EFFECTS OF PLANT ARCHITECTURE AND PREY DISTRIBUTION ON THE FORAGING EFFICIENCY AND BEHAVIOR OF THE PREDATORY MITE *PHYTOSEIULUS PERSIMILIS* (ACARI:PHYTOSEIIDAE)

by

LESSANDO MOREIRA GONTIJO

B.S. Agronomy, Federal University of Viçosa, 2004, Brasil

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2008

Approved by:

Co - Major Professor
James R. Nechols

Approved by:

Co –Major Professor
David C. Margolies

Abstract

The study of how extrinsic factors affect the foraging efficiency and behavior of predaceous arthropods like *Phytoseiulus persimilis* is important to understand their various processes of acquiring prey, mates, refuges, oviposition sites, and overcoming obstacles posed by the environment. Many intrinsic and extrinsic factors affect predator foraging efficiency and behavior. One of the most influential extrinsic factors may be the host plant on which herbivorous prey are found. Recent studies suggest that plant architecture plays an important role in tritrophic interactions. In this work, I studied the effects of cucumber plant architecture and prey distribution on the foraging efficiency (prey-finding time and prey-consumption rate) and behavior (time allocated between moving, resting and feeding) of *P. persimilis*. Plant architecture represented differences in leaf number and size; however, all plants had the same total surface area. Plants with 6 small leaves (ca. 82.98 square cm each) were considered as complex architecture, whereas plants with only 2 large leaves (ca. 240.60 square cm each) were considered as simple. The prey distributions were: prey patch on a single basal leaf (closest leaf to the soil) and prey patch on all leaves. The foraging efficiency was assessed by measuring prey-finding time and prey-consumption rate, whereas the behavior was assessed by conducting observational studies on specific foraging activities. When placed either on the top or at the base of the plant *P. persimilis* encountered prey more rapidly (interval 0-30 minute) on complex and simple plants with prey patches distributed on all leaves. Differences in prey density (number of prey per leaf) had no effect on the prey-finding time of *P. persimilis*. The predator consumed more eggs on complex plants with prey patches distributed on all leaves. *Phytoseiulus perismilis* tended to find prey patches more quickly as well as consume more eggs on leaves close to its release point. Furthermore, the predator was observed to lay more eggs on leaves where it had consumed higher number of prey eggs. The dimensions of individual parts of the plant e.g., stem, petiole and leaf, affected the time allocated by *P. persimilis* between searching, resting and feeding. The predatory mite spent more time foraging on the stems and petioles of the simple plants whereas on complex plants it spent more time foraging on the leaves.

Table of Contents

List of Figures

List of Tables

Acknowledgements

At first I must thank both my advisors, Dr. Nechols and Dr. Margolies, for depositing their confidence upon me and believing in my capability to conduct this study.

Along with that I would like to thank my committee members, Dr. Margolies, Dr. Nechols and Dr. Cloyd for their always insightful and wise guidance throughout my graduate studies.

I also would like to show my appreciation to our technician, Xiaoli Wu, who always worked hard to maintain colonies and keep things functioning properly in our laboratory and greenhouse.

In addition, I would like to extend my thanks to Leslie Campbell for helping to prepare the posters for congresses and providing valuable suggestions during our laboratory meetings.

I want to express my special thanks to Dr. James Higgins at the Department of Statistics who was always willing to advise me on statistical analyses, and also to Dr. Kimberly Williams at the Department of Horticulture Forestry and Recreation who provided me with important advices when choosing the plant species that would fit best into our system.

My sincere thanks to my lab mates Punya Nachappa, Dianna Wilkening and Julin Weng for their support and friendship.

I also wish to thank all the colleagues and staff of this department whose efforts always played an important role in making this department outstanding and a pleasant place to be.

At last I would like to express my gratitude to my family, Jésus, Maria, Cristiano, and my fiancée Angela, who at all moments gave me words of encouragement and support, and provided me with the inspiration that I needed to pursue my dreams.

CHAPTER 1 - Introduction and literature review

The foraging and general movement behavior of a predator typically comprises a set of coordinated adaptive traits that allows efficient acquisition of food, mates, oviposition and nesting sites, and refugia. These resources are essential for growth, development, and maintenance of individual predators. Moreover, efficient searching mechanisms and the ability to accurately assess resources are essential for survival and reproduction, which therefore contributes to the long-term success of future generations (Bell, 1990). The foraging efficiency of predators is considered to be a critical component of fitness, especially in cases regarding short-lived predators (Gingras and Boivin, 2002). Finally, attributes that confer efficient searching for, finding and attacking of prey are important in defining an effective predator when considering suppression of prey/pest populations in biological control programs (Huffaker *et al*., 1976).

Predator foraging efficiency may be influenced both by intrinsic and extrinsic factors. A detailed knowledge of predator foraging behavior, when combined with an adequate understanding of intrinsic factors affecting population growth of a predator and prey, allows better predictions of the dynamics of predator-prey interactions. However, because extrinsic factors often have profoundly different effects on predators and prey, investigating these effects is essential for making meaningful predictions.

When studying the interactions between herbivorous arthropods and their natural enemies, one of the most influential extrinsic factors is the host plant on which herbivorous arthropods feed and/or live (Price, 1986). For example, plant attributes have been found to affect the capacity of natural enemies to encounter herbivorous arthropods (Uetz, 1991). Generally the success of parasitoids and predators to encounter hosts/prey decreases with an increase in plant size (Ables *et al*., 1980; Thorpe 1985), plant complexity (Ramsy, 1977; Bond, 1983; Carter *et al*., 1984; Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992; Mackauer and Volk, 1993; Geitzenauer and Bernays, 1996) and plant surface area and volume (Knipling and McGuire, 1968; Need and Burbutis, 1979; Burbutis and Koepke, 1981; Kanour and Burbutis, 1984; Maini and Burgio, 1990).

With respect to predator foraging, plants may have direct effects on predator movement and prey-finding behavior. Plants also may indirectly influence predator foraging by altering the density and distribution of prey. To gain a mechanistic understanding of predator-plant interactions, we need to distinguish between such direct and indirect effects. It is difficult, however, to quantify these plant effects because prey may change their behavior and distribution in the presence of natural enemies (Gross, 1993; Persson, 1993; Coll and Izraylevich, 1997), and predators often change their searching behavior after encountering a prey item (Dixon and Russel, 1972; Brunner and Burts, 1975; Evans, 1976; Shields and Watson, 1980). Until recently, most research has focused on the effects of specific plant chemicals, e.g., plant volatiles, and/or morphological traits such as leaf trichomes (Obrycki, 1986; Vet and Dicke, 1992) on natural enemy foraging efficiency and behavior. Nevertheless, recent evidence suggests that plant architecture also plays an important role in tritrophic interactions (Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992; Marquis and Whelan, 1996; Clark and Messina, 1998; Cloyd and Sadof, 2000). Architectural traits such as stem or leaf dimensions, branching angles, surface complexity, and canopy spacing may "guide" enemy searching (Ferran and Deconchat, 1992) and, thus, influence either the time a predator spends on a plant or the overlap (coincidence) between predator and prey distributions (Carter *et al*., 1984; Frazer and McGregor, 1994). Plant architecture can simply be described by three variables: size, heterogeneity, and connectivity (Andow and Prokrym 1990, Bell *et al*. 1991). Size is represented by the height and volume of the plant. Heterogeneity is represented by the relative abundance, per unit area or volume, of the different structural components such as leaves, flowers, buds, and fruits, but also to components within the same plant that have different morphologies (e.g., glabrous versus hairy leaves, male versus female flowers). At last, connectivity refers to the absolute abundance, per unit of area or volume, of connections between individual structural components (e.g., number of leaves). It is assumed that simple plant architectures will have low values of plant size, heterogeneity and connectivity, and the opposite holds for the complex plant architectures.

The objective of early studies on plant architecture was essentially to explain patterns of species diversity and abundance (Moran 1980, Lawton 1983, Strong *et al*. 1984). For instance, Lawton (1983) evaluated some data that showed significant correlations between architectural complexity (architecture broadly defined to include a variety of plant attributes such as size and growth form, seasonal development, persistence, and variety of above ground parts) and the species richness of herbivores on the host plant. Species richness was observed to decline as plant architectural complexity decreased. Two hypotheses were provided to explain such a pattern. One dealt with the absolute size of plants, and the other focused on the plant resources made available to herbivores as a consequence of plant architectural complexity. The resource diversity hypothesis suggested that resources such as a diversity of feeding, oviposition and overwintering sites, and escape space are provided with increasing architectural complexity. Lawton (1983) also theorized that the architectural complexity of plants affords a higher degree of 'escape space' for herbivorous prey because the more complex plants provide more refugia.

Plant architecture can have both a direct and indirect impact on the foraging activities of parasitoids and predators. Plant architecture affects predator foraging efficiency and behavior indirectly by mediating prey availability, density, abundance and distribution (Pimentel, 1961; Lawton, 1983; Freese, 1995; Clark and Messina, 1998). The shapes or dimensions of plant parts may affect predation risk by influencing the availability of spatial refuges, i.e., microsites where predators do not have access to prey (Pimentel, 1961; Freese, 1995). For instance, Clark and Messina (1998) studied the foraging efficiency of ladybird beetle *Propylea quatuordecimpunctata* (L.) attacking the Russian aphid wheat *Diuraphis noxia* (Mordvilko) on two grasses (indian ricegrass and crested wheatgrass) with divergent leaf architectures. Their work suggests that the effect of the host plant in the tritrophic system largely depends on differences in the availability of prey refuges rather than on differences in predator searching behavior. Their results showed that more aphids were dislodged, contacted and captured by the predator on indian ricegrass than on crested wheatgrass. This may be a result of indian ricegrass having slender, tightly rolled leaves (where there is not enough space available to shelter many aphids) such that only the abaxial (lower) surface is exposed, thus increasing prey exposure and accessibility to the predatory ladybird beetles. Likewise, Clark and Messina (1998), assessing the foraging behavior of larvae of the green lacewing *Chrysoperla carnea* (Stephens), also on indian ricegrass and crested wheatgrass, concluded that plant architecture appeared to have a greater effect on prey accessibility rather than on predator mobility. In this case the predator also appeared to be more efficient on indian ricegrass, which in turn affected the susceptibility of the prey by influencing the availability of spatial refuges. It is also known that plant architecture affects the success of herbivores in colonizing new host plants. For instance, Marquis *et al*. (2002) found that for leaf-tying caterpillars living on *Quercus alba* a higher damage rate was observed on plants with a higher level of leaf connectedness. These caterpillars use their silk to tie together two leaves to form a "leaf sandwich" or leaftie within which they feed. Their results suggest that architectural traits that minimize leaf-to-leaf contact in *Q. alba* may be defensive traits against leaftying caterpillars.

In addition to indirect effects, plant architecture can also have direct impacts on the foraging activities of predators and parasitoids. A variety of plant physical characteristics, from leaf trichomes to plant architecture (stem and leaf dimensions, leaf numbers, branching angles, surface complexity, and canopy spacing), have been implicated in altering movement, effectiveness, behavior and survival of both predators and parasitoids (Pimentel, 1961; Evans, 1976; Price *et al.*, 1980; Shah, 1982; Carter *et al.*, 1984; Treacy *et al.*, 1985; Obrycki, 1984,1986; Kareiva and Sahakian, 1990; Van Lenteren and de Ponti, 1990; Stadler and Völk, 1991; Grevstad and Klepetka, 1992; Hare, 1992; Walter and O'Dowd, 1992; Weisser, 1995; Romero and Vasconcellos-neto, 2005; Clark and Messina, 1998; Krips *et al.*, 1999; Cloyd and Sadof, 2000). Kareiva and Sahakian (1990) demonstrated the influence of plant morphology on the foraging efficiency of two coccinellid species, *Coccinella septempunctata* L. and *Hippodamia variegata* Goeaze. According to their results, the two coccinellid species fell off significantly more often from normal peas than from leafless peas (leafless peas have tendrils instead of leaflets) with reduced stipules. As a result, the suppression of the population of aphids by the coccinellid species was reduced on the normal leaf (normal stipules). Legrand and Barbosa (2003) tested the efficiency of adults of the ladybird beetle *Coccinella septempunctata* when foraging on three near-isogenic pea lines with different structural architectures (simple, intermediary and complex). They found that *C. septempunctata* consumed significantly fewer aphids and foraged significantly longer on the plants with more complex architecture. Cloyd and Sadof (2000) testing the effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Howard), a parasitoid of the citrus mealybug, concluded that all architectural characteristics tested (leaf number, branch number, leaf surface area and height) were negatively correlated with attack rates of *L. dactylopii*. As with other plant physical characteristics, the effects of plant morphological complexity are difficult to isolate experimentally from other co-occurring, confounding factors such as plant chemistry. However, Andow and Prokym (1990) managed to study the effects of structure complexity by manipulating the structure of paper surfaces while holding surface area constant. Their study showed that the parasitism rates of the parasitoid

Trichogramma nubilale Ertle and Davis were significantly higher on simple surfaces than on complex ones. Unexpectedly, their study revealed that when no hosts were present, searching time on simple surfaces was significantly higher than on complex surfaces. This implies that structural complexity itself can affect the giving-up time of a searching parasitoids.

It is noteworthy that a fairly large number of studies have been conducted to gain a better understanding of the effects of plant architecture on natural enemies. However, most of these studies have focused on insect species and very few have dealt with acarinids. It is important to try to extend this knowledge to non-insect arthropods, especially predatory mites, because they play a key role in suppressing arthropod pest populations in both natural and agricultural ecosystems. The Phytoseiidae is one the most important families of predatory mites; which are chiefly responsible for the control of herbivorous mites belonging to the family Tetranychidae. Phytoseiids have a free-living, terrestrial lifestyle and are encountered in diverse environments such as foliage, bark and humus. Most of the species that have been studied are predaceous on tetranychids and on others small arthropods, but some have other dietary requirements. All phytoseiids have 5 developmental stages: egg, larva, protonymph, deutonymph and adult. The larvae have 3 pairs of legs whereas the other stages have 4 pairs (Chant, 1985).

One of the most important and thoroughly studied species of phytoseiids is the predatory mite *Phytoseiulus persimilis* Athias-Henriot. *Phytoseiulus persimilis* is a specialist on tetranychids and the most frequently-used biological control agent for spider mites, especially in greenhouses (Van Lenteren and Woets, 1988). Survival of *P. persimilis* depends largely on the consumption of tetranychid mites and they show no tendency to reproduce on other types of diet (Mori and Chant, 1996; Ashihara *et al*., 1978), at least not in greenhouses. Although extremely small (approximately 0.5 mm), *P. persimilis* can be distinguished with a hand lens. It is fast-moving, orange to bright reddish orange, has a teardrop-shaped body and long legs, and is slightly larger than its prey. Immatures present a pale salmon color. Eggs are oval and are approximately twice as large as the pest mite eggs. *Phytoseiulus persimilis* eggs hatch in 2-3 days, and although the larval stage does not feed, the subsequent nymphs and adults feed on all stages of prey (eggs, nymphs and adults). Total time from egg to adult ranges from 25.2 days at 15°C (59°F) to 5.0 days at 30°C (86°F) (Hoffmann and Frodsham,1993). The adult female may lay up to 60 eggs during her 50 day-long lifetime at 17-27°C. Generation times range from 7 to 17 days, depending on temperature and humidity. Due to its tropical origin, *P. persimilis* does not have a diapause stage and is active year-round in enclosed habitats such as interior plantscapes and greenhouses.

When predatory mites invade a spider mite-infested plant, the predator population is likely to eliminate the local spider mite population (Chant, 1961; Takafuji *et al*., 1983). This may happen because *P. persimilis* has a high numerical and functional response (Overmeer, 1985). Although this means the local predator-prey interaction is limited and ephemeral, the interaction may persist on a regional scale due to repeated dispersal from and colonization of patches by both species (Nachman, 1987, 1988, 1991; Sabelis *et al*., 1991; Walde, 1991, 1994; Jansen and Sabelis, 1992). As prey density drops to zero, *P. persimilis* will leave and seek other prey patches (Takafuji, 1977; Bernstein, 1984; Zhang and Sanderson, 1993). Successful colonization of new spider mite patches is important for the persistence of the predator population and for biological control (Sabelis *et al*., 1999; Walde and Nachman, 1999; McCauley *et al*., 2000).

One of the main arthropod pest targets of *P. persimilis* is the twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae). *Tetranychus urticae* can be recognized by the presence of two large dark green spots on the dorsal part of the abdomen. Significant variation exists in this trait, however, and it may not be the most reliable character for identifying *T. urticae*. *Tetranychus urticae* development differs somewhat between species, but a typical life cycle is as follows. The eggs are attached to fine silk webbing and hatch in approximately three days. The life cycle is composed of the egg, the larva, two nymphal stages (protonymph and deutonymph) and the adult. The length of time from egg to adult varies greatly depending on temperature. Under optimum conditions (approximately 80ºF), spider mites complete their development in five to twenty days. There are many overlapping generations per year. The adult female life span ranges from two to four weeks and is capable of laying several hundred eggs during her life. *Tetranychus urticae* is a generalist herbivore and a serious pest on a wide variety of crops worldwide, including greenhouse vegetables and floriculture (Van de Vrie *et al*., 1972). *Tetranychus urticae* injures individual leaf cells causing the reduction of total chlorophyll content and net photosynthetic rate of leaves (Iatrou *et al*., 1995). Additionally, high infestations of *T. urtica*e decrease leaf productivity by reducing the total number of leaves per plant, thereby resulting in significant yield losses (Park and Lee, 2005). Usually, *T. urticae* colonizes the undersurface of the leaves where they produce webbing in which all stages live and most activity (e.g., feeding, mating, oviposition) takes place. In spider mites, fertilized eggs produce only females whereas unfertilized eggs produce only males (Crooker, 1985). Adult females deposit eggs close to where they feed, and immatures do not move very far from where they hatch (Kondo and Takafuji, 1985). In this way, clusters, or patches, of spider mite infested leaves develop. As mite feeding destroys leaf tissue within a patch, pests move to new, uninfested parts of a plant. Because of the explosive growth potential of mite populations (Sabelis, 1981), mites can rapidly infest and kill entire plants, and because of their ability to disperse they can rapidly infest large areas. Furthermore, *T. urticae* has the ability to enter diapause when facing extreme environmental conditions, which are driven mainly by temperature, photoperiod and food shortage. Female *T. urticae* enter diapause in the adult stage and may withstand low temperatures up to – 27^0C during the winter.

The fact that *T. urticae* and many other greenhouse pests are highly polyphagous means that natural enemies must search for them on structurally diverse plants if they are to be effective. Even within the same plant species, architectural complexity can still increase as plant development proceeds. The rate and extent of plant architectural complexity may also be manipulated by modifying simple horticultural practices such as manipulating pot size, amount of water and/or fertilization, time of transplanting, control of temperature, and even the use of plant growth regulators (PGR's). Differences in foraging efficiency and behavior of natural enemies are directly related to the success of biological control programs. Studying the effects of plant architecture on predator foraging efficiency and behavior will allow a better understanding of predator-prey interactions on plants with different architectures, thereby contributing to meaningful predictions for improving biological control integrated pest management (IPM) programs in greenhouses and other protected environments. As an example, this knowledge can aid decisions about when and how many predators to release. Improvements in biological control programs that lead to greater adoption not only lead to better pest management recommendations for growers, but also have the indirect benefit of reducing pesticide use by creating more effective management options. A more precise knowledge of how many predators to release for effective biological control will also lead to cost reductions because recommendations will guide growers to avoid excessive releases of predators. Therefore, my thesis has focused on understanding the effects of different architectures of cucumbers (*Cucumis sativus*) and prey distributions on the foraging efficiency and behavior of the predatory mite, *P. persimilis* when searching for the twospotted spider mite, *T. urticae*.

CHAPTER 2 - Constructing Cucumber plants *Cucumis sativus* with different architectures

Introduction

It is a common practice for ornamental plant growers to manipulate plant architecture, especially plant height and canopy volume; to obtain a better product that will fit more adequately with consumer preferences. Besides the aesthetic value of plant architecture for consumers, it has also been documented to have major impact on biological control programs by affecting the interactions between arthropod pests and their natural enemies. Both genetic and extrinsic factors influence plant architecture. Plant architecture is first dictated by the expression of specific morphological genetic traits which are then shaped by extrinsic factors such as light, temperature, photoperiod, etc. Nevertheless, it is of our knowledge that plant architecture can also be manipulated artificially by means of plant breeding practices, use of plant growth regulators, cultural practices such as removal of terminal buds, pruning and control of water, nutrients and light intensity.

Plant architecture can be described based on the physical form and spatial arrangement of some of its morphological traits such as branches, plant height, canopy volume/surface area, leaf connectedness, number of leaves, etc. The objective of this work was to develop a system that would allow us to construct two cucumber plants that would differ in number and size of leaves, but with approximately the same total plant surface area. One of the plant architectures denoted simple plant architecture, hereafter called ‘simple plant’, would have 2 large leaves (ca. 240.60 cm^2 each) whereas the one denoted complex plant architecture, hereafter called ‘complex plant’, would have 6 small leaves (ca. 82.98 cm^2 each) . Nonetheless, both plant types had approximately the same total plant surface area. This study serves a specific, practical purpose. It also provides technical information that may be of general use for those interested in manipulating plant growth or studying the role that plant architecture may play in the interactions between arthropods (predator-prey and/or parasitoid-host interactions). The methodology presented here can aid these people to manipulate plant leaf number and size, and plant surface area. We expect that this knowledge can also be extended and/or adapted for other plant species.

