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Interactions Mediated by Predators in Arthropod Food Webs

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Interações Mediadas por Predadores em Teias Alimentares de Artrópodes

RESUMO - Estudos sobre interações entre plantas, herbívoros e inimigos naturais são importantes para o entendimento da dinâmica populacional das espécies em teias alimentares, bem como para o sucesso do controle de pragas por inimigos naturais. Os programas de controle biológico fundamentam-se na ocorrência de sucessões tróficas, onde a adição de um inimigo natural causa o decréscimo na densidade da presa/hospedeiro e o aumento da biomassa da planta. Entretanto, quando mais de uma espécie de inimigo natural é usada para controlar várias pragas no mesmo sistema, teias alimentares artificiais são criadas e as interações tritróficas simples transformam-se em outras mais complicadas. A ocorrência de interações complexas e de onivoria nestas teias alimentares pode modificar a direção e a intensidade dos efeitos diretos dos inimigos naturais sobre as pragas. Neste artigo, são apresentados e discutidos os resultados experimentais sobre interações mediadas por predadores em uma teia alimentar artificial. Esta teia é formada em plantas de pepino em casa de vegetação onde o controle biológico é aplicado. A teia constitui-se de duas pragas, o ácaro rajado *Tetranychus urticae* Koch e o tripes *Frankliniella occidentalis* (Pergande). Para o controle dos ácaros rajados são liberados os ácaros predadores *Phytoseiulus persimilis* Athias-Henriot e *Neoseiulus californicus* (McGregor). O controle dos tripes é feito através de liberações do percevejo generalista *Orius laevigatus* (Fieber) e do ácaro predador especialista *Neoseiulus cucumeris* (Oudemans). Resultados de estudos comportamentais mostraram que algumas destas espécies são atraídas para o mesma planta e não evitam plantas ocupados por outras espécies. Quando estas espécies são encontradas na mesma planta, interações complexas ocorrem: (a) predação intraguilda de *O. laevigatus* sobre *P. persimilis*, (b) uso da teia produzida pelo ácaro rajado pelas larvas de tripes como refúgio contra seus predadores. As conseqüências destas interações na dinâmica populacional dos predadores e das pragas e no sucesso do controle biológico são discutidos.

PALAVRAS-CHAVE: Defesa de plantas, odor, atração, comportamento antipredador, predação intraguilda, controle biológico.

ABSTRACT – Studies on interactions among plants, herbivores and natural enemies are important for understanding population dynamics of species in food webs, but they are also important for the practice of pest control with natural enemies. Biological control programs heavily rely on the occurrence of trophic cascades, where the addition of one natural enemy causes a decrease of pest densities and an increase of plant biomass. However, when more that one natural enemy is used to control various pests in the same system, artificial food webs are created and simple tritrophic interactions change to more complicated ones. The occurrence of complex interactions and omnivory in these food webs may modify the sign and the strength of direct effects of natural enemies on pests. In this paper, we show and discuss the experimental results on interactions mediated by predators in an artificial food web that occurs on cucumber plants in greenhouses where biological control is applied. The two pests in this food web are the two-spotted spider mite *Tetranychus urticae* Koch, and the western flower thrips *Frankliniella occidentalis* (Pergande). The predatory mites *Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* (McGregor) are used to control spider mites, and the generalist predatory bug *Orius laevigatus* (Fieber) and a specialist predatory mite *Neoseiulus cucumeris* (Oudemans) are predators of thrips. Results from behavioural studies showed that some of these species are attracted to the same

patch and do not avoid each other's presence. We show some complex interactions arising from the meeting of these species: (a) the intraguild predation by *O. laevigatus* on *P. persimilis,* (b) the use of spider-mite web as a refuge by thrips larvae against their predators. The consequences of such interactions for population dynamics of predators and prey and their implications for success of biological control are discussed.

KEY WORDS: Plant defence, odour, attraction, antipredator behavior, intraguild predation, biological control.

