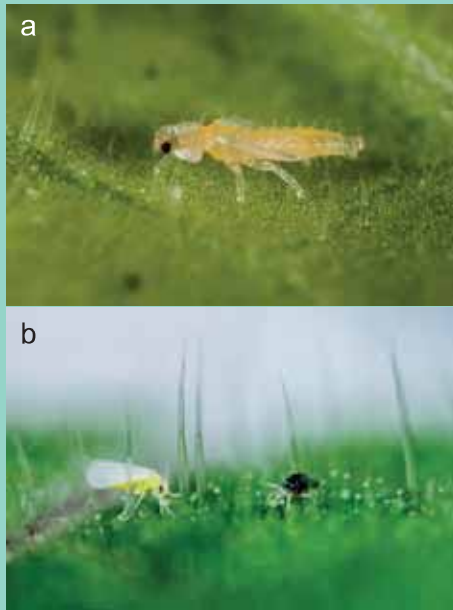


FIGURE 0.4. Main pest species in greenhouse crops: (a) thrips pupae; (b) adults of whitefly (left) and spider mite (right). Photographs J. van Arkel.

piercing epidermal and parenchymal cells, and sucking out their contents. They also transmit viruses (Brødsgaard & Albajes 1999). Damaged plant parts develop characteristic silvery spots or scars. In ornamentals, low densities of thrips can cause aesthetic damage to flowers, the marketable part of roses, making them unsaleable (Brødsgaard & Albajes 1999). Although thrips feed on above-ground plant parts, the pre-pupae and pupae live in the litter or soil (Brødsgaard & Albajes 1999), where they are less affected by chemical control. Biological control with predators is efficient in some crops, such as vegetables (Gillespie 1989; Jacobson et al. 2001; Shipp & Wang 2003; Shipp & Ramakers 2004). Western flower thrips are omnivorous: besides feeding on plant tissue, larvae and adults consume spider mite eggs, predatory mite eggs and whitefly crawlers (Trichilo & Leigh 1986; Faraji et al. 2001; Janssen et al. 2003; van Maanen et al. 2012). Due to all these special characteristics, its control is still a challenge in crops with low damage thresholds, especially ornamentals.

Box 4: Alternative prey: Astigmatic mites

Astigmatic mites such as the mould mite *Tyrophagus putrescentiae* (Schrank) (FIGURE 0.5), the dried fruit mite *Carpoglyphus lactis* (L.) and the flour mite *Acarus siro* (L.) can be used as alternative prey for predators. These species belong to the Acaridae family, they are cosmopolitan, so they can be used in different crops and in different countries. They are easy to rear and are used as food for predators in mass-rearing systems (Ramakers & van Lieburg 1982).

These astigmatic species inhabit the soil, litter, and decaying vegetable material. Species of the genus *Tyrophagus* commonly inhabit soils, old hay, mushrooms, house dust, and bird nests (Walter et al. 1986; Mullen & O'Connor 2009). They feed on yeast,



FIGURE 0.5. *Tyrophagus putrescentiae* adults and eggs. These mites can be used as alternative prey for generalist predators. Photograph J. van Arkel.

algae, nematodes, and possibly also on injured and dead mites (Walter et al. 1986). The mold mite *T. putrescentiae* (FIGURE 0.4b), is considered a pest of stored products with high lipid and protein content, such as cheeses and grains. It is commonly used as food source in rearing systems of different predatory mites of the family Phytoseiidae, and of soil predators of different families, such as Laelapidae (Ramakers 1990; Bolckmans & van Houten 2006; Fidgett & Stinson 2008; Pochubay & Grieshop 2012; Barbosa & de Moraes 2016). *Carpoglyphus lactis* is considered a pest of saccharide-rich stored products such as dried fruits, wine, beer and honey (Hubert et al. 2014). This astigmatic mite species is used to mass-rear phytoseiid predators such as *Amblyseius swirskii* (Athias-Henriot) (Bolckmans & van Houten 2006; Fidgett & Stinson 2008). *Acarus siro* is also considered a pest in stored products such as flour, wheat, and cheese (Solomon 1962). This mite is used to mass-rear phytoseiid predators from the genus *Amblyseius* and *Neoseiulus*, and soil predators from different families such as Macrochelidae and Laelapidae (Ramakers & van Lieburg 1982; Bolckmans et al. 2013).

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