Single and multiple releases of predators for biological control of spider mites *Tetranychus urticae* Koch and western flower thrips *Frankliniella occidentalis* (Pergande)

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Summary

Two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) (TSSM) and western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) are two notorious pests of ornamental plants and vegetables, both in field and especially in greenhouse cultures. They often occur simultaneously on the same plants. Chemical control is difficult mainly because of problems with low efficiency of insecticides, resistance, residues and interference with biocontrol strategies. The predatory mite *Amblyseius cucumeris* Oudemans (Acari: Phytoseiidae) and the predatory bug *Orius insidiosus* Say (Hemiptera: Anthocoridae) are two widely used biological control agents of WFT; both are generalist predators. Besides thrips, spider mites also constitute a main diet of both predators and sometimes *Amblyseius* and *Orius* spp. are used to suppress TSSM populations. One aim of this project was to elucidate whether each of the two predators can significantly suppress both pests when occurring simultaneously on the same plant in different densities, and how one of the two pests influences the control efficiencies of each other by both predators. In combined release systems with more than two predators, intraguild predation (IGP) more or less exists, e.g. *Orius* spp. can also feed on the predatory mite. However, the intensity and consequences of IGPs differ in relation to system parameters like direction of predation (who is predator, who prey) within the predator guild, the density of prey item as well as the availability (density) of and preference for alternative food. Thus another objective of this project was to evaluate such possible intraguild effects with combined releases of *A. cucumeris* and *O. insidiosus* and how they could influence suppression of WFT and TSSM and therefore the efficiency of biocontrol.

Apart from by foliar dwelling predators, prepupae and pupae of WFT can be attacked by soil mites like *Hypoaspis* spp. (Mesostigmata: Laelapidae) during their passage through the subtrate. Traditionally, biological control of WFT targets only the foliar-feeding or soil-dwelling stages using a single biocontrol agent, but the control efficacies were often not satisfactory. However, the combination of predators foraging on the plants with those dwelling in the soil for suppressing WFT has been mostly neglected so far. Thus, a further aim of this project was to elucidate the control efficiency of WFT using combined releases of plant-inhabiting and soil-dwelling predators.

The main results showed that when TSSM or WFT occurred singly, *A. cucumeris* or *O. insidiosus* could significantly suppress their population growth, especially at lower densities of TSSM in case of *A. cucumeris*. *A. cucumeris*, irrespective of its own density, significantly reduced mite populations by 33.8% and 21.9% at initial densities of 10 and 20 TSSM per pot, respectively, but could not suppress initial densities of 40 TSSM per pot. 5 and 10 *A. cucumeris* also resulted in 29.9% and 43.1% corrected mortality (CM) of WFT, respectively, irrespective of the density of WFT (from 20 to 40 thrips per pot). A single *O. insidiosus* was able to reduce mite populations by 52.9, 38.7 and 25.8% at initial densities of 20, 40 and 80 spider mites, respectively. At the same spider mite densities, two bugs achieved control levels of 60.6, 63.1 and 38.4%, respectively. Releases of 1 or 2 *O. insidiosus* resulted in CMs of WFT 62.5 and 46.3%, or 87.9 and 71.9% in WFT at initial larval densities of 100 and 160, respectively.

When *A. cucumeris* was introduced to control TSSM and WFT, the addition of TSSM did not significantly impact the control efficiency of WFT by this predator. If *O. insidiosus* was used against TSSM and WFT, the addition of WFT, however, significantly decreased the efficiency of *O. insidiosus* in controlling TSSM, while the presence of mites at initial densities of 20 to 80 females per pot did not significantly influence its effect on WFT. *A. cucumeris* and *O. insidiosus* preferred preying on WFT compared to TSSM. The presence of WFT resulted in higher oviposition by *O. insidiosus* females than the presence of spider mites, indicating that thrips are a more suitable resource than TSSM for *O. insidiosus*.

In the mix-infestation system of TSSM and WFT, the combined releases of *A. cucumeris* and *O. insidiosus* significantly suppressed the WFT and TSSM population. They caused 31.5-65.8% TSSM suppression and 63.7-92.7% CMs in WFT in the six combinations of TSSM at three initial densities of 20, 40 and 80 mites per pot and WFT at two densities of 100 and 160 thrips per pot. TSSM and WFT suppression were significantly negatively correlated to their densities and positively correlated to the density of *O. insidiosus*. The densities of WFT also negatively affected the control efficiency of TSSM by both predators. *O. insidiosus* suppressed the TSSM population mainly through killing the spider mites adults, while *A. cucumeris* consuming the non-mature stages of TSSM. Both TSSM and WFT decreased the extent of IGPs of *O.*

insidiosus on *A. cucumeris*. *A. cucumeris* and *O. insidiosus* should be compatible for combined suppression of TSSM and WFT.

Individual releases of the soil-dwelling predatory mites *H. aculeifer* significantly suppressed WFT. The combined releases of the plant-inhabiting predators and the soil-dwelling predator against the different developmental stages of WFT, which occupy different niches, showed an additive effect in suppressing WFT.

WFT larvae could consume the eggs of its natural enemy, *A. cucumeris*. Under experimental condition, one 3 to 7 days old WFT larva killed 1.2 eggs per day.

Key words: *Tetranychus urticae*, *Frankliniella occidentalis*, *Orius insidiosus*, *Amblyseius cucumeris*, *Hypoaspis aculeifer*, interaction, biological control, intraguild predation

Zusammenfassung

Die Spinnenmilbe *Tetranychus urticae* Koch (Acari: Tetranychidae) (TSSM) und der Kalifornischen Blütenthrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) sind zwei bedeutende Schädlinge von Zierpflanzen und Gemüse, in Feldkulturen wie auch im Gewächshaus. Sie treten oft simultan auf der selben Pflanze auf. Die chemische Bekämpfung ist sehr problematisch. Die Raubmilbe *Amblyseius cucumeris* Oudemans (Acari: Phytoseiidae) und die Raubwanze *Orius insidiosus* Say (Hemiptera: Anthocoridae) sind zwei häufig eingesetzte Antagonisten in der biologischen Bekämpfung von WFT. *Amblyseius* spp. und *Orius* spp. sind generalistische Prädatoren. Neben Thripsen sind Spinnmilben eine häufige Beute beider Räuber. In verschiedenen Studien wurden beide Antagonisten gemeinsam *Amblyseius* spp. und *Orius* spp. verwendet, um TSSM zu kontrollieren. Ein Ziel der hier vorliegen Arbeit war es einerseits zu untersuchen, ob die beiden Prädatoren beide Schädlingen wesentlich in ihrer Populationsentwicklung begrenzen können, und ob andererseits das gemeinsame Vorkommen der beiden Schädlinge die Leistungsfähigkeit beider Prädatoren beeinflusst. Wenn mehr als zwei Räuber gleichzeit freigesetzt werden, kann es zur Intraguild Prädation (IGP) kommen. Insbesondere für *Orius* spp. ist bekannt, dass sie auch Raubmilbe als Beute annimmt. Die Intensität und Richtung von IGPs ist jedoch von der Struktur des gesamten Systems abhängig. Beutepräferenzen des Intraguild-Räubers für normale Beutetiere oder Intraguild-Beute, die Dichte der Beuten oder die Verfügbarkeit alternativer Nahrung können Grad und Richtung der IGPs bedeutend beeinflussen, und damit kann die Effizienz des gesamten biologischen Bekämfpungssystems beeinflusst werden. Ein weiteres Ziel des Vorhabens war die Beantwortung der Frage ob gemeinsame Freilassungen von *A. cucumeris* und *O. insidiosus* beide Schädlingspopulationen bedeutend verringern können und wie die Dichte beider Schädlingen den Grad möglicher IGPs von *O. insidiosus* auf *A. cucumeris* beeinflusst.

Die Bodenstadien von WFT (Prepuppe und Puppe) können auch von räuberischen Bodenmilben wie *Hypoaspis* spp. (Mesostigmata: Laelapidae) angegriffen werden. Die Verfahren der traditionellenbiologische Bekämpfung von WFT nutzen nur separat

Gegenspieler, die auf der Pflanze foragieren oder solche, die Bodenstadien erbeuten können Die Bekämpfungserfolge sind jeweils für sich oft nicht zufriedenstellen. Eine Kombination beider der unterschiedlichen Beutestrategen könnte die Effizienz der Gesamtkontrolle steigern, ist aber bisher kaum detailliert analysiert worden. Deshalb war ein weiteres Ziel der vorliegenden Arbeit die Bewertung dieses Ansatze. Die Ergebnisse zeigten, dass bei alleinigem Auftreten von TSSM oder WFT, sowohl *A. cucumeris* als auch *O. insidiosus* bedeutende Reduktionen der Schädlingsdichte hervorrufen können, *A. cucumeris* allerdings primär bei niedrigen Dichten von TSSM. Unabhängig von der eigenen Dichte unterdrückte *Amblyseius cucumeris* die TSSM Populationen signifikant um 33,8% und 21,9% bei initialen Dichten von 10 und 20 TSSM pro Versuchseinheit, Anfangsdichten von 40 TSSM pro Versuchseinheit konnten aber nicht kontrolliert werden. 5 und 10 *A. cucumeris* führten zu 29,9% bzw. 43,1% korrigierter Mortalität (CM) von WFT, unabhängig von der Dichte der Thripse (von 20 bis 40 Individuen/Versuchseinheit). Einzelne *O. insidiosus* konnte die Spinnmilbenpopulationen um 52,9, 38,7 und 25,8% bei Anfangsdichten von 20, 40 bzw. 80 TSSM pro Versuchseineheit reduzieren. Bei denselben Milbendichten, erreichten zwei *O. insidiosus* Effizienzen von 60,6, 63,1 und 38,4%. Freilassungen von 1 oder 2 *O. insidiosus* führten zu CMs von 62,5 und 46,3 % bzw. 87,9 und 71,9% bei WFT bei Anfangslarvendichten von 100 und 160 pro Versuchseinheit.

Beim Einsatz von *A. cucumeris* gegen TSSM und WFT beeinflußte die gleichzeitige Anwesenheit von TSSM die Kontrolleffizienz gegenüber WFT nicht bedeutend. Beim Einsatz *O. insidiosus* gegen TSSM und WFT hingegen verminderte ein Zusatz von WFT die Bekämpfungseffizienz der TSSM durch *O. insidiosus* erheblich, während andererseits die Spinnmilben bei Ausgangsdichten von 20 bis 80 Adulten pro Versuchseinheit keinen signifikanten Einfluß auf die Dezimierung der Thripspopulation durch *O. insidiosus* hatten. *Amblyseius cucumeris* und *O. insidiosus* bevorzugten beide WFT als Beute. Die Anwesenheit von *F. occidentalis* führte zu höheren Ovipositionsraten von *O. insidiosus* Weibchen als in der Gegenwart von Spinnenmilben, was ebenfalls als Indikator für eine bessere Ressourcenqualität der Thripseim Vergleich zu den Spinnmilben gewertet werden kann.

Bei gleichzeitigem Befall der Bohnenpflanzen durch TSSM und WFT unterdrückten die gemeinsamen Freilassungen von *A. cucumeris* und *O. insidiosus* die WFT und TSSM Population jeweils signifikant. Es konnten Reduktionsraten der TSSM von 31.5 - 65.8% und korrigierte Mortalitäten (CM) der WFT von 63.7 - 92.7% bei Kombinationen von drei TSSM (20, 40 und 80 Individuen pro Versuchseinheit) und zwei WFT (100 und 160 Individuen pro Versuchseinheit) Ausgangsdichten erreicht werden. Die Reduktion der Dichten von TSSM und WFT war jeweils mit deren Ausgangsdichtensignifikant negativ und mit der Dichte von *O. insidiosus* positiv korreliert. Die Dichte von WFT beeinflusste negativ die Effizienz der Kontrolle von TSSM durch beide Prädatoren. *Orius insidiosus* unterdrückte die TSSM Population hauptsächlich durch Erbeutung adulter Spinnenmilben, während *A. cucumeris* die jungen Entwicklungsstadien von TSSM präferierte. Sowohl TSSM als auch WFT verminderten den Grad der IGP von *O. insidiosus* gegenüber *A. cucumeris*.

Einzelne Freilassung der räuberischen Bodenmilbe *H. aculeifer* hatten einen signifikant reduzierenden Einfluß auf die Entwicklung des WFT. Gemeinsame Freilassungen der auf Pflanze foragierenden Räuber *A. cucumeris* und *O. insidiosus* mit der Bodenmilbe *H. aculeifer*, die somit Entwicklungsstadien von WFT in den verschiedenen Nischen angreifen, hatten eine additive Wirkung auf die Reduktionsrate von WFT.

WFT Larve können in gewissen Umfang auch als Räuber auftreten und damit IGP Effekte hervorrufen. Prädationsversuche mit Eiern von *A. cucumeris* zeigten, dass 3 – 7 Tage alte WFT Larven bis zu 1,2 Eier innerhalb von 24 Stunden erbeuten können.

Stichwörter: *Tetranychus urticae, Frankliniella occidentalis, Orius insidiosus, Amblyseius cucumeris, Hypoaspis aculeifer*, Interaktion, Biologische Schädlingsbekämpfung, Intraguild Prädation

Contents

Abbreviations

WFT	western flower thrips, *Frankliniella occidentalis* (Pergande)
TSSM	two-spotted spider mite, *Tetranychus urticae* Koch
Ac	*Amblyseius cucumeris* Oudemans
Oi	*Orius insidiosus* Say
Ha	*Hypoaspis aculeifer* Canestrini
TSWV	Tomoto Spotted Wilt Virus
INSV	Impatiens Necrotic Spot Viruses
IGP	Intraguild predation
IG-predator	Intraguild predator
IG-prey	Intraguild prey
CRS	Controlled release sachet
L: D	Ratio of light to darkness in a day
r.h.	Relative humidity

Introduction

The two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) (TSSM) and the western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) are widespread over an array of geographical range (CAB International, 2003). WFT is a native insect of the western part of North America and was first reported in 1895. In the 1970s and early 1980s, this species spread throughout North America (Beshear 1983). Soon thereafter it was found in Europe in Dutch greenhouses and since then it has become a major exotic pest of greenhouse production in many countries throughout the world (Tommasini and Maini, 1995, van Lenteren and Loomans 1998, Kirk and Terry, 2003). TSSM is also a cosmopolitan pest. It has been recorded from most countries in Europe, Asia, Africa, Australasia, the Pacific and Caribbean islands, America (CAB International, 2003). In many field crops both species often occur simultaneously on the same plants in the field (Trichilo and Leigh, 1986; Wilson et al., 1996; Colfer et al., 1998, 2000) just as in the greenhouse (Brødsgaard and Enkegaard, 1997; Sterk and Meesters, 1997).

TSSM and WFT are notorious pests particularly of ornamental plants and vegetables. While feeding, both pests penetrate the plant foliage/leaves/flowers with their mouth stylets and suck out the cell contents. Photosynthesis and metabolism of plants are seriously affected. In addition, WFT causes indirect damage by vectoring tomato spotted wilt (TSWV) and impatiens necrotic spot viruses (INSV) (Tommasini and Maini, 1995; van de Wetering et al., 1996). Moreover, in ornamentals even low pest densities can affect the external quality. Quantitative and qualitative damage often results in important economic losses in crops and ornamentals (Rabbinge, R., 1995; Lewis, 1997; Nachman and Zemek, 2002).

Chemical control of both pests is extremely problematic, particularly that of WFT. The core difficulties are reflected by the facts that the organisms are minute and can live sheltered on or in leaves and/or flower buds (Brødsgaard, 1989), where they are often not reached by contact insecticides. More efficient are systemic insecticides with multiple modes of actions, but particularly with WFT even these pesticides are unable to control non-feeding stages like eggs of WFT and TSSM or prepupa and pupa of WFT. Since all insecticides are unable to control these soil-dwelling developmental

stages of WFT, an important source for recolonisation of the plant cannot be eliminated. Moreover, both TSSM and WFT achieve high reproduction rates and short generation cycles especially under warm conditions and under high pesticide load both pests tend to fast selection of resistant biotypes. It is reported that WFT (Gillespie, 1989; Brødsgaard, 1994; Zhao et al., 1995) and TSSM (Cranham and Helle, 1985; Eilenberg et al., 2000) have become resistant to numerous insecticides or acaricides registered for their control. Systemic insecticides are often very persistent which requires long waiting periods after application. Moreover, some efficient pesticides can have undesired side effects on important natural enemies, influencing systems of biocontrol in multiple pest associations where other pests should be controlled by predators or parasitoids (van Lenteren and Loomans, 1998), or they kill bumblebees, which are used in greenhouse tomatoes for pollination (Shipp and Wang, 2003). Highly demanded are safe and environmentally harmonious alternatives to the use of synthetic insecticides like the implementation of biological control as a management tactic.

The important natural enemies of TSSM include phytoseiid mites (Hussey et al., 1965; Oatman and McMurtry, 1966) and *Stethorus* spp. (Coleoptera: Coccinellidae) (Chazeau, 1985). Other useful beneficials include anthocorids (mainly *Orius* spp.), larvae of chrysopids, predatory thrips (e.g. *Scolothrips* spp.) as well as larvae of cecidomyiid midges, in particular *Feltiella acarisuga* Kieffer (i.e., *Therodiplosis persicae*) (Diptera: Cecidomyiidae) (Chazeau, 1985) and fungi, such as *Neozygites* spp. (Klubertanz et al., 1991). However, the most effective natural enemies of TSSM are predatory mites from the family Phytoseiidae. These mites, belonging to a number of genera, such as *Phytoseius*, *Amblyseius*, *Euseius* and *Neoseiulus*, have been shown to regulate populations of TSSM on a range of crops (CAB International, 2003). The most frequently used predator has been the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot, which was first used in glasshouses on various crops in the 1960s (for example, Hussey et al., 1965), and has been used ever since successfully on a wide variety of crops in a range of protected and unprotected environments. However, *P. persimilis* shows a high degree of specialization to tetranychid mites as prey (McMurtry and Croft, 1997; Cross et al., 2001). Its high efficiency can lead to an overexploitation of the prey and the predator will die out because of starvation, the inability of subsistence on alternate food, especially in confined spaces, as in a greenhouse (Wysoki, 1985). This

creates unstable systems with often fast resurgence of the pest. On long-term basis it doesn't always succeed in suppressing TSSM (Sterk and Meesters, 1997). On the other hand, accompanying infestation with WFT cannot be suppressed by this specialized predator. Other phytoseiid mites, such as *Ambyseius* (*Neoseiulus*) *californicus* McGregor (Garciá-Marí and González-Zamora, 1999; Easterbrook et al., 2001) and *A. fallacis* Garman (Raworth, 1990; Cooley et al., 1996) are also used to control spider mites on some certain plants. They are, however, also selective predators of tetranychid mites (McMurtry and Croft, 1997).

The biocontrol agents of WFT include predatory mites (Ramakers, 1987; Gillespie, 1989; Bennison and Jacobson, 1991), anthocorid bugs (van den Meiracker and Ramakers, 1991; Sabelis and Rijn, 1997), nematodes (Ebssa et al., 2001, 2004; Premachandra et al., 2003), predatory thrips (Ramakers et al., 2000), parasitoids (van Lenteren and Loomans, 1998) and fungi (Butt and Brownbridge, 1997; Murphy et al., 1998). Among the most reliable biocontrol agents are phytoseiid mites of the genera *Amblyseius* and anthocorid flower bugs of the genus *Orius*, whereas *A. cucumeris* Oudemans and *O. insidiosus* Say are two often used species. *A. cucumeris* was first associated as a predator of WFT in Dutch greenhouses. It was later fully developed to control thrips and used on a commercial basis in the early 1980's. *O. insidiosus* is a nearctic species. It has been extensively used from the early 1980's in Europe (van den Meiracker and Ramakers, 1991; Sörensson and Nedstam, 1993).

Both *Amblyseius* (Acarina: Phytoseiidae) and *Orius* spp. (Heteroptera: Anthocoridae) are generalist predators. Besides feeding on thrips, they also consume other small arthropods like spider mites (Lewis, 1997; McMurtry and Croft, 1997). For *Orius* spp. thrips and mites are believed to constitute essential parts of their diet (Wright, 1994). Both *Amblyseius* and *Orius* spp. are also sometimes used to control spider mites (Helle and Sabelis, 1985; McMurtry and Croft 1997; Colfer et al., 1998, 2000). Therefore, in a mix-infestation system of TSSM and WFT, *Amblyseius* or *Orius* spp. seem to offer attractive protagonists against both pests. However, the preference even of a generalist predator for different preys may be distinct (Salas-Aguilar and Ehler, 1977; Isenhour and Yeargan, 1981). Likewise, the densities of preys may also influence the preying efficiency of a predator. Therefore, the first objective of this study was to investigate

how TSSM and WFT at their different densities affected each other the control efficiency of *A. cucumeris* or *O. insidiosus* in their mixed infestations.

Amblyseius and *Orius* spp. have been extensively used to control WFT. However, satisfactory control of WFT cannot be easily and reliable achieved with each of the two predators. For instance, *Orius* spp. are only effective if sufficient prey is available. At a lower density of WFT, *Orius* spp. tend to leave the crop or even the greenhouse unless pollen as alternative food source is available (Ramakers and Meiracker, 1991). Likewise, *Amblyseius* spp. are able to prey only on the first instar larvae of thrips (Gillespie and Ramey, 1988; Bakker and Sabelis, 1989; Van der Hoeven et al., 1990), and their dispersal potential is lower than that of WFT (Jacobson et al., 2001b). Abiotic factors, such as temperature (Shipp et al., 1996; Shipp and van Houten, 1997) and humidity (van Houten et al., 1993) also restrict the impact of *Amblyseius* spp. on WFT.

Though *A. cucumeris* is often used as a preventive method with inundative releases at very low infestation densities of WFT, occasions of failure in efficient control with *A. cucumeris* are reported. In particular, if sudden immigration of large WFT numbers from adjacent crops occurs, the predators are not able to limit built-up of damaging populations (Jacobson et al., 2001b). Therefore, sometimes both predators are released together on the same greenhouse ornamentals and vegetables to achieve additive or even synergistic effects and to improve the efficacy of control (Sörensson and Nedstam, 1993; Sterk and Meesters, 1997). During the last decade, because the availability of beneficials for biocontrol in greenhouses has substantially increased and production costs could be reduced (Eilenberg et al., 2000), the combined release of several biocontrol agents simultaneously to combat one or more pests has become a common phenomenon (Meyling et al., 2002).