Arthropod food webs are often complex and species are rarely arranged in linear food chains consisting of plants, herbivores and predators (DeAngelis *et al.* 1996, Polis & Strong 1996). The occurrence of omnivory and indirect interactions in these food webs can make especially difficult to assign species to distinct trophic levels. In a simple model proposed by Hairston *et al*. (1960) where each species in a food web is classified in one of three trophic levels, changes in one trophic level cascade down to lower trophic levels, but this may not be true for more complex food webs. This is because herbivore density and plant biomass affect and are affected by species that occupy more than one trophic level (Polis & Strong 1996).

Feeding on more than one trophic level is a common phenomenon in ecological communities (Polis 1991, Diehl 1993, Winemiller 1996). In arthropod food webs, many predators are generalists and they may not restrict their diets to herbivore species but feed also on other predators and even on conspecifics (Sabelis 1992). Generalist predators are therefore expected not only to interact with other predators through competition for food, but in many cases also through intraguild predation. This is defined as the killing and eating of species that otherwise use similar resources and are thus potential competitors (Polis *et al.* 1989). If a generalist predator preferentially feeds on other predators (intraguild prey), an increase of herbivore populations is expected due to lower numbers of the intraguild prey and/or due to the reduction of time and energy spent by the intraguild predator on the herbivores.

Besides omnivory, indirect interactions in food webs may also modify the strength or even the sign of direct effects of natural enemies on herbivores (Wootton 1994). Numerical indirect interactions occur when one species affects densities of another through an effect on the numbers, density or biomass of an intermediate species (i.e. competition, apparent competition, indirect effects of intraguild predation); functional indirect interactions emerge when changes in the way that two species interact occur through the presence of a third (i.e. induced resistance and susceptibility, indirect plant defenses, avoidance of competition) (see Janssen *et al.* 1998 for a review of indirect interactions). Direct interactions can also be numerical and functional. Predation is a numerical direct interaction; avoidance of predation via behavioural responses of the prey is a functional direct interaction (Janssen *et al.* 1998). Such behavioural changes will normally not only have effect on the functional response of the predator, but will also affect the prey growth rate due to costs involved in displaying the antipredator behavior (Lima & Dill 1990). Besides having a numerical effect on prey through predation, predators also have a functional effect on prey through changes in predator attack rate and prey growth rate. These so-called non-lethal effects cause severe consequences for the dynamics of predators and prey (Schmitz *et al.* 1997, Lima 1998), because the indirect effects mediated through changes in behavior may take place much more rapidly than those due to numerical changes (Abrams 1984) and they affect many more prey than the relatively small numbers that predators actually consume (Mittelbach, 1988). Although the majority of studies on interactions in food webs have concentrated on numerical interactions, experiments and theory have shown that functional interactions can equal numerical interactions in strength (Abrams 1995, 1996, Menge 1997, Schmitz *et al.* 1997, Peckarsky & McIntosh 1998, Peacor & Werner 2000).

Plants too interact with other members of the food web, for instance with the natural enemies of their herbivores. Plants can arrest natural enemies through provision of food or shelter and/or may facilitate prey searching of natural enemies through the production of herbivore-induced plant volatiles signaling the presence of herbivores (see Sabelis *et al.* 1999 for a review). These volatiles vary considerably, depending on plant and herbivore species (Sabelis and van de Baan 1983, Dicke and Sabelis 1988, Takabayashi *et al.* 1991, Dicke 1999), on plant variety (Dicke *et al*. 1990, Dicke 1999), on age of plant tissue (Takabayashi *et al*. 1994, Scutareanu *et al.* 1997), and on degree of infestation (Turlings *et al.* 1990, Scutareanu *et al.* 1997). However, the interaction among plants and natural enemies of their herbivores is prone to exploitation by other members of the food web: other herbivores and omnivores could use the herbivore-induced plant volatiles to find plants or use the food and shelter provided by the plant. Hence, to understand the evolution of such interactions, it is essential to consider their effect in a food web context (Sabelis *et al.* 1999).