Methodology

For this study I used cucumber plants *Cucumis sativus* that belong to the cultivar "Cumlaude". Seeds were obtained from Hydrogarden Company Inc. (USA). For germination the seeds were placed individually into 2.5-inch square pots which were confined within plastic flat. Each flat had 32 pots. The growth media utilized for growing the seedlings was FAFARD® germinating mix whereas the growth media utilized for growing the plants after transplant was FAFARD® growing mix. In order to avoid competition for light the seedlings were taken out of the plastic flat and spaced on the greenhouse table when they had the first leaf completely expanded. To construct plants with different architectures (different leaf size and number) I first attempted to use plant growth regulators (PGRs) Sumagic (uniconazole), Cycocel (chlormequat chloride) and Pro Gibb (Gibberellic Acid), however; due to problems of phytotoxity (burning of leaves) regarding the two first PGRs this approach was no viable and therefore I did not use it anymore. Thereafter another approach was adopted. For such approach I manipulated the pot sizes and the transplanting dates of the cucumber seedlings. The seedlings that would serve as simple plants were transplanted into 6-inch rounded pots when they had 4 leaves completely expanded (the 5th leaf starts to appear), whereas the seedlings that would serve as complex plants were transplanted into 4-inch rounded pots when they had 6 completely expanded leaves (the 7th leaf starts to appear). The seedlings were watered every day, and fertigated with 20-10-20 fertilizer once a week prior to the transplant, and thereafter the plants were fertigated always when they needed to be watered. The solution of fertilizer was prepared by dissolving 1,048 g of 20-10-20 into a 20-gallon container of water. The fertigation was done using a hozon device (1:16).

To equalize the total plant surface area between simple and complex plants I first established a correlation between leaf surface area and its mid rib length. Leaves of diverse sizes, ranging from very small to large, were scanned using the scanner HP scanjet 4850® and the surface area of their images was measured using the software Scion Image®. Subsequently, the correlation between the surface area values and the length of mid rib of the leaves was established (Figure 1 and Appendix B). Based on the equation $y = 1.091x^2 - 5.817x + 19.477$ which was obtained from that regression I created a one-way table in which entering any leaf mid rib length value would allow me to know the correspondent value for leaf surface area (Table 1). Second, to measure the surface area of stems and petioles I constructed a two-way table (Table 2) based on the cylinder formula $2*\pi*r*h$ (π =3.14, r = radius of the cylinder, h = height of the cylinder). By entering the values of petiole/stem diameter and length it allowed me to know the surface area of those plant parts. At last, to measure the total plant surface area I simply summed up the surface area of all parts of each plant (leaf, stem and petioles). The surface areas of the leaves were multiplied by two because table 1 gives the values only for one side of the leaf. To construct the two divergent plant architectures with approximately same total plant surface I first measured the small plants (the ones that would serve as complex plant) and then pruned (removed a few leaves) on the large ones (the ones that would serve as simple plant) so that the latter would have approximately the same total plant surface area as the former. Additionally, I also did a sight prune on the apex of the complex plants removing a newly emerged seventh leaf. This was done just in order to experimentally make sure that all experimental units received the same treatment, the prune. This prune was done approximately 4 days after the transplant of the complex plants. Given the fact that most of the plants grow uniformly through time it was possible to guess how the plants would be pruned every time prior to an experiment. The plants obtained were cucumber plant architectures that differed in leaf number and leaf size, but had approximately the same total surface area (Figure 2). Simple and complex plant had individual parts (stem, petiole and leaf) that differed in dimensions (surface area). Simple plants had longer and thicker internodes, longer and thicker petioles and larger leaves compared to complex plants (Table 2.3). Although simple plants had fewer internodes, they were still higher compared to complex plants. This was so because the distance from the growth media to the first internode was far longer on simple plants (Table 2.3). These plant characteristics could be recreated consistently regardless of the time of the year.

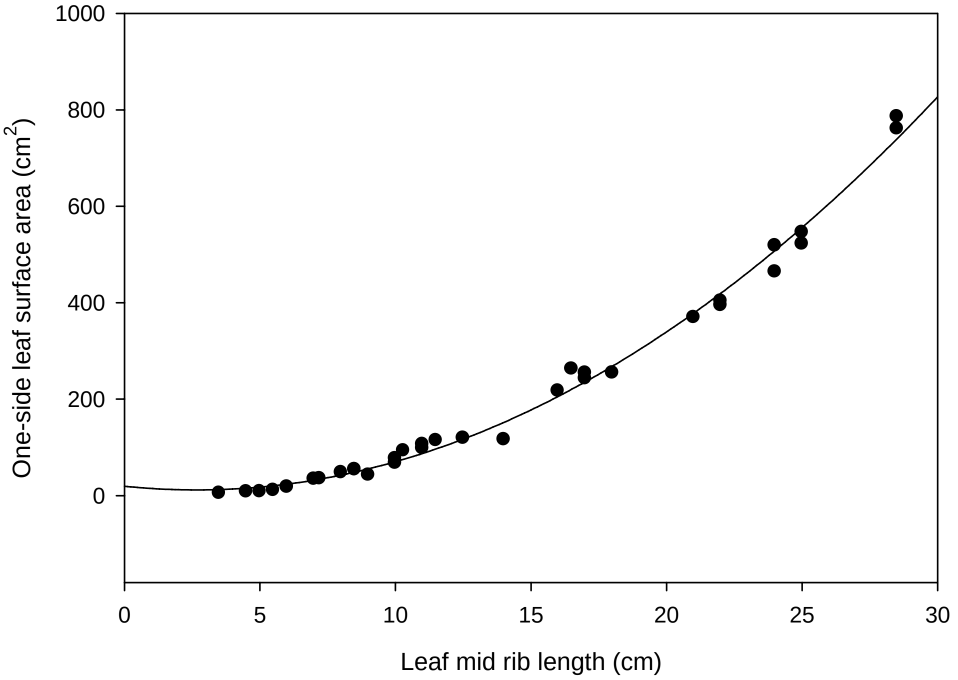

Figure 2-1 Regression between cucumber leaf mid rib length and surface area. (equation: $y = 1.09x^2 - 5.81x + 19.47$, R^2, $P < 0.0001$)

Figure 2-2 Typical cucumber plant architectures used during the experiments ("simple" architecture on left and "complex" architecture on right)

Table 2-1 One-sided cucumber leaf surface area estimate based on the leaf mid rib length

Mid rib length (cm)	**Leaf surface area (cm^2)**	Mid rib length (cm)	**Leaf surface area (cm^2)**
2.00	**12.21**	11.00	**87.50**
2.50	**11.75**	11.50	**96.87**
3.00	**11.85**	12.00	**106.78**
3.50	**12.48**	12.50	**117.23**
4.00	**13.67**	13.00	**128.24**
4.50	**15.39**	13.50	**139.78**
5.00	**17.67**	14.00	**151.88**
5.50	**20.49**	14.50	**164.51**
6.00	**23.85**	15.00	**177.70**
6.50	**27.76**	15.50	**191.43**
7.00	**32.22**	16.00	**205.70**
7.50	**37.22**	16.50	**220.52**
8.00	**42.77**	17.00	**235.89**
8.50	**48.86**	17.50	**251.80**
9.00	**55.50**	18.00	**268.26**
9.50	**62.68**	18.50	**285.26**
10.00	**70.41**	19.00	**302.81**

Table 2-2 Estimate of the surface area (cm^2) of petioles and stems of cucumber plants by using the mathematical formula of cylinder (diameter*π*length)

Petiole or stem length (cm)										
		2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Diameter (cm)	**0.20**	1.26	1.88	2.51	3.14	3.77	4.40	5.02	5.65	6.28
	0.30	1.88	2.83	3.77	4.71	5.65	6.59	7.54	8.48	9.42
	0.40	2.51	3.77	5.02	6.28	7.54	8.79	10.05	11.30	12.56
	0.50	3.14	4.71	6.28	7.85	9.42	10.99	12.56	14.13	15.70
	0.60	3.77	5.65	7.54	9.42	11.30	13.19	15.07	16.96	18.84
	0.70	4.40	6.59	8.79	10.99	13.19	15.39	17.58	19.78	21.98
	0.80	5.02	7.54	10.05	12.56	15.07	17.58	20.10	22.61	25.12
	0.90	5.65	8.48	11.30	14.13	16.96	19.78	22.61	25.43	28.26
	1.00	6.28	9.42	12.56	15.70	18.84	21.98	25.12	28.26	31.40

Table 2-3 Measurements of simple and complex cucumber plant architectures

Measurements of cucumber stems, petioles and leaves									
plt. arch.	N	pt Ø *	pt lg *	st Ø *	d *	int *	hgt *	lf s.a *	plt s.a ^{NS}
complex	18	0.32 ± 0.005	3.61 ± 0.06	0.86 ± 0.02	6.89 ± 0.14	0.93 ± 0.02	12.61 ± 0.26	82.98 ± 1.87	554.8 ± 10.05
simple	20	0.45 ± 0.008	7.4 ± 0.09	1.04 ± 0.02	10.5 ± 0.24	2.66 ± 0.05	15.34 ± 0.37	240.6 ± 4.11	551.91 ± 9.90

N= number of plants used, pt Ø= mean petiole diameter (cm), pt lg= mean petiole length (cm), st Ø= mean stem diameter (cm), d= mean distance from the soil to first internode (cm); int= mean length internode (cm); hgt, mean plant height (cm), lf s.a= mean leaf surface area (cm^2), plt s.a= total mean plant surface area (cm^2)

* Means within the same column are significantly different at $p<0.01$(t-test)

^{NS} Means within the same column are considered equal (t-test)

CHAPTER 3 - The effects of cucumber plant architecture and prey distribution on the prey-finding time of *Phytoseiulus persimilis* (Acari: Phytoseiidae)

Introduction

The foraging efficiency of natural enemies is broadly defined as their ability to acquire hosts or prey. Therefore, foraging efficiency may play a key role in the development, survival and reproduction of natural enemies. The foraging efficiency of a natural enemy may be affected by both intrinsic and extrinsic factors. One of the major extrinsic factors that affects foraging efficiency is the plant on which natural enemies search for hosts or prey. For example, a number of studies have shown either a positive or negative influence of plant morphological features on natural enemy's foraging. These include leaf trichomes (Obrycki, 1984, 1986; Krips *et al*., 1999), surface smoothness of leaves (Carter *et al*., 1984; Kareiva and Sahakian, 1990), leaf and plant connectedness (Marquis *et al*., 2002; Skirvin. and Fenlon, 2003), plant size (Thorpe, 1985; Cloyd and Sadof, 2000), leaf number (Stamp and Browers, 1993; Cloyd and Sadof, 2000) and plant surface area or volume (Burbutis and Koepke, 1981; Kanour and Burbutis, 1984; Maini and Burgio, 1990). Some of these structural features, such as leaf and plant connectedness, plant size, leaf number and plant surface area can be part of plant architecture.

The impact of plant architecture on tritrophic interactions and, thus, biological control, has been documented. For instance, Grevstad and Klepetka (1992) observed that the architecture of cruciferous plants can substantially alter the foraging success of various ladybird beetles species by impeding or facilitating movement, causing them to fall, or otherwise making prey less accessible. Plant species exhibiting differences in architectural traits can also modify the functional response of predators. For example, Skirvin and Fenlon (2001) reported that the number of eggs of the twospotted spider mite, *Tetranychus urticae* Koch, consumed by its predator, *Phytoseiulus persimilis* Athias-Henriot, was lower on plant species with hairy leaves and higher on those with smoother leaves. Cloyd and Sadof (2000) reported that the attack rate of *Leptomastix dactylopii* (Howard), a parasitoid of citrus mealybug *Planococcus citri* (Risso), was negatively correlated with the number of leaves of the host plant.

One method of measuring the foraging efficiency of a predator or parasitoid on plant with different architectural traits is to quantify its prey-finding time. Prey-finding time can be defined as the amount of time required by the predator to encounter its first prey after being released. Thus, predators with low values of prey-finding time will encounter prey more quickly, and thereby be more efficient at foraging; and the opposite holds for high values of prey-finding time. A number of studies have been conducted to gain a better understanding of the effects of plant architecture on insects that are considered to be natural enemies. However, very few of these have involved predatory mites. Therefore, the aim of this study was to gain a better understanding of the effects of plant architecture (leaf number and size) on the foraging efficiency of the predatory mite, *Phytoseiulus persimilis*. I hypothesized that the prey-finding time of *P. persimilis* would increase with plant architectural complexity (number of leaves). In addition, it is possible that there will be an interaction between plant architecture and prey distribution. The specific objectives were to: 1) quantify the prey-finding time of *P. persimilis* when foraging on cucumber plants with different numbers of leaves and different leaf sizes, but similar overall surface areas, 2) evaluate the effect of prey distribution on prey-finding time, and 3) assess whether there is an interaction between plant architecture and prey distribution.

Materials and Methods

Mite colonies and general experimental conditions

Twospotted spider mite

Tetranychus urticae were obtained from colonies maintained in greenhouses at Kansas State University, Manhattan – KS, under a photoperiod of 16:8 L:D, relative humidity of 60 ± 10% and temperature of 25 ± 2^0C. Twospotted spider mites were reared on lima bean (*Phaseolus lunatus*) plants inside 0.3 x 0.6 m plastic flats. New lima beans were added every other day.

Predatory mites

Phytoseiulus persimilis was obtained from Koppert Inc (Romulus, MI) and kept on spider mite-infested lima bean plants inside a 0.01 m^3 plastic chambers with a fine mesh covering the tops and sides. Newly infested lima bean plants were added every other day. The *P. persimilis* population was maintained under a photoperiod of 16:8 L:D, relative humidity of 60 ± 10% and temperature of 25 ± 2^0C. All experiments were conducted in greenhouses under similar conditions to the ones described above.

Prey-finding time of Phytoseiulus persimilis in response to different plant architectures and prey distributions (predator placed at the base of the plant)

Complex and simple plant architectures were created as described in chapter 2. This experiment was set up as a completely randomized design. The structure was a 2 x 2 factorial which consisted of 2 plant architectures and 2 prey distributions resulting in 4 treatment combinations. There were 20 replicates for a total of 80 experimental units (plants). The plant architectures tested were simple (2 large leaves) and complex (6 small leaves). The prey were distributed either on a single basal leaf or on all leaves. Leaves designated to receive spider mites were infested by transferring a 1 cm^2 bean leaf containing 10 adult female *T. urticae* onto the experimental cucumber plants and holding the squares in place with toothpick tips. The *T. urticae* females were allowed to migrate off onto the cucumber leaves, lay eggs, and produce webbing for a period of 24 hours after which a 2-hour starved female *P. persimilis* was positioned at the base of the main stem of each plant with the aid of a fine-haired paint brush. To assess prey-finding time, observations of all infested leaves were done for the presence/absence of *P. persimilis* every 30 minutes for a 2-hour period.

Prey-finding time of Phytoseiulus persimilis in response to different plant architectures and prey distributions (predator placed on the top of the plant)

This experiment was similar to the one described above except that the predator was positioned on the top of the plant (on the main stem, 1-2 cm above the insertion of the highest leaf) and there were 12 to 14 replicates. We had fewer replicates because some of the plants died.

Prey-finding time of Phytoseiulus persimilis in response to different plant architectures and prey densities

This experiment was a factorial 2 x 2 with 2 levels of plant architecture and 2 levels of prey density. There were 10 replicates, and the treatments were distributed in a completely randomized design. The plant architectures tested were the same as the first experiment. Predators were exposed to one of two prey densities: 10 or 20 adult female *T. urticae* per leaf. To increase the likelihood that *P. persimilis* would have an equal chance of prey encounter on both plant architectures, half of the leaves were infested with *T. urticae*. Thus, for the simple plant architecture the basal leaf was infested and the other was left uninfested. On the complex plant, three alternate leaves (1st, 3rd and 5th, from the base to the top) were infested, theoretically giving predators a 0.5 probability of encountering an infested leaf, and perhaps the prey patch. The predator was positioned at the base of the plant 24 h after prey were released. The duration and schedule for assessing prey-finding time by *P. persimilis* were the same as described in the previous experiments.

Statistical analyses

The prey-finding times were assigned to one of 5 categories: predators that encountered the first prey patch within 0-30, 31-60, 61-90, or 91-120 minutes, or did not locate a prey patch within the 2-hr experiment. A non-parametric analysis (Kruskal-Wallis test) was used to test for differences in prey-finding time. However, the Kruskal-Wallis test cannot assess differences among treatment means nor treatment interactions. Therefore, once a significant treatment effect was shown, I conducted an analysis of variance using PROC GLM (SAS®). To do so I arbitrarily graded the predators accordingly to the time interval in which they encountered a prey patch or did not encounter it. The grades were 1, 2, 3 4 and 5 for the intervals of 0-30, 31-60, 61-90, 91-120 minutes or did not find prey, respectively. Values closer to 1 represented faster encounters and values closer to 5 represented slower or no encounters.

Results

Prey-finding time in response to different plant architectures and prey distributions when Phytoseiulus persimilis was placed at the base of the plant

There was a significant treatment effect (Kruskal-Wallis; chi-square= 28.78 and *p*= 0.012). More predators failed to find a prey patch during 2-h tests on cucumber plants with a simple architecture regardless of prey distribution than on plants with other treatment combinations (Figure 3.1). Plants with a more complex architecture and all leaves infested, the highest percentage (85%) of predators found a prey patch, and they did so in the shortest time (all within 0-30 min) (Table 3.1 and Figure 3.4). The fewest predators found a prey patch (40%) on plants with only two leaves (simple architecture) regardless of plant architecture. On the treatments 'complex + base leaf' (complex architecture with single base leaf infested) and ‘simple + all leaves’ (simple architecture with all leaves infested) a relatively low percentage of predators encountered a prey patch during the interval 0-30 minute; however, there was a large increase in the number of predators that found a prey patch during the following interval (31-60 minutes) (Table 3.1 and Figure 3.4). Very few encounters of prey patches occurred between 61-90 minutes or 91-120 minutes (Figure 3.2). There was a significant effect of both plant architecture (GLM; F = 9.74 and p = 0.0025) and prey distribution (GLM; F= 8.91 and p = 0.0038) on prey-finding time of *P. persimilis*. However, the interaction between plant architecture and prey distribution was not significant (GLM; F = 0.04and p = 0.85). Predators foraging on ‘complex + all leaves’ were able to encounter prey patch the fastest, followed by predators foraging on ‘complex + base leaf’ and ‘simple + all leaves’; while predator foraging on ‘simple + base leaf’ took the longest to encounter prey patch (Table 3.2).

When *P. persimilis* had a choice of prey-infested leaves (all leaves infested) on plants with complex architecture, most found a prey patch on the lowest two leaves first; thereafter the percentage of predators that found prey patches decreased the further away the leaf was from the predator positioning point (Figure 3.7). In contrast to that, when *P. persimilis* had a choice of prey-infested leaves on simple plants, most found prey patch on the upper most leaf (Figure 3.8).

Prey-finding time in response to different plant architectures and prey distributions when Phytoseiulus persimilis was placed on the top of the plant

There was a significant effect due to treatment (Kruskal-Wallis; Chi square = 34.77 and p < 0.01). When predators were positioned on the top of the plant, fewer found a prey patch on complex (6 small leaves) and simple (two large leaves) plants with a single basal leaf infested compared to the other treatments (Figure 3.2). However, by shifting the point of where the predator was positioned from the base to the top of the plant it was possible to increase the overall success of predators in encountering a prey patch during the experiment. Nearly all predators foraging on ‘complex’ plants with all leaves infested were able to find a prey patch within 30 minutes, and all found a prey patch within the 31-60 minute interval (Table 3.3 and Figure 3.5). Approximately 60% of the predators foraging on ‘simple’ plants with all leaves infested found a prey patch within 0-30 minutes (Table 3.3 and Figure 3.5). Thereafter prey patch finding increased by 25 and 16.67% over the next two intervals, reaching 100% success in 61-90 minutes (Table 3.3 and Figure 3.5). There was a difference in prey-finding time between ‘simple’ and ‘complex’ plants with only the base leaf infested that was kept constant through time (Table 3.5 and Figure 3.5). However, the percentage of predators that were successful at finding a prey patch on ‘complex’ plants was always lower, for all time intervals, than on ‘simple’ plants (Table 3.2 and Figure 3.5). Using the categorical (grading) analysis of prey-finding times, there was a significant effect from prey distribution (F= 39.88, *p*>0.0001) and a significant interaction between plant architecture and prey distribution (F= 5.87, *p*>0.019). Predators foraging on ‘complex’ plants with all leaves infested, and on ‘simple’ plants with all leaves infested, encountered the prey patch more rapidly than those in the other treatments (Table 3.4). Predators foraging on ‘simple’ plants with only the base leaf infested found prey at an intermediate rate (time grade = 2.75) compared to other treatments (Table 3.4). Predators foraging on ‘complex’ plants with only the base leaf infested took the longest to encounter a prey patch (time grade = 3.68) (Table 3.4).