However, with the combined release of beneficials, especially with generalist predators in same environment, the risk of competition increases. One predator may be consumed by the other, a general phenomenon, called intraguild predation (IGP) (Polis et al., 1989; Rosenheim et al., 1995). The predator, which preys on the other one, is called intraguild predator (IG-predator), and the victim is the intraguild prey (IG-prey). The extent of IGP can vary due to differences in the preference of the IG-predator for the IG-prey or the herbivorous pest, thereby possibly affecting the outcome of biological

control. For example, if the IG-predator indiscriminately preys on both the IG-prey and the herbivorous pest, combined releases of the IG-predator and the IG-prey may lead to a decreased control efficiency of the herbivorous pest. For instance, Wittmann and Leather (1997) recorded that *O. laevigatus* (Fieber) did not distinguish between *A. cucumeris* and WFT as prey. Hence, a combination of *O. laevigutus* and *A. cucumeris* is not likely to result in efficient biological control of WFT. However, biological control should be enhanced if the IG-predator prefers preying on the herbivorous pest compared to the IG-prey. In the mentioned study Wittmann and Leather (1997) observed that *O. laevigatus* preferred to prey on WFT compared to another predatory mite species *A. degenerans* (Berlese), which would improve WFT control. Gillespie and Quiring (1992) found that *O. tristicolor* (White) favoured WFT over *A. cucumeris*, indicating that a combination of these predators might also improve biological control of WFT.

Additionally anti-predation behaviour of the IG-prey in the presence of the IG-predator may affect the extent of IGP. For example, TSSM produce webbings, which can be used by other pests like WFT and also small predators to seek refuge from carnivory (Pallini et al., 1998). Finally the prey density may also influence the extent of IGP by reducing the competition for prey between the IG-predator and the IG-prey.

Thus, in the biological control system including multi-pests and predators, the relationships among them can be complicated. In this study, the outcome of combined releases of *A. cucumeris* and *O. insidiosus* on mixed infestations of TSSM and WFT at varying initial densities were investigated. The specific objectives were to study (1) whether TSSM and WFT can be effectively controlled by combined releases of both predators, and (2) if and how pest densities affect IGP of *O. insidiosus* on *A. cucumeris*.

Currently, the biological control of WFT focuses primarily on the foliar dwelling developmental stages, with little attention to the soil inhabiting stages. However, the late second instar larvae of WFT will leave the plant, prepupate and pupate in the soil (Palmer, 1989; Tommasini and Maini, 1995; Berndt, 2004), where they spend about one-third of their life cycle (Loomans and van Lenteren, 1995). This developmental stage of WFT in the soil is excluded from the prey spectrum of the common predators foraging on the plants. Soil predatory mites like *Stratiolaelaps (Hypoaspis) miles*

(Berlese) and *Hypoaspis aculeifer* Canestrini (Acarina: Laelapidae) commercially produced for the control of mushroom sciarid larvae (Folker-Hansen and Krogh, 1988; Enkegaard et al., 1997; Ydergaard et al., 1997; Ali et al., 1999; Jess and Kilpatrick, 2000), or of bulb mites, *Rhizoglyphus robini* Claparede (Lesna et al., 1996, 2000), also prey on thrips dropping to the ground to pupate (Gillespie and Quiring, 1990; Brødsgaard et al., 1996; Borgemeister et al., 2002; Berndt et al., 2002, 2004). But in general, the potential of *Hypoaspis* spp. to manage thrips appears to be restricted. Berndt et al. (2004) summarized that availability of too much alternative prey, such as nematodes, mites, springtails and small insect larvae in the soil, low encounter rates between predators and preys as well as interference between predators can be responsible for the limitation of the predatory efficiency. Thus, the third aim of this study was to achieve an improved suppression of WFT with a simultaneous release of plant and soil dwelling predators, combining *A. cucumeris* or *O. insidiosus* with *H. aculeifer*, respectively.

Interactions of western flower thrips *Frankliniella occidentalis* (Pergande), two-spotted spider mites *Tetranychus urticae* Koch and the predatory mite *Amblyseius cucumeris* (Oudemans) on beans

2.1 Introduction

Western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) and two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) (TSSM) are economically important pests of ornamentals and vegetables. WFT is native to the western part of North America and since the late 1970s has become a highly cosmopolitan pest. Today it is considered to be the number one pest of many crops, particularly in greenhouses (Beshear, 1983; van Lenteren and Loomans, 1995; Kirk and Terry, 2003). TSSM is likewise a universally occurring pest and often invades greenhouses where it can cause serious damage to many economically important crops.

Both pests are difficult to control with synthetic insecticides / acaricides, especially because of wide spread resistance in WFT (Gillespie, 1989; Brødsgaard, 1994; Zhao et al., 1995) and TSSM (Cranham and Helle, 1985). Moreover, because of the cryptic feeding behaviour, with thrips often found in flowers, buds and leaf axils, and spider mites hidden in their webs, they are often not attainable by contact insecticides / acaricides. Finally chemical control often leads to unacceptable high residue levels on marketable products such as fresh vegetables and has a negative effect on important beneficials such as predators, parasitoids and pollinators. A highly promising and environmentally friendly alternative is the use of biological control through inundative releases of natural enemies of the pests in greenhouses.

Amblyseius cucumeris (Oudemans) (Acarina: Phytoseiidae) is a polyphagous predatory mite, preying on a number of mites and insect species (McMurtry and Croft, 1997). It is widely used as a biological control agent to combat thrips outbreaks on ornamentals (Hessein and Parrella, 1990; De Courcy Williams, 1993, 2001) and vegetable crops such as sweet pepper (Ramakers, 1987), cucumber (Gillespie, 1989; Ramakers et al., 1989; Bennison and Jacobson, 1991; Jacobson, 1995, 2001), and also tomatoes (Shipp and Wang, 2003). However, thrips control by *A. cucumeris* is not equally successful in every crop. In some crops, such as cucumber (*Cucumis sativus* L.), *A. cucumeris* is not a very

effective control agent (van Houten et al., 1995). In contrast, _A. cucumeris_ has been rarely used for biological control of phytophagous mites. Only in recent years, _A. cucumeris_ has been sporadically used for control of the cyclamen mite _Phytonemus pallidus_ (Banks) and TSSM on strawberry (Croft et al., 1998; Easterbrook et al., 2001) and the broad mite _Polyphagotarsonemus latus_ (Banks) (both Acari: Tarsonemidae) on sweet pepper (Weintraub et al., 2003). Hence, the first objective of this study was to investigate whether _A. cucumeris_ is capable of successfully suppressing TSSM and/ or WFT populations, using kidney beans as the model plant.

Plants are often simultaneously infested by both WFT and TSSM (Trichilo and Leigh, 1986; Lewis, 1973; Sterk and Meesters, 1997). Little is known about biological control of WFT in the dual presence of other pests like TSSM. Hence the second objective of this study was to investigate whether the extent of biological control of WFT by _A. cucumeris_ is affected in a mixed infestation situation with TSSM.

WFT is an omnivore, feeding on plant tissues but occasionally also preying on mite eggs (Trichilo and Leigh, 1986; Agrawal et al., 1999; Agrawal and Klein, 2000). Some reports have even indicated that WFT can also feed on phytoseiid eggs like _Iphiseius degenerans_ (Berl.) (Faraji et al., 2001, 2002) and _Phytoseiulus presimilis_ Athias-Henriot (Janssen et al., 1998). Thus an additional objective of this study was to investigate whether WFT can prey on _A. cucumeris_ eggs.

2.2 Materials and Methods

2.2.1 Plant material

Bean (_Phaseolus vulgaris_ [Fabaceae] cv. Merona) seedlings with the first two true leaves unfolded, i.e., younger than 10 days, were used as test plants. Plants were grown in the nursery of the Institute of Plant Diseases and Plant Protection (IPP), University of Hannover, Germany, at a temperature of 20°C, 75% relative humidity (r.h.) and 16:8 h L: D photoperiod. In the experiment of the potential ability of WFT to prey on _A. cucumeris_ eggs, for easy observation, leaf discs cut from the above-mentioned bean plants were used (for details see below). To avoid that the leaf surface influences the behaviour of the thrips, the leaf discs did not contain the midribs.

2.2.2 Insects and mites

WFT and TSSM were obtained from stock cultures maintained at IPP. Spider mites and thrips were reared at 23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod on bean plants and pods, respectively. In all experiments, younger than two-day-old WFT larvae and neonate gravid females of TSSM were used. *Amblyseius cucumeris* was purchased from Katz Biotech. Services (Baruth, Germany) and kept at 9°C for less than one week before use in the experiments. During this period no extra food in addition to the flour mites (*Tyrophagus putrescentiae* (Schrank)) provided by the supplier was given to the predatory mites. One day before being transferred onto the bean plants, predatory mites were separated from the packaging material and kept together with some additional flour mites as prey. Only active *A. cucumeris* females were used in the experiments.

Similar aged eggs of *A. cucumeris* were produced by keeping adult predatory mites on TSSM infested detached bean leaves. Under the before mentioned conditions, eggs of *A. cucumeris* hatch in about 2.5 days (X. Xuenong, unpubl. data), Thus, only eggs younger than 18h were used in the experiments. WFT larvae of varying age, i.e., 3- to 7-day-old, were obtained from the stock culture.

2.2.3 Experimental procedures

The experimental set-up consisted of single bean seedling, which were individually transplanted into a plastic pot (diameter 11cm) and covered with a plexiglass cylinder (diameter 10cm, height: 30cm). To insure ventilation and for releasing mites and insects, the cylinder walls were equipped with eight holes, which were sealed with thrips-proof nylon gauze (pore size ca. 60µm, Sefar Ltd., Rüschlikon, Switzerland) except for one which was left open for transferring test insects and mites. This hole was later closed with a sticky tape and paper. At the beginning of the experiments 10, 20 or 40 gravid TSSM females were transferred with a fine hairbrush onto one leaf per plant. One day later 20 or 40 WFT larvae and 5 or 10 *A. cucumeris* were transferred to the TSSM infested leaf. All treatments are listed in detail in table 1. Plants were then incubated for eight days in a climate chamber (23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod) and thereafter cut at the ground level. The cut plants (leaves and stems) were immediately examined for presence of thrips larvae, prepupae and pupae. If found, they were transferred to a fresh bean leaf which was returned to the original pot. According to Berndt et al. (2004), approximately 98% of the late second instar larvae of WFT descend from the plants to pupate in the soil. The emerging WFT adults are photosensitive and

leave the soil to re-colonise the plants. Thus, the pots were enclosed with another pot of the same size, whose bottom was cut and covered with a Petri dish. The inner surface of the Petri dish was painted with insect glue, constituting a sticky trap to catch the emerging thrips adults. To prevent high humidity, three holes (diameter 1.5cm) were drilled into the walls of the upper pot and were sealed with thrips-proof nylon gauze. The gap between the two pots was sealed with plasticine. The sticky traps and the pot were daily monitored until no more thrips emerged. After inspection for the different life stages of WFT, the cut plant parts were placed separately in a Petri dish, sealed with parafilm, and then kept at 5°C until further examination. Each treatment was replicated 15 times over time

The experiment on the potential ability of WFT to prey on *A. cucumeris* eggs was conducted in Petri dishes (diameter 6 cm) equipped with a water-soaked sponge ($3 \times 3 \times 0.7 \text{cm}^3$). Additionally a piece of filter paper (diameter 2.1 cm) was placed on the sponge. A single bean leaf disc (3.14 cm^2, diameter 2cm) was then put upside down on the filter paper and served as the experimental arena. Twenty *A. cucumeris* eggs per leaf disc were then transferred with a fine brush. Two similar-aged WFT larvae were subsequently released per Petri dish. In total five different treatments were compared, i.e., *A. cucumeris* eggs without WFT (control), and four treatments with 3-4-, 4-5-, 5-6- and 6-7-days-old WFT larvae. Each treatment was replicated 15 times. The number of surviving eggs was counted after 24 hours. The experiment was conducted in a climatic chamber at 23±1°C, 65%±5% r.h. and 16:8 h L: D photoperiod.

2.2.4 Statistical analysis

To compare the control efficacy of a biological agent, percentages of TSSM suppression and the corrected mortality of WFT are used. Percentages of TSSM suppression were calculated according to the formula of Colfer et al. (2000), and corrected mortality (CM) values in WFT were computed using Schneider-Orelli's formula (Schneider-Orelli, 1947). Data of experiments repeated over time were checked for homogeneity of variance using the HOVTEST = Levene option of SAS (1996) and pooled only when variance homogeneity could be assumed. The percentages of TSSM suppression or CM values of WFT in T6-T11 (TSSM and *A. cucumeris*) and T12-T15 (WFT and *A. cucumeris*) (for details see table 1) were analysed by ANOVA and compared to zero (the

percentages of TSSM suppression and corrected mortality in WFT in the TSSM (T1-T3) and WFT (T4-T5) only treatments, respectively). In case the ANOVAs yielded significant F-values, means were compared using the Dunnett test. The interactions among TSSM, WFT and *A. cucumeris* were analysed using the GLM procedure of SPSS (SPSS 10.0, 2000). If significant factor effects were detected by means of ANOVA, the means of the percentages of TSSM suppression and CM of WFT in the different treatments were compared using Tukey's multiple range tests. The control efficiencies of 5 and 10 *A. cucumeris* were compared using the t-test. In the experiment on the potential ability of WFT to prey on *A. cucumeris* eggs, the numbers of killed eggs per WFT larva were square root transformed and analysed by means of ANOVA. A significance level of $\alpha=0.05$ was used in all the analyses.

Table 1. Initial densities and combinations of TSSM, WFT and *A. cucumeris* adults.

Treatments	TSSM	WFT	*A. cucumeris*
T1	10	0	0
T2	20	0	0
T3	40	0	0
T4	0	20	0
T5	0	40	0
T6	10	0	5
T7	10	0	10
T8	20	0	5
T9	20	0	10
T10	40	0	5
T11	40	0	10
T12	0	20	5
T13	0	20	10
T14	0	40	5
T15	0	40	10
T16	10	20	5
T17	10	20	10
T18	10	40	5
T19	10	40	10
T20	20	20	5
T21	20	20	10
T22	20	40	5
T23	20	40	10
T24	40	20	5
T25	40	20	10
T26	40	40	5
T27	40	40	10

2.3. Results

2.3.1 Experiment I

2.3.1.1 Effects of A. cucumeris on TSSM

At both releases densities *A. cucumeris* could significantly suppress TSSM populations with an initial density of 10 and 20, but not 40 mites (table 2). TSSM control by *A. cucumeris* was significantly influenced by prey but not by predator densities, nor by the interaction between spider mites and predatory mites (table 3). TSSM suppression was significantly different at the three different mite densities.

Table 2. Summary of ANOVA results of the percentages of TSSM suppression at three different mite densities (i.e., 10, 20 and 40) caused by 5 or 10 *A. cucumeris* adults

Source	df	F	P
TSSM	2	18.504	<0.001
A. cucumeris	1	3.110	0.091
TSSM × A. cucumeris	2	0.067	0.935

Table 3. Suppression of TSSM at three initial densities (i.e., 10, 20 and 40) by 5 or 10 *A. cucumeris* adults.

% TSSM suppression (mean ± SE)		
10	20	40
33.8 ± 3.0 a	21.9 ± 3.3 b	6.5 ± 3.2 c

Means (± SE) within a row followed by different letters show significant difference among different densities of TSSM, irrespective of the density of *A. cucumeris* (Tukey test).

2.3.1.2 Effects of A. cucumeris on WFT

Compared to the no-predators controls, *A. cucumeris* at both release rates could significantly suppress WFT ($p<0.01$, Dunnett test). The extent of thrips control was significantly influenced by predator but not by prey density nor by the interaction of both factors (table 4). As prey density did not affect the extent of predation in *A. cucumeris*, data was analysed irrespective of the initial thrips densities. With more than 40% corrected mortality, the higher release rate of *A. cucumeris* resulted in significantly greater thrips control than the lower *A. cucumeris* density (table 5).

Table 4. Summary of ANOVA results of the corrected mortalities of WFT at two different densities (20 and 40) caused by 5 and 10 *A. cucumeris* adults

Source	df	F	*P*
WFT	1	1.347	0.263
A. cucumeris	1	7.728	0.013
WFT × *A. cucumeris*	1	1.351	0.262

Table 5. Corrected mortalities (CM) of WFT caused by 5 and 10 *A. cucumeris* adults irrespective of the thrips densities.

A. cucumeris	CM of WFT (mean ± SE)
5	29.9 ± 3.2 a
10	43.1 ± 3.6 b

Means (± SE) within the column followed by different letters indicate significant difference between two predatory mite densities (i.e., 5 and 10), irrespective of the thrips densities (t test).

2.3.1.3 Effects of A. cucumeris on TSSM in the presence of WFT

Compared to the no-predators controls, in the dual presence of WFT and TSSM, *A. cucumeris* at both release rates could significantly suppress mite populations at the lower and intermediate TSMM densities, and 10 *A. cucumeris* even at the highest mite density ($P < 0.05$, Dunnett test). Only the initial TSSM and predator but not WFT densities significantly affected the extent of spider mite control (table 6). Moreover, all interaction terms were not significant. Hence, percentages of TSSM suppression were compared, irrespective of the thrips densities. At the lower *A. cucumeris* release rate, the percentages of mite suppression significantly differed among the three initial TSSM densities, whereas at the higher release rate of *A. cucumeris* TSSM control differed between the lowest and middle or highest density of TSSM (Fig. 1). Moreover, only at the highest initial density of TSSM did mite suppression significantly differ between the two predator release rates.
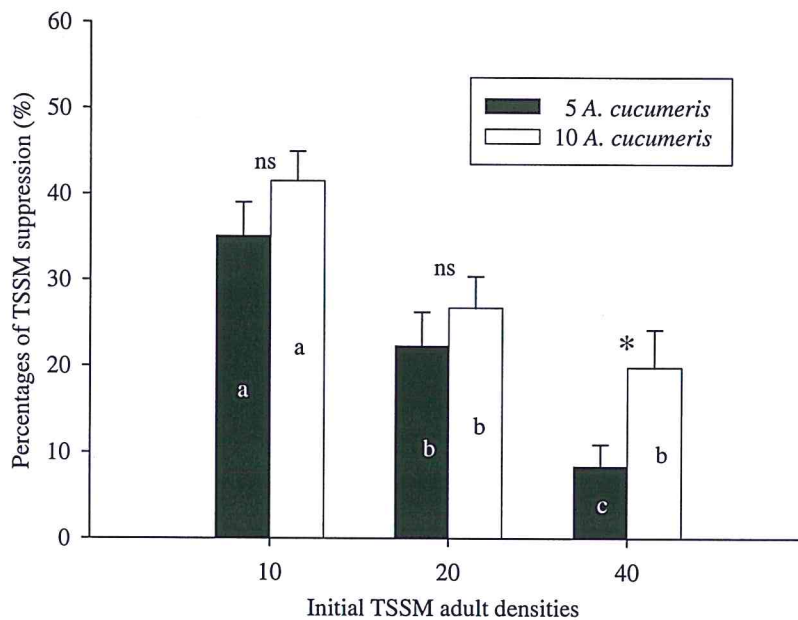
Fig. 1. Percentages of TSSM suppression (mean ± SE) at three spider mite densities (i.e., 10, 20 and 40) by *A. cucumeris* at two densities (i.e., 5 and 10), irrespective of the thrips densities. Means of percentages of TSSM suppression at a given density of *A. cucumeris* marked by different letters are significantly different (Tukey test). ns and * means non-significant and significant difference in TSSM suppression by 5 and 10 *A. cucumeris* at a given density of TSSM (t test).

Table 6. Summary of ANOVA results of the percentages of TSSM suppression at three initial different mite densities (i.e., 10, 20 and 40) caused by 5 or 10 *A. cucumeris* adults in the presence of WFT at three densities of WFT (i.e., 0, 20 and 40)

Source	df	F	P
TSSM	2	20.860	<0.001
WFT	2	2.598	0.081
A. cucumeris	1	5.863	0.018
TSSM × WFT	4	0.895	0.471
TSSM × *A. cucumeris*	2	0.465	0.630
WFT × *A. cucumeris*	2	0.028	0.973
TSSM × WFT × *A. cucumeris*	4	0.150	0.962

2.3.1.4 Effects of A. cucumeris on WFT in the presence of TSSM

Like in TSSM compared to the no-predator controls, in mixed infestations of TSSM and WFT *A. cucumeris* at both releases rates significantly reduced thrips numbers at both initial WFT densities ($P < 0.01$, Dunnett test). Only predator but not thrips and spider

mite densities significantly affected the extent of WFT control (table 7). Moreover, all interaction terms were not significant. Hence, corrected mortalities of WFT were compared irrespective of the initial WFT and TSSM densities. With 45.9% significantly higher corrected mortality was recorded following releases of 10 *A. cucumeris* compared to 32.7% at the lower predator release rate (Fig. 2).

Table 7. Summary of ANOVA results of the corrected mortalities of WFT at two densities (i.e., 20 and 40) caused by 5 and 10 *A. cucumeris* adults in the presence of TSSM at four different initial densities (i.e., 0, 10, 20 and 40)

Source	df	F	P
TSSM	3	1.577	0.204
WFT	1	2.090	0.153
A. cucumeris	1	29.349	<0.001
TSSM × WFT	3	0.128	0.943
TSSM × *A. cucumeris*	3	0.163	0.921
WFT × *A. cucumeris*	1	2.138	0.149
TSSM × WFT × *A. cucumeris*	3	0.200	0.896
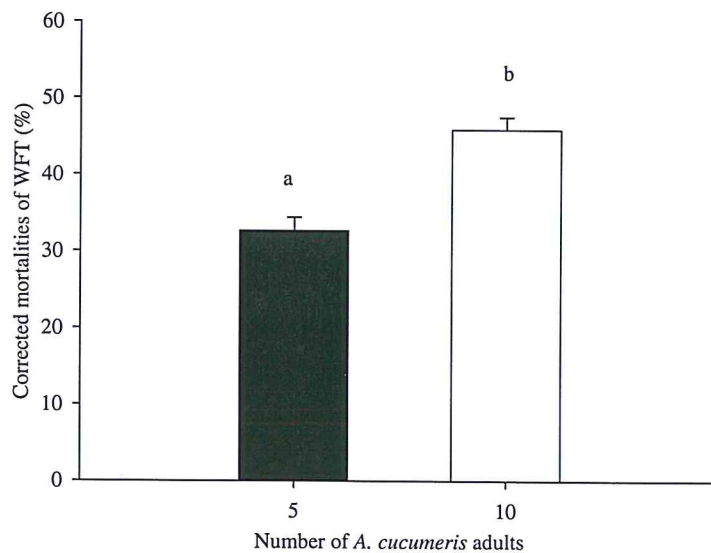
Fig. 2: Corrected mortalities (CM) of WFT caused by *A. cucumeris*, irrespective of the TSSM and WFT densities. Means marked by different letters indicate significant difference between two predator densities (i.e., 5 and 10) (t test).