Interactions such as indirect plant defense and predator avoidance by prey have spatial consequences since they cause the redistribution of animals and therefore affect the probability of species interacting. They also have in common that volatile chemical stimuli play an important role, which is not surprising since odours are of general importance in the foraging behavior of arthropods. When predators assess the profitability and risks of feeding in a given patch, they often use chemical cues related to that patch. Apart from the volatiles produced by plants under herbivore attack, other odours such as those emanating directly from the herbivorous prey (Whitman 1988, Vet & Dicke 1992, Raffa & Dahlsten

1995, Mendel *et al*. 1995) and from their by-products (e.g. faeces, honeydew) (Tumlinson *et al*. 1992) are likely to be related to food availability, thereby guiding predators towards the source. Moreover, predators and prey can also use odours associated with the presence of other con- or heterospecifics on the patches to avoid competition or (intraguild) predation (Lima & Dill 1990, Janssen *et al.* 1997, Pallini *et al*. 1997, 1999). Additionally, prey can distinguish dangerous from harmless predators, through odours related to predation on conspecifics of the prey, e.g. alarm pheromones released by attacked prey (Kats & Dill 1998, Chivers & Smith 1998, Venzon *et al*. 2000).

Besides being of general significance for arthropod food webs, these interactions among plants, herbivores and natural enemies become important for biological control. With the increased use of biological control agents, artificial food webs have been created in agriculture crops, and the interactions among plants, herbivores and natural enemies change from tritrophic interactions to food web interactions. Herbivore densities will be determined not only by direct predator-prey interactions and direct and indirect plant defence against herbivores (Sabelis *et al.* 1998) but also by the other direct and indirect interactions (Sabelis *et al.* 1999). Biological control researchers should therefore carefully consider the direct and indirect effects that may be caused by natural enemy releases.

To determine the occurrence and strength of interactions in food webs, a logical first step is to study the searching behavior of the species in the food web in response to odours associated with the presence of food, predators (intraguild) and competitors. Research should then focus on those combinations of species that were shown to be attracted to the same patch type and do not avoid each other. We use this approach to study interactions mediated by predators in an artificial food web that occurs on cucumber plants in greenhouses where biological control is applied.

The Arthropod Food Web on Cucumber Plants

The studied food web consists of the generalist predatory bug *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae); the specialist predatory mites *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus cucumeris* (Oudemans) and *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae), the herbivores two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), and the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), and cucumber plants (*Cucumis sativa* var. Ventura) (Fig. 1). The predatory bug and *N. cucumeris* are often used in greenhouses in Europe to control thrips, whereas either *P. persimilis* or *N. californicus* is used in the same greenhouses to control spider mites.

Although this arthropod food web is quite small, many direct and indirect interactions can occur among these species. For instance, competition may occur between the two herbivores, as well as between the natural enemies. Being polyphagous, the predatory bug may prey on both pests, but also on the predatory mites. Possibly, some of the predatory mites also prey on each other and thrips can prey on spider mite eggs (Trichilo & Leigh 1986, Milner & Walter 1997). Interference between several species of natural enemies is another distinct possibility. Moreover, the occurrence and strength of all these interactions can be modified by indirect plant defense, avoidance of competition or predation and prey preference of natural enemies. We first studied antipredator behavior of prey and the response of predators towards plants infested with prey; secondly, we looked at avoidance behavior of predators. Finally, after finding which species are attracted to the same patches and do not avoid each other's presence, we looked at interactions that occur when these species meet on the same plants.