Treatments where *P. persimilis* were placed at the top of complex plants with all leaves infested, they tended to find prey patches equally well on the upper two-thirds of plants (~21-29%); whereas a very low percentage of the predators found the first prey patch when it was on the lowest two leaves (Figure 3.9). When foraging on ‘simple’ plants with both leaves infested, predators encountered the prey patch equally on the two leaves (Figure 3.10).

Prey-finding time of Phytoseiulus persimilis in response to different plant architectures and prey densities (predator placed at the base of the plant)

There was a marginal difference among the treatment effects (Kruskal-Wallis, chi-square = 18.12 and *p*= 0.07). Nevertheless, using the categorical (grading) analysis of prey-finding times it was possible to observe a significant effect of plant architecture on the prey-finding time of *P. persimilis* (GLM; F=11.15 and *p*=0.002). However, neither prey density (GLM; F=0.09 and *p*= 0.76) nor the interaction between plant architecture and prey density (GLM; F= 0.26 and *p*= 0.61) were significant. The predators foraging on ‘complex’ plants were able to find prey patch more quickly than predators foraging on ‘simple’ plants regardless of prey density (table 3.6). Nearly all successful predators on ‘complex’ plants found a prey patch within the first 30 minutes (Table 3.5 and Figure 3.6). The percentage of predators encountering a prey patch on either ‘simple + high’ or ‘simple + low’ was low at all time intervals (Table 3.5 and Figure 3.6).

Discussion

Three factors affected the prey-finding time and percentage of predators that encountered a prey patch within the timeframe of the experiment (2 hours): (1) place (base or top of plant) where the predatory mite was positioned, (2) prey distribution, and (3) plant architecture (leaf number). When predators were positioned at the base of 'complex' plants (6 small infested leaves), they were more likely to encounter a prey patch on the lower leaves. When the predatory mite was positioned at the top of the plant, proportionately more predators encountered prey patches on the upper two-thirds of the plant than on the lower third. On plants with simple architecture (2 large infested leaves), the pattern was different. Predators positioned at the base of the plant were twice as likely to find a prey patch on the upper leaf than on the lower one. It is possible that the predator foraging on those plants and positioned at the base might be missing the first petiole and hitting the uppermost one. And predators positioned on the top found prey patches equally well on the upper and lower leaves. These differences in number of predators being able to find prey patches on either lower or upper leaf may be due to differences in the distances between the place where the predator was positioned and the closest petiole. Differences in foraging success between plant architectures may be related to differences in distance and/or surface area between the positioning point of the predator and the prey patch. It is expected that the greater the distance and/or surface area between the positioning point of the predator and the prey patch, the more time would be required for *P. persimilis* to find that prey patch. For instance, predators foraging on the treatment 'complex + base', when placed on the top, would have a greater surface area to cover before getting onto the prey patch whereas a predator released at the base would have much smaller surface area to cover and consequently would be able to find prey patch more rapidly. The opposite holds for the treatment 'simple + base'. A work done by Stavrinides and Skirvin (2003) suggests that *P. persimilis* encounters prey more quickly on leaves close to the point where the predator was positioned. The finding of their study is in accordance with what we observed on the treatment 'complex + all' where predators positioned on the top tended to encounter prey patch first at the superior third part of the plant while predators positioned at the base tented to encounter prey patch first at the inferior third of the plant.

Plant architectural complexity also had an effect on prey-finding time and success of *P. persimilis*. The number of leaves infested or not infested has played an important role in determining the prey-finding time of *P. perismilis*. That is, considering the same plant architecture, *P. persimilis* took longer to find a prey patch on those plants with a higher ratio of uninfested to infested leaves. This outcome may be related to the number of "wrong choices" that can be made by the predator, e.g. turning onto a petiole of an uninfested leaf, would likely increase as the ratio of uninfested /infested leaves. This explanation is supported by the results of our experiments where *P. persimilis* found prey patch more quickly on 'complex + all' and 'simple + all' compared to 'complex + base' and 'simple + base'. Additionally, although comparing two treatments from different experiments, it was still clear that increasing the number of infested leaves on complex plants from 1 to 3 helped to lower the prey finding time of *P. persimilis* (compare figures 3.4 and 3.6). This finding is in agreement with work done by Cloyd and Sadof (2000). In their study they found that the number of leaves a coleus plant *Solenostemon scutellarioides* (L.) Codd had was negatively correlated with the attack rate of the parasitoid *Leptomastix dactylopii* on citrus mealybugs; however, they did not control for host distribution (number of uninfested and infested leaves) which was random. Therefore, my study provides additional evidence that in addition to the effect of leaf number on foraging success of natural enemies, the proportion of uninfested and infested leaves (prey distribution) is also important. My experiments also showed that there was neither an effect of prey density itself on the prey-finding time of *P. persimilis* nor an interaction between prey density and plant architecture. We envisioned that plants with higher densities of *T. urticae* would either be surrounded by higher concentrations of kairomones or produce greater quantities of synomones. The reason why prey density did not have any effect might be because either the time *T. urticae* was feeding on the plant (24 hours) was not long enough, or its density was not large enough to induce the production of volatiles. Accordingly, Takabayashi *et al.* (1994) showed that *Phytoseiulus persimilis* will only respond to odors produced by attacked cucumber plants when the latter are infested with at least 800 *Tetranychus urticae*. Nonetheless, the approach of having such high number of spider mites (at least 800) on our plants would not be feasible. It is possible that at this high density, prey-finding time would be affected by factors that obscure the effects of either plant architectural complexity or prey distribution. Furthermore, the time duration of the infestation ought to be at least three days accordingly to a work done with cucumber plants in greenhouse by Janssen (1999). However, in our work we could not wait this long otherwise plant architecture would have changed and spider mites would have dispersed from leaves. Another procedure that could have influenced spider mite-induced plant volatiles is the pruning of leaves, which was done to manipulate plant architectural complexity. But accordingly to Takabayashi *et al*. (1994), cucumber plants do not emit or emit volatiles in minor quantities in response to mechanical damage.

The results obtained in this study serve to show that it might be possible to create a model based on plant architecture, e.g. number of leaves, and prey distribution within the plant to optimize the predator-prey-release ratio and aid the decision of where and when to release predatory mites during twospotted spider mite infestations. For example, our results show that the predatory mite may be less efficient on plants with complex architecture (many leaves) and having prey distributed contagiously. In that case either a release closer to the infested spot (less realistic approach) or a higher number of predatory mites might be necessary to increase the efficiency of the biological control programs using *Phytoseiulus persimilis*.

Figures and Tables

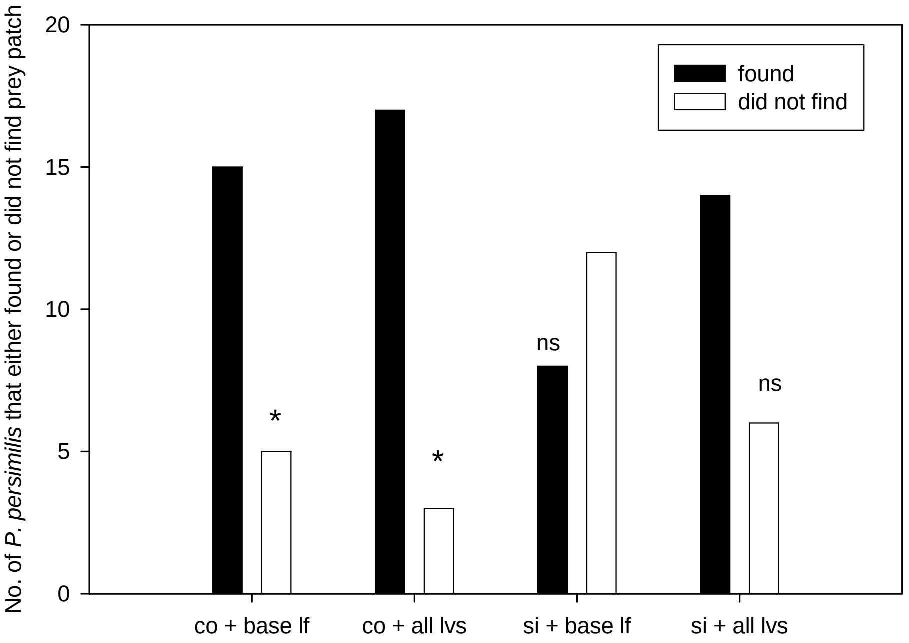

Figure 3-1 Numbers of *Phytoseiulus persimilis* that either found or did not find prey patch in 2-hour experiment when the predators were placed at the base (main stem) of a cucumber plant with a 'simple' (2 large leaves) and 'complex' (6 small leaves) architecture. Leaves were infested with 10 female adults of *Tetranychus urticae*. Treatment combinations: co + base lf = complex plants with a single base leaf infested, co + all lvs = complex plant with all leaves infested, si + base lf = simple plant with a single base leaf infested, si + all lvs = simple plant with all leaves infested. N = 20.* Paired bars differ significantly at $p< 0.05$ (Chi-Square), ^{NS} Paired bars do not differ significantly at $p< 0.005$ (Chi-Square).

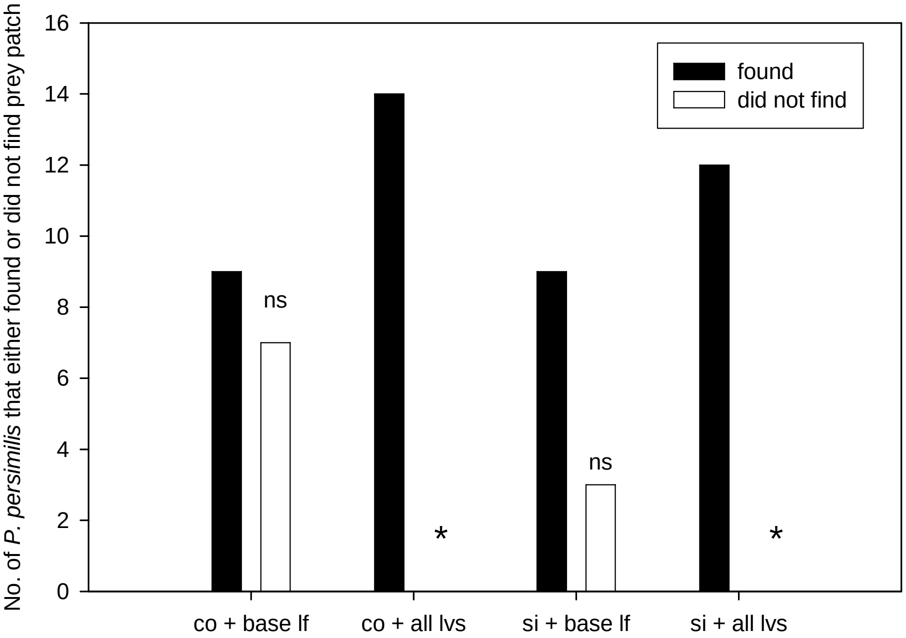

Figure 3-2 Numbers of *Phytoseiulus persimilis* that either found or did not find prey patch in 2-hour experiment when predators were placed at the top of a cucumber plant with a simple (2 large leaves) or complex (6 small leaves) architecture. Leaves were infested with 10 female adults of *Tetranychus urticae*. Treatment combinations: co + base lf = complex plants with single base leaf infested, co + all lvs = complex plant with all leaves infested, si + base lf = simple plant with single base leaf infested, si + all lvs = simple plant with all leaves infested. N = 12-14. * Paired bars differ significantly at $p< 0.05$ (Chi-Square), ^{NS} Paired bars do not differ significantly at $p< 0.005$ (Chi-Square).

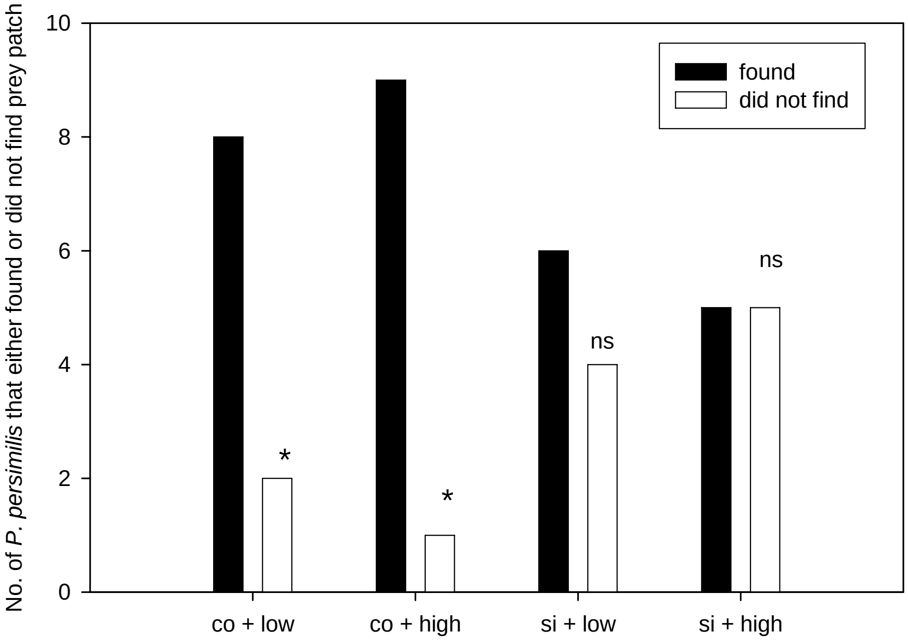

Figure 3-3 Numbers of *Phytoseiulus persimilis* that either found or did not find prey patch in 2-hour experiment when predators were placed at the base of cucumber plants with 'simple' (2 large leaves) and 'complex' (6 small leaves) architectures. Prey distribution: 'simple' had basal leaf infested, 'complex' had 3 leaves infested (1st, 2nd and 3rd , from the bottom to the top). Treatment combinations: co + low =complex plant with 10 female adults of *Tetranychus urticae* on each infested leaf, co + high = complex plant with 20 female adults of *Tetranychus urticae* on each infested leaf, si + low = simple plant with 10 female adults of *Tetranychus urticae* on single base leaf, si + high = simple plant with 20 female adults of *Tetranychus urticae* on a single base leaf. N=10. * Paired bars differ significantly at $p< 0.05$ (Chi-Square), ^{NS} Paired bars do not differ significantly at $p< 0.005$ (Chi-Square).

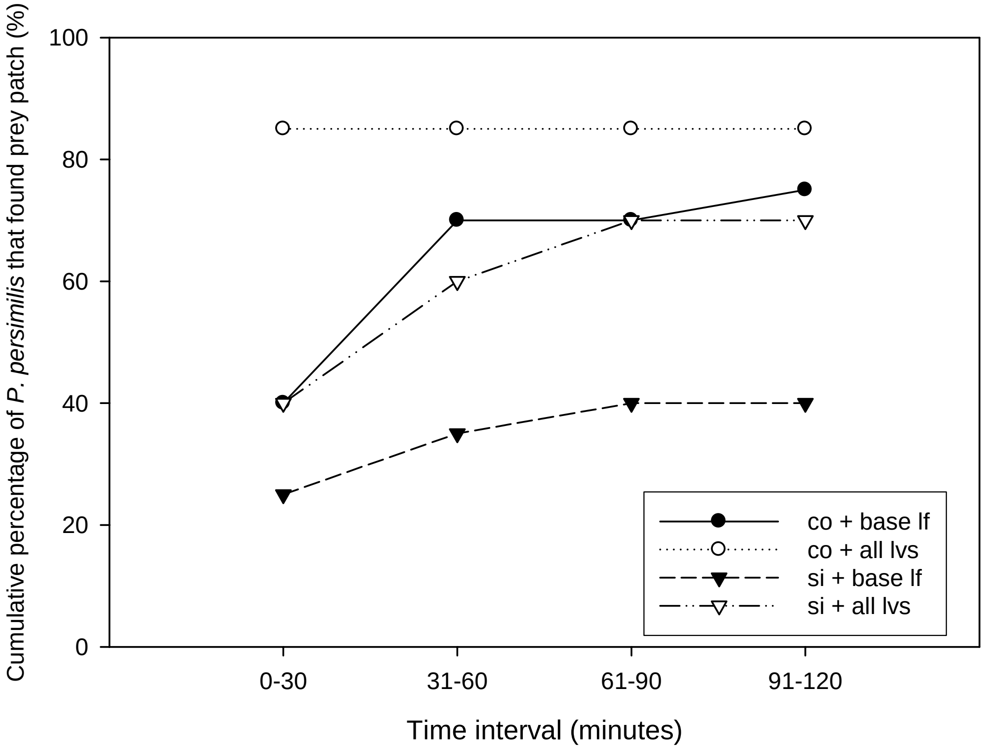

Figure 3-4 Prey-finding time of *Phytoseiulus persimilis* when placed at the base (main stem) of the plant. Leaves were infested with 10 female adults of *Tetranychus urticae*. Treatment combinations: co + base lf = complex plants with single base leaf infested, co + all lvs = complex plant with all leaves infested, si + base lf = simple plant with single base leaf infested, si + all lvs = simple plant with all leaves infested. N=20.

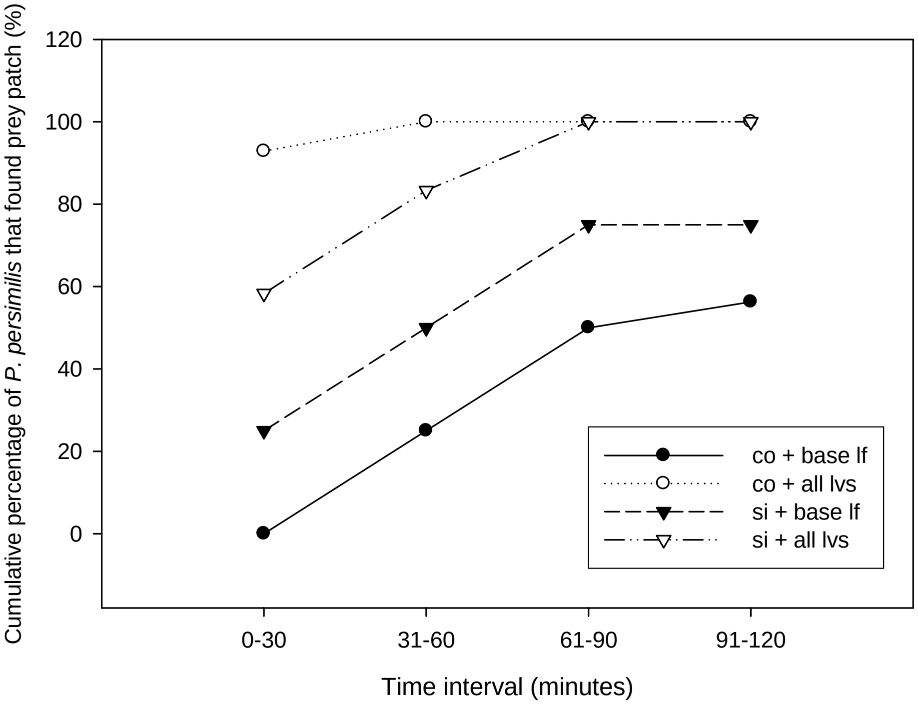

Figure 3-5 Prey-finding time of *Phytoseiulus persimilis* **when placed on the top (main stem) of the plant. Treatment combinations: co + base lf = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, co + all lvs = complex plant with 10 adults of *Tetranychus urticae* on all leaves, si + base lf = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, si + all lvs = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 12-16.**

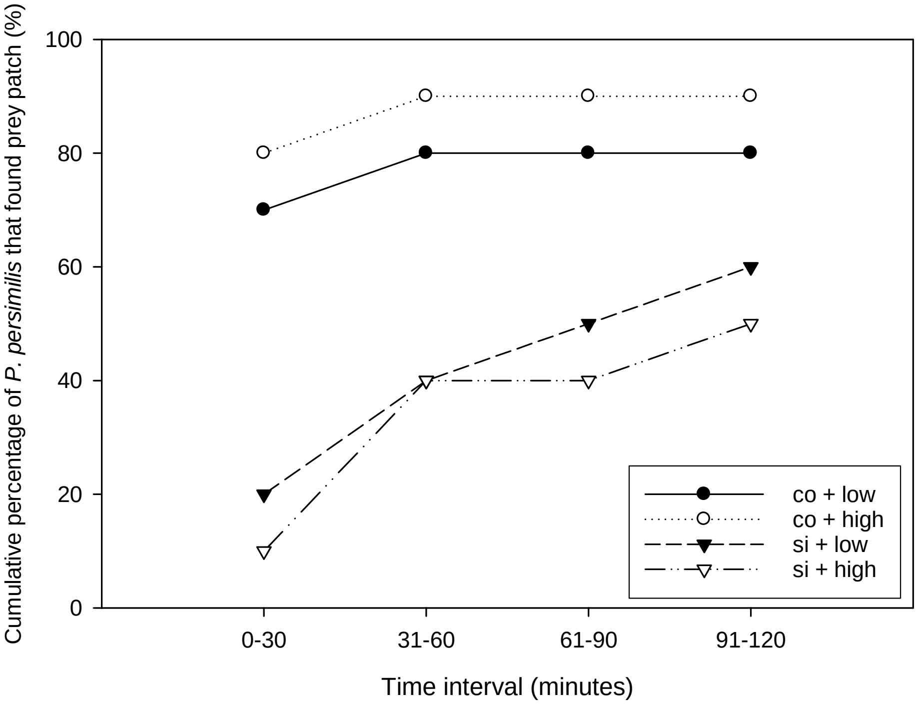

Figure 3-6 Prey-finding time of *Phytoseiulus persimilis* in response to different plant architectures and prey densities. Prey distribution: 'simple' had base leaf infested, 'complex' had 3 leaves infested (1st, 2nd and 3rd, from the bottom to the top). Treatment combinations: co + low = complex plant with 10 adults of *Tetranychus urticae* on each infested leaf, co + low = complex plant with 20 adults of *Tetranychus urticae* on each infested leaf, si + low = simple plant with 10 adults of *Tetranychus urticae* on the base leaf, si + high = 20 adults of *Tetranychus urticae* on the base leaf. N=10.