2.3.2 Experiment II: Predation of WFT larvae on A. cucumeris eggs

In the control treatment, no natural mortality of *A. cucumeris* eggs was found. WFT larvae could kill eggs of *A. cucumeris*, and the age of WFT larvae (ranging from 3-7 days) did not significantly affect egg predation ($F_{3, 49} = 0.02$, $P=0.996$). Under the experimental conditions on average one thrips larva could kill 1.2 (±0.1) *A. cucumeris* eggs per day.

2.4 Discussion

Most often the phytoseiid *Phytoseiulus persimilis* Athias-Henriot is used for biological control of TSSM (Helle and Sabelis, 1985b; McMurtry and Croft, 1997), though on some plants TSSM can also be successfully controlled by other predacious mites like *Neoseiulus californicus* McGregor (Garciá-Marí and González-Zamora, 1999; Easterbrook et al., 2001), and *N. fallacis* Garman (both Acarina: Phytoseiidae) (Raworth, 1990; Cooley et al., 1996; Croft et al., 1998). However, *P. persimilis* has a high degree of specialization to tetranychid mites as prey (McMurtry and Croft, 1997; Cross et al., 2001). Moreover *P. persimilis* and the two *Neoseiulus* spp. do not prey upon WFT. In contrast, *A. cucumeris* is a more polyphagous predator and is widely used for control of WFT (Ramakers, 1987; Gillespie, 1989; Ramakers et al., 1989; Bennison and Jacobson, 1991; Jacobson, 1995, 2001). Moreover, it has also been used to control cyclamen mite *Phytonemus pallidus* (Banks) on strawberry (Croft et al., 1998; Easterbrook et al., 2001) and the broad mite *Polyphagotarsonemus latus* (Banks) (both Acari: Tarsonemidae) on sweet pepper (Weintraub et al., 2003). In our experiments *A. cucumeris* could significantly reduce population levels of spider mites and WFT in individual infestations of both pests. However, the extent of control by *A. cucumeris* differed greatly between TSSM and thrips. The predators were only capable of exerting a significant impact on TSSM populations at low and intermediate pest densities. Moreover, even at the higher release rate of *A. cucumeris* and at low TSSM densities, the level of spider mite suppression did not exceed 34%. Thus it seems that *A. cucumeris* has only a limited ability to control TSSM populations.

Using the same predator: prey ratio of 1:4, *A. cucumeris* could significantly suppress TSSM at low and intermediate but not at high densities. At the highest initial density of 40 gravid female TSSM, the mites appeared to be more gregarious (Xu, unpublished

data) and produced considerably more webbings. McMurtry and Croft (1997) categorised the life-style of phytoseiids into four groups, and in the group to which *A. cucumeris* belongs, many species are adversely affected by dense spider mite webbings (Sabelis and Bakker, 1992). Consequently at higher TSSM densities suppression of the spider mite by *A. cucumeris* is greatly reduced. These results stress that the extent of biological control not only depends on the initial predator: prey ratio but also on the absolute density of the prey. Another example shows this problem but the other way round with decreasing pest densities. Garciá-Marí and González-Zamora (1999) reported that for biological control of TSSM on strawberry plantings by *N. californicus*, at higher TSSM densities (1-10 mites per leaflet) predator: prey ratios of 1:5 to 1:10 suffice to effectively control spider mites during 1-2 weeks. However, at lower TSSM densities (0.1-1 mite per leaflet) due to the increased searching time of *N. californicus* predator: prey ratios of 1:1 to 1:5 are required, stressing the importance to adjust predator release rates to the fluctuating pest densities. In biological control of TSSM by *P. persimilis* Opit et al. (2004) found no interactions between the release ratios and TSSM densities. However, in some of their experiments the extent of mite suppression at higher TSSM densities using the same predator: prey ratio was significantly lower than at lower TSSM densities.

In individual infestations *A. cucumeris* could significantly suppress WFT on bean plants. However, irrespective of the WFT densities, releases of 5 and 10 *A. cucumeris* only resulted in corrected mortalities of 29.9 and 43.1%, respectively. Thus, on average an individual *A. cucumeris* only fed 1.3-1.8 WFT larvae during the entire experiment. In contrast, van Houten et al. (1995) reported a daily consumption of six first instar larvae of WFT by *A. cucumeris*. However, these results were obtained on cucumber leaf discs, and in the three-dimensional space of our experiments *A. cucumeris* apparently had greater difficulties to find its prey. In practical biocontrol of WFT, *A. cucumeris* is often released in very high numbers. For instance on greenhouse tomatoes, *A. cucumeris* were curatively released at 4-weeks intervals at a rate of one sachet of 1,000 predatory mites per plant at a mean initial thrips density of approximately 120 WFT per plant, leading to 77.6% reduction of WFT populations 11 weeks after the first *A. cucumeris* release (Shipp and Wang, 2003). These as well as our results indicate that for achieving greater thrips control efficiency higher numbers of *A. cucumeris* need to be released on beans.

In our experiments with dual infestations of WFT and TSSM, thrips control by *A. cucumeris* was not significantly affected by the additional presence of spider mites. Contrary to that Janssen et al. (1998) recorded a 48.6% lower predation rate of *A. cucumeris* on thrips larvae with the presence of TSSM webbings compared to sole infestations by WFT. The authors attributed this decline in prey efficacy of *A. cucumeris* on WFT in the presence of TSSM to the fact that the thrips can seek refuge in the spider mite webbings, thereby avoiding to be preyed upon. Most likely in our experiments the extent of webbings produced by TSSM did not suffice to provide enough protection for the WFT larvae. Another possible reason for the lack of differences in WFT control by *A. cucumeris* with and without TSSM might be a prey preference of *A. cucumeris* for WFT larvae compared to TSSM. In the study of chapter 3, a similar result was recorded in the biological control system of TSSM and WFT by *O. insidiosus*. *Amblyseius cucumeris* can feed on all developmental stages of TSSM (Blaeser and Şengonca, 2001; Blaeser et al., 2002), whereas in thrips only the first instar larvae can be consumed by *A. cucumeris* (Gillespie and Ramey, 1988; Bakker and Sabelis, 1989; van der Hoeven et al., 1990). In case *A. cucumeris* would have a prey preference for TSSM, then the extent of thrips control should be negatively affected in a mixed compared to a sole (thrips) infestation systems. As this was not the case, we conclude that *A. cucumeris* prefers first instar larvae of WFT as prey compared to spider mites.

Likewise TSSM control by *A. cucumeris* was also not affected by the additional presence of WFT larvae. Possible reasons for these results are: (i) TSSM constitute a low-value prey for *A. cucumeris* as mite control in sole infestations never exceeded 34%; (ii) apparently *A. cucumeris* prefers feeding on first instar larvae of WFT compared to TSSM; but (iii) as our experiments lasted only eight days, first instar larvae of *F. occidentalis* were only present during the first 1-2 days of the experiments. However, in greenhouses and in the field, WFT can develop several generations per year, especially in warmer regions, leading to overlapping generations and thus a continuous presence of first instar larvae. Hence under such conditions, TSSM control by *A. cucumeris* in the presence of WFT is probably even lower.

Some cases of unsuccessful biological control of WFT by *A. cucumeris* have been attributed to (i) wrong release times with bad synchronisation of prey and predator as *A. cucumeris* feeds only on the first instar larvae of thrips (Gillespie and Ramey, 1988;

Bakker and Sabelis, 1989; van der Hoeven et al., 1990), (ii) not convenient prey: predator ratios, or (iii) not convenient abiotic conditions like low humidity (van Houten et al., 1993), leading to reduced larval emergence in *A. cucumeris*. *A. cucumeirs* is a generalist predator. The presence of alternative food sources may also affect the efficacy of *A. cucumeris*. Alterna and Ravensberg (1990) reported that the effectiveness of *A. cucumeris* depended on its reproduction, which is dependent upon availability of pollen. van Rijn and Sabelis (1993) showed that pollen feeding resulted in higher predator densities and consequently in lower thrips densities, compared to situations where pollen is absent. On cucumber biological control has not given good results due to the limited availability of pollen in the crop (Riudavets, 1995). The ability of the predatory mite to use pollen as alternative food resources compensate for periods of insufficient prey availability (Ramakers, 1990; van Rijn and Sabelis, 1990). Thus, the presence of pollen keeps a high and stable efficacy of *A. cucumeris* on suppressing thrips population. Finally the control efficacy of *A. cucumeris* can be also influenced by direct competition between pest and predators, particularly if pest species with ambivalent feeding strategies, which can also act periodically as predators like WFT, which inhabits in the same patch. Our results show that three- to seven-days old WFT larvae can kill the eggs of *A. cucumeris*, with an average of 1.2 *A. cucumeris* eggs killed per thrips larva during 24 h on healthy bean leaves. On damaged leaves possibly WFT can prey even more on *A. cucumeris* eggs as reduced plant quality can cause *F. occidentalis* to shift from herbivory to predation (Agrawal et al., 1999; Janssen et al., 2003). Thus, WFT-induced mortality in *A. cucumeris* eggs can potentially reduce the extent of biological control of *F. occidentalis* by *A. cucumeris*. Fortunately, *A. cucumeris* has the advantage of being readily and cheaply mass-produced (Ramakers and van Leiburg, 1982; Ravensberg and Altena, 1987; Gillespie and Ramey, 1988), which makes it suitable for inundative releases (De Courcy Williams, 2001) and thus the predatory egg mortality imposed by the thrips larvae may be neglected. However, this trait enlightens us in biological control of WFT using *A. cucumeris,* the predatory mite should be released as early as possible to avoid the second instar WFT larvae. And a better approach to the release of *A. cucumeris* is to use one *A. cucumeris* culture sachet per plant compared to using sprinkling method. By using culture sachet, as a controlled release system, more *A. cucumeris* active stages can be continuously offered to the plants. This method has

proved to be an ideal approach in controlling WFT (Jacobson et al. 2001; Shipp and Wang, 2003).

In conclusion our results indicate the predator prefers the first instar larvae of WFT compared to TSSM. Consequently biological control of WFT by *A. cucumeris* is not affected by the additional presence of TSSM. The increasing density of *A. cucumeris* significantly increased the biological control efficiency of WFT. WFT can consume the predatory mite eggs, which should be one of the factors to be considered when releasing *A. cucumeris* for biological control of *F. occidentalis*.

Interactions in the biological control of western flower thrips *Frankliniella occidentalis* (Pergande) and two-spotted spider mites *Tetranychus urticae* Koch by the predatory bug *Orius insidiosus* (Say) on beans

3.1 Introduction

The western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) and the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychiidae) (TSSM) are economically important pests in ornamentals and vegetables. WFT is native to the western part of North America, and since the late 1970s it has become a highly cosmopolitan pest; today it is considered to be the number one pest of many crops, particularly in greenhouses (Beshear, 1983; Kirk and Terry, 2003). TSSM is likewise a universally occurring pest and often invades greenhouses (Cloutier and Johnson, 1993).

Orius spp. (Hemiptera: Anthocoridae) are omnivores, feeding on a variety of preys, including thrips, spider mites, insect eggs, aphids, and small caterpillars. However, thrips and mites are believed to constitute essential parts of an *Orius* spp. diet (Wright, 1994). *Orius* spp. have been successfully used as biological control agents against WFT, for instance in cucumbers (Ravensberg et al., 1992; Chamber et al., 1993; Michelakis et al., 1997), sweet pepper (van den Meiracker and Ramakers, 1991; Chamber et al., 1993; Dissevelt et al., 1995; Sanchez et al., 1997; Funderburk et al., 2000; Ramachandran et al., 2001), strawberries (Frescata and Mexia, 1996; Sterk et al., 1997), sunflower (Chyzik and Klein, 1995), and gerbera (Brødsgaard and Enkegaard, 1997). Yet, bi-weekly releases of *O. insidiosus* (Say) on tomatoes at a rate of 10 adults per plant failed to reduce thrips populations to economically acceptable levels (Shipp and Wang, 2003). TSSM constitutes an alternative prey for predatory bugs (Cloutier and Johnson, 1993). Yet although predatory bugs are considered to be important predators of TSSM (Oatman and McMurthry, 1966), they are rarely used for biological control of mites. However, in selective exclusion of *Orius* with acephate or release of predators in cotton, Colfer et al. (1998, 2000) could demonstrate that *O. tristicolor* (White) and *Geocoris* spp. (Hemiptera: Lydaeidae) could efficiently control TSSM. Hence, the first objective of this study was to investigate whether *O. insidiosus* is capable of successfully suppressing TSSM or WFT populations, using kidney beans as the model plant.

Plants are often simultaneously infested by both WFT and TSSM (Trichilo and Leigh, 1986; Wilson et al., 1996; Lewis, 1997; Sterk and Meesters, 1997; Fejt and Jarosík, 2000), where they compete for food resources. In addition, WFT is an omnivore, feeding on plant tissues but occasionally also preying on TSSM eggs (Trichilo and Leigh, 1986). Thrips respond to the presence of predatory bugs by hiding in the webbings of TSSM (Cloutier and Johnson, 1993; Venzon et al., 2000), thereby enhancing the probability that they feed on TSSM eggs. Damage of bean leaves by WFT but not by TSSM leads to an increase in search time of *O. tristicolor*, indicating that the predator uses WFT-specific infochemicals to locate thrips as prey (van Laerhover et al., 2000). Hence, dual infestations by thrips and mites might increase TSSM control by *O. tristicolor* and possibly other *Orius* spp. through an increased likelihood of encounters between bugs and mites. TSSM webbings can also provide refuges for WFT and thus decrease the control efficacy of predatory bugs with regard to thrips (Cloutier and Johnson, 1993; Venzon et al., 2000). Therefore, dual infestations by TSSM and WFT in the presence of predatory bugs presumably favor thrips rather than mites. However, this might be affected among others by the prey preference of the predators, prey density, and host plants. Thus, the second objective of this study was to investigate how TSSM and WFT affect each other and the control efficiency of *O. insidiosus* in mixed infestations.

3.2 Materials and methods

3.2.1 Plant material

Bean (*Phaseolus vulgaris* [Fabaceae] cv. Merona) seedlings with the two first true leaves unfolded, i.e., younger than 10 days, were used as test plants. Plants were grown in the nursery of the Institute of Plant Diseases and Plant Protection (IPP), University of Hannover, Germany, at a temperature of 20°C, 75% relative humidity (r.h.) and 16:8 h L: D photoperiod.

3.2.2 Insects and mites

WFT and TSSM were obtained from stock cultures maintained at IPP. Mites and thrips were reared at 23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod on potted bean plants and bean pods, respectively. In all the experiments, two-day-old WFT larvae and

neonate gravid females of TSSM were used. *Orius insidiosus* were purchased from Katz Biotech. (Baruth, Germany). One day before the start of the experiments, males and females were isolated in a plastic bottle (200 ml) and bean pods were offered as food. Only active *O. insidiosus* females were used in the experiments.

3.2.3 Experimental procedures

The experimental unit consisted of four bean seedlings, which were transplanted into a plastic pot (16 cm diameter) and covered with a plexiglass cylinder (diameter 15 cm, height 40 cm). To insure ventilation and for releasing mites and insects, four holes were drilled into the cylinder walls (diameter 35 mm), three of which were sealed with thrips-proof nylon gauze (pore size ca. 60 µm, Sefar Ltd., Rüschlikon, Switzerland) and the fourth was left open for mite and insect transfer and was later closed by piece of paper using sticky tape. At the beginning of the experiment 5, 10 or 20 gravid TSSM females were transferred with a fine hairbrush on one leaf per plant, thus totalling 20, 40 or 80 TSSM. One day later, on the same leaves, 25 or 40 WFT larvae were transferred, thus adding 100 and 160 thrips larvae to an experimental unit. After WFT was transferred, 1 or 2 *O. insidiosus* were introduced in each experimental unit. More details of the treatments are provided in table 1. Plants were subsequently incubated for eight days in a climate chamber (23±1°C 65±5% r.h. and 16:8 h L: D photoperiod) and thereafter cut at the ground level. The cut plants (leaves and stems) were immediately examined for presence of thrips larvae, prepupae and pupae. If found, they were transferred to a fresh bean leaf which was returned to the original pot. Leaves with TSSM, and eggs and larvae of *O. insidiosus* were stored in a cold room (5±1°C) before all development stages of mites and bugs were counted. In all treatments with WFT, the emerging adults were counted. According to Berndt et al. (2004), approximately 98% of the late second instar larvae of WFT descend from the plants to pupate in the soil. The emerging WFT adults are photosensitive and leave the soil to re-colonize plants. Thus, the pots were enclosed with another pot of the same size, whose bottom was cut and covered with a Petri dish. The inner surface of the Petri dish was painted with insect glue, constituting a sticky trap to catch the emerging adult thrips. To prevent high humidity and increase ventilation, three holes (diameter 1.5 cm) were drilled into the walls of the upper pot and sealed with thrips-proof nylon gauze. The gap between the two pots was closed with plasticine. The sticky traps were daily monitored until no more thrips emerged. All

experiments were conducted in a climate chamber at 23±1°C, 65%±5% r.h. and 16:8 h L: D photoperiod. Each treatment was replicated five times.

Table 1. Initial densities at the beginning of the experiments and combinations of TSSM, WFT and *Orius insidiosus* adults.

Treatments	TSSM	WFT	*O. insidiosus*
T1	20	0	0
T2	40	0	0
T3	80	0	0
T4	0	100	0
T5	0	160	0
T6	20	0	1
T7	20	0	2
T8	40	0	1
T9	40	0	2
T10	80	0	1
T11	80	0	2
T12	0	100	1
T13	0	100	2
T14	0	160	1
T15	0	160	2
T16	20	100	1
T17	20	100	2
T18	20	160	1
T19	20	160	2
T20	40	100	1
T21	40	100	2
T22	40	160	1
T23	40	160	2
T24	80	100	1
T25	80	100	2
T26	80	160	1
T27	80	160	2

3.2.4 Data analyses

Percentages of TSSM suppression were calculated according to the formula of Colfer et al. (2000), and corrected mortality (CM) values in WFT were computed using Schneider-Orelli's formula (Schneider-Orelli, 1947). Data of experiments repeated over

time were checked for homogeneity of variance using the HOVTEST = Levene option of SAS (1996) and pooled only when variance homogeneity could be assumed. The percentages of TSSM suppression or CM values of WFT in T6-T11 (TSSM and *O. insidiosus*) and T12-T15 (WFT and *O. insidiosus*) were analyzed by ANOVA and compared to zero (the percentages of TSSM and CM in the TSSM (T1-T3) and WFT (T4-T5) only treatments, respectively). In case the ANOVAs yielded significant F-values, means were compared using the Dunnett test. The interactions among TSSM, WFT and *O. insidiosus* were analyzed using the GLM procedure of SPSS (SPSS 10.0, 2000). If significant factor effects were detected by means of ANOVA, the means of the percentages of TSSM suppression and CM of WFT in the different treatments were compared using Tukey's multiple range tests. The differences of the control efficiencies between 1 and 2 *O. insidiosus* were compared using the t-test. Data on *O. insidiosus* offspring was square root transformed prior to ANOVA. Repetitions in which *O. insidiosus* females did not oviposit were excluded from the analysis. A significance level of α=0.05 was used in all analyses.

3.3 Results

3.3.1 Effects of O. insidious on the TSSM population

TSSM suppression was significantly influenced by both mite and bug densities but not by the interaction of mites and bugs (table 2). Moreover, at all TSSM densities both predator densities resulted in significantly lower mite densities compared to the no-predator controls ($P < 0.001$, Dunnett test). At both predator densities TSSM control was significantly lower at the highest compared to the lowest mite densities (table 3). In addition, only in the intermediate TSSM density doubling the higher predator density caused significantly higher mite suppression (table 3).

Table 2. Summary of ANOVA results of the percentages of TSSM suppression at three different initial mite densities (i.e., 20, 40 and 80) caused by 1 or 2 *O. insidiosus* adults.

Source	df	F	P
TSSM	2	9.232	0.001
O. insidiosus	1	9.226	0.006
TSSM × *O. insidiosus*	2	1.020	0.376

Table 3. Suppression of TSSM at three initial densities by 1 or 2 *O. insidiosus* adults.

O. insidiosus	% TSSM suppression (mean ± SE)		
	20	40	80
1	52.9 ± 5.5 A a	38.7 ± 5.5 A ab	25.8 ± 6.1 A b
2	60.6 ± 9.2 A ab	63.1 ± 5.4 B b	38.4 ± 4.4 A a

Means within a column followed by different upper case letters indicate significant differences between the two *O. insidiosus* densities at a given TSSM density (t-test). Means within a row followed by different lower case letters show significant differences among different densities of TSSM at a given *O. insidiosus* density (Tukey test).

3.3.2 Effects of O. insidiosus on the WFT population

Like in the previous experiment, thrips control was significantly influenced by both WFT and *O. insidiosus* densities but not by the interaction of thrips and bugs (table 4). Likewise, in the two thrips densities both *O. insidiosus* densities resulted in significantly lower WFT numbers compared to the no-predator controls ($P < 0.001$, Dunnett test). In both WFT densities, the higher predator density caused significantly greater thrips mortality (table 5). However, only in the higher predator density significantly lower WFT control was recorded at the higher thrips density (table 5).

Table 4. Summary of ANOVA results of corrected mortality values in WFT at two different thrips densities (i.e., 100 and 160) caused by 1 or 2 *O. insidiosus* adults.

Source	df	F	P
WFT	1	8.374	0.011
O. insidiosus	1	21.068	<0.001
WFT × *O. insidiosus*	1	0.001	0.987

Table 5. Corrected mortalities (CM) of 100 and 160 WFT larvae caused by 1 or 2 *O. insidiosus*.

O. insidiosus density	CM of WFT (mean ± SE)	
	100	160
1	62.9 ± 9.3 A a	46.3 ± 3.5 A a
2	87.9 ± 4.0 B a	71.9 ± 2.9 B b

Means within a column followed by different upper case letters indicate significant differences between the two *O. insidiosus* densities at a given WFT density. Means within a row followed by different lower case letters show significant differences between two WFT densities at a given *O. insidiosus* density (t-test).