Antipredator Behavior of Prey

Prey can avoid predation by using odours related to the presence of predators. Spider mites are know to use odours from plants infested with thrips to avoid competition and intraguild predation (thrips larvae consume eggs of spider mites) (Pallini *et al*. 1997). To investigate whether spider mites use odours to avoid predation, an experiment was carried out testing the response of spider mites towards plants with or without predators. It was found that spider mites strongly avoid plants occupied by spider mites plus *P. persimilis*, but do not avoid plants with spider mites plus *N. californicus* (Pallini *et al.* 1999). *P. persimilis* is commonly used in the greenhouse where the *T. urticae* strain was collected. Besides, strains of this pest are known to persist in greenhouses and to adapt to the pesticide regime of this environment (Overmeer *et al.* 1975, 1980). Hence, one hypothesis is that there has been selection on the pest to recognise and avoid its enemy (Pallini *et al.* 1999). As *N. californicus* is not used against two-spotted spider mites in this greenhouse, there has been no selection to recognise this predator. The avoidance of plants with predators by spider mites might have a negative effect on their biological control because spider mites will mainly settle on plants without predators, where they will produce damage and reproduce for some time before being detected and attacked by predators. However, these negative effects may be alleviated by the so-called nonlethal effects of predation (Abrams 1995, Lima 1998).

Given that thrips can co-occur on plants with spider mites, where they can also feed on spider-mite eggs (Pallini *et al.* 1997), and *P. persimilis* is normally released to control spider mites, it becomes important to know how thrips respond to plants that are not only infested by spider mites but also occupied by *P. persimilis*. It was found that thrips avoid plants infested with spider mites plus *P. persimilis* when plants infested with spider mites only were offered as an alternative (A. Pallini, unpublished). This is somewhat surprising because from a functional viewpoint there is no reason for the avoidance. Thrips do not run any risk of predation when visiting plants with *P. persimilis* because this predator, being a spider-mite specialist, is unable to prey upon thrips. Actually, the reverse is true: thrips were observed attacking eggs of *P. persimilis*. Since thrips and spider mites are often found inhabiting the same plants in greenhouses and share common predators such as *N. californicus* and *O. laevigatus*