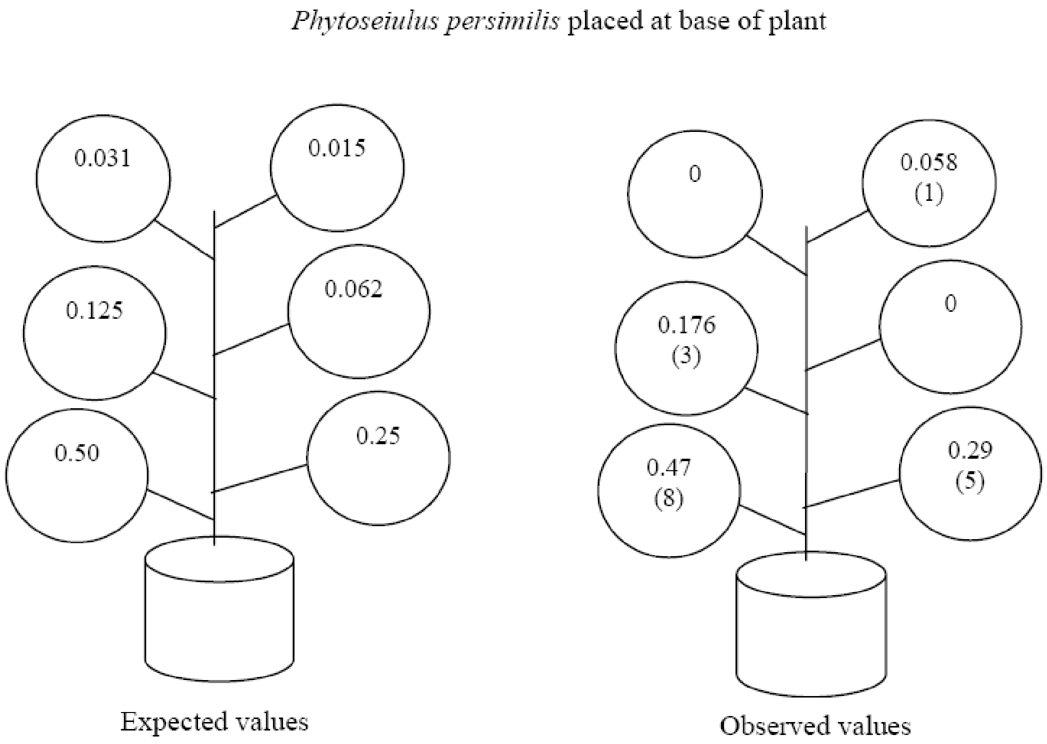

Figure 3-7 Expected and observed numbers of *Phytoseiulus persimilis* that first found prey patch on each leaf of 'complex' plants when placed at the base (main stem) of the plant. N=20.

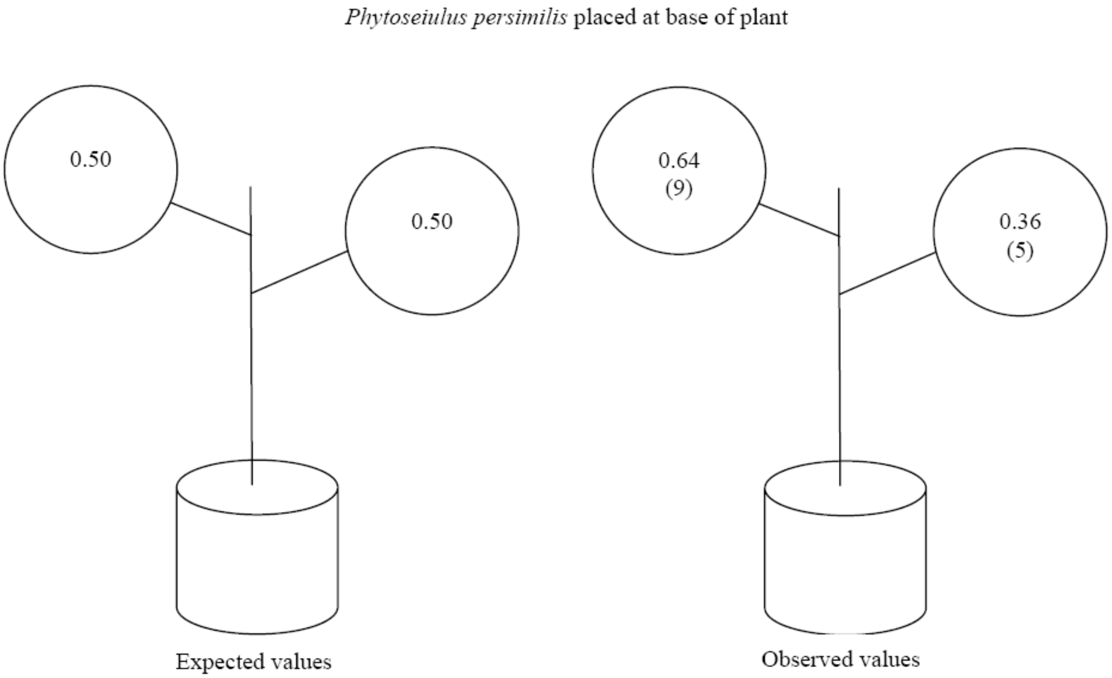

Figure 3-8 Expected and observed numbers of *Phytoseiulus persimilis* that first found prey patch on each leaf of 'simple' plants when placed at the base (main stem) of the plant. N=20.

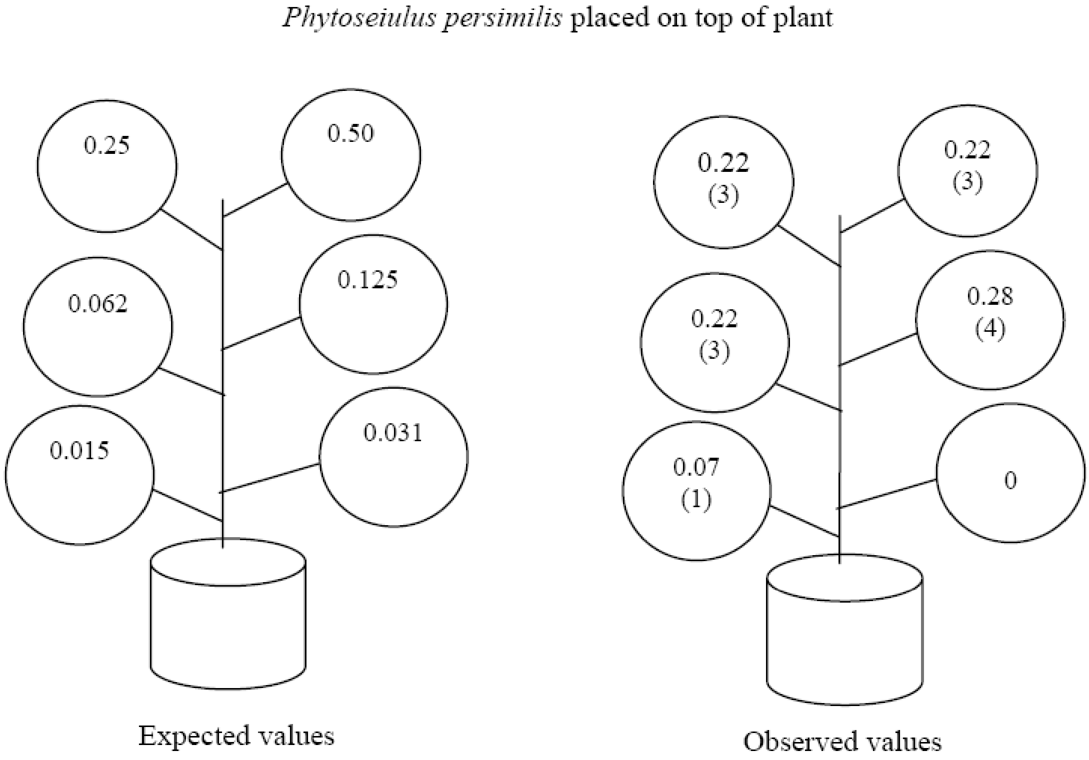

Figure 3-9 Expected and observed numbers of *Phytoseiulus persimilis* that first found prey patch on each leaf of 'complex' plants when placed on the top (main stem) of the plants. N=12.

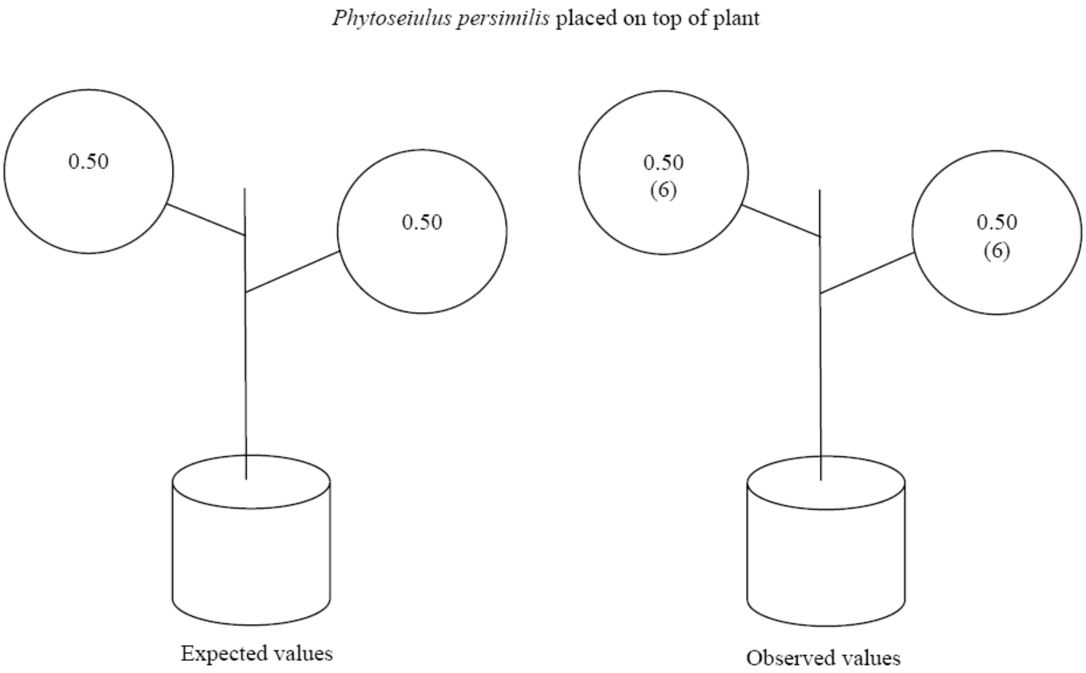

Figure 3-10 Expected and observed numbers of *Phytoseiulus persimilis* that first found prey patch on each leaf of 'simple' plants when placed on the top (main stem) of the plants. N=12.

Table 3-1 Number and percentage of *Phytoseiulus persimilis* that found or did not find a prey patch at different time intervals when placed at the base of the plants

Treatments		Time interval (minutes)					
Plant architecture	Prey distribution	0-30	31-60	61-90	91-120	did not find	Total
complex	base leaf	8 (40%)	6 (30%)	0	1 (5%)	5 (25%)	20 (100%)
complex	all leaves	17 (85%)	0	0	0	3 (15%)	20 (100%)
simple	base leaf	5 (25%)	2 (10%)	1 (5%)	0	12 (60%)	20 (100%)
simple	all leaves	8 (40%)	4 (20%)	2 (10%)	0	6 (30%)	20 (100%)
Total		38 (47.50%)	12 (15%)	3 (3.75%)	1 (1.25%)	26 (32.50%)	80 (100%)

Table 3-2 PROC GLM - Prey-finding time grading (scores) of *Phytoseiulus persimilis*

Plant architecture	Prey distribution	mean score ± SE	time interval (minutes)
complex	base leaf	2.45 ± 0.37 b	61-90
complex	all leaves	1.60 ± 0.37 a	31-60
simple	base leaf	3.60 ± 0.37 c	91-120
simple	all leaves	2.60 ± 0.37 b	61-90

-Mean values closer to 1 = predator finds prey patch more rapidly whereas values closer to 5 = predator takes longer to find prey patch

-Means followed by different letters (last column) differ significantly at $P < 0.05$

Table 3-3 Number and percentage of *Phytoseiulus persimilis* that found or did not find prey patch at different time intervals when placed on the top of the plants

Treatments		Time interval (minutes)					
Plant architecture	Prey distribution	0-30	31-60	61-90	91-120	did not find	Total
complex	base leaf	0	4 (25%)	4 (25%)	1 (6.25%)	7 (43.75%)	16 (100%)
complex	all leaves	13 (92.86%)	1 (7.14%)	0	0	0	14 (100%)
simple	base leaf	3 (25%)	3 (25%)	3 (25%)	0	3 (25%)	12 (100%)
simple	all leaves	7 (58.33%)	3 (25%)	2 (16.67%)	0	0	12 (100%)
Total		23 (42.59%)	11 (20.37%)	9 (16.67%)	1 (1.85%)	10 (18.52%)	54 (100%)

Table 3-4 PROC GLM - Prey-finding time grading (scores) of *Phytoseiulus persimilis*

Plant architecture	Prey distribution	mean grade ± SE	time interval (minutes)
complex	base leaf	3.68 ± 0.27 c	91-120
complex	all leaves	1.07 ± 0.29 a	31-60
simple	base leaf	2.75 ± 0.31 b	61-90
simple	all leaves	1.58 ± 0.31 a	31-60

Mean values closer to 1 = predator finds prey patch more rapidly whereas values closer to

5 = predator takes longer to find prey patch

Means followed by different letters (last column) differ significantly at $P<0.05$

Table 3-5 Number and percentage of predators that found or did not find a prey patch at different time intervals (testing different prey densities)

Treatments		Time interval (minutes)					
Plant architecture	Prey density	0-30	31-60	61-90	91-120	did not find	Total
complex	low	7 (70%)	1 (10%)	0	0	2 (20%)	10 (100%)
complex	high	8 (80%)	1 (10%)	0	0	1 (10%)	10 (100%)
simple	low	2 (20%)	2 (20%)	1 (10%)	1 (10%)	4 (40%)	10 (100%)
simple	high	1 (10%)	3 (30%)	0	1 (10%)	5 (50%)	10 (100%)
Total		18 (45%)	7 (17.5%)	1 (2.5%)	2 (5%)	12 (30%)	40 (100%)

Table 3-6 Prey-finding time grading (scores) of *Phytoseiulus persimilis*

Plant architecture	Prey density	mean grade ± SE	time interval (minutes)
complex	low	1.90 ± 0.49 a	31-60
complex	high	1.50 ± 0.49 a	31-60
simple	low	3.30 ± 0.49 b	91-120
simple	high	3.40 ± 0.49 b	91-120

-Mean values closer to 1 = predator finds prey patch more rapidly whereas values closer to 5 = predator takes longer to find prey patch

-Means followed by different letters (last column) differ significantly at P<0.05

CHAPTER 4 - Prey-consumption rate and oviposition of *Phytoseiulus persimilis* (Acari: Phytoseiidae) when foraging on cucumber plants with different architectures and prey distributions

Introduction

Biological control of spider mites and insect pests has increased notably during the past years. Increased use of biological control is most likely due to two factors: current governmental and consumer pressure to reduce chemical inputs on crops; and increased incidence of pesticide resistance resulting from selection pressures associated with widespread or exclusive use of chemical control. Nonetheless, biological control programs require practitioners to have a broader knowledge of pest management than pesticide users. This may be so because many more variables affect a biological control agent compared to pesticides. Those variables include both intrinsic and extrinsic factors. One of the most interesting, and perhaps most influential, extrinsic factor is the host plant on which insect pests live. It has been well documented that the host plant has major impacts on the efficiency and efficacy of predators and parasitoids (Rabb and Bradley, 1968; McGovern and Cross, 1976; Bergman and Tingey, 1979; Belcher and Thurston, 1982; Barbosa and Letourneau, 1988; Dicke and Sabelis, 1989; Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992, Peitsch *et al*. 1992; Coll and Bottrell, 1994). A particular segment of the study of host plant influences on natural enemies, which has gained considerable attention by researchers lately, is the effects of plant architecture. Plant architecture can be described as the spatial arrangement of leaves, stems and branches any point in time (Cloyd and Sadof, 2000). Plant architecture can be regulated by genetic as well as environmental factors. Factors that alter plant structure include light, water and soil nutrients (DeReffye *et al*. 1995). Additionally, plant architecture may also be manipulated artificially by plant breeding practices, removal of terminal buds and use of plant growth regulators (Ball, 1985). Plant architecture has been documented to affect natural enemies directly by mediating host plant choice (Romero and Vasconcellos-neto, 2005), altering movement and survival (Obrycki and Tauber,1984; Clarck & Messina, 1998) and modifying their behavior (Kareiva and Sahakian, 1990). Likewise, plant architecture can also affect natural enemies indirectly by influencing the availability of spatial refuges for prey

(Freese, 1995), the spatial distribution of prey/hosts (Clark & Messina, 1998) and the abundance and diversity of herbivores (Lawton, 1983). Furthermore, recent ecological studies have shown that plant architecture can have a major impact on the prey-consumption rate of predators. For instance, Legrand and Barbosa (2003) observed that *Coccinella septempunctata* ate more aphids on pea plants that had a simple architecture than on those with a complex architecture. Plant architecture can be a key factor affecting the development, reproduction and survival of natural enemies. Therefore, understanding the role that plant architecture plays in predator-prey interactions is important to achieve success in biological control programs. This study focused on the effects of different cucumber plant architectures (different leaf number and size) and prey distributions on the prey-consumption rate and oviposition of the predatory mite, *Phytoseiulus persimilis* when foraging for eggs of the twospotted mite, *Tetranychus urticae*. My hypotheses were: 1 - Assuming that *P. persimilis* finds a prey patch, consumes some prey and leaves, I predict that the predator will eat more prey and lay more of its own eggs on complex plants (many small leaves) having prey distributed evenly within plant canopy (regardless of prey density). 2 - Assuming that *P. persimilis* finds a prey patch and leaves it only after depletion, I predict that the predator will eat more prey and oviposit more on plants having leaves infested with higher prey density regardless of plant architecture and prey distribution.

Materials and Methods

Twospotted spider mite

Tetranychus urticae were obtained from our colonies which are reared at Kansas State University greenhouse facilities. *Tetranychus urticae* were reared on plastic flats 0.3 x 0.6 m containing from 40 to 60 young lima bean plants, *Phaseolus lunatus*. *Tetranychus urticae* were kept under photoperiod 16:8 L:D, relative humidity 60 ± 10% and temperature of 25 ± 2^0C. These mites were fed with new lima bean plants every other day.

Predatory mites

Phytoseiulus persimilis were obtained from Koppert Inc. (Romulus, MI), a commercial supplier of natural enemies, and kept on spider mite-infested lima bean plants inside 0.01 m^3 plastic chamber with a fine mesh covering its top and part of its lateral side. *Phytoseiulus persimilis* were fed with fresh spider mite-infested lima bean plants every other day. The *P.*

persimilis population was maintained under photoperiod 16:8 L:D, humidity 60 ± 10% and temperature of 25 ± 2^0C.