3.3.3 Effects of O. insidiosus on the TSSM population in the presence of WFT

All individual factors but only the interactions of TSSM and WFT and of WFT and *O. insidiosus* significantly affected the extent of TSSM suppression (table 6). In the 100 WFT and 1 *O. insidiosus* treatments only at the lowest TSSM density significantly higher mite suppression than in the no-predator and no-thrips control were recorded, whereas at the higher bug density TSSM suppression was always significantly higher than in the controls (table 7). Similarly at the higher thrips density adding 1 *O. insidiosus* did not yield a significantly higher mite suppression in all TSSM densities compared to the respective controls, and at the high bug density significantly higher mite suppression was only recorded at the intermediate and highest TSSM densities (table 7). Only in the combination of 1 *O. insidiosus* and 100 WFT significantly higher mite suppression was recorded at the lowest compared to the intermediate and highest TSSM density (table 7). However, in all other bug and WFT combinations mite suppression did not differ significantly among the three TSSM density levels. At 20 TSSM and 1 *O. insidiosus* adding 100 or 160 WFT to the system resulted in significantly lower mite suppression than in the no-thrips treatment (Fig. 1a). However, in the two bugs treatments only at the highest WFT density significantly lower mite suppression was recorded compared to the mite-only treatment (Fig. 1a). Similarly at the intermediate TSSM density adding thrips resulted in significantly lower mite suppression than in no-thrips treatments, and additionally at the higher predator density TSSM suppression at the higher WFT density was significantly lower than at the lower WFT density (Fig. 1b). At the highest TSSM density level adding thrips to the system did not affect mite suppression at both *O. insidiosus* densities (Fig. 1c).

Table 6. Summary of ANOVA results of the percentages of TSSM suppression at three different initial mite densities (i.e., 20, 40 and 80) caused by 1 or 2 *O. insidiosus* adults in the presence of WFT at three densities (i.e., 0, 100 and 160).

Source	df	F	P
TSSM	2	7.849	0.001
WFT	2	49.801	<0.001
O. insidiosus	1	31.160	<0.001
TSSM × WFT	4	4.639	0.002
TSSM × *O. insidiosus*	2	2.919	0.061
WFT × *O. insidiosus*	2	3.229	0.046
TSSM × WFT × *O. insidiosus*	4	0.386	0.818

Table 7. Percentages of TSSM suppression at three initial densities (i.e., 20, 40 and 80) caused by 1 or 2 *O. insidiosus* in the presence of WFT at two densities (i.e., 100 and 160).

O. insidiosus ×WFT	% TSSM suppression (mean ± SE)		
	20	40	80
1×100	27.8 ± 6.7 a *	6.9 ± 5.3 b ns	5.3 ± 4.0 b ns
2×100	40.7 ± 3.7 a *	42.7 ± 7.4 a *	25.9 ± 7.6 a *
1×160	11.7 ± 7.0 a ns	12.9 ± 2.3 a ns	12.8 ± 6.2 a ns
2×160	11.6 ± 4.5 a ns	21.4 ± 2.7 a *	23.6 ± 4.9 a *

Means within a row followed by different letters means significant difference among different densities of TSSM (Tukey test); ns or * within a column indicate non-significant or significant differences to the no-thrips and no-predator controls at a given density of TSSM (Dunnett test).

3.3.4 Effects of O. insidiosus on the WFT population in the presence of TSSM

Irrespective of the TSSM densities at both thrips and *O. insidiosus* densities significantly lower WFT densities were recorded compared to the no-predator controls ($P < 0.01$, Dunnett test). Only WFT and *O. insidiosus* but not TSSM densities significantly affected the extent of thrips control (table 8). Moreover, all interactions terms were not significant. Hence, corrected mortalities of WFT were compared irrespective of the TSSM densities. At both thrips densities adding two predators resulted in significantly higher WFT control than only one (Fig. 2). In addition, at both predator density levels significantly lower thrips mortality was recorded at the higher compared to the lower WFT density (Fig. 2).

Table 8. Summary of ANOVA results of corrected mortality values in WFT at two different thrips densities (i.e., 100 and 160) caused by 1 or 2 *O. insidiosus* adults in the presence of TSSM at four initial densities (i.e., 0, 20, 40 and 80).

Source	df	F	*P*
TSSM	3	2.745	0.051
WFT	1	22.747	<0.001
O. insidiosus	1	33.616	<0.001
TSSM × WFT	3	0.053	0.984
TSSM × *O. insidiosus*	3	0.886	0.454
WFT × *O. insidiosus*	1	0.497	0.484
TSSM × WFT × *O. insidiosus*	3	0.486	0.693
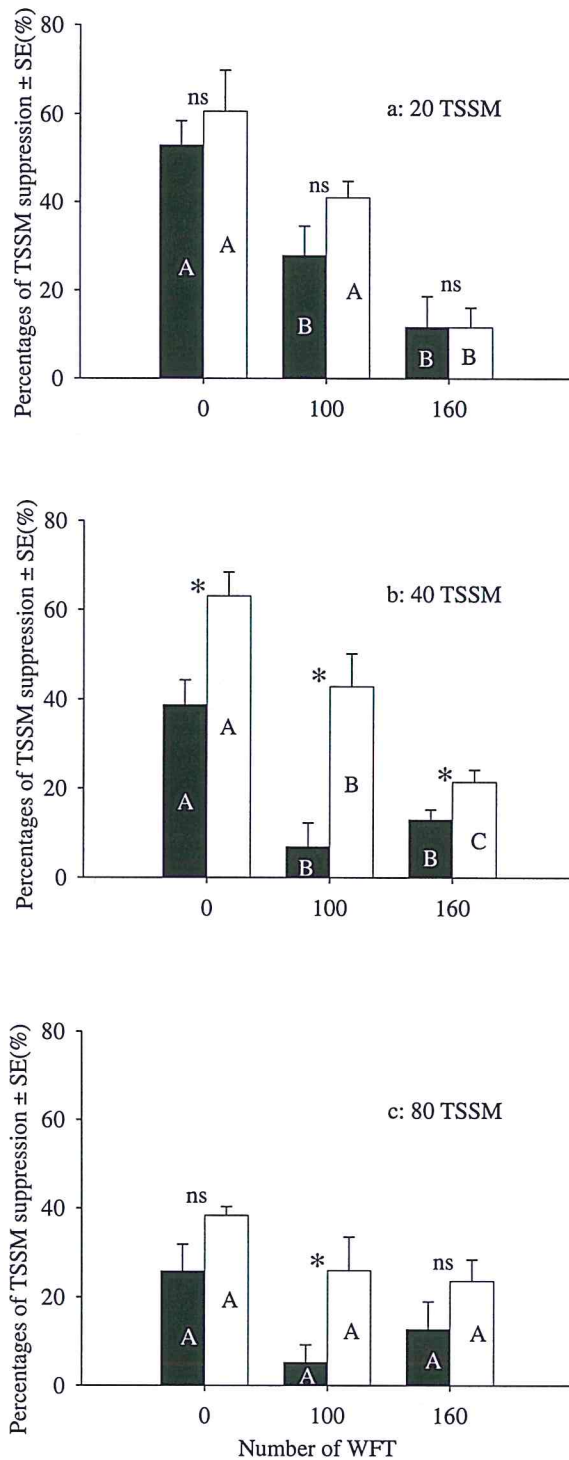
Fig. 1. Mean percentages (± SE) of TSSM suppression at different TSSM initial densities (a: 20 TSSM; b: 40 TSSM; c: 80 TSSM) by *O. insidiosus* alone and in the presence of WFT. Closed and open bars show the mean percentages of TSSM suppression by 1 and 2 *O. insidiosus*. Means of percentages of TSSM suppression for a given *Orius* density followed by different letters are significantly different (Tukey Test). ns or * indicate non-significant or significant differences in TSSM suppression by 1 and 2 *O. insidiosus* at a given WFT density.
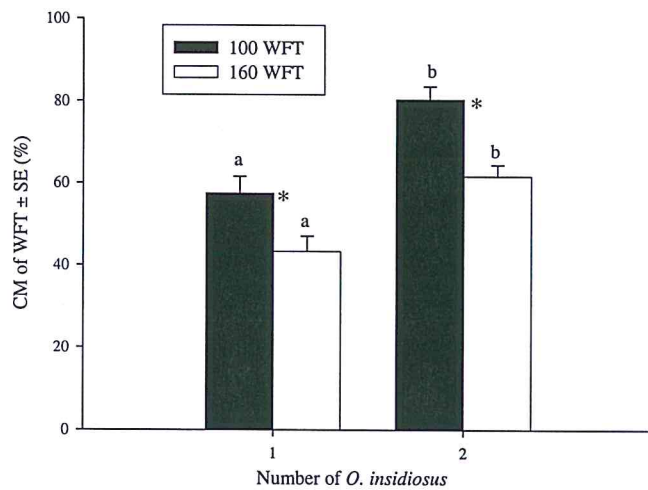
Fig. 2. Corrected mortalities (CM) of WFT caused by two densities of *O. insidiosus*. CM of WFT was compared irrespective of TSSM densities (see text for detail). CM values at a given WFT density followed by different letters indicate significant differences between 1 and 2 *O. insidiosus*. * indicate significant differences in CM between the two WFT densities at a given predator density (t-test).

3.3.5 Influence of WFT and TSSM on the reproduction of O. insidiosus

The ANOVA analysis (GLM procedure) yielded no significant factor interactions, and only WFT densities significantly affected oviposition in *O. insidiosus* (table 9). Hence, data on predator offspring were compared irrespective of TSSM and WFT densities and combinations between mites and thrips. Significantly lower numbers of *O. insidiosus* offspring were recorded in the TSSM-only compared to the WFT-only and combined mites and thrips treatments (table 10).

Table 9. Summary of ANOVA results on the effects of two different *O. insdiosus* densities (i.e., 1 and 2), four initial TSSM (i.e., 0, 20, 40 and 80) and three WFT densities (i.e., 0, 100 and 160) on the oviposition rate (eggs/day) of *O. insidiosus* during 8 days.

Source	df	F	P
TSSM	3	0.404	0.751
WFT	2	13.836	<0.001
O. insidiosus	1	3.160	0.081
TSSM × WFT	5	0.955	0.454
TSSM × *O. insidiosus*	3	0.611	0.611
WFT × *O. insidiosus*	2	0.789	0.460
TSSM × WFT × *O. insidiosus*	5	1.098	0.373

Table 10. Mean (± SE) oviposition rate (eggs/day) of *O. insidiosus* feeding on TSSM, WFT or both[1].

TSSM	WFT	TSSM + WFT
$0.7 \pm 0.2\ a^2$	$1.9 \pm 0.3\ b$	$2.5 \pm 0.3\ b$

[1] Data on oviposition were square root transformed; however, back-transformed values are presented in the table; [2] means followed by different letters are significantly different (Tukey test).

3.4 Discussion

Orius insidiosus can considerably suppress both WFT and TSSM populations when they occur individually on bean plants. On cotton Colfer et al. (2000) recorded highly efficient suppression of TSSM by *O. tristicolor* and *Geocoris* spp., with pest population levels 76-99% lower than in the absence of the predators. With 63%, in our experiments the highest mite control was achieved when 2 *O. insidiosus* were released for control of an initial density of 40 TSSM (Fig. 1b). In general the extent of TSSM suppression by *O. insidiosus* decreased with increasing mite density.

On sweet pepper, van den Meiracker and Ramakers (1991) observed that WFT densities sharply declined within three weeks and were reduced to less than one per flower after four weeks even at a high initial density of 36.7 thrips per flower after releases of approximately 2 *O. insidiosus* adults per plant. Likewise, Funderburk et al. (2000) using different treatments of biological and synthetic insecticides which altered the population densities of prey and predators recorded a near extinction of WFT adults and larvae once predatory bugs (*O. insidiosus*) - prey ratios reached 1:40. According to Michelakis and Amri (1997) the optimum predator: prey ratio in *O. insidiosus* for WFT control on cucumbers is 1: 2.5. Finally, on Gerbera, Brødsgaard and Enkegaard (1997) showed that releases of anthocorids at a predator: prey ratio of 1:150 can reduce thrips densities to less than one WFT per leaf within 4-6 weeks. Our results illustrate that on beans *O. insidiosus* can substantially suppress WFT population already at a adult predator: prey larvae ratio of 1:160.

When TSSM and WFT occur simultaneously, the presence of mites does not affect the extent of WFT control by *O. insidiosus*. Yet, suppression of TSSM was considerably reduced in the presence of WFT and was additionally affected by mite and predator densities. This suggests that the generalist predator *O. insidiosus* clearly prefers WFT as

prey compared to TSSM. Except at the lowest mite densities generally predator: prey ratios of adult *O. insidiosus* and WFT larvae of 1: 80 and greater were needed for a significant suppression of TSSM populations. Thus, when ample WFT larvae are present on the plants, *O. insidiosus* preferably preys on thrips, leading to insufficient control of *TSSM* in mixed mite and thrips infestations. Hence, in such situations higher release rates of predatory bugs will be required to assure an adequate control of both pests.

The addition of WFT larvae not only decreases the TSSM suppression by *O. insidiosus*, but also reduces the differences in TSSM suppression at three tested mite densities. In the no-thrips treatments we recorded significantly higher TSSM control at the lower and intermediate compared to the highest densities of *TSSM* (table 3). However, when adding WFT to the system TSSM suppression did not differ significantly among the three mite densities except at the lower density of both thrips and *O. insidiosus* (table 7).

In their studies both Cloutier and Johnson (1993) and Venzon et al. (2000) recorded a decrease in control efficiency of WFT by predatory bugs in the presence of TSSM and attributed this to the protection of the mite webbings for the thrips. However, in our experiments bug-induced mortality in WFT was not affected by additional mite infestations. These contrasting results are most likely due to considerable differences in TSSM densities in Cloutier and Johnson (1993) and Venzon et al. (2000) and in our studies. Cloutier and Johnson (1993) and Venzon et al. (2000) used 120 TSSM females for 2 days on a cucumber leaf disc (diameter 7 cm) or 100 TSSM females on a cucumber leaf disc (diameter 2.5 cm), respectively, which resulted in roughly two-thirds of the discs being covered with the webbings. However, in our experiments we used 20 TSSM females per bean leaf as the highest mite density. Consequently the thrips found considerably less refuges in our experimental arenas compared to the ones in Cloutier and Johnson (1993) and Venzon et al. (2000) experiments.

A further evidence for the greater prey value of WFT for *O. insidiosus* compared to TSSM was the significantly higher numbers of bug offspring when offered WFT alone or both mites and thrips compared to TSSM only. This might also explain the reduced mite suppression by *O. insidiosus* in the presence of WFT. Our results corroborate earlier findings by Venzon et al. (2002) who showed that under ample prey supply

O. laevigatus females fed with thrips or with a mixture of thrips and TSSM laid significantly more eggs than females fed with mites alone. Moreover, these authors also did not record any significant differences in the oviposition rate of *Orius* spp. females fed with thrips or with a mixture of thrips and spider mites.

In summary our results indicate complex interactions between *O. insidiosus*, WFT and TSSM when the predators are simultaneously exposed to two different prey species at varying densities and proportions. The presence of spider mites apparently has little to no influence on the control efficiency of WFT by *O. insidiosus*. Yet, in the presence of WFT spider mites were less preferred as prey, most likely because of the greater prey value of thrips compared to mites for *O. insidiosus*. Hence, in dual infestations of TSSM and WFT higher releases rates for predatory bugs are needed to assure a sufficient mite control.

The effects of combined releases of the predatory mite *Amblyseius cucumeris* Oudemans and the predatory bug *Orius insidiosus* Say on mixed infestations of beans by western flower thrips *Frankliniella occidentalis* (Pergande) and two-spotted spider mites *Tetranychus urticae* Koch

4.1 Introduction

Two spotted spider mites *Tetranychus urticae* Koch (Acari: Tetranychidae) (TSSM) and western flower thrips *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) (WFT) are two cosmopolitan pests, which seriously damage ornamentals and vegetables both in the field and in greenhouse cultures. Plants are often simultaneously infested by WFT and TSSM (Trichilo and Leigh, 1986; Wilson et al., 1996; Sterk and Meesters, 1997; Fejt and Jarosík, 2000).

Chemical control of WFT and TSSM is often very difficult, among others because of widespread resistance of both pests to insecticides and acaricides (Gillespie, 1989; Cranham & Helle, 1985). Consequently, for both pests biological control strategies, based on releases of predators in greenhouses, have been developed (Hussey et al., 1965; Jacobsen et al., 2001b). Most often the phytoseiid *Phytoseiulus persimilis* Athias-Henriot is used for biological control of TSSM (Hussey et al., 1965; Helle and Sabelis, 1985). However, *P. persimilis* is rather specific in its prey preference, preferably preying on tetranychid mites (McMurtry and Croft, 1997; Cross et al., 2001). In biological control of WFT often *Amblyseius* spp. (Acari: Phytoseiidae) (Gillespie, 1989; Tellier and Steiner, 1990; De Courcy Williams, 1993) and/or *Orius* spp. (Heteroptera: Anthocoridae) are used (Isenhour and Yeargan, 1981; van den Meiracker, 1991, Funderburk et al., 2000). Especially on high value crops like ornamentals, however, biological control of WFT has not always been successful (Ramakers et al., 1989; Bennison et al., 1990). One alternative to individual releases of one predator species is combined releases of two or more predators (Gillespie and Quiring, 1992; Ramakers, 1993; Sörensson and Nedstam, 1993).

Both *Amblyseius* and *Orius* spp. are generalist predators. Apart from feeding on thrips, they also consume other small arthropods like mites (Wright, 1994; McMurtry and Croft, 1997). Yet, for *Orius* spp. thrips and mites are believed to constitute essential

parts of their diet (Wright, 1994). Moreover both *Amblyseius* and *Orius* spp. are sometimes used to control spider mites (Helle and Sabelis, 1985; McMurtry and Croft, 1997; Colfer et al., 1998, 2000).

Amblyseius cucumeris Oudemans and *O. insidiosus* Say are among the most frequently used predators for biological control of WFT. However, little is known about their ability to suppress TSSM populations. Results from previous studies indicate that both predators can successfully control individual infestations of TSSM, especially at low mite densities; yet in mixed infestations of WFT and TSSM *O. insidiosus* and *A. cucumeris* show a distinct prey preference for thrips (Xuenong Xu, unpubl. data). The predatory mite can only feed on the first instar larvae of thrips (Gillespie and Ramey, 1988; Bakker and Sabelis, 1989; Van der Hoeven and van Rijn, 1990). Thus, in mixed infestations of spider mites and thrips and in the dual presence of both predators, suitable WFT prey stages for *A. cucumeris* might be scarce, among others due to the competition with *O. insidiosus*. In such situations *A. cucumeris* might switch to preying on TSSM, thereby offsetting the reduced control efficiency of *O. insidiosus* on TSSM.

Orius spp. can also prey on small predators like phytoseiid mites (Wittmann and Leather, 1997), a phenomenon generally termed intraguild predation (IGP) (Polis et al., 1989; Rosenheim et al., 1995). The extent of IGP can vary due to differences in the preference of the intraguild predator (IG-predator) for the intraguild prey (IG-prey) or the herbivorous pest, thereby possibly affecting the outcome of biological control. For example, if the IG-predator indiscriminately preys on both the IG-prey and the herbivorous pest, combined releases of the IG-predator and the IG-prey may lead to a decreased control efficiency of the herbivorous pest. For instance, Wittmann and Leather (1997) recorded that *O. laevigatus* (Fieber) did not distinguish between *A. cucumeris* and WFT as prey. Hence, a combination of *O. laevigutus* and *A. cucumeris* is not likely to result in efficient biological control of WFT. However, biological control should be enhanced if the IG-predator prefers preying on the herbivorous pest compared to the IG-prey. Wittmann and Leather (1997) observed that *O. laevigatus* preferred to prey on WFT rather than on *A. degenerans* (Berlese), and Gillespie and Quiring (1992) found that *O. tristicolor* (White) favoured WFT over *A. cucumeris*, indicating that combinations of these predators might improve biological control of WFT.

Additionally anti-predation behaviour of the IG-prey in the presence of the IG-predator may affect the extent of IGP. For example TSSM produce webbings, which can be used by other pests like WFT and also small predators to seek refuge from carnivory (Pallini et al., 1998). Finally the prey density may also influence the extent of IGP by reducing the competition between the IG-predator and the IG-prey for prey.

In this study, the outcome of combined releases of *A. cucumeris* and *O. insidiosus* on mixed infestations by TSSM and WFT at varying initial densities were investigated. The specific objectives were to study (1) whether TSSM and WFT can be effectively controlled by combined releases of both predators, and (2) if and how pest densities affect IGP of *O. insidiosus* on *A. cucumeris*.

4.2 Materials and methods

4.2.1 Plant material

Bean (*Phaseolus vulgaris* [Fabaceae] cv. Merona) seedlings with the two first true leaves unfolded, i.e., younger than 10 days, were used as test plants. Plants were grown in the nursery of the Institute of Plant Diseases and Plant Protection (IPP), University of Hannover, Germany, at a temperature of 20°C, 75% relative humidity (r.h.) and 16:8 h L: D photoperiod.

4.2.2 Insects and mites

WFT and TSSM were obtained from stock cultures maintained at IPP. Mites and thrips were reared at 23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod on potted bean plants and bean pods, respectively. In all experiments, younger than two-days-old WFT larvae and neonate gravid females of TSSM were used. *Amblyseius cucumeris* and *O. insidiosus* were purchased from Katz Biotech. (Baruth, Germany) and kept at 9°C for less than one week before experimental use. One day before being transferred onto the bean plants, adults of both predators were isolated. *Orius insidiosus* was kept in a plastic bottle (200ml) with bean pods as food, whereas *A. cucumeris* were separated from the packing materials and kept together with some additional flour mites as prey. Only active adult females of *O. insidiosus* and *A. cucumeris* were used in the experiments.