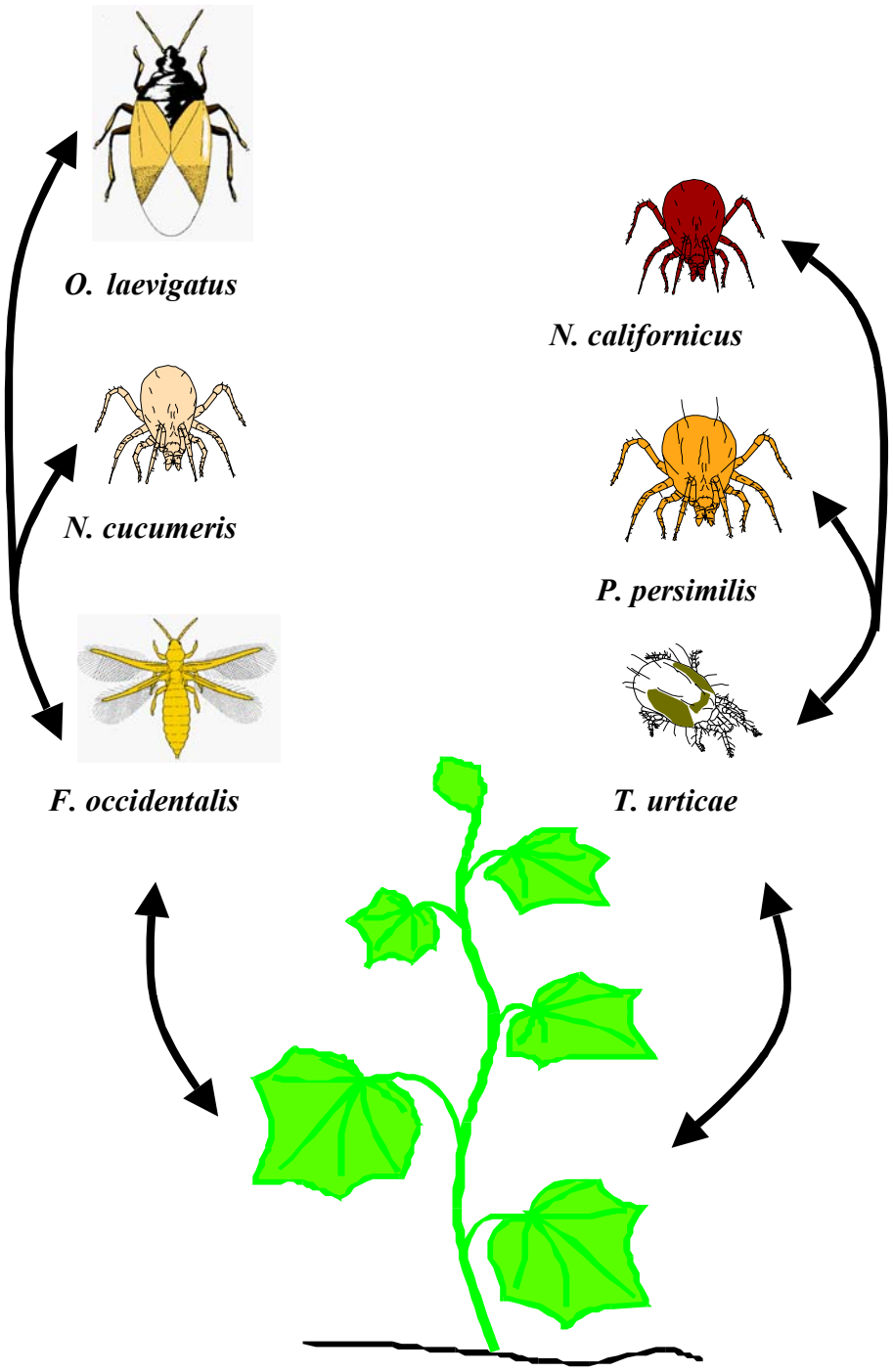

Figure 1. Part of the artificial food web on cucumber in greenhouses in The Netherlands where biological control is applied. Shown are the cucumber plant (*C. sativa*), two pest species, the western flower thrips (*F. occidentalis*) and the two-spotted spider mite (*T. urticae*) and the natural enemies used to control them. Natural enemies of thrips are the predatory mite *N. cucumeris* and the generalist predatory bug *O. laevigatus*. The predatory mites *P. persimilis* and *N. californicus* are used to control spider mites. Arrows indicate direct effects between members of different trophic levels (i.e. predation and herbivory).

(Sabelis & van Rijn 1997), thrips could have evolved to exploit the chemical communication of spider mites. Hence, it is possible that the warning signals produced by alerted spider mites under predation by *P. persimilis* may be translated into a general predation risk by thrips.

Attraction of Predators Towards Plants Infested with Herbivores

To investigate the searching behavior of the predators towards herbivore-infested plants, we offered them a choice between odours from clean plants and plants infested either with spider mites or thrips. Olfactometer and greenhouse release-recapture experiments showed that *O. laevigatus* and *P. persimilis* preferred plants infested either with spider mites or with thrips over clean plants (Janssen *et al.* 1998, Janssen 1999, Venzon *et al*. 1999); *N. cucumeris* was attracted to plants infested with thrips but showed no preference for plants with spider mites over clean plants (Janssen *et al.* 1998).

Subsequently, predators were offered a choice between plants with spider mites and plants with thrips. *N. cucumeris* was found to be attracted more strongly to thrips infested plants; *P. persimilis* and *O. laevigatus* showed preference for plants with spider mites over plants with thrips (Janssen *et al.* 1998, Venzon *et al*. 1999). The response of *P. persimilis* is in agreement with the observation that it is predominantly a spider mite predator and does not feed on thrips, but the response of *O. laevigatus* was not really expected. Although thrips and spider mites are both successfully attacked and fed upon by *O. laevigatus,* thrips is a superior diet for this bug as it allows for a higher intrinsic rate of population growth under ample prey supply (Venzon *et al.* unpublished). To elucidate the preference of *O. laevigatus* for plants infested with spider mites, a second experiment was carried out using a higher density of thrips per plant than used before and the same density of spider mites. Now, the preference for spider mites infested plants disappeared, and *O. laevigatus* showed no preference. Thus, when searching for patches, predators may not only consider the prey quality, but also the quantity of prey per patch. Moreover, this decision may also depend on the quality of the patch in the future, i.e. increase or decrease of prey numbers during patch exploitation (Kindlmann & Dixon 1999).