Prey-consumption rate assessment

Complex and simple plant architectures using cucumber plants *Cucumis sativus* were created as described in chapter 2. This experiment was conducted in the late summer and early fall, 2007, in a greenhouse at Kansas State University; Manhattan, KS. The temperature was 28 ± 2 ^{o}C., photoperiod was 16:8 (L:D) and relative humidity was 55 ± 5%. This experiment was designed as a factorial 2x2 with 2 plant architectures and 2 prey distributions. Additionally, the experiment included controls (check leaves) where cucumber leaves were infested with twospotted spider mites but no predator was released. This control had the purpose of allowing us to estimate the number of *T. urticae* eggs consumed by *P. persimilis* by comparison. The experiment was blocked by date (3 dates = 08/21 - 08/23, 08/28 - 08/30 and 09/19 - 09/21) and had approximately 10 replicates for each treatment per date. The plant architectures used were simple plant architecture, hereafter called 'simple plant'; and complex plant architecture, hereafter called 'complex plant'. Simple plants had two large leaves, whereas complex plant had six small leaves (Table 2.3). The total plant surface area was the same for both architectures (Table 2.3). The different prey distributions consisted of: 1) a single base leaf infested and, 2) all leaves infested. For the prey distribution having a single base leaf infested the prey density was about 60 *T.urticae* eggs on the base leaf, whereas the prey density when they were distributed on all leaves was about 30 *T. urticae* eggs per leaf. These different prey densities were used to ensure that the mites would move within the plant canopy in case they found a prey patch and left it only after depletion. Infestation of leaves was done based on results of a previous 24-hour assay which showed that 6 adult female *T. urticae* can lay approximately 30 eggs on cucumber leaves and 12 females can lay about 60 eggs in 24 hours. Therefore, the leaves that were pre-assigned to have 60 eggs were infested with 12 adult female of *T. urticae*, whereas the leaves that were pre-assigned to have 30 eggs were infested with 6 adults. These *T. urticae* females were allowed to lay eggs and produce webbing for a period of 24 hours. Thereafter all *T. urticae* females were eliminated from the cucumber leaves by killing them with a fine needle leaving only webbing and eggs. Each plant was placed on top of an inverted 5-inch pot contained within a plastic plate filled with water to prevent the predator from escaping. Thereafter, a single nonstarved female *P. persimilis* (experimental unit) was placed close to a prey patch on the basal leaf of each plant (closest to the growth median), and allowed to remain on the plant for 48 hours. For the ‘check leaves’ *T. urticae* were placed on leaves of both plant architectures. However, after its removal no predatory mite was released on the plant. The number of *T. urticae* eggs consumed by *P. persimilis* was estimated by subtracting the remaining number of eggs on each infested leaf from the mean number of eggs laid by *T. urticae* on the check leaves (leaves without predator). Estimation of prey consumption was made by date. For instance, on date 1 the estimated number of eggs consumed by *P. persimilis* on leaves infested with 12 female *T. urticae* was the mean number of eggs produced by 12 *T. urticae* on the check leaves minus the number of remaining eggs (48 hours after predator was released) on leaves previously infested with that number of *T. urticae*. Subsequently, in cases where the plants had two or six infested leaves, such as treatments ‘complex + all’ and ‘simple + all’, the estimated numbers of *T. urticae* eggs consumed on each leaf were summed to obtain the total prey consumption value per plant. Likewise, the numbers of predator eggs observed on those leaves were also summed to obtain the total number of predator eggs laid per plant. To compare the prey consumption and oviposition of *P. persimilis* per plant for possible statistical differences among treatments, a PROC GLM analysis was done using SAS$^{®}$. In cases where two and six leaves were infested with *T. urticae,* I also wanted to know on which leaves the predator was feeding the most and laying the most eggs. To do so I summed the estimated numbers of consumed *T. urticae* eggs and number of predator eggs laid on the leaves that were located on the same position of their respective plant architecture, thus providing a mean value of prey consumption and predator oviposition for those leaves. To compare the prey consumption and predator oviposition among those leaves and within their respective treatments, an ANOVA procedure was conducted using SAS$^{®}$. Additionally, a Pearson correlation was carried out between the number of *T. urticae* eggs consumed by *P. persimilis* and its eggs laid across the leaves of treatment ‘complex + all’ and ‘simple + all’.

Results

The number of eggs laid by female *Tetranychus urticae* on the check leaves were not affected by either date or leaf size. However; it was affected by the number of *T. urticae* (Table 2). Six adult females of *T. urticae* under greenhouse conditions infesting either small or large leaves will lay 31.97 ± 0.55 eggs/24 hours (N=39), whereas 12 adult females of *T. urticae* will lay 61.17 ± 0.53 eggs/24 hours (N=40). I noticed that *T. urticae* females would produce from 1-2 patches on average on each leaf during the experiment period. The total prey consumption rate of *Phytoseiulus persimilis* was affected by date (GLM, F= 17.07 and *p*= <.0001), plant architecture (GLM, F= and *p*= <.0001), prey distribution (GLM, F= 11.14 and *p*= 0.0012) and the interactions plant architecture*prey distribution (GLM, F= 6.46 and *p*= <.0125) and date*plant architecture*prey distribution (GLM, F= 6.21 and *p*= 0.0029). However, there was no effect of the interactions date*plant architecture (GLM, F= 1.03 and *p*= 0.35) and date*distribution (GLM, F= 2.54 and *p*= 0.083). *Phytoseiulus persimilis* consumed significantly more eggs in the treatment ‘complex +all’ (cucumber plants with 6 small leaves infested) than in all other treatments (Table 4.2 and Figure 4.1). In the treatment ‘complex + base’ (cucumber plants with 6 small leaves, but only base leaf infested) *P. persimilis* consumed significantly more eggs than the other two treatments ‘simple + base’ (cucumber plants with 2 large leaves, but only base leaf infested) and ‘simple +all’ (cucumber plants with 2 large leaves infested) (Table 4.2 and Figure 4.1). *Phytoseiulus persimilis* consumed a similar number of eggs in the treatment ‘simple + base’ and ‘simple + all’. *Phytoseiulus persimilis* tended to consume more eggs on leaves where it was placed at the beginning of the experiment regardless of plant architecture or prey distribution (Table 4.3 and 4.4, Figure 4.2 and 4.3). The predator was also generally observed to eat a higher number of eggs on leaves closer to where the predatory mite was released (basal leaf) compared to leaves located further away (Table 4.3 and Figure 4.2). The predator seemed to be moving within the plant canopy of either simple or complex plant architecture. Furthermore, predator oviposition seemed to follow the trend of prey consumption (predator laid more eggs where more *T. urticae* eggs consumed and vice-versa) on either treatment ‘complex + all’ or ‘simple +all’ (compare Figure 4.2 vs. 4.4 and 4.3 vs. 4.5). A positive correlation between the number of *T. urticae* eggs consumed by *P. perismilis* and the number of its eggs laid on a leaf was detected for both treatments ‘complex + all’ (Pearson, r = 0.40 and *p* = > 0.0001) and ‘simple + all’ (Pearson, r = 0.30 and $p = 0.0225$). Therefore, *P. persimilis* tended to lay more eggs on the leaves where it had consumed more *T. urticae* eggs (Table 4.4 and 4.5). However, the total number of eggs laid by *P. persimilis* on the entire plant was not significantly different among treatments (Table 4.2 and 4.3).

Discussion

Phytoseiulus persimilis consumed significantly more *T. urticae* eggs on complex plants that had all 6 leaves infested with prey eggs than on plants with a simple architecture and/or a patchy prey distribution. This likely was because predators were able to more easily encounter prey that were distributed evenly within the canopy, and because plants that had a complex architecture had smaller leaves than ‘simple’ plants. In respect to leaf size, it is reasonable to envision that the predator would find a prey patch more quickly on leaves with a smaller surface area to search. Surprisingly, *P. persimilis* consumed the second highest amount of *T. urticae* eggs on complex (6-leafed) plants with just the base leaf infested. Based on other studies, predators and parasitoids may take longer to encounter prey or host patch on plants with complex architecture (Lukianchuk and Smith, 1997; Cloyd and Sadof, 2000; Legrand and Barbosa, 2003) and prey distributed patchily. However, when they find a prey patch, they may consume more. For example, Yasuda and Ishikawa (1999) observed ladybird beetles to consume more aphids when they were distributed contagiously. *Phytoseiulus persimilis* consumed fewer eggs on simple plant architectures regardless of prey distribution or prey number per leaf. It is possible that an experiment lasting 48 hours was excessively long for revealing differences in prey consumption on the simple plants, regardless of prey distribution or prey number per leaf. For example, it is known that *P. persimilis* is able to encounter prey patches more quickly on simple architectures when prey is distributed evenly within the canopy than otherwise (Gontijo, *unpublished data*). Thus, it is reasonable to expect that the prey consumption on those plants would be different, at least in a short time frame. Additionally, Gingras and Boivin (2002) found that host density significantly affected parasitism efficiency of *Trichogramma evanescens*, but only when females foraged for 4 hours; when foraging was longer than that, no host density effect could be detected.

Phytoseiulus persimilis tended to consume more eggs on the leaf where it was placed first or leaves closer to it. Stavrinides and Skirvin (2003) observed the same pattern where *P.*

perimilis consumed more prey eggs on leaves adjacent to its release point on chrysanthemum plants. This finding has important implications for biological control programs in terms of where predatory mites should be released. It is likely that biological control practitioners who consider plant architecture and prey distribution will have a better understanding of where and when to release the predatory mites to increase efficiency of biological control. In my work observations showed that the predator visited different leaves on the plant and did not deplete the patches it visited during the timeframe of the experiment. This pattern of consumption conforms to a theoretical strategy known as “milker”, as described by Van Baalen and Sabelis (1995). These researchers referred to predators in this category as “prudent” because by not depleting prey patches, they left food behind for offspring. This strategy may be important for ensuring the survival of offspring, thereby enhancing fitness. In my study, *P. persimilis* tended to lay more eggs on leaves where it had consumed more *T. urticae* eggs regardless of plant architecture. It is possible that there is a direct relationship between the amount of energy acquired by *P. persimilis* on a leaf through feeding and the number of eggs to be laid on the same leaf. The predator may have to “decide” whether to utilize the energy acquired on the prey patch to go in search of a new one or to utilize that energy to lay eggs. The optimal strategy depends on the current and future profitability of the present and the surrounding patches, on the time it takes to find another patch, and on the risk of dying during a transit (e.g., Krebs *et al*. 1974; Charnov 1976; Iwasa *et al*. 1981). Considering that the predator does not know its chances of encountering a new prey patch within the plant canopy, the strategy of laying more eggs where it feeds more might be reasonable. Such an act can decrease risks of starvation and/or death during transits among leaves within the plant canopy. Furthermore, it may guarantee the production of offspring. The results of this study show that *P. persimilis* may be more efficient at consuming prey eggs on plants with complex architectures (many small leaves) than on plants with simple architecture (few large leaves). Therefore, it is expected that biological control practitioners would need to release a higher number of predatory mites on plants with simple architecture.

Figures and Tables

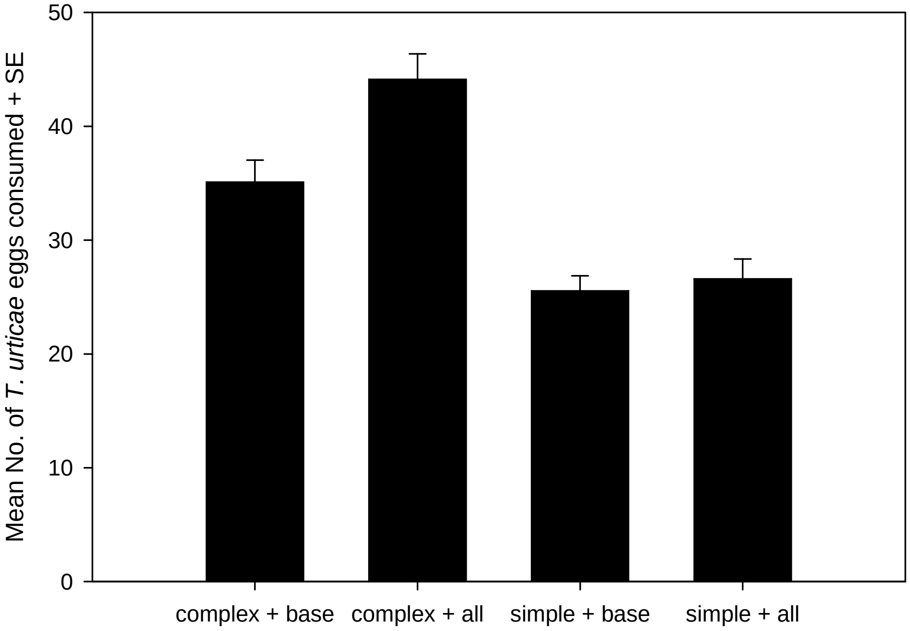

Figure 4-1 Prey consumption rate of *Phytoseiulus persimilis* upon eggs of *Tetranychus urticae* on cucumber plants with a simple (2 large leaves) or complex (6 small leaves) architecture. Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 27-30.

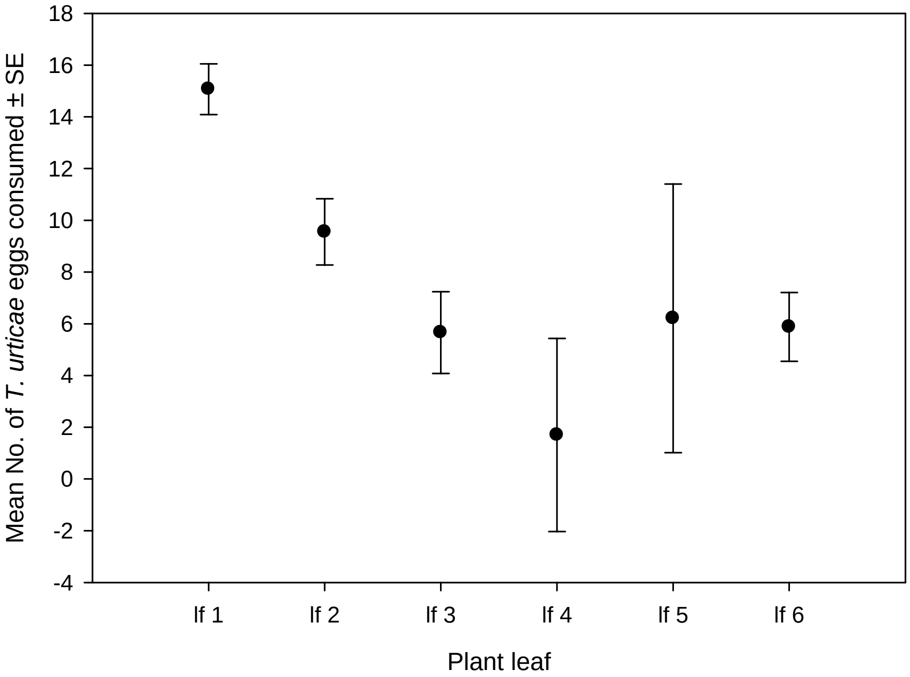

Figure 4-2 Mean number of *Tetranychus urticae* eggs consumed by *Phytoseiulus persimilis* within the canopy of complex plant architecture (6 leaves). N= 27 leaves for each leaf category. leaf 1 =closest to growth media and leaf 6 = uppermost leaf

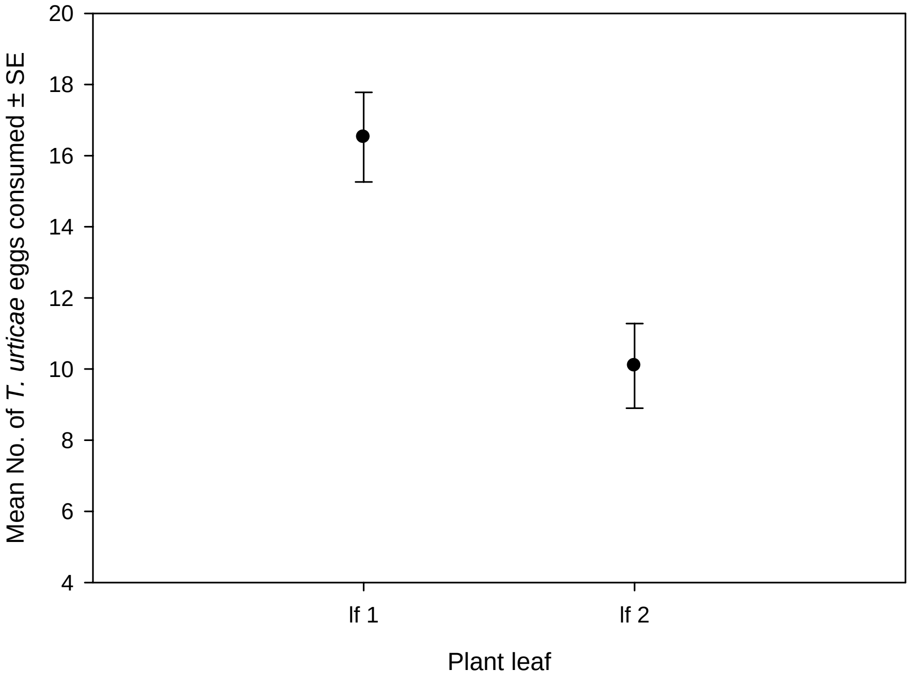

Figure 4-3 Mean number of *Tetranychus urticae* eggs consumed by *Phytoseiulus persimilis* on the two leaves of simple architecture. N= 30 leaves for each leaf category. leaf 1= closest to growth media.

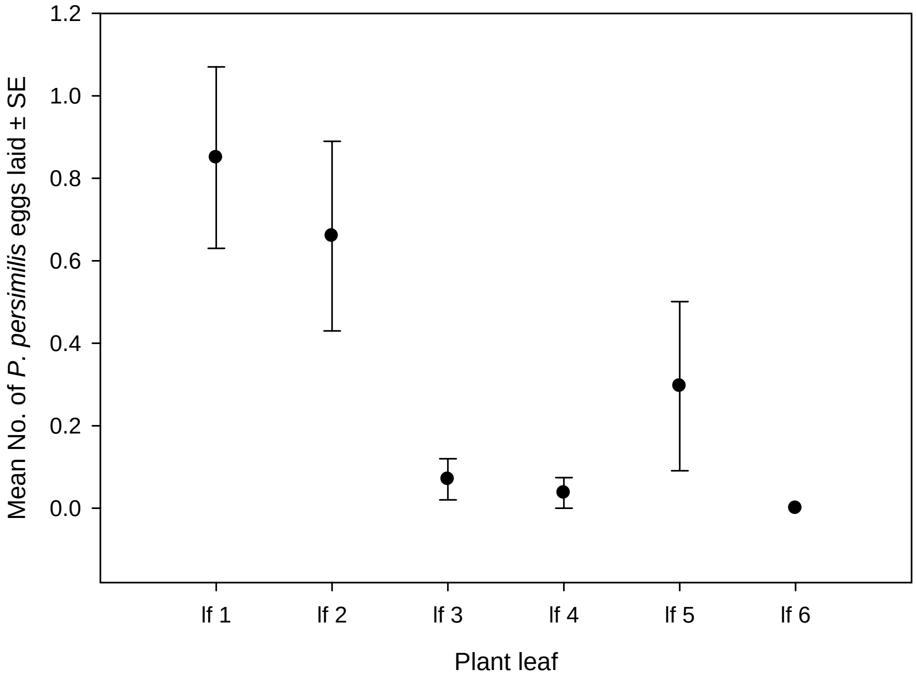

Figure 4-4 Oviposition of *Phytoseiulus persimilis* within the canopy of cucumber plants with complex architecture (6 leaves). N= 27 leaves for each leaf category. leaf 1= closest to growth media and leaf 6= uppermost leaf.

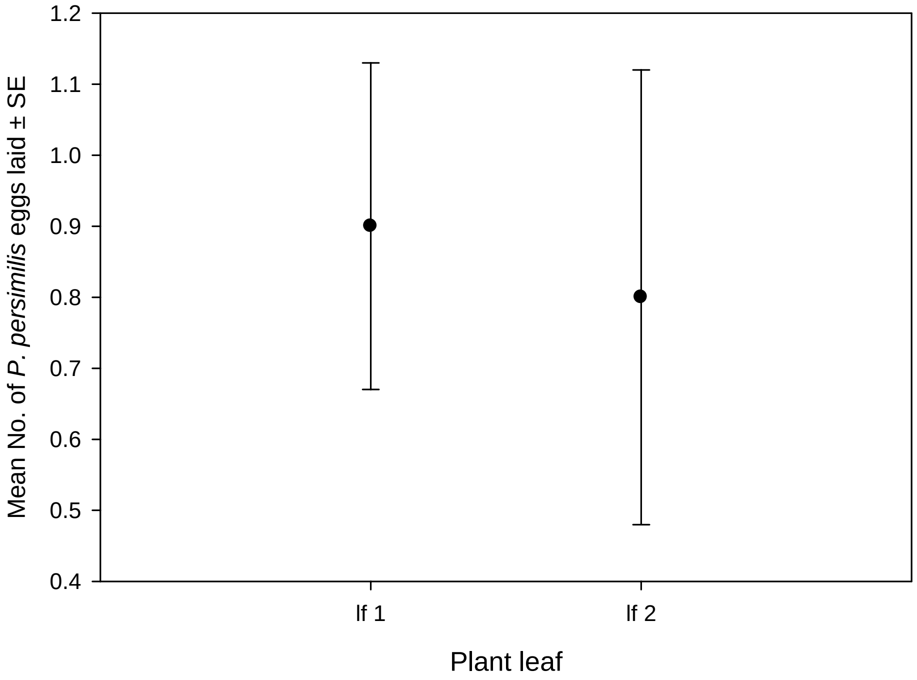

Figure 4-5 Oviposition of *Phytoseiulus persimilis* within the canopy of cucumber plants with simple architecture (2 leaves). N= 30 leaves for each leaf category. leaf 1= closest growth media.