4.2.3 Experimental procedures

The experimental unit consisted of four bean seedlings, which were transplanted into a plastic pot (diameter 16 cm) and covered with a plexiglass cylinder (diameter 15 cm, height 40 cm). To insure ventilation and for releasing mites and insects, four holes were drilled into the cylinder walls (diameter 35 mm), three of which were sealed with thrips-proof nylon gauze (pore size ca. 60 μm, Sefar Ltd., Rüschlikon, Switzerland) and the fourth was left open for mite and insect transfer; it was later closed by piece of paper using sticky tape. At the beginning of an experiment 5, 10 or 20 gravid TSSM females were transferred with a fine hairbrush on one leaf per plant, thus totalling 20, 40 or 80 TSSM, respectively. One day later, on the same leaves, 25 or 40 WFT larvae were added, thus totalling 100 or 160 thrips larvae per experimental unit. Thereafter 5 or 10 *A. cucumeris* adults were transferred onto the same leaf, resulting in 20 or 40 predatory mite adults per experimental unit. Then 1 or 2 *O. insidiosus* were introduced into each experimental unit (for more details on the different treatments refer to table 1). Plants were subsequently incubated for eight days in a climate chamber (23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod) and thereafter cut at the ground level. The cut plants (leaves and stems) were immediately examined for presence of thrips larvae, prepupae and pupae. If found, they were transferred to a fresh bean leaf which was then returned to the original pot. Plants with TSSM, *A. cucumeris* and *O. insidiosus* were stored in a cold room (5±1°C) for subsequent checking. In all treatments, the emerging WFT adults were counted. According to Berndt et al. (2004), approximately 98% of the late second instar larvae of WFT descend from the plants to pupate in the soil. The emerging WFT adults are photosensitive and leave the soil to re-colonize the plants. Thus, the pots were enclosed with another pot of the same size, whose bottom was cut and covered with a Petri dish. The inner surface of the Petri dish was painted with insect glue, constituting a sticky trap to catch the emerging adult thrips. To prevent high humidity and increase ventilation, three holes (diameter 1.5 cm) were drilled into the walls of the upper pot and sealed with thrips-proof nylon gauze. The gap between the two pots was closed with plasticine. The sticky traps were daily monitored until no more thrips adults emerged. All experiments were conducted in a climate chamber at 23±1°C, 65%±5% r.h. and 16:8 h L: D photoperiod. Each treatment was replicated five times over time.

Table 1. Initial densities and combinations of TSSM, WFT, *A. cucumeris* and *O. insidiosus*

Treatments	TSSM	WFT	*A. cucumeris*	*O. insidiosus*
T1	20	100	0	0
T2	20	160	0	0
T3	40	100	0	0
T4	40	160	0	0
T5	40	100	0	0
T6	40	160	0	0
T7	20	100	20	1
T8	20	160	20	1
T9	40	100	20	1
T10	40	160	20	1
T11	40	100	20	1
T12	40	160	20	1
T13	20	100	20	2
T14	20	160	20	2
T15	40	100	20	2
T16	40	160	20	2
T17	40	100	20	2
T18	40	160	20	2
T19	20	100	40	1
T20	20	160	40	1
T21	40	100	40	1
T22	40	160	40	1
T23	40	100	40	1
T24	40	160	40	1
T25	20	100	40	2
T26	20	160	40	2
T27	40	100	40	2
T28	40	160	40	2
T29	40	100	40	2
T30	40	160	40	2

4.2.4 Data analyses

Percentages of TSSM suppression were calculated according to the formula of Colfer et al. (2000), and corrected mortality (CM) values in WFT were computed using Schneider-Orelli's formula (Schneider-Orelli, 1947). Data of the experiments repeated

over time were checked for homogeneity of variance using the HOVTEST = Levene option of SAS (1996) and pooled only when variance homogeneity could be assumed. The percentages of TSSM suppression or CM values of WFT in T7-T30 were analysed by ANOVA and compared to zero (the percentages of TSSM suppression and CM of WFT in T1-T6, respectively). In case the ANOVAs yielded significant F-values, means were compared using the Dunnett test. The interactions among TSSM, WFT, A. cucumeris and O. insidiosus were analysed using the GLM procedure of SPSS (SPSS 10.0, 2000). If the ANOVAs yielded significant factor effects, the means of the percentages of TSSM suppression and CM of WFT in the different treatments were compared using Tukey's multiple range tests. Differences in control efficiencies between the predator densities were compared using the t-test. Data on number of offspring per A. cucumeris and O. insidiosus females and the number of A. cucumeris adults at the end of the experiments were square root transformed prior to analysis by ANOVA. A significance level of $\alpha=0.05$ was used in all analyses.

4.3 Results

4.3.1 Effects of A. cucumeris and O. insidiosus on TSSM populations in the presence of WFT

4.3.1.1 TSSM population suppression by both predators

In all tested densities of pests and predators, the combined releases of *A. cucumeris* and *O. insidiosus* always significantly decreased the TSSM populations compared to the no-predator controls (table 2). With 65.8% the highest TSSM suppression was recorded in the 20 TSSM and 100 WFT treatment following releases of 20 *A. cucumeris* and 2 *O. insidiosus*. The lowest levels of TSSM suppression were obtained at intermediate and high densities of TSSM together with the higher WFT density and releases of 20 *A. cucumeris* and 1 *O. insidiosus* (table 2).

Table 2: Percentages of TSSM suppression (%) caused by releases of two densities of *A. cucumeris* (i.e., 20 and 40) and *O. insidiosus* (i.e., 1 and 2) in the presence of WFT at two initial densities (i.e., 100 and 160) in comparison to the no-predator controls.

WFT	Ac[1]	Oi[2]	Percentages of TSSM suppression (mean ± SE)		
			20 TSSM	40 TSSM	80 TSSM
100	20	1	46.9 ± 6.0 *	46.9 ± 8.2 *	38.2 ± 5.8 *
		2	65.8 ± 2.3 *	54.0 ± 9.4 *	49.6 ± 5.7 *
	40	1	63.9 ± 6.2 *	50.5 ± 6.0 *	46.1 ± 5.2 *
		2	62.3 ± 3.5 *	46.9 ± 5.8 *	41.2 ± 4.4 *
160	20	1	41.0 ± 6.2 *	31.5 ± 1.0 *	33.2 ± 2.0 *
		2	52.5 ± 6.3 *	37.9 ± 3.8 *	44.0 ± 2.7 *
	40	1	43.4 ± 6.2 *	39.3 ± 4.1 *	43.2 ± 8.8 *
		2	55.6 ± 3.4 *	51.1 ± 8.3 *	43.6 ± 5.1 *

[1] Ac = *A. cucumeris*, [2] Oi = *O. insidiosus*; * indicate significant differences in TSSM suppression in predator release treatments compared to the no-predator controls (Dunnett test).

4.3.1.2 Effects of the predator and pest densities on the percentages of TSSM suppression

ANOVA results showed that both TSSM and WFT densities as well as *O. insidiosus* but not *A. cucumeris* releases significantly affected the extent of suppression in TSSM (table 3). In addition, all two-, three-, and four-way interactions turned out to be not significant. As TSSM suppression was not significantly affected by *A. cucumeris* releases, data on spider mite suppression was compared irrespective of the tested *A. cucumeris* densities. In general the level of TSSM suppression decreased with increasing densities of TSSM. However, significant differences were only found between the combination of 20 and 80 TSSM with 100 WFT and 2 *O. insidiosus* (Fig. 1). WFT densities significantly affected the extent of spider mite control only at the lowest and intermediate initial densities of TSSM in combination with releases of 2 and 1 *O. insidiosus*, respectively. The higher release *O. insidiosus* rate yielded significantly higher TSSM suppression only at the lowest spider mite, combined with the higher thrips densities (Fig. 1).

Table 3. Summary of ANOVA results of the percentages of TSSM suppression at three different initial spider mite densities (i.e., 20, 40 and 80) caused by releases of 20 and 40 *A. cucumeris* and 1 and 2 *O. insidiosus* in the presence of WFT at two initial thrips densities (i.e., 100 and 160).

Source	df	F	P
TSSM	2	8.785	0.000
WFT	1	11.197	0.001
Ac^1	1	2.539	0.115
Oi^2	1	7.902	0.006
TSSM × WFT	2	1.236	0.295
TSSM × Ac	2	0.099	0.906
WFT × Ac	1	0.867	0.354
TSSM × WFT × Ac	2	0.981	0.379
TSSM × Oi	2	0.581	0.562
WFT × Oi	1	0.814	0.369
TSSM × WFT × Oi	2	0.101	0.904
A. cucumeris × Oi	1	3.272	0.074
TSSM × Ac × Oi	2	0.430	0.652
WFT × Ac × Oi	1	2.282	0.134
TSSM × WFT × Ac × Oi	2	0.223	0.800

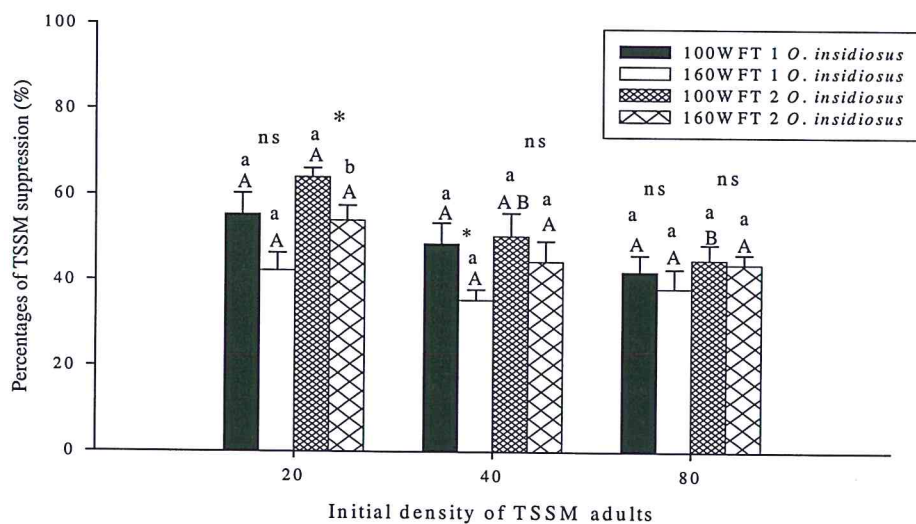[1] *Ac = A. cucumeris*; [2] *Oi = O. insidiosus*.

Figure 1. Percentages of TSSM suppression caused by *O. insidiosus* in the presence of WFT (simultaneous releases of *A. cucumeris* had no significant effect on TSSM suppression; hence data was analysed irrespective of the *A. cucumeris* releases, see text for details). Columns (mean ± SE) marked by different upper case letters are significantly different among the different TSSM densities at a given density of *O. insidiosus* and WFT (Tukey test). Columns (mean ± SE) marked by different lower case letters are significantly different between the two *O. insidiosus* densities (t-test) at a given density of TSSM and WFT. ns and * indicate non-significant and significant differences in TSSM suppression between two different WFT densities (i.e., 100 and 160) at a given density of TSSM and *O. insidiosus* (t-test).

4.3.1.3 Proportion of TSSM active stages (larvae, nymphs) and eggs to the total offspring of TSSM under the influence of both predators

The proportions of active stages (i.e., larvae and nymphs) and eggs of TSSM to the total offspring of TSSM were not affected by releases of the two predators (table 4). The proportion of active stages in the no-predator and predator release treatments ranged between 26.8 - 30.0% and 21.3 - 37.4%, respectively. For the proportion of eggs the corresponding values were 70.0 - 73.2% and 62.6 - 78.7% (table 4).

Table 4: Proportion (mean ± SE) of active stages (larvae and nymphs) and eggs of TSSM to the total offspring of TSSM in the presence of WFT, as influenced by releases of _A. cucumeris_ and _O. insidiosus_ at two different release rates [1].

WFT	Ac^2	Oi^3	Proportion of active stage		
			20 TSSM	40 TSSM	80 TSSM
	0	0	30.0 ± 2.5	28.0 ± 1.4	29.2 ± 2.0
100	20	1	25.2 ± 3.0	30.2 ± 2.9	32.0 ± 1.9
		2	37.2 ± 2.3	37.4 ± 7.4	36.8 ± 2.9
	40	1	29.4 ± 7.7	26.2 ± 2.6	27.8 ± 2.3
		2	30.8 ± 7.0	28.0 ± 3.5	29.0 ± 4.1
	0	0	29.2 ± 1.6	28.4 ± 1.3	26.8 ± 2.3
160	20	1	30.5 ± 0.7	27.8 ± 3.8	27.4 ± 2.1
		2	35.0 ± 5.9	31.8 ± 4.8	33.6 ± 1.5
	40	1	24.4 ± 2.8	21.3 ± 2.6	22.2 ± 2.0
		2	30.2 ± 4.2	36.0 ± 5.9	29.3 ± 6.7
WFT	Ac^2	Oi^3	Proportion of eggs		
			20 TSSM	40 TSSM	80 TSSM
	0	0	70.0 ± 2.5	72.0 ± 1.4	70.8 ± 2.0
100	20	1	74.8 ± 3.0	69.8 ± 2.9	68.0 ± 1.9
		2	62.8 ± 2.3	62.6 ± 7.4	63.3 ± 2.9
	40	1	70.6 ± 7.7	73.8 ± 2.6	72.2 ± 2.3
		2	69.2 ± 7.0	72.0 ± 3.5	71.0 ± 4.1
	0	0	70.8 ± 1.6	71.6 ± 1.3	73.2 ± 2.3
160	20	1	69.5 ± 0.7	72.3 ± 3.8	72.6 ± 2.1
		2	65.0 ± 5.9	68.2 ± 4.8	66.4 ± 1.5
	40	1	75.6 ± 2.8	78.8 ± 2.6	77.8 ± 2.0
		2	69.8 ± 4.2	64.0 ± 5.9	70.7 ± 6.7

[1] There were no significant differences of the ratios of active stages and eggs of TSSM between the treatments with two predators and without predator controls (Dunnett test).
[2] Ac = _A. cucumeris_; [3] Oi = _O. insidiosus_.

4.3.1.4 Effects of the predator and prey densities on the proportions of TSSM active stages (larvae, nymphs) and eggs

ANOVA results showed that only the release rates of *O. insidiosus* and *A. cucumeris*, but not WFT and TSSM densities significantly affected the proportions of eggs and active stages of TSSM to the total TSSM offspring (table 5). The proportions of spider mite eggs significantly increased with increasing *A. cucumeris* density at the lower *O. insidiosus* release rate, and significantly decreased with increasing *O. insidiosus* density (Fig. 2). For the proportion of active stages of TSSM the opposite results were recorded, i.e., significantly decreased with increasing *A. cucumeris* density at the lower *O. insidiosus* release rate, and significantly increased with increasing *O. insidiosus* density (Fig. 2).

Table 5. Summary of ANOVA results on the effects of releases of *O. insidiosus* (i.e., 1 and 2) and *A. cucumeris* (20 and 40) and two WFT densities (i.e., 100 and 160) on the proportions of eggs and active stages of TSSM to the total TSSM offspring at three TSSM densities (i.e., 20, 40 and 80).

Source	df	F	P
TSSM	2	0.044	0.957
WFT	1	0.945	0.334
Ac^1	1	5.659	0.019
Oi^2	1	11.243	0.001
TSSM × WFT	2	0.200	0.819
TSSM × Ac	2	0.120	0.887
WFT × Ac	1	0.054	0.818
TSSM × WFT × Ac	2	0.679	0.510
TSSM × Oi	2	0.120	0.887
WFT × Oi	1	0.445	0.506
TSSM × WFT × Oi	2	0.324	0.724
A. cucumeris × Oi	1	0.098	0.755
TSSM × Ac × Oi	2	0.367	0.694
WFT × Ac × Oi	1	2.368	0.127
TSSM × WFT × Ac × Oi	2	0.228	0.797

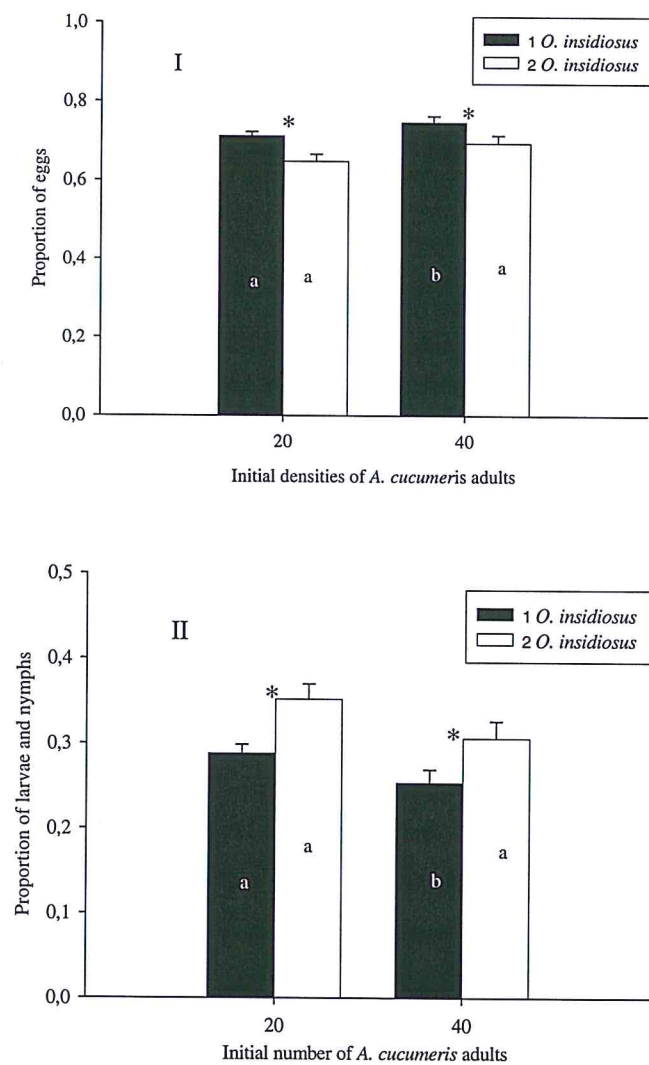[1] *Ac = A. cucumeris*; [2] *Oi = O. insidiosus*.

Figure 2: Proportion of eggs (I), and larvae and nymphs (II) of TSSM as affected by releases of *O. insidiosus* at two densities (i.e., 1 and 2) and *A. cucumeris* at two densities (i.e., 20 and 40), irrespective of the TSSM and WFT densities. Columns (mean ± SE) marked by different letters indicate significant differences between the two *A. cucumeris* densities at a given *O. insidiosus* density. * indicate significant differences between two *O. insidiosus* densities at a given *A. cucumeris* density (t-test).

4.3.1.5 Total number of TSSM adults and the proportion of live TSSM adults on plants at the end of the experiment.

There was no significant difference in the total number of TSSM adults (alive and dead) in the presence or absence of the two predators (table 6). However, at the end of the experiments, except for one treatment combination, the proportions of live TSSM adults on the initially released number of TSSM were always significantly lower in the predator release treatments compared to the no-predators controls (Table 7).

Table 6: Total numbers of TSSM adults (alive and dead) at the end of the experiments in predator release treatments, i.e. *O. insidiosus* (i.e., 1 and 2) and *A. cucumeris* (20 and 40), and in the no-predator controls in the presence of two WFT densities (i.e., 100 and 160).

WFT	Ac^1	Oi^2	Total number of TSSM adults (alive and dead) (mean ± SE) [3]		
			20 TSSM	40 TSSM	80 TSSM
100	0	0	18.8 ± 0.2	37.2 ± 1.2	76.4 ± 0.9
	20	1	18.6 ± 1.5	34.8 ± 0.9	70.4 ± 1.7
		2	16.2 ± 1.2	31.8 ± 0.2	69.5 ± 1.9
	40	1	16.4 ± 0.7	35.2 ± 1.7	71.6 ± 2.4
		2	17.0 ± 0.7	34.6 ± 1.8	70.6 ± 2.1
160	0	0	18.2 ± 0.6	38.0 ± 0.6	75.4 ± 1.4
	20	1	18.0 ± 1.0	36.3 ± 0.9	70.0 ± 2.2
		2	17.8 ± 1.1	35.2 ± 0.5	72.2 ± 0.7
	40	1	18.4 ± 0.9	34.3 ± 1.6	72.0 ± 1.0
		2	17.0 ± 1.2	35.2 ± 1.4	71.7 ± 0.9

[1] Ac = *A. cucumeris*, [2] Oi = *O. insidiosus*; [3] there were no significant differences in the total number of TSSM adults in the presence or absence of the two predators (Dunnett test).

Table 7: Proportion of live TSSM adults (in %) at the end of the experiments in predator release treatments, i.e., *O. insidiosus* (i.e., 1 and 2) and *A. cucumeris* (i.e., 20 and 40), and in the no-predator controls in the presence of two WFT densities (i.e., 100 and 160) on the initial numbers of introduced TSSM adults.

WFT	Ac^1	Oi^2	Proportion of live TSSM adults (mean % ± SE)		
			20 TSSM	40 TSSM	80 TSSM
100	0	0	88.0 ± 3.0	84.0 ± 2.8	83.1 ± 2.7
	20	1	50.0 ± 10.6 *	46.0 ± 10.9 *	59.4 ± 7.6 *
		2	21.0 ± 2.4 *	39.6 ± 12.4 *	39.5 ± 9.5 *
	40	1	28.0 ± 9.7 *	48.0 ± 3.8 *	52.0 ± 6.2 *
		2	30.0 ± 8.9 *	49.5 ± 6.0 *	47.1 ± 5.6 *
160	0	0	77.0 ± 4.4	77.6 ± 4.7	84.6 ± 3.4
	20	1	46.3 ± 10.5 *	59.4 ± 6.3 ns	58.0 ± 3.8 *
		2	42.0 ± 8.0 *	50.6 ± 8.2 *	46.7 ± 5.2 *
	40	1	48.0 ± 4.1 *	50.1 ± 4.4 *	52.8 ± 5.9 *
		2	29.0 ± 5.6 *	40.6 ± 8.4 *	48.8 ± 3.6 *

[1] Ac = *A. cucumeris*, [2] Oi = *O. insidiosus*; * and ns indicate significant differences between predator release treatments and the no-predator controls at a given density of TSSM and WFT (Dunnett test)

4.3.1.6 Effect of the predator and prey densities on the proportion of live TSSM adults on plants at the end of the experiment

Only the initial densities of TSSM adults and releases of _O. insidiosus_ significantly affected the proportion of live TSSM adults at the end of the experiments (table 8). Moreover, all interaction terms were not significant. Therefore, the effects of the different initial TSSM densities and releases of _O. insidiosus_ on the proportion of live TSSM adults at the end of the experiments were analysed irrespective of the WFT densities and _A. cucumeris_ releases. At the higher _O. insidiosus_ release rate the proportions of live TSSM adults at the end of the experiments were significantly higher at the intermediate and higher compared to the lower initial densities of TSSM (Table 9). Moreover, in the lower and higher but not in the intermediate initial densities of TSSM, the proportion of live TSSM adults at the end of the experiments were significantly lower at the higher compared to the lower _O. insidiosus_ release rates.

Table 8. Summary of ANOVA results on the proportion of live TSSM adults at the end of the experiments as affected by three initial TSSM release densities (i.e., 20, 40 and 80), the presence of WFT in two densities (i.e., 100 and 160), and releases of _O. insidiosus_ (i.e., 1 and 2) and _A. cucumeris_ (i.e., 20 and 40).