Summarizing, *O. laevigatus* as well as *P. persimilis* and *N. cucumeris* are attracted to plants with thrips, whereas both *O. laevigatus* and *P. persimilis* are attracted to plants with spider mites (Fig. 2). Interactions such as intraguild predation, competition, and interference are more likely to occur between predators that are attracted to plants carrying the same species of herbivore. Interactions between other combinations of species on plants with any of the herbivore species are less likely to occur. However, the occurrence and intensity of interactions between species that are attracted to plants with same prey can be reduced because predators avoid plants occupied with other predators. Similarly, prey can reduce the occurrence of predation or competition by avoiding plants occupied with predators or herbivores, respectively.

Avoidance Behavior

The occurrence of avoidance among predators was investigated by offering them plants infested with prey and plants infested with prey plus heterospecific predators. Results from olfactometer and greenhouse release-recapture experiments showed that *P. persimilis* did not avoid plants with spider mites plus either *O. laevigatus*, *N. californicus* or *F. occidentalis* (this thrips species can attack eggs of *P. persimilis*) (Janssen *et al.* 1999). This contrasts with the finding that *P. persimilis* does avoid plants with spider mites and conspecifics (Janssen *et al.* 1997). In this latter case, the odours that enabled *P. persimilis* to discriminate between plants with and without competitors were not produced by the conspecifics themselves, since odours from conspecifics were proven to be attractive rather than unattractive. There is evidence that the odours are produced by the adult spider mite prey in response to the presence of predators or their odours (Janssen *et al.* 1997). These volatiles may serve as alarm pheromone to warn related spider mites. Hence, the adult prey probably produce volatiles that convey a signal to downwind predators that the plant is already occupied by predators and is therefore a less profitable place to visit. It seems that the heterospecific predators, *O. laevigatus*, *N. californicus* and *F. occidentalis,* do not elicit production of such odours in the adult prey, or that *P. persimilis* does not respond to these odours in a similar way as when conspecifics are present on plants with prey. With respect to the latter explanation, it is important to realise that *O. laevigatus* and *F. occidentalis* are not only competitors of *P. persimilis*, but also prey on it. Hence, *P. persimilis* would have every reason to avoid plants occupied with these species.

Absence of avoidance was also found when *O. laevigatus* was offered a choice between plants with spider mites and plants with spider mites plus *P. persimilis.* This response is not surprising because both spider mites and *P. persimilis* are attacked and fed upon by *O. laevigatus.* Taking together this and the previous results, there is a great possibility that *O. laevigatus* and *P. persimilis* will meet on plants infested with spider mites. The interactions resulting from this meeting may have profound effects on spider mite population dynamics.

Interactions Resulting from Attraction and Absence of Avoidance of Arthropods Towards the Same Plants

On plants infested with spider mites, *O. laevigatus* may interact through intraguild predation and/or competition with *P. persimilis.* Therefore, the effects of releasing *O. laevigatus* on populations dynamics of spider mites and *P. persimilis,* and on the performance of cucumber plants were investigated. Only small or no effect of the release of *O. laevigatus* on numbers of spider mites, plant damage, and numbers of *P. persimilis* were found. These results were unexpected, as *O. laevigatus* was observed to attack and feed upon *P. persimilis* when they were on the same leaf disc with spider mites. Besides, the presence of spider mites did not prevent