Table 4-1 Effects of day and cucumber leaf size on oviposition of *Tetranychus urticae*

Test variable	F value	df	*P*- value
No. female *T. urticae*	1272.22	1	< .0001
Day	1.72	2	0.1867
Leaf size	0.02	1	0.885
No. female *T. urticae**Day	0.11	2	0.9004
No. female *T. urticae**Leaf size	0.61	1	0.4369
Day*Leaf size	0.12	2	0.8859
No. female *T. urticae**Day*Leaf size	0.33	2	0.7207

Table 4-2 PROC GLM - Number of *Tetranychus urticae* eggs consumed and number of eggs laid by *Phytoseiulus persimilis*

Plant architecture	Prey distribution	Mean no. prey eggs consumed ± SE	Mean no. predator eggs laid ± SE
complex	base	35.10 ± 1.47 B	1.55 ± 0.36 A
complex	all	44.10 ± 1.55 A	1.96 ± 0.37 A
simple	base	26.61 ± 1.62 C	1.76± 0.39 A
simple	all	25.39 ± 1.47 C	1.70 ± 0.35 A

Means followed by different letters within the same column differ significantly at GLM $p<0.05$

Table 4-3 ANOVA - Consumption and oviposition rate of *Phytoseiulus persimilis* within the canopy of complex cucumber plant architecture

Complex plant architecture		
Plant leaf	Mean no. prey eggs consumed ± SE	Mean no. predator eggs laid ± SE
1st leaf	15.07 ± 0.98 A	0.86 ± 0.22 A
2nd leaf	9.55± 1.28 B	0.67 ± 0.23 AB
3rd leaf	5.66 ± 1.58 C	0.07 ± 0.05 C
4th leaf	1.70 ± 0.92 D	0.03 ± 0.03 BC
5th leaf	6.22 ± 1.23 BC	0.30 ± 0.20 C
6^{th} leaf	5.86 ± 1.33 C	0.00 ± 0.00 C

Means followed by different letters within the same column differ significantly at ANOVA $p<0.05$

Table 4-4 ANOVA - Consumption and oviposition rate of *Phytoseiulus persimilis* within the canopy of simple cucumber plant architecture

Simple plant architecture		
Plant leaf	Mean no. prey eggs consumed ± SE	Mean no. predator eggs laid ± SE
1st leaf	16.52 ± 1.26 A	0.90 ± 0.23A
2nd leaf	10.09 ± 1.19 B	0.80 ± 0.32A

Means followed by different letters within the same column differ significantly at ANOVA $p<0.05$

Table 4-5 Number of *Tetranychus urticae* eggs consumed by *Phytoseiulus persimilis*/ number of eggs laid by *Phytoseiulus persimilis* on different leaves of cucumber plants with complex architecture (6 leaves) in three different dates

date	predator	leaf 1	leaf 2	leaf 3	leaf 4	leaf 5	leaf 6
1	1	3.00/0	0.00/0	16.00/0	0.00/0	16.00/5	16.00/0
1	2	11.00/1	15.00/2	0.00/0	0.00/0	13.00/0	0.00/0
1	3	21.00/0	19.00/2	3.00/0	1.00/1	2.00/0	21.00/0
1	4	11.00/1	9.00/2	11.00/0	0.00/0	6.00/0	2.00/0
1	5	20.00/0	11.00/0	16.00/0	0.00/0	0.00/0	3.00/0
1	6	21.00/1	2.00/0	2.00/0	11.00/0	13.00/0	1.00/0
1	7	12.00/0	3.00/0	14.00/0	0.00/0	11.00/0	0.0/0
1	8	19.00/3	6.00/0	0.00/1	1.00/0	13.00/0	1.00/0
1	9	13.00/1	7.00/0	1.00/0	0.00/0	0.00/0	13.00/0
2	10	4.84/0	1.84/0	17.84/0	0.00/0	17.84/4	17.84/0
2	11	16.84/1	17.84/4	0.84/0	0.00/0	0.84/0	2.84/0
2	12	18.84/0	20.84/2	0.00/0	10.84/0	0.84/0	14.84/0
2	13	12.84/1	10.84/2	12.84/0	0.00/0	7.84/0	3.84/0
2	14	21.84/0	14.84/0	0.00/0	1.84/0	0.84/0	4.84/0
2	15	12.84/1	23.84/0	0.00/0	1.84/0	2.84/0	2.84/0
2	16	12.84/0	1.84/0	11.84/0	1.84/0	14.84/0	0.84/0
2	17	22.84/3	6.84/0	0.00/1	2.84/0	16.84/0	0.00/0
2	18	9.84/1	7.84/0	0.84/0	9.84/0	0.00/0	14.84/0
3	19	13.93/0	10.93/0	2.93/0	4.93/0	0.00/0	0.00/0
3	20	10.93/0	9.93/0	2.93/0	0.00/0	8.83/0	14.93/0
3	21	15.93/0	1.93/0	13.9/0	0.00/0	0.93/0	7.23/0
3	22	14.93/0	0.00/0	5.93/0	1.93/0	0.00/0	11.93/0
3	23	20.93/0	8.93/0	0.00/0	4.93/0	0.93/0	0.00/0
3	24	20.93/4	8.93/0	18.93/0	0.93/0	5.93/0	0.00/0
3	25	11.93/0	16.93/0	3.93/0	0.00/0	2.93/0	0.00/0
3	26	15.93/3	6.93/1	0.00/0	0.00/0	5.93/0	3.93/0
3	27	16.93/1	15.93/1	0.00/0	13.93/0	10.93/0	5.93/0

leaf 1 = closest to growth media and leaf 6 = upmost leaf

Table 4-6 Number of *Tetranychus urticae* eggs consumed by *Phytoseiulus persimilis*/ number of eggs laid by *Phytoseiulus persimilis* on different leaves of cucumber plants with simple architecture (2 leaves) in three different dates

Date	predator	leaf 1	leaf 2
1	1	10.00/0	8.00/0
1	2	21.00/0	7.00/2
1	3	23.00/1	16.00/0
1	4	21.00/0	7.00/0
1	5	21.00/1	15.00/0
1	6	0.00/0	12.00/0
1	7	21.00/0	3.00/0
1	8	18.00/0	12.00/0
1	9	18.00/0	3.00/0
1	10	20.00/2	9.00/0
2	11	15.40/0	7.84/0
2	12	22.84/0	8.84/2
2	13	20.84/1	24.84/6
2	14	22.84/0	10.84/0
2	15	20.84/1	18.84/0
2	16	1.84/0	13.84/0
2	17	20.84/0	15.84/0
2	18	19.84/0	13.84/0
2	19	22.84/3	20.84/4
2	20	22.84/2	14.84/0
3	21	13.93/0	0.93/0
3	22	3.93/0	10.93/0
3	23	5.93/0	10.92/0
3	24	6.93/0	10.93/0
3	25	20.93/2	1.93/0
3	26	18.93/2	1.93/0
3	27	20.93/4	0.00/0
3	28	10.93/4	15.93/0
3	29	18.93/0	0.00/0
3	30	9.93/0	10.93/0

leaf 1 = lower leaf

CHAPTER 5 - The influence of cucumber plant architecture and prey distribution on the foraging behavior of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae)

Introduction

Foraging may be defined as a group of behaviors exerted to acquire resource. Foraging behavior is important for development, survival and reproduction. It is difficult to know how natural enemies perceive and search for resources within their environment. For natural enemies, including predators and parasitoids, perception and search is probably a hierarchal system that proceeds step-wise according to habitat, patch and individual resource items (Hassell and Southwood, 1978). Natural selection should favor foraging behaviors that maximize the difference between searching costs and benefits, and reduce several types of risks that may occur when a natural enemy is foraging for resources. It may be expected that natural enemies exhibiting efficient foraging behavior would have higher likelihood for effective biological control.

The foraging behavior of a natural enemy may be influenced by both intrinsic and extrinsic factors. One important extrinsic factor is the host plant on which prey are found. Both plant morphology (Arthur, 1966; Belcher and Thurston, 1982; Shah, 1982; Grevstad and Klepetka, 1992; Clark and Messina, 1998) and plant semiochemicals (Espelie and Brown,1990; Lewis and Martin, 1990; Turlings *et al*. 1990, Coll and Ridgway, 1995) affect foraging behavior of natural enemies. Therefore, it is important to take the plant into consideration when making pest management decisions, e.g. number of predators to release. An important morphological characteristic of plants that has been reported to play a key role in multitrophic interactions is the plant architecture (Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992; Cloyd and Sadof, 2000; Marquis *et al*. 2002; Legrand and Barbosa, 2003). Certain architectural traits such as branching angle and number, surface area and leaf number can influence the direction and rate of natural enemies' search, and thus influence the searching time, encounter rate and spatial overlap with prey/host. For example, high plant architectural complexity in terms of increased leaf edge to leaf area ratio and increased number of junctions (leaf number and branch ramification) reduced the new area search efficiency and foraging success of the lady beetle, *Coccinella* *septempunctata*, when foraging on pea plants with divergent plant architectural complexity (Legrand and Barbosa, 2003). Additionally, many natural enemies with poor vision must rely on plant morphological cues which many times happen to be plant architectural traits, as with the predatory mite *Amblyseius potentillae* which follows leaf veins or edges when foraging for prey (Sabelis and Dicke, 1985). The spatial distribution of prey is another factor that may influence natural enemy foraging behavior and success (capacity to find and consume enough resource to develop, survive and reproduce), and may interact with plant architecture (Ryoo, 1996; Stavrinides and Skirvin, 2003). Recent studies have been conducted to evaluate the influence of plant architecture on the foraging behavior and success of natural enemies. However; very few have separated the effects of total plant surface area itself from the effects of other specific architectural traits. Additionally, most of these studies have focused only on insects, thereby omitting another important group of natural enemies such as the acarinids, especially phytoseiid mites. Of the few published works dealing with interactions between phytoseiids, efficiency and plant architectural traits, nearly all have looked only at the effects of leaf trichomes. Therefore, my objectives were to: 1) quantify the effects of leaf number on the foraging behavior (time allocated between moving, resting and feeding) of *Phytoseiulus persimilis*, 2) separate the effects of total plant surface area from the effects of leaf number, and 3) assess the possible interaction between the effects of plant architecture (leaf number) and prey distribution. The following hypotheses were tested: 1) assuming that prey distribution is constant, the foraging time of *P. persimilis* will increase with number of leaves; 2) on plants with prey distributed contagiously, *P. persimilis* will require a longer time to find a prey patch compared to plants with a more uniform prey distribution; 3) the amount of time spent moving, resting and feeding by *P. persimilis* will be influenced by differences in the relative surface areas of individual plant parts, such as the stem, petiole and leaf.

Materials and Methods

Mites and general experimental conditions

Twospotted spider mite

Tetranychus urticae were obtained from colonies maintained at Kansas State University. They were reared in plastic flats (0.3 x 0.6 m) containing young lima bean plants (*Phaseolus lunatus*). *Tetranychus urticae* were kept under a photoperiod of 16:8 L:D, 60 ± 10% R.H. and temperature of 25 ± 20^0C. The mites were given new lima bean plants every other day.

Predatory mites

Phytoseiulus persimilis were purchased from Koppert Inc. (Romulus, MI), and maintained on spider mite-infested lima bean plants inside $0.01m^3$ plastic chambers with a fine mesh covering the top and part of the sides. *Phytoseiulus persimilis* were fed with fresh spider mite-infested lima bean plants every other day. The *P. persimilis* population was maintained under a photoperiod of 16:8 L:D, 60 ± 10% R.H. and temperature of 25 ± 2^0C.

Experimental conditions

Complex and simple plant architectures were created on cucumber plants (*Cucumis sativus*) as described in chapter 2. The experiment was conducted in the laboratory at Kansas State University, Manhattan, KS. The experimental design was a 2 x 2 factorial with two plant architectures and two prey distributions. Plant architectures were represented by plants having only two large leaves, hereafter called 'simple plants', and plants having 6 small leaves, hereafter called 'complex plants'. However, regardless of plant architecture, all plants had approximately the same total plant surface area. The prey distributions were a single basal leaf infested and all leaves infested. The treatments were blocked through time and there were 2-3 replicates of each treatment per day for a total of 11 replicates at the end of four days. Leaves were infested with 10 adult female *T. urticae*. Each cohort of *T. urticae* adults previously had been placed on a 1-cm^2 square piece of bean leaf, which was floated bottom-side up on cotton wool in a plastic tray filled with water. This procedure kept the leaf squares from drying out and inhibited spider mites from leaving the leaf squares. Subsequently, the infested square leaves were attached to the cucumber leaves by using the tips of tooth picks (1 tooth pick on the center of each leaf square). Female *T. urticae* were allowed to migrate off the square bean leaves and settle on the cucumber leaves, lay eggs and produce webbing for a period of 24 hours, after which a 2-hour starved female *P. persimilis* was placed at the base of the main stem of each plant with the aid of a fine-haired paint brush. Each predatory mite was watched individually for 20 minutes after release. Predators that were released but failed to move during the first 5 minutes were removed and new one was released. During the 20-minute observation I recorded the frequency and duration of moving, resting and feeding, plus the plant part (stem, petiole and leaf) where these behaviors occurred.

Statistical analyses

The predator behavioral data were organized in four forms: 1) time spent moving and resting on the stem before moving onto a petiole, and on the petiole before moving onto a leaf; 2) total time spent moving, resting and feeding on the plant stem, petioles and leaves; 3) total time spent moving and resting on the entire plant; and 4) the percentage of time spent resting, moving and feeding on stems, petioles and leaves. The effects of day, plant architectural complexity, prey distribution and their interactions were tested using the PROC GLM procedure in SAS®.

Results

Although the total plant surface area of both 'simple' and 'complex' plant was approximately the same, the surface areas for other plant parts were shown to be significantly different between the two plant architectures (see Chapter 2, Table 2.3). The 'simple' plants had longer stems and petioles, and the leaves had a larger surface area compared to the leaves of 'complex' plants. In most of the observations, *P. persimilis* walked upwards and around the stem after being placed at the base of the plant (main stem). The predator always changed direction when facing an obstacle such as a large stem trichome or a simple stem protuberance (callus-like appearance). In most cases, turns were made onto the first petiole the predator encountered. The predators searched actively for prey and made many stops when engaged in foraging. However; the stops were very short (seconds), and the longer stops took place on leaves. When walking, *P. persimilis* was observed to consistently move its front legs to and fro to assess the substrate. When on a leaf, *P. persimilis* walked slower, and in the case of an uninfested leaf, it would walk more along the leaf margins. Occasionally *P. persimilis* moved from one leaf to another on the same plant (complex plants) that had leaves overlapping (leaf connectedness). The predator spent significantly more time moving on the stem of ‘simple’ plants before turning onto a petiole (Figure 5.1 and Table 5.1; GLM, F= 2.05 and $p<0.04$). This effect apparently is due to plant architecture (GLM, F= 11.20 and $p<0.002$). Likewise, *Phytoseiulus persimilis* also spent more time moving on petioles of simple plants before reaching the leaf blade (Figure 5.2 and Table 5.1; GLM, F= 3.28 and $p<0.003$). There was a significant effect of day (GLM, F=5.68 and $p=0.003$), plant architecture (GLM, F=13.06 and $p=0.0012$) and the interaction between day and architecture (GLM, F= 5.03 and $p=0.006$) with respect to time spent by *P. persimilis* moving on the petiole before moving onto a leaf. Treatments had no effect on time spent resting by *P. persimilis* on either the stem before moving onto a petiole, or on the petiole before moving onto a leaf blade. The total time (predator may visit the stem or petiole more than once) spent by *P. persimilis* moving on the stem and petiole was significantly greater on simple plants than on complex plants (Figure 5.3 and Table 5.2), whereas no significant difference was observed on the total time spent by *P. persimilis* resting either on the stem (GLM, F=1.84 and $p=0.07$) or petiole (GLM, F=1.54 and $p=0.15$) (Figure 5.3 and Table 5.2). In respect to total time moving on the plant leaves, *P. persimilis* moved significantly more (GLM, F=7.23 and $p=0.011$) on the leaves of the treatment ‘complex + base’ compared to the other ones (Figure 5.3 and Table 5.2). *Phytoseiulus persimilis* seemed to spend more time feeding on prey when on the leaves of the treatment ‘complex + all’ (Figure 5.3, 5.4 and Table 2). The total time that *P. persimilis* moved on the entire plant was significantly higher on the treatments ‘complex + base’, ‘simple + base’ and ‘simple + all’ compared to ‘complex + all’. There was no significant difference on the total time spent resting on the entire plants (GLM, F=1.25 and $p=0.29$) (Figure 5.4). *Phytoseiulus persimilis* spent more time moving than resting during the 20-minute observation on the entire plant (Figure 5.4). In all treatments *P. persimilis* encountered the petioles and leaves of the plants (Figure 5.5). However, a higher percentage of *P. persimilis* encountered prey patches on the leaves of ‘complex’ plants with prey on all leaves compared to the other treatment combinations (Figure 5.5). *Phytoseiulus persimilis* spent a greater part of the observation time on leaves of cucumber plants with complex architecture (6 small leaves) whereas on plants with simple architecture (2 large leaves) *P. persimilis* spent shorter, but about the same time between stems and leaves (Figure 5.6).

Discussion

On simple plants, predators spent more time moving on the stems before turning onto a petiole compared to the complex plants. The predators also moved for a longer time on the petiole of simple plants before moving to a leaf blade, compared to complex plants. These differences may be associated with the relatively greater surface areas of those structures on plants with a simple architecture. Thus, from the point of release a randomly searching *P. persimilis* female would have to forage over more area on a simple plant before encountering the boundary between plant parts than on a complex plant. Besides plant architecture, foraging efficiency should also be affected by prey distribution on a plant.

The total time (predator may visit stem or petiole more than once) spent moving on the stem and petioles was also higher on simple plants. The total time moving on the stem did not differ from the time spent moving on stem before turning onto a petiole (predator visit stem only once) as well as the total time of moving on the petiole did not differ from the time moving on the petiole before getting onto a leaf (predator visit petiole only once). It may be so because generally the predator could not frequently forage on the same plant part twice or more due to the time frame they were allowed to forage (20 minutes each).

Phytoseiulus persimilis spent the most time moving on complex plants where the prey were only on the basal leaf. This is consistent with the fact that these plants not only had a more complex architecture (many leaves), but because prey were distributed patchily, the chances of the predator making a wrong choice (turning onto an uninfested leaf) were the greatest. The time spent by *P. persimilis* resting on the stem before moving onto a petiole, and the time spent resting on the petiole before entering a leaf, was not significantly different among treatments. Neither the total time spent resting on stem, petiole nor leaf was significantly different among treatments, indicating that resting was not affected by plant architectural differences, and resting and movement behaviors are not interdependent. The observation period (20 minutes) was not long enough for the predator to find a prey patch, leave it, and find another one. Multiple encounters with prey patches would likely involve more 'rest' (absence of movement). For example, it has been documented that *P. persimilis* rests more on leaves nearby prey, especially where there is a high density of prey and webbing (Bancroft and Margolies, 1996).

Phytoseiulus persimilis tended to spend more time feeding on plants with a complex architecture and all leaves infested. Most likely the observed higher time spent feeding on ‘complex + all’ by *P. persimilis* was due to its lower prey-finding time on those plants. If predators find prey patches more quickly, they should have more time to spend feeding within a short observation period. For example, in Chapter 2 where I report on the effects of cucumber plant architecture on prey-finding time of *P. persimilis*, I observed that predators encountered a prey patch more rapidly on complex plants (cucumber with many small leaves) with prey distributed evenly among the leaves. Thus, plant architecture can indirectly affect feeding time of *P. persimilis*. Plant architectures that require a longer time for a predator to encounter a prey patch can also increase the hunger of a predator when foraging. This, in turn, may affect handling times and the latter may affect the amount of time spent by predator exploiting a prey patch. The total time spent moving by *P. persimilis* on the entire plant was lower on complex plant with prey on all leaves compared to the other treatment combinations. It may have happened due to the fact that *P. persimilis* were able to find prey more quickly and spend more time feeding on those plants, and hence; less time moving. Because total plant surface area was kept constant in my experiments, it appears that differences in architecture and corresponding differences in relative time spent on different plant parts do not affect the overall proportion of time predators move and rest, however; plant architecture and prey distribution are found to interact in this case.

In my study, *P. persimilis* spent more time moving than resting. In contrast, Bancroft and Margolies (1996), who measured the time *P. persimilis* allocated between feeding, resting and moving, observed that the predator rested more than moved. At least two factors might account for the differences in results between the two studies. First, the duration of their observation period was 1 hour (compared to 20 minutes), which might give the predator sufficient time to find prey and feed, but also to rest more. Second, unlike our studies, all their observations were conducted on leaf discs which would have significantly increased the proximity of the predator to prey patch, thereby reducing the searching time and allowing more time for resting or feeding. The predatory mite *P. persimilis* was also observed to spend greater part of the experimental time on the leaves of plants with complex architecture compared to plants with simple architecture. It may happen due to the size of the petioles on simple plants which are smaller compared to complex plants, thereby; allowing the predator to arrive quicker to leave blades of those plants and there spend more time either moving, resting or feeding (in case of infested leaf).

Phytoseiulus persimilis was observed to forage along the edges of the leaves, especially leaves without spider mites. Moreover, a few times *P. persimilis* was observed to move from one leaf to another on complex plants (within the same plant) due to a certain level of leaf connectedness (leaves touching each other) on those plants. This could not occur on simple plants because the two alternate leaves never touched each other. Leaf connectedness might be considered an "energy-saving feature" for *Phytoseiulus persimlis* because the surface area covered between the predator release point and a prey patch may be reduced.