Source	df	F	P
TSSM	2	7.397	0.001
WFT	1	2.747	0.101
Ac^1	1	0.850	0.359
Oi^2	1	9.177	0.003
TSSM × WFT	2	0.437	0.647
TSSM × _Ac_	2	0.273	0.761
WFT× _Ac_	1	0.769	0.383
TSSM × WFT × _Ac_	2	0.675	0.512
TSSM × _Oi_	2	0.406	0.667
WFT × _Oi_	1	0.000	0.996
TSSM × WFT × _Oi_	2	0.300	0.741
A. cucumeris × _Oi_	1	1.485	0.226
TSSM × _Ac_ × _Oi_	2	0.122	0.885
WFT × _Ac_ × _Oi_	1	2.743	0.101
TSSM × WFT × _Ac_ × _Oi_	2	1.025	0.363

[1] _Ac = A. cucumeri_, [2] _Oi = O. insidiosus_.

Table 9: The effects of three initial TSSM densities (i.e., 20, 40 and 80) and releases of _O. insidiosus_ (i.e., 1 and 2) on the proportion of live TSSM adults (in %) at the end of the experiments irrespective of the WFT densities and releases of _A. cucumeris_ (see text for details).

| Treatments | Proportion of live TSSM adults (%) | | |
| | Initial TSSM densities | | |
	20	40	80
1 _O. insidiosus_	42.9 ± 4.6 a A	50.4 ± 3.5 a A	55.5 ± 2.9 a A
2 _O. insidiosus_	30.5 ± 3.5 b A	45.1 ± 4.3 a B	45.5 ± 3.1 b B

Means within a column followed by different lower case letters indicate significant differences between the two _O. insidiosus_ densities at a given TSSM density (t test); means within a row followed by different upper case letters indicate significant differences among the different initial TSSM densities at a given _O. insidiosus_ density (Tukey test).

4.3.2 Effects of A. cucumeris and O. insidiosus on the corrected mortality of WFT in the presence of TSSM
4.3.2.1 Effects of both predators on the corrected mortality of WFT in the presence of TSSM

In all predator release treatments CM levels in WFT significantly differed from the no-predator controls (table 10). In general releases of the two predators resulted in high CM values in WFT, which in only three treatment combinations were lower than 70%. The highest and lowest CM values were recorded at the lower and higher initial densities of WFT, respectively (table 10).

Table 10: Corrected mortalities (CM) of WFT at two densities (i.e., 100 and 160) caused by releases of two densities of _A. cucumeris_ (i.e., 20 and 40) and _O. insidiosus_ (i.e., 1 and 2) in the presence of TSSM at three initial densities (i.e., 20, 40 and 80) in comparison to the no-predator controls.

| WFT | Ac[1] | Oi[2] | CM of WFT (mean ± SE) | | |
			20 TSSM	40 TSSM	80 TSSM
100	20	1	81.2 ± 5.0 *	77.2 ± 9.9 *	74.6 ± 5.9 *
		2	92.7 ± 2.4 *	88.1 ± 5.1 *	92.5 ± 4.5 *
	40	1	82.7 ± 6.9 *	82.7 ± 6.5 *	79.2 ± 3.5 *
		2	91.6 ± 3.2 *	72.7 ± 8.1 *	80.1 ± 1.6 *
160	20	1	78.9 ± 9.9 *	75.0 ± 8.9 *	65.3 ± 4.9 *
		2	80.0 ± 9.5 *	82.4 ± 3.9 *	83.6 ± 2.5 *
	40	1	63.7 ± 4.4 *	74.9 ± 4.9 *	68.0 ± 6.7 *
		2	88.8 ± 2.5 *	81.6 ± 6.5 *	78.0 ± 3.2 *

[1] Ac = _A. cucumeris_, [2] Oi = _O. insidiosus_; * indicate significant differences in CM of WFT in predator release treatments compared to the no-predator controls (Dunnett test).

4.3.2.2 Effects of the densities of A. cucumeris and O. insidiosus on the corrected mortality of WFT in the presence of TSSM

ANOVA results showed that among the individual factors only WFT densities and *O. insidiosus* releases significantly affected the corrected mortality in WFT (table 11). Moreover, all interaction terms turned out to be not significant. Therefore the effects of the different initial WFT densities and releases of *O. insidiosus* on corrected mortality in WFT were analysed irrespective of the initial TSSM densities and *A. cucumeris* releases. At the higher but not at the lower initial WFT density the higher compared to the lower *O. insidiosus* release rate resulted in significantly higher CM of WFT (Fig. 4). Increasing the WFT density caused significantly lower CM in thrips after releases of 1 but not 2 *O. insidiosus*.

Table 11. Summary of ANOVA results of corrected mortalities in WFT at two initial densities (i.e., 100 and 160) caused by releases of 20 and 40 *A. cucumeris* and 1 or 2 *O. insidiosus* in the presence of TSSM at three initial densities (i.e., 20, 40 and 80).

Source	df	F	P
TSSM	2	1.309	0.275
WFT	1	6.529	0.012
Ac^1	1	0.868	0.354
Oi^2	1	13.673	0.000
TSSM × WFT	2	0.897	0.411
TSSM × Ac	2	0.027	0.974
WFT× Ac	1	0.061	0.806
TSSM × WFT × Ac	2	0.235	0.791
TSSM × Oi	2	1.190	0.309
WFT × Oi	1	0.953	0.332
TSSM × WFT × Oi	2	0.051	0.951
A. cucumeris × Oi	1	0.755	0.387
TSSM × Ac × Oi	2	2.370	0.099
WFT × Ac × Oi	1	3.592	0.061
TSSM × WFT × Ac × Oi	2	0.284	0.754

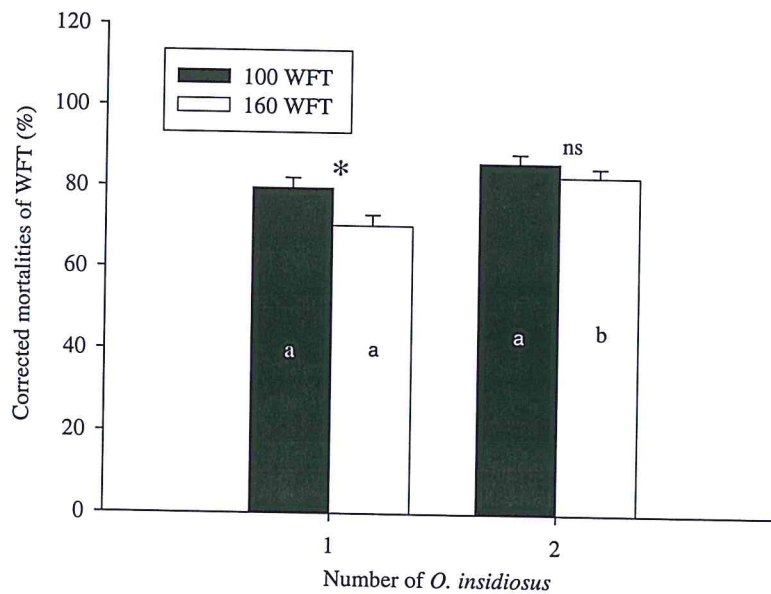[1] Ac = *A. cucumeris*, [2] Oi = *O. insidiosus*.

Figure 4. Corrected mortalities (CM) in WFT caused by *O. insidiosus* in the presence of TSSM (initial densities of TSSM and simultaneous releases of *A. cucumeris* had no significant effects on CM in WFT; hence data was analysed irrespective of the *A. cucumeris* releases and initial TSSM densities, see text for details). CM values (mean ± SE) at a given WFT density marked with different letters indicate significant differences between two *O. insidiosus* densities (t-test). ns and * indicate non-significant and significant differences in CM between the two WFT densities at a given *O. insidiosus* density (t-test).

4.3.3 Fluctuation of A. cucumeris population

4.3.3.1 Effects of both predators and pests on the number of offspring per A. cucumeris female

ANOVA results showed that all single factors, i.e. initial densities of TSSM and WFT and the different release rates of *A. cucumeris* and *O. insidiosus*, had a significant influence on the total number of offspring produced per *A. cucumeris* female (table 12). However, all interaction terms were not significant. Significantly higher reproduction in *A. cucumeris* was recorded in four out of eight different WFT and predator combinations at the higher compared to the lower initial TSSM density (Fig. 5a). The higher WFT density resulted in significantly higher numbers of offspring in *A. cucumeris* only in the two lower predator release rate combinations at the intermediate and higher initial densities of TSSM. In four out of 12 different TSSM, WFT and predator combinations a significantly reduced reproduction per *A. cucumeris* females was recorded at the higher compared to the lower predatory mite release rates

(Fig. 5b). The higher compared to the lower release rates of _O. insidiosus_ only caused a significant reduction in offspring number of _A. cucumeris_ at the highest initial densities of TSSM and WFT and at the lower _A. cucumeris_ release rate. In general individual reproduction in _A. cucumeris_ females increased with increasing TSSM and WFT densities, but decreased with increasing _A. cucumeris_ and _O. insidiosus_ release rates.

Table 12. Summary of ANOVA results on the effects of releases of _O. insidiosus_ adults (i.e., 1 or 2) in the presence of TSSM and WFT at three and two initial densities (i.e., 20, 40 and 80, and 100 and 160, respectively) on the number of offspring per _A. cucumeris_ female at two release rates (i.e., 20, 40).

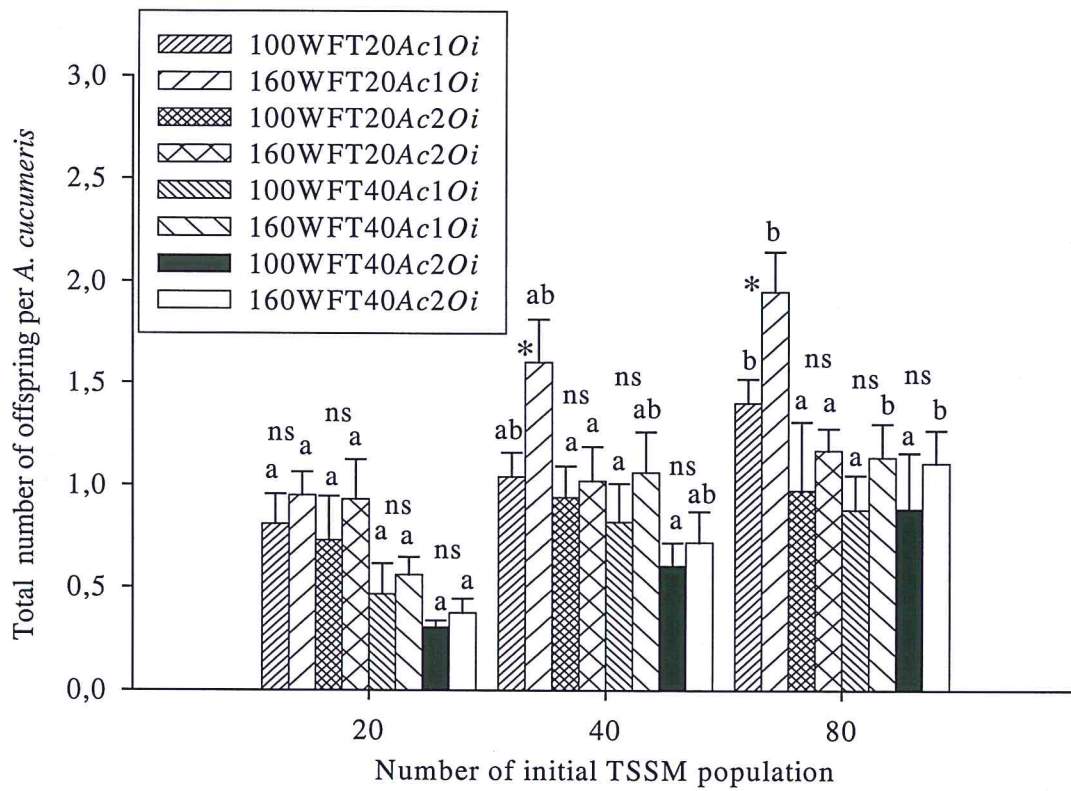| Source	df	F	P
TSSM	2	18.316	0.000
WFT	1	10.113	0.002
Ac^1	1	27.848	0.000
Oi^2	1	10.833	0.001
TSSM × WFT	2	0.361	0.698
TSSM × Ac	2	0.548	0.580
WFT× Ac	1	0.128	0.721
TSSM × WFT × Ac	2	0.011	0.989
TSSM × Oi	2	0.363	0.697
WFT × Oi	1	0.413	0.522
TSSM × WFT × Oi	2	0.368	0.693
A. cucumeris × Oi	1	0.615	0.435
TSSM × Ac × Oi	2	1.405	0.251
WFT × Ac × Oi	1	0.118	0.732
TSSM × WFT × Ac × Oi	2	0.175	0.840

[1] Ac = _A. cucumeris_, [2] Oi = _O. insidiosus_.

Figure 5a. Total number of offspring per *A. cucumeris* female (mean ± SE) following releases of *A. cucumeris* (i.e., 20 and 40) and *O. insidiosus* (i.e., 1 and 2) at three (i.e., 20, 40 and 80) and two (i.e., 100 and 160) in initial densities of TSSM and WFT. Means marked by different letters indicate significant differences between the three different initial TSSM densities at a given density of *O. insidiosus*, *A. cucumeris* and WFT (Tukey test). * and ns indicate significant and non-significant differences between the two initial WFT densities at a given density of *O. insidiosus*, *A. cucumeris* and TSSM (t-test). *Ac* = *A. cucumeris*, *Oi* = *O. insidiosus*.
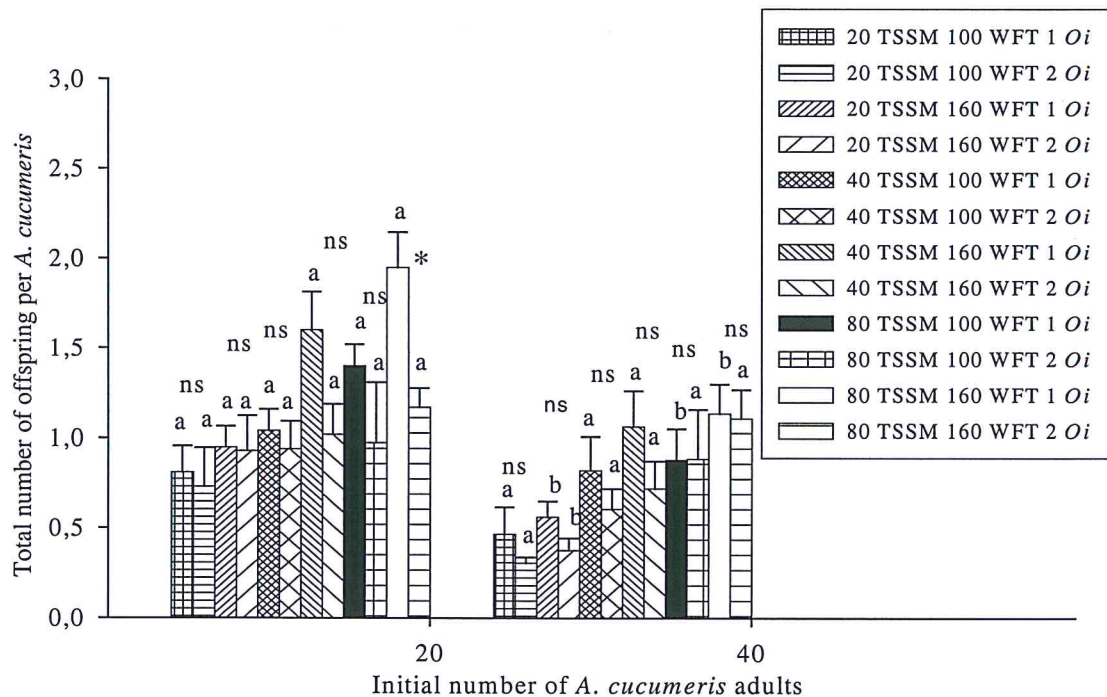
Figure 5b. Total number of offspring per *A. cucumeris* female (mean ± SE) following releases of *A. cucumeris* (i.e., 20 and 40) and *O. insidiosus* (i.e., 1 and 2) at three (i.e., 20, 40 and 80) and two (i.e., 100 and 160) in initial densities of TSSM and WFT. Means marked by different letters indicate significant differences between the two predatory mite release rates at a given density of *O. insidiosus*, TSSM and WFT (t-test). * and ns indicate significant or non-significant differences between the two *O. insidiosus* densities at a given density of *A. cucumeris*, TSSM and WFT (t-test). *Oi* = *O. insidiosus*

4.3.3.2 Total number of adults and proportion of live A. cucumeris adults on the plant at the end of the experiment

ANOVA results indicated that the total number of *A. cucumeris* adults (alive and dead) at the end of the experiments were significantly affected by the initial TSSM densities as well as releases of *A. cucumeris*; in contrast, *O. insidiosus* releases and the initial TSSM densities significantly influenced the proportion of live *A. cucumeris* adults at the end of the experiments (table 13). In both analyses all interaction terms were not significant (table 13). Thus for the total number of *A. cucumeris* adults (alive and dead) at the end of the experiments, the effects of the initial TSSM densities and release rates of *A. cucumeris* were compared irrespective of the WFT densities and releases of *O. insidiosus*. In the analyses of the proportion of live *A. cucumeris* adults at the end of the experiments, the effects of the initial TSSM densities and *O. insidiosus* releases were compared irrespective of the WFT densities and the *A. cucumeris* releases.

At the end of the experiments at both *A. cucumeris* release rates significantly higher total numbers of predatory mite adults were recorded in the higher compared to the lower initial TSSM densities (Fig. 6a). Moreover, at all initial densities of TSSM significantly higher total numbers of *A. cucumeris* adults were observed at the end of the experiments in the higher compared to the lower predatory mites release rate treatments. Similarly for the proportion of live *A. cucumeris* adults at the end of the experiments, in both *O. insidiosus* release rates significantly higher proportions of live *A. cucumeris* adults were found in the higher compared to the lower initial TSSM densities (Fig. 6b). However, at all initial TSSM densities, and significant at the intermediate and highest levels, reduced proportions of live *A. cucumeris* adults at the end of the experiments were recorded in the higher compared to the lower *O. insidiosus* treatments.

Table 13. Summary of ANOVA results on the total numbers of *A. cucumeris* adults (alive and dead) and the proportion of live *A. cucumeris* adults at the end of the experiments as affected by three initial *TSSM* (i.e., 20, 40 and 80) and two initial WFT densities (i.e., 100 and 160), and releases of *O. insidiosus* (i.e., 1 and 2) and *A. cucumeris* (i.e., 20 and 40).

| Source	df	Total number of *Ac* adults		Proportion of live *Ac*	
		F	P	F	P
TSSM	2	9.118	0.000	6.926	0.002
WFT	1	2.482	0.119	1.252	0.266
Ac[1]	1	129.197	0.000	0.011	0.916
Oi[2]	1	0.000	0.987	13.024	0.001
TSSM × WFT	2	0.313	0.732	0.449	0.639
TSSM × *Ac*	2	0.686	0.506	1.629	0.202
WFT × *Ac*	1	1.033	0.312	0.021	0.884
TSSM × WFT × *Ac*	2	2.743	0.070	0.033	0.968
TSSM × *Oi*	2	0.852	0.430	0.149	0.861
WFT × *Oi*	1	0.897	0.346	1.405	0.239
TSSM × WFT × *Oi*	2	1.871	0.160	0.828	0.440
Ac × *Oi*	1	0.045	0.832	0.493	0.485
TSSM × *Ac* × *Oi*	2	2.429	0.094	0.018	0.983
WFT × *Ac* × *Oi*	1	0.426	0.515	0.859	0.356
TSSM × WFT × *Ac* × *Oi*	2	0.237	0.790	0.200	0.819

[1] *Ac = A. cucumeris*, [2] *Oi = O. insidiosus*.
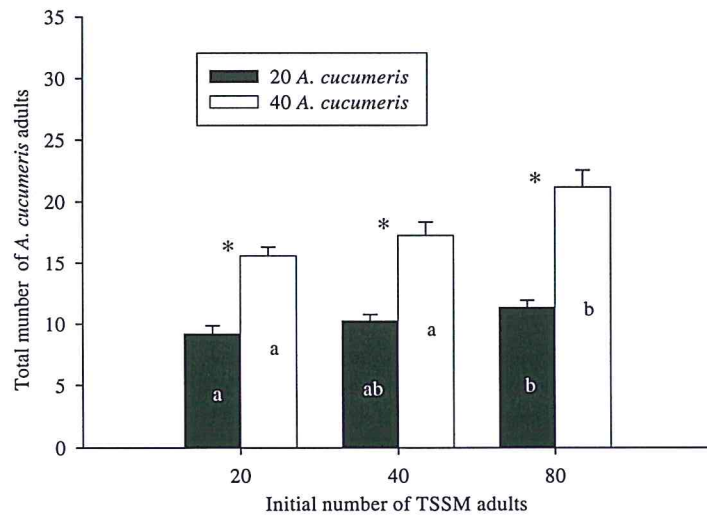
Figure 6a: Total number of *A. cucumeris* adults (alive and dead) (means ± SE) at the end of the experiments as affected by the two release rates of the predatory mites (i.e., 20 and 40) and the three initial TSSM densities (i.e., 20, 40 and 80), irrespective of the densities of *O. insidiosus* and WFT (see text for details). Columns marked by different letters indicate significant differences between the three initial TSSM densities at a given *A. cucumeris* density (Tukey test). * indicate significant differences between the two *A. cucumeris* release rates at a given TSSM density (t-test).
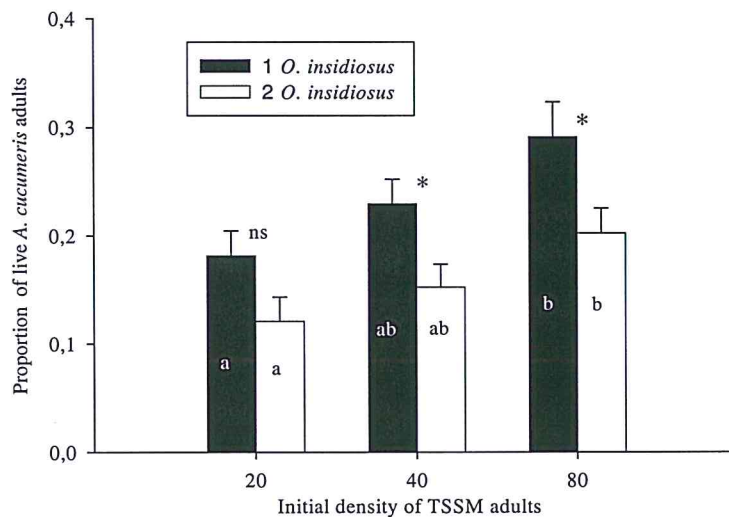
Figure 6b: Proportion of live *A. cucumeris* adults (means ± SE) at the end of the experiments as affected by the two release rates of *O. insidiosus* (i.e., 1 and 2) and the three initial TSSM densities (i.e., 20, 40 and 80), irrespective of the densities of *A. cucumeris* and WFT (see text for details). Columns marked by different letters indicate significant differences between the three initial TSSM densities at a given *O. insidiosus* density (Tukey test). * and ns indicate significant and non-significant differences between the two *O. insidiosus* densities at a given TSSM density (t-test).