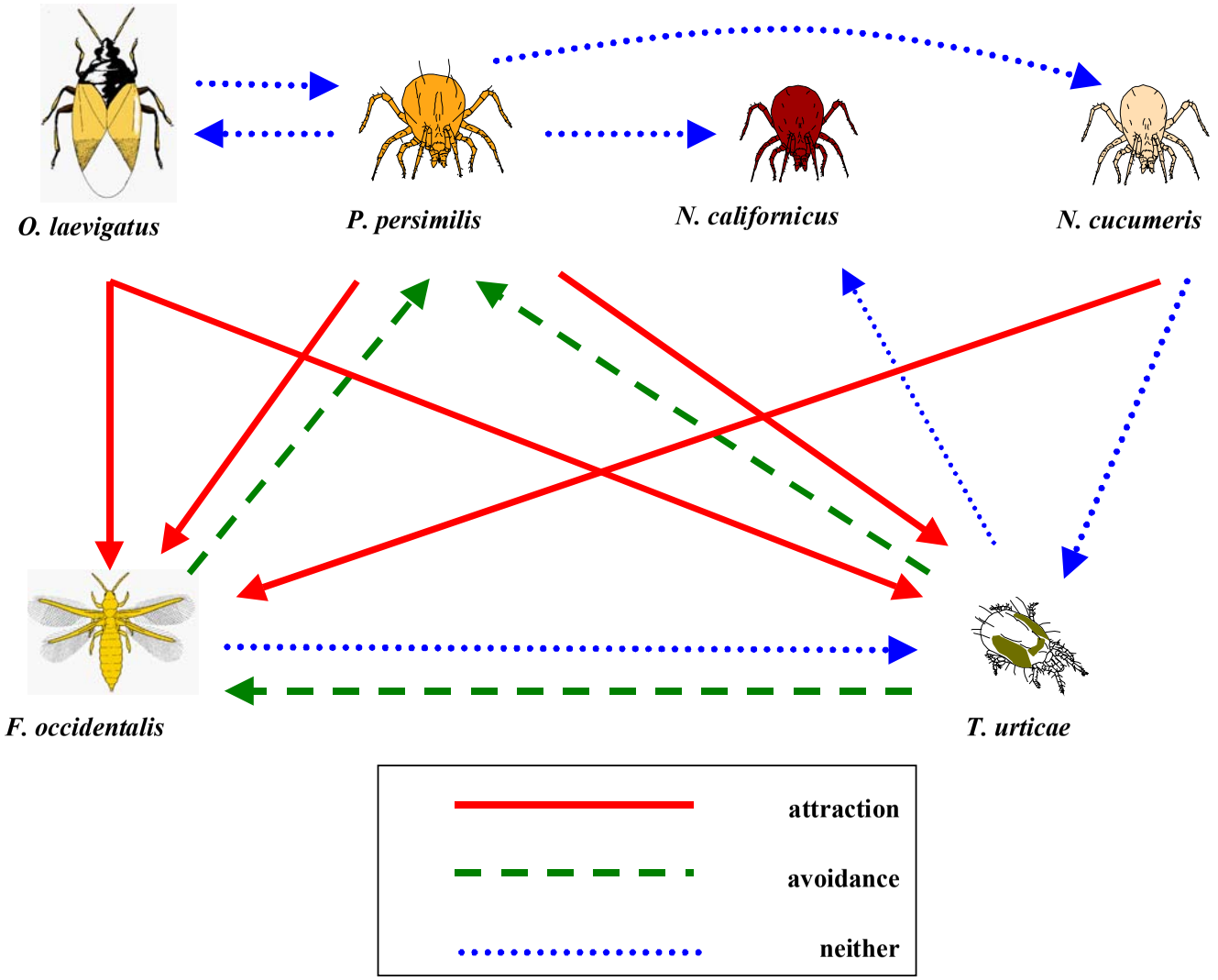

Figure 2. Summary of responses of predators (top row of arthropods) towards cucumber plants infested either with herbivores (bottom row) or the combination of herbivores and predators. Full arrows indicate attraction, broken arrows show avoidance and dotted arrows show neither attraction nor avoidance.

intraguild predation. The reason why intraguild predation is manifested in the behavioural experiments, but not in the population experiments, remains an open question. One potential reason for the absence of an effect of intraguild predation at the population level is the increased escape or mortality of the predatory bugs due to the webbing of spider mites (Venzon *et al.* 2000).