From this study I conclude that *P. persimilis* can allocate more time feeding and less time moving (plant as whole) on plants with complex architecture and prey evenly distributed. The differences in dimensions (e.g. surface area) of individual plant parts such as stem, petiole and leaves may help explain this. Therefore, this behavioral study provides further evidence that plant architecture and prey distribution affects the foraging activities of *P. persimilis*. With adequate knowledge of how plant architecture and the prey distribution affect foraging behavior and efficiency of *P. persimilis*, it may be possible to predict numbers of predators to release, and release points on the plant, to achieve consistently high levels of biological control.

Figures and Tables

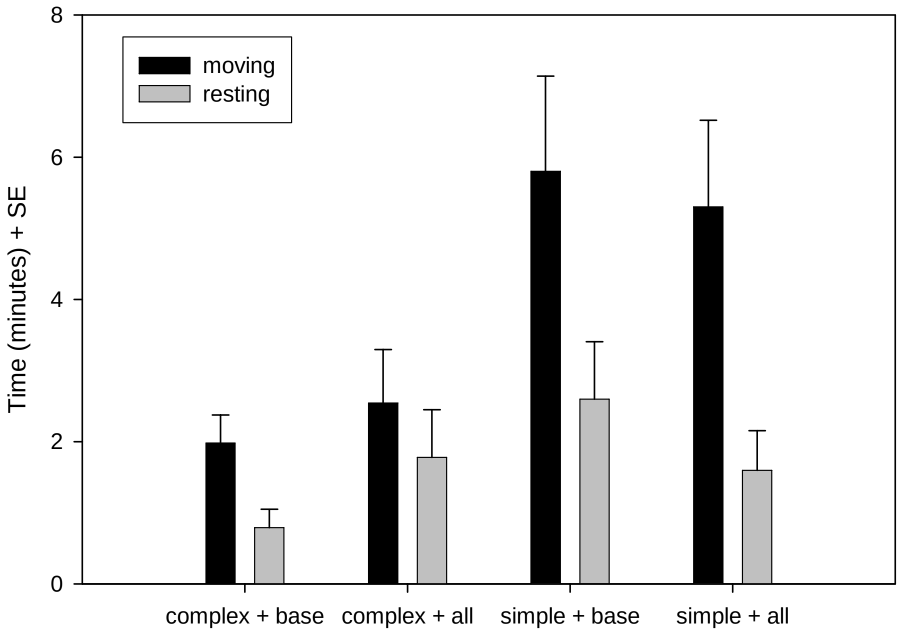

Figure 5-1 Time spent by *Phytoseiulus persimilis* moving and resting on the stem of cucumber plants before moving onto a petiole. Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 11.

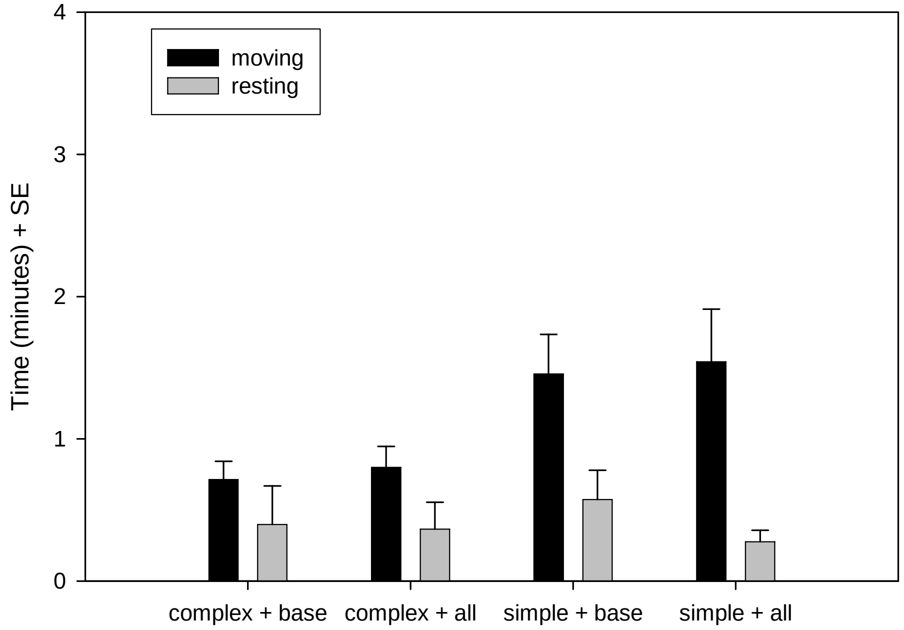

Figure 5-2 Time spent by *Phytoseiulus persimilis* moving and resting on the petiole of cucumber plants before moving onto a leaf. Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 11.

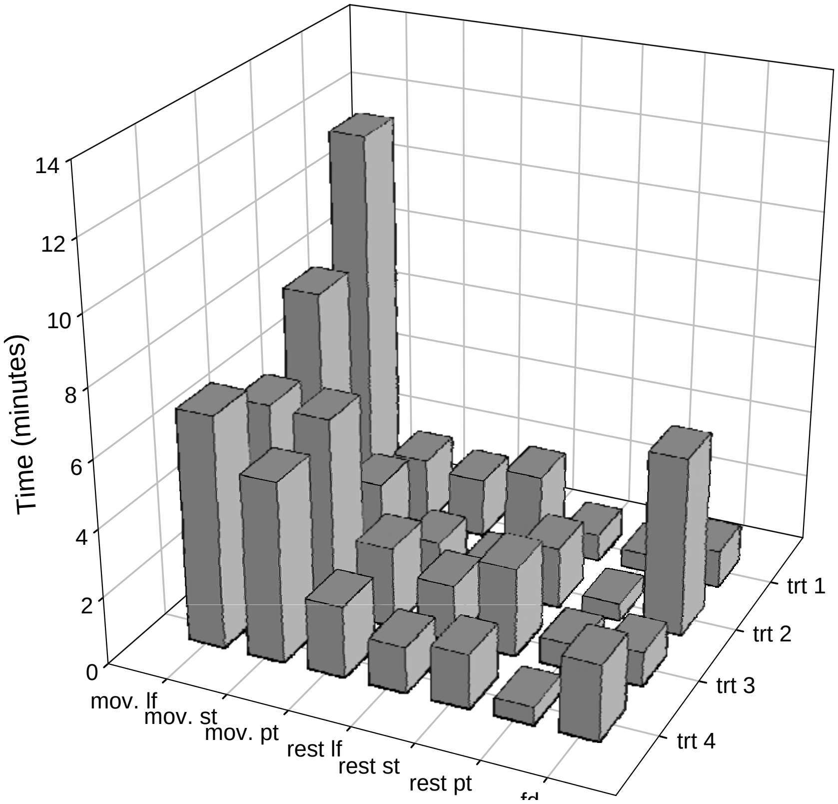

Figure 5-3 total time spent by *Phytoseiulus persimilis* moving, resting, and feeding on either the plant stem, petiole or leaf. mov. lf: moving on the leaf, mov. st.: moving on the stem, mov. pt.: moving on the petiole, rest lf: resting on the leaf, rest st.: resting on the stem, rest pt.: resting on the petiole, fd.: feeding, trt 1: complex + base leaf, trt 2: complex + all leaves, trt 3: simple + base leaf, trt 4: simple + all leaves

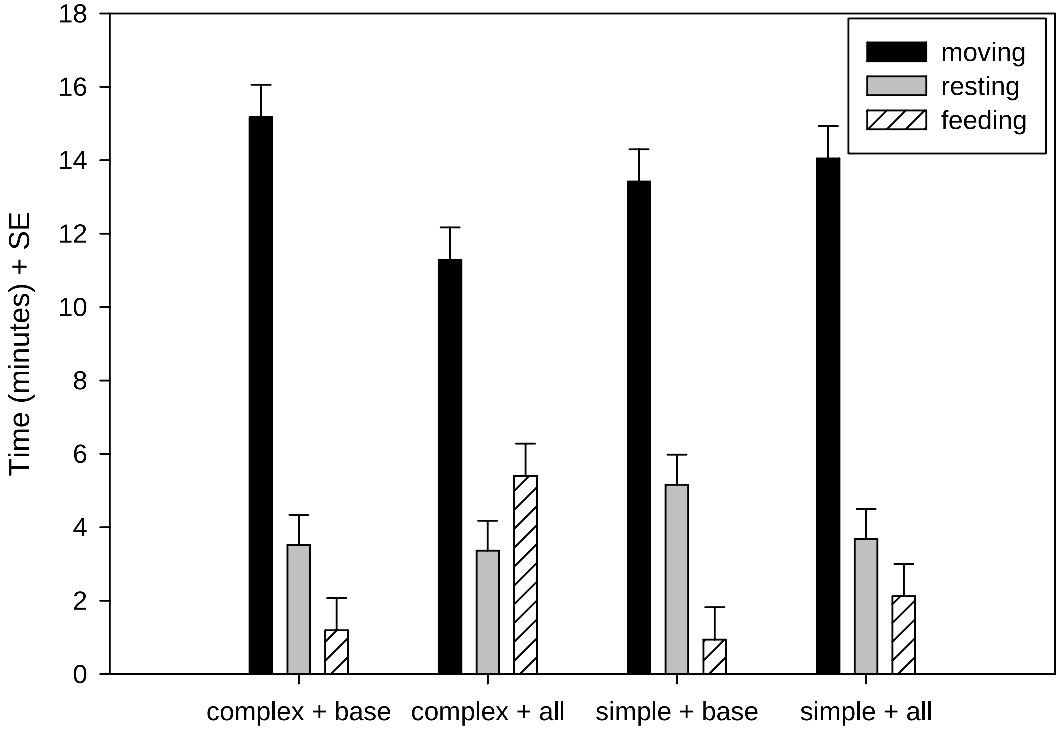

Figure 5-4 Total time spent by *P. persimilis* moving and resting on the entire cucumber plant. Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 11.

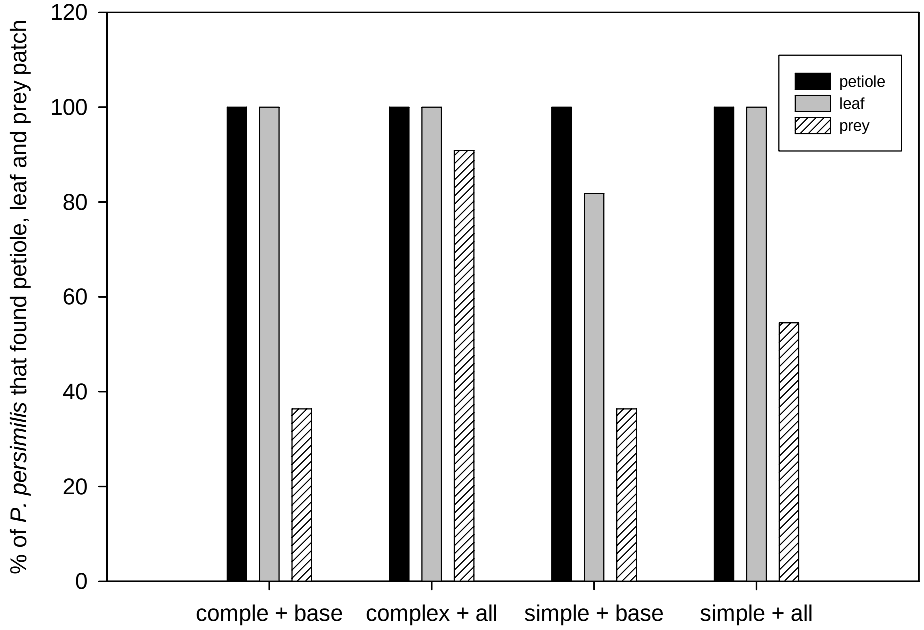

Figure 5-5 Percentage of *Phytoseiulus persimilis* that were able to encounter petiole, leaf and prey patch on either simple or complex cucumber plant architecture. Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 11.

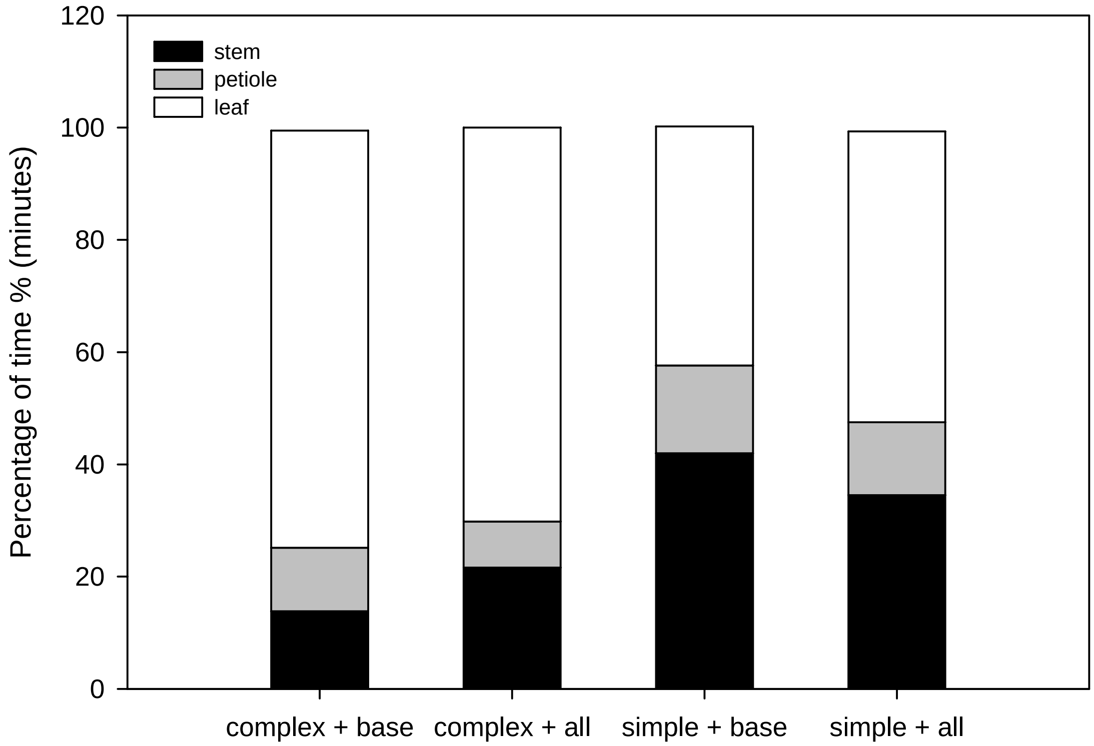

Figure 5-6 Percentage of time in minutes spent by *Phytoseiulus persimilis* on stems, petioles and leaves of cucumber plants with simple (2 large leaves) and complex (6 small leaves). Treatment combinations: complex + base = complex plants with 10 adults of *Tetranychus urticae* on a single base leaf, complex + all = complex plant with 10 adults of *Tetranychus urticae* on all leaves, simple + base = simple plant with 10 adults of *Tetranychus urticae* on a single base leaf, simple + all = simple plant with 10 adults of *Tetranychus urticae* on all leaves. N = 27-30.

Table 5-1 PROC GLM - analysis for comparing the time spent by *Phytoseiulus persimilis* moving and resting on stem before getting onto a petiole, and time spent on the petiole before getting onto a leaf

plant parts	behavior	complex + base leaf	complex + all leaves	simple+ base leaf	simple + all leaves
stem	moving	1.58 ± 0.37 B	21.77 ± 0.27 B	4.72 ± 1.14 A	4.70 ± 1.21 A
	resting	0.75 ± 0.24A	1.30 ± 0.41 A	1.83 ± 0.61 A	1.54 ± 0.54 A
petiole	moving	0.71 ± 0.12 B	0.86 ± 0.12 B	1.45 ± 0.27 A	1.54 ± 0.37 A
	resting	0.39 ± 0.27 A	0.36 ± 0.18 A	0.57 ± 0.20 A	0.28 ± 0.0 8A

Means followed by different letters within the same row differ significantly at GLM $p<0.05$

Table 5-2 PROC GLM - analysis for comparing the total time spent by *Phytoseiulus persimilis* moving, resting and feeding on plant stem, petiole and leaf

plant parts	behavior	complex + base leaf	complex + all leaves	simple + base leaf	simple + all leaves
stem	moving	1.91 ± 0.94 B	2.56 ± 0.94 B	5.38 ± 0.94 A	5.20 ± 0.94 A
	resting	0.88 ± 0.55 A	1.87 ± 0.55 A	2.39 ± 0.55 A	1.63 ± 0.55 A
petiole	moving	1.72 ± 0.30 AB	1.08± 0.30 B	2.26 ± 0.30 A	2.11 ± 0.30 A
	resting	0.52 ± 0.21 A	0.47 ± 0.21 A	0.71 ± 0.21 A	0.60 ± 0.21 A
leaf	moving	11.54 ± 1.15 A	7.65± 1.15 B	6.27 ± 1.15 B	6.73 ± 1.15 B
	resting	2.11 ± 0.50 A	0.94 ± 0.50 A	2.06 ± 0.50 A	1.44 ± 0.50 A
	feeding	1.19 ± 0.88 A	5.40 ± 0.88 A	0.94 ± 0.88 A	2.12 ± 0.88 A

Means followed by different letters within the same row differ significantly at GLM $p<0.05$

CHAPTER 6 - Conclusions

Tetranychus urticae is considered to be a major arthropod pest on over 30 economically important crops, including cucumbers. *T. urticae* injures individual leaf cells, causing a reduction in total chlorophyll content and in the net photosynthetic rate of leaves. Under high infestations it can decimate plants. One of the most specialized biological control agents used to control *T. urticae* is *Phytoseiulus persimilis*. This predatory mite feeds chiefly on spider mites belonging to the family Tetranychidae. The success of biological control of *T. urticae* utilizing *P. persimilis* can be influenced by both genetic and extrinsic factors associated with the predator and prey/pest. In terms of extrinsic influences, the host plant on which the predator and prey interact may be quite important. For example, the plant may have many effects on predator survival and foraging efficiency. In terms of the latter, plants are known to produce semiochemicals that influence predator behavior. In addition, leaf toughness, nutritional value that affects prey, toxins, and plant architecture (leaf trichomes, number and size of leaves, plant height, plant volume/surface area, leaf connectedness, etc) have effects on predators.

Plant architecture has been documented to affect predators directly by mediating host plant choice, altering movement and survival, and modifying behavior. Similarly, plant architecture can also affect predators indirectly by influencing the availability of spatial refuges for prey, the spatial distribution of prey, and the abundance and diversity of herbivorous prey. It is therefore crucial for growers and biological control practitioners to take the factor “plant” into account when making pest management decisions. Studying the role played by plant architecture on the interaction between prey and predator is of paramount importance to understanding predator-prey dynamics on plants with different architectures. Thus, the knowledge obtained from such studies can lead to meaningful predictions in both biological control and IPM programs. My study, in particular, enabled a better understanding of the effects of plant architecture (number and size of leaves) and prey distribution on prey-finding time, prey-consumption rate and foraging behavior of *P. persimilis*. Plant architecture was found to affect all of those behavioral components. Moreover, those effects were observed to interact with prey distribution and predator release point. When prey are distributed uniformly among leaves within the canopy, *P. perismilis* finds prey patches more quickly on complex plants (many small leaves) than on simple plants (few large leaves), regardless of predator release point. When prey are distributed patchily (e.g., a single base leaf infested) within the canopy and the predator is released away from the prey location (i.e., at the top of the plant), then *P. persimilis* tends to find the prey patch more quickly on leaves of simple plants (2 large leaves). In my studies, prey density seemed not to affect the prey-finding time of *P. perismilis*. The predator was able to consume more eggs on complex plants than on simple plants, regardless of prey distribution. However, within complex architecture treatments *P. persmilis* was found to consume more eggs when prey were distributed uniformly among the canopy leaves than on plants where prey were located only on a single base leaf. On simple plants, regardless of prey distribution, *P. persimilis* showed no difference in prey-consumption during a 48-experiment. The predator tended to find prey patches more quickly, as well as consume more eggs, on leaves adjacent to its release point. Furthermore, the predator was observed to lay more eggs on leaves where it had consumed a higher number of prey eggs. However; overall, *P. persimilis* was able to consume eggs on all infested leaves, which may be indicative of coincidence between prey and predator.

In respect to foraging behavior, *P. persimilis* was found to walk upwards and around the stem after being released (released at plant base). The predator would change its course of direction always when facing an obstacle such as a large stem trichome or a simple stem protuberance. In most of the cases, turns were observed on the first petiole with which the predator was confronted. The predators searched actively for prey and made many stops when engaged in foraging. However, the stops were very short (seconds) when searching on stem and petioles; the longer stops were observed to happen on the leaves. Always when walking *P. persimilis* was observed to move its front legs to and fro in order to tap the substrate in search of prey cues. Furthermore, differences in plant architecture of specific plant parts (e.g., stem, petiole and leaf) were shown to affect the relative time allocated by *P. persimilis* for searching, resting and feeding. Predators spent more time foraging on the stem and petiole of simple plants; whereas on complex plants it spent more time foraging on the leaves.