4.3.4 The daily number of offspring per O. insidiosus female

Only the initial release rates of *O. insidiosus* significantly influenced the daily number of offspring per *O. insidiosus* female (table 14). Densities of TSSM and WFT as well as releases of *A. cucumeirs* had no effect on the reproduction in *O. insidiosus*. In addition, all interaction terms were not significant (table 14). With 2.7 (± 0.2) the daily reproduction of *O. insidiosus* females in the lower release rate treatment was significantly higher than the 1.6 (± 0.1) recorded in the higher *O. insidiosus* release rate treatment ($P < 0.05$, t-test).

Table 14. Summary of ANOVA results on the effects of releases of *A. cucumeris* adults (i.e., 20 or 40) in the presence of TSSM and WFT at three and two initial densities (i.e., 20, 40 and 80, and 100 and 160, respectively) on the number of offspring per *O. insidiosus* female per day at two release rates (i.e., 1 and 2).

Source	df	F	P
TSSM	2	0.361	0.698
WFT	1	2.910	0.093
Ac^1	1	0.002	0.964
Oi^2	1	13.314	0.001
TSSM × WFT	2	0.525	0.594
TSSM × Ac	2	0.059	0.943
WFT × Ac	1	1.101	0.298
TSSM × WFT × Ac	2	0.032	0.969
TSSM × Oi	2	0.515	0.600
WFT × Oi	1	0.006	0.941
TSSM × WFT × Oi	2	0.531	0.591
Ac × Oi	1	0.067	0.797
TSSM × Ac × Oi	2	1.336	0.271
WFT × Ac × Oi	1	3.205	0.079
TSSM × WFT × Ac × Oi	2	0.177	0.838

[1] *Ac = A. cucumeris*, [2] *Oi = O. insidiosus*.

4.4 Discussion.

Our results clearly show that combined releases of *A. cucumeris* and *O. insidiosus* lead to a significant suppression of mixed infestations by WFT and TSSM populations at all pest densities and predator release combinations tested. In a previous study individual releases of *A. cucumeris* and *O. insidiosus* at the same releses rates were tested for

control of mixed infestations of WFT and TSSM at a single pest density combination, i.e., 80 TSSM and 160 WFT (more detail see chapter 5). TSSM control by _A. cucumeris_ alone vs. combined releases of _A. cucumeris_ and _O. insidiosus_ lead to an approximate doubling of spider mite suppression by all _A. cucumeris_ densities tested versus the varying combinations of the two predators. Similarly WFT control by combined releases of _A. cucumeris_ and _O. insidiosus_ largely increased compared to individual releases (compared to chapter 5). Enhanced WFT control was particularly striking when comparing individual releases of _A. cucumeris_ with combined releases of the predatory mite and _O. insidiosus_. Here corrected mortalities in WFT increased from 29.5 and 47.5% at individual releases of 20 and 40 _A. cucumeris_, respectively, to a maximum of 83.6% following the releases of 20 _A. cucumeris_ and 2 _O. insidiosus_. The differences between combined releases of the two predators and single releases of _O. insidiosus_ were less pronounced. Here the highest corrected mortality recorded after individual releases of predatory bugs was 63.4%. On many greenhouse crops thrips and spider mite infestations often occur simultaneously (Sterk and Meesters, 1997; Fejt and Jarosík, 2000). However, this is the first report on the combined impact of _A. cucumeris_ and _O. insidiosus_ on dual infestations of WFT and TSSM. In previous studies the combined effect of _A. cucumeris_ and several _Orius_ spp. on WFT control have been investigated. For instance, Sörensson and Nedstam (1993) compared individual and combined releases of _A. cucumeris_ and _O. insidiosus_. They found that the combination of the two predators were most effective for control of WFT on potted ornamentals. Likewise, Tellier and Steiner (1990) recorded that sequential introductions of _A. cucumeris_ and _O. tristicolor_ for WFT control on sweet pepper crops in greenhouses were both compatible and complementary.

The prey preference of the two predators between the two pests differ, as well as their preference for certain developmental stages within a given pest species. For instance, _O. insidiosus_ rarely feeds on TSSM eggs (Venzon et al., 2000). Our results indicate that _O. insidiosus_ preferably preys on TSSM adults, as shown by the decreasing proportion of live TSSM adults at the end of the experiments with increasing release rates of _O. insidiosus_. On the contrary it seems that _A. cucumeris_ prefers to prey on TSSM eggs and small larvae and nymphs rather than on TSSM adults. For instance the proportion of live TSSM adults at the end of the experiments were not significantly affected by

increasing the release rates of *A. cucumeris*. Results from this and a previous study (more detail see chapter 3) clearly show that *O. insidiosus* adults prefer preying on WFT compared to TSSM. Except for the thrips eggs, the predatory bug can feed on all developmental stages of WFT (Funderburk et al. 2000). In our experiments only 1st and 2nd instar larvae of WFT were present, and the predatory bugs successfully preyed on both developmental stages. However, *A. cucumeris*, though also preferring WFT over TSSM as a prey, can only feed on 1st instar larvae of thrips (Bakker and Sabelis, 1989). When comparing the efficacy of the two predators for WFT control, our results indicate that *O. insidiosus* is the more efficient predator of thrips than *A. cucumeris*, as shown by the significant and non-significant increase in corrected mortality of *WFT* as affected by increasing release densities of *O. insidiosus* and *A. cucumeris*, respectively. The prey preference of *O. insidiosus* for WFT negatively affected the extent of TSSM control, as with increasing WFT densities TSSM suppression significantly decreased. However, when both predators were released, the negative effects of WFT on TSSM suppression were reduced due to the predation of *A. cucumeris* on TSSM eggs and larvae and nymphs.

In previous studies IGP of *Orius* spp. on *Amblyseius* spp. could well be documented. For instance, Wittmann and Leather (1997) showed that *O. laevigatus* fed on *A. cucumeris* to a similar extent to on WFT. However, so far in most studies on IGP between two and more predator species only one prey species have been used (one example, Wittmann and Leather, 1997). Yet the addition of a second prey species might affect the outcome of IGP. Our results indicate that in dual infestations by WFT and TSSM the extent of IGP of *O. insidiosus* on *A. cucumeris* is considerably reduced. For example, with increasing TSSM densities the number of *A. cucumeris* offspring and the proportion of live adult predatory mites at the end of the experiments significantly increased in the presence of WFT and *O. insidiosus*. TSSM produce webbings and for instance thrips can seek refuge in these webbings as a reponse to the presence of predators (Janssen et al., 1998; Venzon et al., 2000). However, predators can also show a similar escape behaviour when confronted with superior intraguild predators (Moran and Hurd, 1994; Moran *et al.*, 1996). Our data indicate that in the presence of *O. insidiosus* the predatory mite *A. cucumeris* benefited from increasing TSSM densities, possibly by hiding in the TSSM webbings. As a consequence spider mite

infestations in the presence of WFT lead to a reduction of IGP of *O. insidiosus* on *A. cucumeris*. Increasing WFT densities lead to a significant increase in reproduction of *A. cucumeris*. However, increasing the release rates of *A. cucumeris* did not significantly affect the level of corrected mortality in WFT. We believe that these results indicate that WFT like TSSM infestations decreased the extent of IGP of *O. insidiosus* on *A. cucumeris*. As *O. insidiosus* preferably preys on thrips compared to *A. cucumeris*, increasing WFT densities possibly reduced the level of IGP of the predatory bugs on the predatory mites.

In conclusion our data show that in dual infestations of TSSM and WFT, IGP of *O. insidiosus* on *A. cucumeris* is considerably reduced, mainly due to the protection and/or refuge the TSSM webbings provide for the predatory mites, as well as the prey preference of *O. insidiosus* for thrips. We believe that these are the main factors for the increased control of WFT and TSSM following combined releases of *O. insidiosus* and *A. cucumeris* compared to individual releases of both predators. Thus, despite of potential IGP of *O. insidiosus* on *A. cucumeris,* both predators can be successfully combined for biological control of WFT and *TSSM*.

Biocontrol of western flower thrips *Franklinilla occidentalis* (Pergande) by combined releases of plant-inhabiting predatory mites, *Amblyseius cucumeris* Oudemans or bugs, *Orius insidiosus* Say with soil-dwelling mites, *Hypoaspis aculeifer* Canestrini in the presence of two-spotted spider mite *Tetranychus urticae* Koch

5.1 Introduction

The western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (WFT) is economically one of the most important pests of ornamentals and vegetables. Native to the western part of North America, since the late 1970s it has become a highly cosmopolitan pest and is often considered to be the number one pest of many crops, particularly in greenhouses (Beshear, 1983; Kirk and Terry, 2003).

Chemical control of WFT is difficult. Adults and larvae live sheltered in leaf axils and/or flower buds (Brødsgaard, 1989), where they are often not reached by contact insecticides. Systemic insecticides with multiple modes of actions are often highly persistent, have residual effects on marketable products such as fresh vegetables and are harmful to important natural enemies like *Orius* spp. (Hemiptera: Anthocoridae) when sucking plant juices. Moreover, WFT have become resistant to almost all the insecticides registered for its control (Brødsgaard, 1994; Zhao et al., 1995).

In recent years strategies for biological control of WFT have been extensively researched. Amongst the most frequently used biocontrol agents are phytoseiid mites of the genus *Amblyseius* (Manjunatha et al., 1998; De Courcy Williams, 2001; Jacobson et al., 2001b) and anthocorid flower bugs of the genus *Orius* (Riudavets, 1995; Sabelis and Rijn, 1997; Wittmann and Leather, 1997; Riudavets and Castane, 1998; van den Meiracker and Sabelis, 1999; De Courcy Williams, 2001). However, so far often biocontrol efficiency have not always been sufficient, especially in high value crops with low economic threshold levels like ornamentals. For instance *Orius* spp. were only effective when used at appreciable thrips densities unless pollen as alternative food source were available (Ramakers and Meiracker, 1991). Likewise *Amblyseius* spp. are able to prey only on first instar larvae of WFT (Gillespie and Ramey, 1988; Bakker and Sabelis, 1989; Van der Hoeven et al., 1990; Higgins, 1992; Jacobson et al., 2001a), and

their dispersal potential is lower than that of WFT (Jacobson et al., 2001b). Moreover, abiotic factors, such as temperature (Shipp et al., 1996; Shipp and van Houten, 1997), and humidity (van Houten et al., 1993b) limit the impact of *Amblyseius* spp. on WFT. Finally, both *Amblyseius* and *Orius* spp. are omnivores that prey in addition to WFT on many other mites and insects (Riudavets, 1985), thereby reducing their potential to control WFT if they occur at the same time.

In recent years the simultaneous use of two or more beneficials has been widespread for biological control of pests in greenhouses, especially in greenhouse ornamentals (Brødsgaard & Enkegaard, 2001). However, combined releases of parasitoids and/or predators might lead to interactions between the biocontrol agents, possibly negatively affecting the control efficacy (Ferguson and Stiling, 1996), a phenomenon often termed intraguild predation (IGP) (Polis et al., 1989). For instance, Wittmann and Leather (1997) showed that *O. laevigatus* Fieber did not distinguish in its preying behaviour between *A. cucumeris* and WFT.

In WFT the majority of late second instar larvae leave the plants to pupate in the soil (Palmer, 1989; Helyer et al., 1995; Tommasini and Maini, 1995; Berndt et al., 2004), where the thrips spend about one-third of their life time (Loomans and van Lenteren, 1995). The soil-dwelling life stages are usually not targeted in biocontrol of WFT. The soil-inhabiting predatory mites *Stratiolaelaps* (*Hypoaspis*) *miles* (Berlese) and *H. aculeifer* Canestrini (Acarina: Laelapidae) are commercially produced for control of fungus gnads (Enkegaard et al., 1997; Ydergaard et al., 1997; Folker-Hansen and Krogh, 1998; Ali et al., 1999; Jess and Kilpatrick, 2000) and bulb mite *Rhizoglyphus robini* Claparede (Astigmata: Acaridae) (Lesna et al., 1996, 2000). However, they also prey on soil-dwelling life stages of WFT (Gillespie and Quiring, 1990; Brødsgaard et al., 1996; Premachandra et al., 2003; Berndt et al., 2004), though their potential for thrips control is limited (Berndt et al., 2004).

Thus the present approach in biocontrol of WFT through releases of plant-inhabiting or soil-dwelling predators does not always assure sufficient pest control. Therefore, the objectives of this study were to investigate whether combined releases of plant-inhabiting predatory mites or bugs together with soil-dwelling predatory mites possibly resulted in more improved thrips control than individual releases and to study potential

IGP between the predators. As plants are often simultaneously infested by WFT and two-spotted spider mites *Tetranychus urticae* Koch (Acarina: Tetranychidae) (TSSM) (Trichilo and Leigh, 1986; Wilson et al., 1996; Lewis, 1997; Sterk and Meesters, 1997; Fejt and Jarosik, 2000) and since TSSM is an alternative prey for *A. cucumeris* and *O. insidiosus*, we included TSSM in our experiments and studied whether TSSM was in addition to WFT also suppressed by *A. cucumeris* or *O. insidisous*.

5.2 Materials and methods

5.2.1. Plant material

Bean (*Phaseolus vulgaris* [Fabaceae] cv. Merona) seedlings with the first two true leaves unfolded, i.e., younger than 10 days, were used as test plants. Plants were grown in the nursery of the Institute of Plant Diseases and Plant Protection (IPP), University of Hannover, Germany, at a temperature of 20°C, 75% relative humidity (r.h.) and 16:8 h L: D photoperiod.

5.2.2. Insects and mites

WFT and TSSM were obtained from stock cultures maintained at IPP. Mites and thrips were reared at 23±1°C, 65±5% r.h. and 16:8 h L: D photoperiod on potted bean plants and bean pods, respectively. In all experiments, two-day-old WFT larvae and neonate gravid females of TSSM were used. *Orius insidiosus, A. cucumeris* and *H. aculeifer* were purchased from Katz Biotech. (Baruth, Germany). Only active female predators were used in the experiments.

5.2.3. Experimental procedures

The experimental unit consisted of four bean seedlings, which were transplanted into a plastic pot (diameter 16cm) and covered with a plexiglass cylinder (diameter 15cm, height 40cm). To insure ventilation and for releasing mites and insects, four holes were drilled into the cylinder walls (diameter 35mm), three of which were sealed with thrips-proof nylon gauze (pore size ca. 60μm, Sefar Ltd., Rüschlikon, Switzerland) and the fourth was left open for mite and insect transfer and was later closed by a piece of paper, using sticky tape. At the beginning of experiment, 20 gravid TSSM females were transferred with a fine hairbrush onto one leaf per plant, thus totalling 80 TSSM. One day later, on the same leaves, 40 WFT larvae were transferred, thus adding 160 thrips

larvae to an experimental unit. After WFT was transferred, 5 or 10 *A. cucumeris* were transferred on the same leaf, thus adding 20 or 40 predatory mites to an experimental unit. Alternatively 1 or 2 *O. insidiosus* were introduced in each experimental unit. Three days later, 5, 10 or 20 *H. aculeifer* were transferred into each unit (in the second experiment only 5 and 10 *H. aculeifer* were used). More details of the treatments are provided in table 1. Plants were subsequently incubated for five days in a climate chamber (23 ± 1°C, 65 ± 5% r.h. and 16:8 h L: D photoperiod) and thereafter cut at the ground level. The cut plants (leaves and stems) were immediately examined for presence of thrips larvae, prepuape and pupae. If found, they were transferred to a fresh bean leaf and returned to another pot. Leaves with TSSM were stored in a cold room (5 ± 1°C) for later checking. According to Berndt et al. (2004), approximately 98% of the late second instar larvae of WFT descend from the plants to pupate in the soil. The emerging WFT adults are photosensitive and leave the soil to re-colonise plants. Thus, all pots were enclosed with another pot of the same size, whose bottom was cut and covered with a Petri dish. The inner surface of the Petri dish was painted with insect glue, constituting a sticky trap to catch the emerging thrips adults. To prevent high humidity and increase ventilation, three holes (diameter 1.5cm) were drilled into the walls of the upper pot and were sealed with thrips-proof nylon gauze. The gap between the two pots was closed with plasticine. The sticky traps were daily monitored until no more thrips emergence could be recorded. All experiments were conducted in a climate chamber at 23 ± 1°C, 65%±5% r.h. and 16:8 h L: D photoperiod. Each treatment was replicated five times over time.

5.2.4. Data analysis

Percentages of TSSM suppression were calculated according to the formula of Colfer et al. (2000), and corrected mortality (CM) values in WFT were computed using Schneider-Orelli's formula (Schneider-Orelli, 1947). Data of experiments repeated over time were checked for homogeneity of variance using the HOVTEST = Levene option of SAS (1996) and pooled only when variance homogeneity could be assumed. The percentages of TSSM suppression or CM values of WFT were analysed by ANOVA and compared to zero (the percentages of TSSM suppression and CM in the no-predator TSSM and WFT control treatments, respectively). In case the ANOVAs yielded significant F-values, means were compared using the Dunnett test. The CM values in

the different treatments with predators were compared using Tukey's multiple range test. A significance level of α=0.05 was set in all the performed analyses.

Table 1. Initial densities at the beginning of the experiments (160 WFT larvae and 80 TSSM TSSM adult females) and combinations of *A. cucumeris* or *O. insidiosus* with *H. aculeifer*.

Treatments	Experiment 1		Experiment 2	
	A. cucumeris	*H. aculeifer*	*O. insidiosus*	*H. aculeifer*
T1	0	0	0	0
T2	0	5	0	5
T3	0	10	0	10
T4	0	20	-	-
T5	20	0	1	0
T6	40	0	2	0
T7	20	5	1	5
T8	20	10	1	10
T9	20	20	-	-
T10	40	5	2	5
T11	40	10	2	10
T12	40	20	-	-

5.3 Results

5.3.1 Experiment 1.

5.3.1.1 Effects of A. cucumeris on TSSM

Densities of 20 and 40 *A. cucumeris* significantly suppressed 80 TSSM in the presence of 160 WFT larvae (table 2) ($F_{2, 12} = 27.26$, $P < 0.001$) though no significant differences in the percentages of TSSM suppression were recorded between the two predator densities (table 2).

Table 2. Percentages of TSSM suppression by 20 or 40 *A. cucumeris* adults in the presence of 160 thrips larvae.

Treatment	% TSSM suppression (means ± SE)
20 *A. cucumeris*	17.4 ± 3.4 a *
40 *A. cucumeris*	26.7 ± 2.9 a *

Means within a column followed by the same letter indicate non-significant differences between the two predatory mite densities (i.e., 20 and 40) (t-test). * indicate significant difference between the treatments with predator and no-predator treatment (Dunnett test).

5.3.1.2 Thrips control by A. cucumeris and H. aculeifer alone and in combination

At all tested densities of the two predatory mites or their combinations WFT populations were significantly suppressed ($F_{11,\ 48}=55.21$ $P<0.001$). The higher *A. cucumeris* density resulted in significantly higher WFT mortality, whereas in *H. aculeifer* only the lowest and the highest release rates differed significantly (Fig. 1). At a given density of *H. aculeifer* all combined releases with *A. cucumeris* significantly improved WFT control (Fig. 1). Likewise, in *A. cucumeris* all combinations, except for 40 *A. cucumeris* with 5 *H. aculeifer*, lead to a significant increase in thrips mortality compared to individual releases of *A. cucumeris* at a given predator density (Fig. 1)
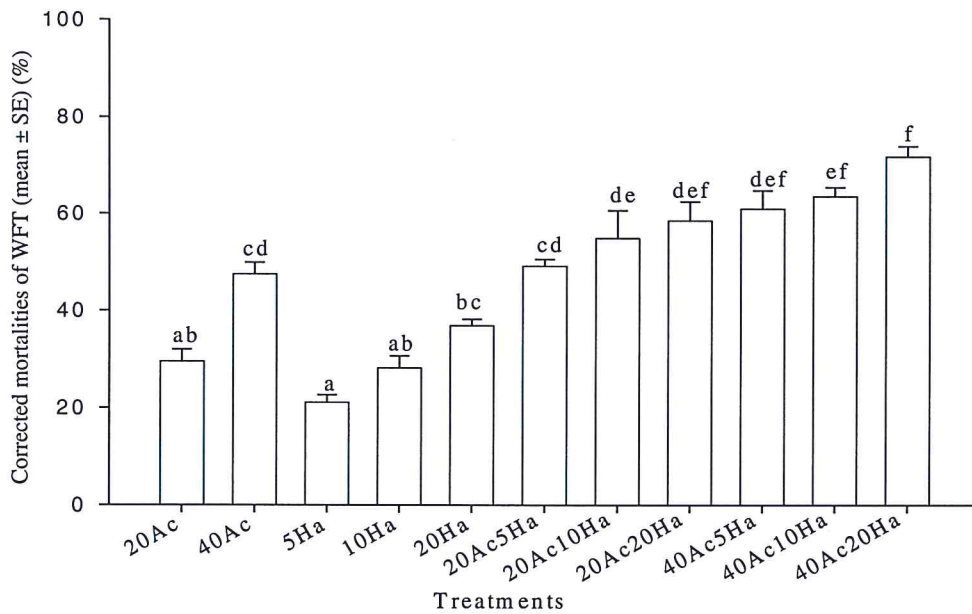
Figure 1. Corrected mortalities (CM) of western flower thrips caused by individual and combined releases of *Amblyseius cucumeris* (Ac) and *Hypoaspis aculeifer* (Ha) at varying predator densities. Columns represent means (± SE) of CM of WFT. Columns marked with different letters are significantly different at $P < 0.05$ (Tukey test).

5.3.2 Experiment 2.

5.3.2.1 Effects of O. insidiosus on the TSSM population

Only the higher *O. insidiosus* significantly suppressed mites compared to the no-predator control ($F_{2,\ 12}=5.337$, $P=0.022$) (table 3).