These results raise an important point for the debate on complex interactions and their role in food web dynamics. Clearly, one should be cautious in extrapolating experiments carried out in confined environments (cages, dishes) to the population level. Even though intraguild predation was observed in small scale experiments, it did not affect the interaction between the predatory mites and the spider mites on large scale experiments. The absence of such complexities implies that complex food webs may actually behave as simple tritrophic food chains (Sabelis *et al.* 1999). If this generally holds, it becomes more understandable why plants invest in indirect defenses, i.e. by promoting the effectiveness of natural enemies of the herbivores despite the investments being open to exploitation by other members of the food web.

Another group of species that can be found on the same plant consists of thrips, spider mites and the predators *N. cucumeris* and *O. laevigatus:* the two pests are often found attacking the same plants in greenhouses (Lewis 1997); both predators are attracted to plants with thrips; *O. laevigatus* is attracted to plants with spider mites and *N. cucumeris* is not repelled by plants with spider mites. One special interaction known to occur among these species is that thrips larvae use web produced by spider mites as a refuge from predation by *N. cucumeris* and by O. *laevigatus* (Pallini *et al.* 1998, Venzon *et al.* 2000). In webbed areas thrips larvae experience lower predation risk because the predators are hindered by the dense, sticky spider mite web. Although, the predation rate is lower in webbed areas, thrips compete with spider mites, resulting in a reduced rate of development and reproduction. To minimize these costs of refuge use, thrips larvae move into webbing only when perceiving volatile cues associated with thrips being attacked and eaten by predators (Pallini *et al.* 1998, Venzon *et al.* 2000).

The consequences of this antipredator behavior on the population dynamics of thrips are yet to be explored. The redistribution of thrips to webbed plant parts due to presence of predators will lead to effects on the population levels of thrips. First of all, refuge use results in a lower predation rate (Pallini *et al.* 1998, Venzon *et al.* 2000). Secondly, thrips developmental rate and fecundity are lower in refuges (Pallini *et al.* 1998). Hence, the use of refuges leads to two opposite effects on thrips numbers, and the net result of these two effects is not clear. Furthermore, because prey inside the refuge are difficult to catch, predators may concentrate searching efforts on plants or plant parts where prey refuges are absent. The resulting absence of predators near refuges would stimulate thrips to move out of refuges to the more profitable unwebbed plant parts. The effect of antipredator behavior on thrips population levels will greatly depend on flexibility of the behavior in response to changes in predation risk. Moreover, antipredator behavior may not only influence prey population dynamics, but may also lead to trophic level effects that are comparable in form and strength to those from direct predation events (Abrams 1995, Schmitz *et al.* 1997, Peckarsky & McIntosh 1998).

Concluding Remarks

Studies on food web interactions are important for understanding population dynamics of species in food webs and for understanding the existence of indirect plant defenses, but they are also important for the practice of pest control with predators. The success of biological control hinges on top-down control of herbivores, but with multiple introduction of natural enemies, artificial food webs are created, and the interactions among plants, herbivores and natural enemies change from simple tritrophic interactions to more complex food web interactions. These complex interactions may all affect pest densities and success of biological control. It is important not only to study the compatibility of natural enemies by evaluating numerical indirect interactions, but also through study of functional indirect interactions.

An inventory of such interactions and their effects on population dynamics of herbivores and predators is essential to understand the behavior of food webs in crops as well as in natural ecosystems. When food webs are disturbed by adding (the introduction of natural enemies) or removing species (through use of pesticides), as is the case in agroecosystems, a variety of important indirect interactions may be expected. These interactions may have both positive and negative effects on biological control of the herbivores. Hence, the population-dynamical consequences of these effects deserve further investigation. The study presented here illustrates that ecologists and biocontrol practitioners should not underestimate the importance of interactions mediated by predators in determining community-level interactions both in artificial and in natural food webs.

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