Table 3. Percentages of TSSM suppression by 1 or 2 *O. insidiosus* adults in the presence of 160 thrips larvae.

Treatment	% TSSM suppression (means ± SE)
1 *O. insidiosus*	1.5 ± 3.7 ns
2 *O. insidiosus*	10.5 ± 2.1 *

ns and * indicates non-significant and significant difference between the treatments with predator and no-predator treatment (Dunnett test).

5.3.2.2 Thrips control by O. insidiosus and H. aculeifer alone and in combination

At all tested densities of *O. insidiosus* and *H. aculeifer* alone or in combinations significantly higher WFT mortality were recorded compared to the no-predator controls ($F_{8, 35}$=54.51 $P<0.001$). Contrary to *H. aculeifer* in *O. insidiosus* the higher predator density resulted in significantly higher WFT control (Fig. 2). Like in experiment 1 in *H. aculeifer* all combinations with *O. insidiosus* caused significantly higher levels of thrips mortality than sole releases of *H. aculeifer* at a give predator density. However, in *O. insidiosus* only the combination of the lower bug density with 10 *H. aculeifer* caused a significantly higher WFT control compared to individual releases of *O. insidiosus* at a given predator density (Fig. 2).

Figure 2. Corrected mortalities (CM) of western flower thrips caused by individual and
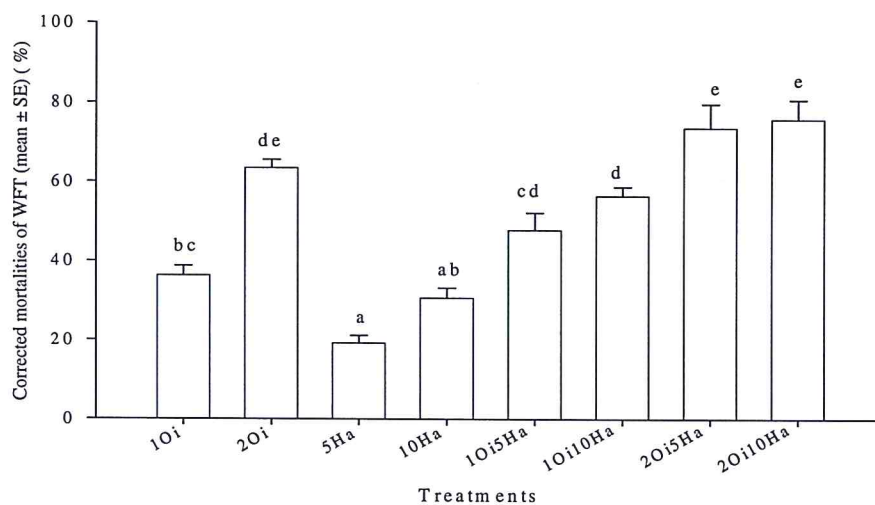
combined releases of *O. insidiosus* (Oi), *H. aculeifer* (Ha) at varying predator densities. Columns represent means (± SE) of CM of WFT. Columns marked with different letters are significantly different at $P < 0.05$ (Tukey test).

5.4 Discussions

In our experiments thrips control by *H. aculeifer* ranged between 20-37% at release rates of approximately 250 and 1,000 mites per square meter. Gillespie and Quiring (1990) recorded about 30% reduced WFT emergence following inundative releases of *H. aculeifer* at a rate of 1,600 mites per cucumber plant over a 40 days trial period, whereas Premachandra et al. (2003) observed a reduction in WFT densities of 46% after releases of approximate 1,400 *H. aculeifer* per square meter. Finally, in experiments in microcosms similar to the one used in our study Berndt et al. (2004) found that WFT population densities on French beans could be decreased by 57.6, 69.3 and 80.5% following releases of 5, 10 and 20 *H. aculeifer*, respectively, which is equivalent to approximately 700, 1,400 and 2,800 mites per square meter. However, with 10 and 50 WFT larvae their thrips densities were substantially lower than the 160 adult thrips used in this study. In general, it seems that *H. aculeifer* can cause only low to intermediate levels of thrips control, which is probably due to the rather polyphagous feeding habit of the mite, which preys in addition to thrips on a great variety of other small arthropods. Berndt et al. (2004) summarized that many alternative preys, for instance, nematodes, mites, springtail, small insect larvae in the soil (Karg, 1995), the lower encounter rates between predators and preys and interference between predators (possible cannibalism) were responsible for the limitation of the predatory efficiency.

At both release densities *A. cucumeris* significantly suppressed TSSM populations, though the maximum mite mortality did not exceed 27%. In *O. insidiosus* only the higher predator density resulted in a significantly higher mite mortality compared to the no-predator control, and the highest mortality in mites was only 10.5%. One reason is probably the strong prey preference of *Orius* spp. especially *O. insidiosus* for WFT compared to TSSM (more detail see chapter 3). Easterbrook et al. (2001) reported that the numbers of TSSM eggs were reduced significantly (ca. 60%) when 20 *A. cucumeris* per strawberry plant were released against both TSSM and tarsonemid mite *Phytonemus pallidus*. Also on strawberry and co-occurrence of the two pests, Croft et al. (1998) recorded that *A. cucumeris* suppressed about 50% TSSM population at the peak density of TSSM.

For WFT, individual releases of *A. cucumeris* or *O. insidiosus* significantly suppressed thrips populations, with higher levels of WFT control following releases of the

predatory bug than the mite at the predator densities tested in this study. Moreover, all combinations of these plant-inhabiting predators with *H. aculeifer* lead to higher CM of thrips compared to individual releases of *A. cucumeris* and *O. insidiosus* though the extent varied among the different predator combinations tested. For *H. aculeifer* all combinations with *A. cucumeris* and/ or *O. insidiosus* significantly improved WFT control compared to individual releases of *H. aculeifer* at the predator densities tested. In *A. cucumeris* all combinations with *H. aculeifer* except for one (i.e., 40 *A. cucumeris* and 5 *H. aculeifer*) significantly increased thrips mortality compared to individual releases of *A. cucumeris*. However, for *O. insidiosus* only the combination of 1 *O. insidiosus* and 10 *H. aculeifer* lead to a significantly higher thrips control than individual releases of *O. insidiosus* at the two predator densities tested.

During the last decade, the availability of beneficials for biocontrol in greenhouses has substantially increased (Eilenberg et al., 2000), opening up possibilities of using several biocontrol agents simultaneously to combat one or more pests at the same time (Meyling et al., 2002). However, so far releases of multiple biocontrol agents not always resulted in improved control levels. For instance, Ferguson and Stiling (1996) recorded that interference of predators and parasitoids used for aphid control lead to a reduced mortality in the pest. Moreover, predator-predator interactions can also reduce the efficacy of biological control (Rosenheim et al., 1993; Cisneros and Rosenheim, 1997; Rosenheim, 2001, Snyder and Wise, 2001). In a recent review paper Denoth et al. (2002) analysed 59 and 108 biological control projects against weeds and insect pests, respectively. They found no relationship between the number of biocontrol agents released and successful control in insect pests. In addition, in more than 50% of the successful projects where multiple biocontrol agents were used for weed and pest control, a single agent was responsible for the success. Hence, negative interactions among biocontrol agents can greatly affect the success of biological control (Denoth et al., 2002). In predators, two main types of negative interactions exist, i.e., IGP where one predator preys on a second (Polis et al., 1989; Rosenheim et al., 1995), and exploitative competition where one predator can have a detrimental effect on a second predator by depleting essential resources of the latter species (Schoener, 1993). Hence, negative interactions between predators should be as much as possible avoided for instance by releasing predators that occupy different niches, e.g. on the plants and in the

soil, where pests at their different developmental stages dwell. In our experiments, WFT was more effectively controlled by releasing the plant-inhabiting predators *A. cucumeris* and *O. insidiosus* that prey on plant-feeding thrips larvae than by releases of the soil-dwelling predator *H. aculeifer* that, among others, feed on WFT prepupae and pupae. Yet, in all combinations of the plant-inhabiting predators with *H. aculeifer* additive effects in terms of biological control of WFT were recorded. For *A. cucumeris* combinations with *H. aculeifer* mostly resulted in significantly higher thrips control than sole releases of *A. cucumeris*. However, in *O. insidiosus* in only one case of combined releases with *H. aculeifer* significantly improved thrips control. Probably the greater extent of predation on thrips larvae by the bugs considerably reduced the amount of available prey for *H. aculeifer*, thereby reducing its control potential indicating a resource depletion for the predatory mite. However, our strategy of releasing predators that considerably differ in their niche preferences lead to a complete avoidance of any IGP and thus additive effects in terms of thrips mortality.

In conclusion, our results show that for multiple predator releases selecting species that differ in their niche preference can result in additive control effects in WFT. Combining *A. cucumeris* with *H. aculeifer* seems to be the major strategy in terms of thrips and TSSM control compared to the dual releases of *O. insidiosus* and *H. aculeifer*. However, with 26.7% TSSM suppression the extent of mite control by the combination of *A. cucumeris* and *H. aculeifer* was comparatively low. Hence, in case of TSSM outbreaks additional releases of more mite specific predators like *Phytoseiulus persimilis* Athias-Henriot (Mesostigmata: Phytoseiidae) might be needed.

6. General Discussion

Two-spotted spider mite (TSSM) and western flower thrips (WFT) are notorious pests of ornamental plants and vegetables both in field (Trichilo and Leigh, 1986; Wilson et al., 1996; Colfer et al., 1998, 2000) and in greenhouse cultures (Brødsgaard and Enkegaard, 1997; Sterk and Meesters, 1997; Fejt and Jarosík, 2000). They often occur on the same plants simultaneously. The plant dwelling predators *A. cucumeris* and *O. insidiosus* have been extensively used to control WFT in many greenhouse ornamentals and vegetables. As more generalized predators they attack not exclusively WFT but can prey also on TSSM. Development of WFT is not restricted to the crop canopy; more than 98% late second instar larvae leave the plants to pupate in the soil (Berndt et al., 2004) where they are protected from the above-mentioned predators. On the other hand, polyphagous soil born predators like *Hypoaspis aculeifer* Canestrini (Acarina: Laelapidae) which are commercially produced for control of fungus gnats (Folker-Hansen and Krogh, 1988; Enkegaard et al., 1997; Ydergaard et al., 1997) and bulb mite *Rhizoglyphus robini* Claparede (Astigmata: Acaridae) (Lesna et al., 1996, 2000) also prey on WFT (Gillespie and Quiring, 1990; Brødsgaard et al., 1996; Berndt et al., 2004). The potential relationships among this predator guild and their prey are shown in figure 1: TSSM exclusively feeds on the foliage, flowers and pods of bean plants, whereas WFT larvae and adults prefer leaves and flowers, and WFT larvae can also feed on spider mite eggs and eggs of *A. cucumeris*. The predatory mite consumes only the first instar larvae of WFT and all developmental stages of TSSM. For the latter prey it prefers eggs and nymphal stages. *Orius insidiosus* is a typically polyphagous predator that preys on both TSSM and WFT but also on *A. cucumeris*. However, WFT seems to be the most suitable diet for the predatory bug. Sometimes *A. cucumeris* and *O. insidiosus* can use plant material as alternative food to avoid starvation during periods with low availability of prey. A separated niche is occupied by *H. aculeifer* which is polyphagous too, but restricted to the soil where in case of WFT it can only encounter the prepupae and pupae.

During the last decade, the availability of beneficials for biocontrol in greenhouses has substantially increased (Eilenberg et al., 2000), opening up possibilities of using several biocontrol agents simultaneously to combat one or more pests at the same time (Brødsgaard and Enkegaard, 2001; Meyling et al., 2002). However, when more than
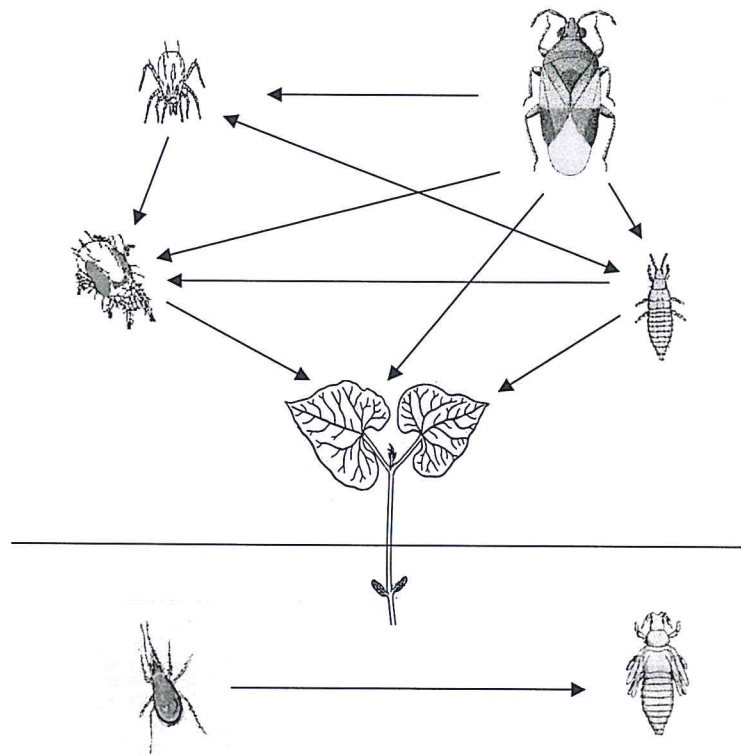
Fig. 1: Relationships among *T. urticae*, *F. occidentalis*, two plant-inhabiting predators, i.e., *A. cucumeris* and *O. insidiosus* and the soil-dwelling predator *H. aculeifer*. Arrows indicate direct effects between members of different trophic levels (i.e., predation and herbivory). Pictures of *T. urticae* and *A. cucumeris* are adopted from Janssan et al. (1998). Sources for images of *F. occidentalis* and *O. insidiosus* http://www.ipmofalaska.com, for *H. aculeifer* http://www.ibacon, and for beans http://www.botit.botany.wisc.edu.

two beneficials are introduced into a biological control system, the risk of competition among antagonists will increase. Intraguild predation (IGP) is a general phenomenon in systems where more than one natural enemy and one or more pests occur simultaneously (Polis et. 1989; Rosenheim et al. 1995). Strong IGP may cause biological control to fail. For instance, Ferguson and Stiling (1996) recorded that interference of predators and parasitoids used for aphid control lead to reduced mortality in the pest. Likewise, predator-predator interactions can also reduce the efficacy of biological control (Rosenheim et al., 1993; Cisneros and Rosenheim, 1997; Rosenheim, 2001, Snyder and Wise, 2001). Denoth et al. (2002) analysed 59 and 108 biological control projects against weeds and insect pests, respectively. They found no relationship between the number of biocontrol agents released and successful control in insect pests.

In addition, in more than 50% of the successful projects where multiple biocontrol agents were used for weed and pest control, a single agent was responsible for the success. Hence, negative interactions among biocontrol agents can greatly affect the success of biological control (Denoth et al., 2002). Hence a better understanding of IGP can possibly lead to a higher success rate in biological control.

6.1 Compatibility of combined releases of *Amblyseius* and *Orius* spp. for suppression of western flower thrips on greenhouse crops

The control efficiency of a single release of *Amblyseius* or *Orius* spp. is not always satisfactory. For improvement sometimes combined releases of both predators have been recommended (Hubert, 1992). However, as *Orius* spp. can feed on *Amblyseius* spp., IGP between the two predators might affect control of WFT. Consequently, a prerequisite for successfully using both predators simultaneously against WFT is a low level of IGP. For example, at varying densities of *A. cucumeris* and WFT in the presence of a single *O. laevigatus* female, the predatory bug fed on both arthropods to a similar extent. Thus, Wittmann and Leather (1997) questioned the suitability of this combination of predators for WFT biocontrol. On the other hand, Sanchez et al. (1997) and Van der Blom et al. (1997) reported that on greenhouse sweet pepper, *F. occidentalis* could be effectively controlled by the combined applications of *A. cucumeris* and *O. laevigatus*. These findings correspond with results of this study (for details see chapter 4). The combined releases of *A. cucumeris* and *O. insidiosus* significantly suppressed WFT in the presence of TSSM, although *O. insidiosus* can also feed on *A. cucumeris*. Similar results were obtained by Sörensson and Nedstam (1993) and Ramakers (1993) in a biological control system using *O. insidiosus* and *A. cucumeris* against WFT. The main conclusion from our studies and those reported in the literature is that adverse effects of predatory bugs on predatory mites do not affect to a great extent the biological control of WFT. The main reasons for this are the following:

(1) *O. insidiosus* prefers WFT to predatory mites (see also chapter 4).

(2) Releasing *Orius* and *Amblyseius* spp. at comparatively low ratios on greenhouse crops, as often practiced in commercial biocontrol, should limit the pressure of the bugs on *A. cucumeris*. An often recommended release strategy is the inundative release of *A. cucumeris* using controlled release sachets (CRS) or sprinkler once every week or every

second week. In contrast the recommend release numbers of and the release frequency for *O. insidiosus* are much lower. For example, on greenhouse cucumbers the recommended release rate for *A. cucumeris* is 5,000 CRS, containing at least 250 mites per bag, per hectare. Such a release rate should lead to a density of approximately 125 *A. cucumeris* per square meter. Releases might be repeated after 4-6 weeks. In contrast, *O. insidiosus* is released at least two times with one adult per square meter (Biobest, http://www.biobest.be). On other horticultural crops like sweet pepper or strawberry, decreased or increased release rates, respectively, of both predators are needed because of the differing prey potential of *A. cucumeris* and *O. insidiosus* on these plants. Nevertheless, the release ratio of *O insidiosus* to *A. cucumeris* is in general not greater than 1: 50. In our experiments, reported in chapter 4, the ratios of *O. insidiosus* to *A. cucumeris* were 1: 10 to 1: 40, which are comparatively higher than the before mentioned ones. As mentioned before, at lower release ratios the IGP pressure of *Orius* spp. on *Amblyseius* spp. should be reduced.

(3) Different release strategies for *O. insidiosus* and *A. cucumeris* may also decrease the pressure of the predatory bugs on the predatory mites. *Amblyseius* spp. are often released as a preventative measure, while *O. insidiosus*, because of its high mobility and aggressiveness, can be applied later, for instance once WFT numbers start to increase. With increasing prey density, *Amblyseius* spp. will be more and more released from the pressure of *Orius* spp. because of their preference for thrips.

(4) *Orius* spp. are typical omnivores which in addition to preying on various arthropods also feed on plants even when prey is readily available (Armer, 1996).

In summary, for combined releases of predatory bugs and predatory mites for WFT control, strong intraguild effects with *Orius* spp. as the predator and *Amblyseius* spp. as the prey are not very likely. Thus this predator combination seems to be well adapted for control of *F. occidentalis* on various greenhouse crops.

6.2 *Amblyseius cucumeris* and *Orius insidiosus* as predators of spider mites

Although *A. cucumeris* at a ratio of greater than 1: 4 could significantly suppress TSSM populations at low and moderate spider mite densities, doubling the number of released predators did not significantly increase the control efficiency. Moreover, even at low

TSSM densities, the suppression rate did not exceed 34% (for details see chapter 2). Thus, a single release of even high numbers of *A. cucumeris* against TSSM does not seem to be a very successful strategy to combat *T. urticae* infestations. Likewise releases of *O. insidiosus* at predator/prey ratios greater than 1: 80 resulted in a significant suppression of TSSM populations, but the control efficacy was also not very high (for details see chapter 3). Moreover, *O. insidiosus* suppressed TSSM populations mainly through selective killing of adult spider mites (chapter 4), which limits its potential for long-term suppression of TSSM populations even more. However, this drawback of *O. insidiosus* can be compensated by additional releases of *A. cucumeris*, because it mainly preys on eggs, larvae and nymphs of *T. urticae*.

Additionally *A. cucumeris* can benefit from the spider mite webbings, where it can find refuge from intraguild attacks by *Orius* spp. Thus, also for TSSM control combined releases of both predators are compatible. In the literature only very few studies report on such effects. For example in a field study on cotton, Colfer et al. (2003) observed that the naturally occurring generalist predatory bugs *Geocoris* spp. (Hemiptera: Lygaeidae) and *O. tristicolor* improved spider mite suppression by the augmentatively released predatory mite *Galendromus occidentalis* Nesbitt (Acari: Phytoseiidae).

Thus, in conclusion combined releases of predatory bugs and predatory mites can improve spider mite control, though both *O. insidiosus* and *A. cucumeris* are not very efficient predators of TSSM.

6.3 Combined releases of plant-inhabiting and soil-dwelling predators against WFT

IGP can be avoided when the predators forage in spatially separated niches, where they feed on different developmental stages of the pest. In such a situation predators that theoretically are IGP predators or IGP prey can work "hand in hand", thereby increasing the control efficiency. In chapter 5, the combined releases of the plant-inhabiting predators *A. cucumeris* or *O. insidiosus* with the soil-dwelling predator *H. aculeifer* in most cases significantly increased the control efficiency of WFT compared to single releases.

The spatial separation between the two predators prevents direct IGP effects. Moreover, in our system the two predators fed on different developmental stages of the prey. However, they still compete for the same resource, i.e. WFT. Thus overexploitation of this resource by one predator will affect the fitness of the other. Thus well balanced release rates of the two predators and the availability of alternative food resources will stabilise the system. The results in chapter 5 show that in most cases stronger additive control effects were recorded after combined releases of *A. cucumeris* and *H. aculeifer* than of *O. insidiosus* and *H. aculeifer*. This indicates that combined releases of two predators with similar control potential, like *A. cucumeris* and *H. aculeifer*, are more likely to yield additive effects than combining one very strong and one less efficient predator like in the combination of *O. insidiosus* and *H. aculeifer*. For the latter type of combination it is very essential that the release ratio is well balanced.

6.4 Conclusion

In dual infestations of *F. occidentalis* and *T. urticae* both pests can be significantly suppressed by *A. cucumeris* and *O. insidiosus*. Because of the distinct prey preference of *O. insidiosus* for WFT to TSSM, its control efficiency in *T. urticae* is limited. However, this can be partly compensated by the simultaneous release of *A. cucumeris*. Combined releases of predatory bugs and predatory mites are compatible for suppression of both thrips and spider mites. Potential IGP is avoided by combined releases of plant-inhabiting and soil-dwelling predators and are very efficient for WFT control. However, when combining two predators the ratio of the two beneficials needs to be well balanced to reduce IGP and/ or to limit overexploitation of resources by one predator and its potential negative effects on the fitness of the second predator.

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