At last, this investigation provides us with valuable information, as well as new insights, on the effects of plant architecture, prey-distribution, and their interactions on the predator-prey dynamics, and these have important implications for biological control programs. For example, growers and biological control practitioners who monitor their crop periodically and get to know the plant architecture and prey distribution, can use that information to optimize the predator-prey release ratio and time of release of predators, thereby defining a better and more efficient threshold. Additionally, understanding plant architecture and prey distribution can help those using biological control to make more reliable decisions regarding where on the plant the predators should be released. Overall, I expect the combination of all information collected during this work to lead to a wider range of pest management options, leading to a net reduction in pesticide use. Lastly, it may be realistic to consider the possibility that plant breeders might manipulate the architecture of cultivated plants in order to favor biological control agents.

References

Ables, J. R., D.W.J. McCommas, S. L. Jones, and R. K. Morrison. 1980. Effect of cotton plant size, host egg location, and location of parasite release on parasitism by *Trichogramma pretiosum*. Southwest. Entomol. 5: 261-264

Andow, D. A., and D. R. Prokym. 1990. Plant structural complexity and host-finding by a parasitoid. Oecologia (Berl.). 82: 162-165

Arthur, A. P. 1966. Associative learning in *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). Can. Entomol. 98:213–23

Ashihara, W., Hamanura, T. and Shinkaji, N. 1978. Feeding, reproduction, and development of *Phytoseiulus persimilis* Athias-Henriot (Acarina:Phytoseiidae) on various food substances. Bull. Fruit Tree Res. Stn., Jpn., Ser. E, 2: 91-98

Ball, V. (ed.). 1985. Ball red book greenhouse growing, 14th ed. Reston Publishing, Reston, VA

Bancroft, J. S. and Margolies, D. C. 1996. Allocating time between feeding, resting and moving by the two-spotted spider mite, *Tetranychus urticae* and its predator *Phytoseiulus persimilis*. Experimental and Applied Acarology. 20: 391-404

Barbosa P, Letourneau D.K., (eds). 1988. Novel Aspects of Insect-Plant Interactions. New York: Wiley. 362 pp

Belcher, D. W. and Thurston, R. 1982. Inhibition of movement of larvae of the convergent lady beetle by leaf trichomes of tobacco. Environ. Entomol. 11: 91–94

Bell, W. J. 1990. Searching behavior patterns in insects. Annual Review of Entomology. 35: 447-467

Bell, S. S., D.McCoy, E. and Mushinsky, H. R. 1991. Habitat structure, the physical arrangement of objects in space. Chapman and Hall, New York

Bergman, J. M and Tingey, W. M. 1979. Aspects of interaction between plant genotypes and biological control. Bull. Entomol. Soc. Am. 25:275–79

Bernstein, C. 1984. Prey and predator emigration responses in the acarine system *Phytoseiulus persimilis-Tetranychus urticae*. Oecologia 61:134-142

Bond, A. B. 1983. The foraging behaviour of lacewing larvae on vertical rods. Anim. Behav. 31: 990-1004

Brunner, J. F. and Burts, E. C. 1975. Searching behavior and growth rates of *Anthocoris nemoralis* (Hemiptera: Anthocoridae), a predator of the pear psylla, *Psylla pyricola*. Annals Entomol. Soc. Am. 68: 311–315

Burbutis, P. P., and Koepke, C. H. 1981. European corn borer control in peppers by *Trichogramma nubilale*. J. Econ. Entomol. 74: 246-247

Carter, M. C. and Dixon, A.F.G. 1984. Honeydew: an arrestant stimulus for coccinellids. Ecol. Entomol. 9: 383-387

Carter, M. C., Sutherland, D. and Dixon, A.F.G. 1984. Plant structure and searching efficiency of coccinellid larvae. Oecologia 63: 394-397

Chant, D. A. 1961. An experiment in biological control of *Tetranychus telarius* (L.) (Acarina Tetranychidae) in a greenhouse using the predacious mite *Phytoseiulus persimilis* Athias-Henriot (Phytoseiidae). Can. Entomol. 93: 437-443

Chant, D. A. 1985. Systematics and morphology. Pp.3-10, In W. Helle and M. W. Sabelis (eds), Spider Mites: Their Biology, Natural Enemies and Control. Volume 1B. Elsevier, Amsterdam

Charnov, E. L. 1976. Optimal foraging, the marginal theorem. Theor. Popul. Biol. 9: 129–136

Clark, T. L., and Messina, F. J. 1998. Foraging behavior of lacewing larvae (Neuroptera: Chrysopidae) on plants with divergent architectures. J. Insect Behavior. 11:303-317

Clark, T. L., and Messina, F. J. 1998. Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. Entomol. Exp. Appl. 86: 153-161

Cloyd, R. A. and Sadof, C. S. 2000. Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera: Pseudococcidae). Environ. Entomol. 29 (3): 535 – 541

Coll, M. and Bottrell, D. G. 1994. Effects of nonhost plants on an insect herbivore in diverse habitats. Ecology 75:723–31

Coll, M. and Ridgway, R. L. 1995. Functional and numerical responses of *Orius insidiosus* (Heteroptera: Anthocoridae) to its prey in different vegetable crops. Ann. Entomol. Soc. Am. 88:732–38

Coll, M. and Izraylevich, S. 1997. When predators also feed on plants: effects of competition and plant quality on omnivore-prey population dynamics. Annals of the Entomological Society of America (in press)

Crooker, A. 1985. Embryonic and Juvenile development. Pp. 149-163, In W. Helle and M.W. Sabelis (eds.), Spider Mites: Their Biology, Natural Enemies and Control. Volume 1A . Elsevier, Amsterdam

DeReffye, P., Houllier, F., Blaise, F., Barthelemy, D., Dauzat, J. and Auclair, D. 1995. A model simulating above- and below-ground tree architecture with agroforestry applications. Agrofor. Syst. 30: 175-197

Dicke, M. and Sabelis M. W. 1989. Does it pay plants to advertise for bodyguards? Towards a cost-benefit analysis of induced synomone production, Pp. 341–58, In H. Lambers, M. L. Cambridge, H. Connings, and T.L. Pons (ed.), Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. The Hague: SPB Acad.

Dixon, A. F. G. and Russel, R. J. 1972. The effectiveness of *Anthocoris nemorum* and *A. confusus* as predators of the sycamore aphid *Drepanosiphum platanoides*. II. Searching behaviour and the incidence of predation in the field. Entomologia Experimentalis et Applicata 15: 35–50

Eigenbrode, S. D., Castagnola, T., Roux, M. B., Steljes, L. 1996. Mobility of three generalist predators is greater on cabbage with glossy leaf wax that on cabbage with a wax bloom. Entomol. Exp. Appl. 81: 335–343

Espelie, K. E. and Brown, J. J. 1990. Cuticular hydrocarbons of species which interact on four trophic levels: apple, *Malus pumila* Mill.; codling moth, *Cydia pomonella* L.; a hymenopteran parasitoid, *Ascogaster quadridentata* Wesmael; and a hyperparasite, *Perilampus fulvicornis* Ashmead. Comp. Biochem. Physiol. 95B:131–36

Evans, H. F. 1976. The searching behaviour of *Anthocoris confuses* (Reuter) in relation to prey density and plant surface topography. Ecological Entomology 1: 163–169

Ferran, A. and Deconchat, M. 1992. Exploration of wheat leaves by *Coccinella septempunctata* L. (Coleoptera, Coccinellidae) larvae. J. Insect Behav. 5: 147-159

Frazer, B. D. and McGregor, R. R. 1994. Searching behaviour of adult female Coccinellidae (Coleoptera) on stem and leaf models. Can. Entomol 126: 389-399

Freese, G. 1995. Structural refuges in two stem boring weevils on *Rumex crispus*. Ecol. Entomol. 20: 351-358

Fujii, K., Holling, C. S. and Mace, P. M. 1986. A simple generalized model of attack by predators and parasites. Ecological Research 1(2): 141-156

Geitzenauer, H. L., and Bernays, E. A. 1996. Plant effects on prey choice by a vespid wasp, *Polistes arizonensis*. Ecol. Entomol. 21: 227-234

Gingras, D. and Boivin, G. 2002. Effect of plant structure, host density and foraging duration on host finding by *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). Environ. Entomol. 31: 1153-1157

Grevstad, F. and Klepetka, B. W. 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. Oecologia 92: 399-404

Gross, P. 1993. Insect behavioral and morphological defenses against parasitoids. Annu. Rev. Entomol. 38: 251–273

Hare, J. D. 1992. Effects of plant variation on herbivore natural enemy interactions, pp. 278-298. In R. S. Fritz and E. L. Simms (eds.), Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics. The University of Chicago Press, Chicago, IL

Hassell, M. P., Southwood, T. R. E. 1978. Foraging strategies of insects. Annu. Rev. Ecol. Syst. 9: 75-98

Hassell, M.P. and May, R.M. 1985. From individual behavior to population dynamics. In R. M. Sibly and R. H. Smith (eds.), Behavioural Ecology. Blackwell Scientific Publ., Oxford

Hoffmann, M. P. and Frodsham, A. C. 1993. Natural Enemies of Vegetable Insect Pests. Cooperative Extension, Cornell University, Ithaca, NY. 63 pp

Huffaker, C. B., Luck, R. F. and Messenger, P. S. 1976. The ecological basis of biological control, pp. 560-586, In D. White (ed.), Proceedings of the 15th International Congress of Entomology, Washington D.C.

Iatrou, G., Cook, C. M., Stamou, G. and Lanaras, T. 1995. Chlorophyll fluorescence and leaf chlorophyll content of bean leaves injured by spider mites (Acari: Tetranychidae). Exp. Appl. Acarol. 19: 581-591

Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. 117: 710–723

Jansen, V. A. A. and Sabelis, M. W. 1992. Prey dispersal and predator persistence. Exp. Appl. Acarol. 14: 215-231

Janssen, A. 1999. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. Entomologia Experimentalis et. Applicata. 90: 191-198

Kanour, W. W. and Burbutis, P. P. 1984. *Trichogramma nubilale* (Hym. Trichogrammatidae) field releases in corn and a hypothetical model for control of European corn borer (Lep.: Pyralidae). J. Econ. Entomol. 77: 103-107

Kareiva, P., and Sahakian, R. 1990. Tritrophic effects of a simple architectural mutation in pea plants. Nature 345: 433-434

Knipling, E. F. and McGuire, J. U. 1968. Population models to appraise the limitations and potentialities of *Trichogramma* in managing host insect populations. U.S. Dep. Agric. Tech. Bull. 1387: 1-44

Kondo, A. and Takafuji, A. 1985. Resource utilization pattern of two species of tetranychid mites (Acarina: Tetranychidae). Res. Popul. Ecol. 27: 145-157

Krebs J. R., Ryan J. C. and Charnov E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees Anim. Behav. 22: 953–964

Krips, O. E., Kleijn, P. W., Willems, P. E. L., Golds, G. J. Z. and Dicke, M. 1999. Leaf hairs influence searching efficiency and predation rate of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae). Experimental and Applied Acarology 23: 119-131

Krips, O. E., Willems, P. E. L., Gols, R., Posthumus, M. A., and Dicke, M. 1999. The response of *Phytoseiulus persimilis* to spider-mite induced volatiles from gerbera: influence of starvation and experience. J. Chem. Ecol. (in press)

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annu. Rev. Entomol. 28: 23-39

Legranda, A. and Barbosa, P. 2003. Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Environ. Entomol. 32: 1219-1226

Lewis, W. J and Martin, W. R. 1990. Semiochemicals for use with parasitoids: status and future. J. Chem. Ecol. 16: 3067–3089

Lukianchuk, J. L. and Smith, S. M. 1997. Influence of plant structural complexity on the foraging success of *Trichogramma minutum*: a comparison of search on artificial and foliage models. Entomol. Exp. Appl. 84: 221-228

Mackauer, M. and Volkl, W. 1993. Regulation of aphid populations by aphidiid wasps: does parasitoid foraging behavior or hyperparasitism limit impact? Oecologia 94: 339-350

Maeda, T. and Takabayashi, J. 2001. Production of herbivore-induced plant volatiles and their attractiveness to *Phytoseiulus persimilis* (Acari: Phytoseiidae) with changes of *Tetranychus urticae* (Acari: Tetranychidae) density on a plant. Appl. Entomol. Zool. 36: 47-52

Maini, S. and Burgio, G. 1990. Biological control of the European corn borer in protected pepper by *Trichogramma maidis* Pint. and Voeg. and *Bacillus thuringiensis* Berl, pp. 213-216. In E. Wajnberg and S. B. Vinson (eds.), *Trichogramma* and other egg parasitoids. Proceedings, 3rd International Symposium, Sept. 23-27, 1990, San Antonio, TX. Les Colloques, No 56. Institut National de la Recherche Agronomique (INRA), Paris

Marquis, R. J. and Whelan, C. 1996. Plant morphology and recruitment of the third trophic level: subtle and little-recognized defenses? Oikos 75: 330-334

Marquis, R. J., Lill, J. T. and Piccinni, A. 2002. Effect of plant architecture on the colonization and damage by leaftying caterpillars of *Quercus alba*. Oikos 99: 531-537

McCauley, E., Kendall, B. E., Janssen, A., Wood, S., Murdoch, W. W., Hosseini, P., Briggs, C. J., Ellner, S. P., Nisbet, R. M., Sabelis, M. W. and Turchin, P. 2000. Inferring colonization processes from population dynamics in spatially structured predator-prey systems. Ecology 81: 3350-3361

McGovern, W. L. and Cross, W. H. 1976. Effects of two cotton varieties on levels of boll weevil parasitism (Coleoptera: Curculionidae). Entomophaga 21: 123–25

Moran, V. C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. Ecol. Entomol. 5: 153-164

Mori, H. and Chant, D. A. 1966. The influence of humidity on the activity of *Phytoseiulus persimilis* Athias-Henriot and its prey *Tetranychus urticae* C.L. Koch (Acarica:Phytoseiidae, Tetranychidae). Can. J. Zool. 44: 863-871

Nachman, G. 1987. Systems analysis of acarine predator-prey interactions. II. The role of spatial processes in system stability. J. Anim. Ecol. 56: 267-281

Nachman, G. 1988. Regional persistence of locally unstable predator-prey populations. Exp. Appl. Acarol. 5: 293-318

Nachman, G. 1991. An acarine predator-prey metapopulation system inhabiting greenhouse cucumbers. Biol. J. Linn. Soc. 42: 285-303

Need, J. T., and Burbutis, P. P. 1979. Searching efficiency of *Trichogramma nubilae*. Environ. Entomol. 8: 224-227

Obrycki, J. J. and Tauber, M. J. 1984. Natural enemy activity on glandular pubescent potato plants in the greenhouse: An unreliable predictor of effects in the field. Environ. Entomol. 13: 679–683

Obrycki, J. J. 1986. The influence of foliar pubescence on entomophagous speciesm, Pp. 61-83, In D. J. Boethel and R. D. Eikenbarry (eds.), Interactions of Plant Resistance and Parasitoids and Predators of Insects, Wiley, New York,

Overmeer, W. P.J. 1985. Alternative prey and other food resources, Pp.131-139, In W. Helle and M. W. Sabelis (eds.), Spider Mites: Their Biology, Natural Enemies and Control. Volume 1B. Elsevier, Amsterdam

Park, Y. L. and Lee, J. H. 2005. Impact of twospotted spider mite (Acari: Tetranychidae) on growth and productivity of glasshouse cucumbers. J. Econ. Entomol. 98: 457-463.

Peitsch, D., Fietz, A., Hertel, H. de Souza. J., Ventura, D. F., Menzel, R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. J. Comp. Physiol. A 170: 23–40

Persson, L., 1993. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. Oikos 68: 12–22

Pimentel, D. 1961. An evaluation of insect resistance in broccoli, brussels sprouts, cabbage, collards, and kale. J. Econ. Entomol. 54: 156-158

Price, P. W. 1986. Ecological aspects of host plant resistance and biological control: Interactions among three trophic levels, Pp. 11-30, In D. J. Boethel and R. D. Eikenbarry (eds.), Interactions of Plant Resistance and Parasitoids and Predators of Insects, Wiley, New York,

Rabb, R. L and Bradley, J. R. 1968. The influence of host plants on parasitism of the eggs of the tobacco budworm. J. Econ. Entomol. 61: 1249–1252

Ramsy, A. H. 1977. Predatory efficiency and biology of the predatory mite, *Amblyseius gossipi* (Acarina: Phytoseiidae) as affected by plant surfaces. Entomophaga 22: 421-423

Romero, G. Q. and Vasconcellos-Neto, J. 2005. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). Journal of Animal Ecology 74: 12-21.

Ryoo, M. I. 1996. Influence of the spatial distribution pattern of prey among patches and spatial coincidence on the functional and numerical response of *Phytoseiulus persimilis* (Acarina, Phytoseiidae). J. Appl. Entomol. 120: 187–192

Sabelis, M.W. 1981. Biological control of two-spotted spider mite using phytoseiid predators. Part I: Modelling the predator-prey interaction at the individual level. Agricultural Research Reports 910, Pudoc, Wageningen, Netherlands. 242 pp

Sabelis, M. W., Dicke, M. 1985. Long-range dispersal and searching behaviour, Pp. 141-60 In W. Helle and M. W. Sabelis (eds.), Spider Mites, Their Biology, Natural Enemies and Control, Vol. IB, Amsterdam:Elsevier Sci

Sabelis, M. W., O. Diekmann, and V. A. A. Jansen. 1991. Metapopulation persistence despite local extinction: predator-prey patch models of the Lotka-Volterra type. Biol. J. Linn. Soc. 42: 267-283

Sabelis, M. W., Van Baalen, M., Bruin, J., Egas, M., Cansen, V. A. A., Janssen, A. and Bas Pels. 1999. The evolution of overexploitation and mutualism in plant-herbivore-predator interactions and its impact on population dynamics, Pp. 259-282 In B.A. Hawkins and H.V. Cornell (eds.), Theoretical Approaches to Biological Control. Cambridge University Press, Cambridge, England

SAS (Statistical Analysis System). Version 8.2. SAS Institute, Cary NC

Shah, M. A. 1982. The influence of plant surfaces on the searching behaviour of coccinellid larvae. Entomol. Exp. Appl. 31: 377-380.

Shields, E. J. and T. F. Watson, 1980. Searching behavior of female *Orius tristicolor*. Annals of the Entomological Society of America 73: 533–535

Skirvin, D. and J. S. Fenlon. 2001. Plant species modifies the functional response of *Phytoseiulus persimilis* (Acari: Phytoseiidae) to *Tetranychus urticae* (Acari: Tetranychidae): implications for biological control. Bulletin of Entomological Research 91: 61-67

Skirvin, D. and J. S. Fenlon. 2003. Of mites and movement: the effects of plant connectedness and temperature on movement of *Phytoseiulus persimilis*. Biological Control 27: 242-250

Stadler, B., and Völk, W. 1991. Foraging patterns of two aphid parasitoids, *Lysiphlebus testaceipes* and *Aphidius colemani* on banana. Entomol. Exp. Appl. 58: 221-229

Stamp, N. E. and Browers, M. D. 1993. Presence of predatory wasps and stinkbugs alters foraging behavior of cryptic and non-cryptic on plantain (Plantago lanceolata). Oecologia 95: 376-384

Stavrinides, M. C. and Skirvin, D. J. 2003. The effect of chrysanthemum leaf trichome density and prey spatial distribution on predation of *Tetranychus urticae* (Acari: Tetranychidae) by *Phytoseiulus persimilis* (Acari: Phytoseiidae). Bull. Ent. Res. 93: 343-350

Strong, D. R., Lawton, J. H. and Southwood, T. R. 1984. Insects on Plants. Harvard University Press. Cambridge,MA

Takabayashi, J., Dicke, M. and Posthumus, M. A. 1994. Volatile herbivore-induced terpenoids in plant-mite interactions: variation caused by biotic and abiotic factors. J Chem Ecol 20: 1329–1354

Takafuji, A. 1977. The effect of the rate of successful dispersal of a phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) on the persistence in the interactive system between the predator and its prey. Res. Popul. Ecol. 18: 210-222

Takafuji, A., Tsuda, Y. and Mori, T. 1983. System behaviour in predator-prey interaction, with special reference to acarine predator-prey systems. Res. Popul. Ecol. Suppl. 3: 75-92

Thorpe, K. W. 1985. Effects of height and habitat type on egg parasitism by *Trichogramma minutum* and *T. pretiosum* (Hymenoptera: Trichogrammatidae). Agric. Ecosyst. Environ. 12: 117-126

Treacy, M. F., Zummo, G. R. and Benedict, J. H. 1985. Interactions of host-plant resistance in cotton with predators and parasites. Agric. Ecosyst. Environ. 13: 151-157

Turlings, T. C. J., Scheepmaker, J. W. A., Vet, L. E. M., Tumlinson, J. H., Lewis, W. J. 1990. How contact foraging experiences affect preferences for host-related odors in the larval parasitoid *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae). J. Chem. Ecol. 16: 1577–1589

Uetz, G. W. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems, pp. 325-348. In S. S. Bell, E. D. McCoy, and H. R. Mushinsky (eds.), Habitat Structure, the Physical Arrangement of Objects in Space. Chapman and Hall, New York

Van Baalen, M. and Sabelis, M. W. 1995. The milker-killer dilemma in spatially structured predator–prey interactions. Oikos 74: 391–400

Van de Vrie, M., McMurtry, J. A. and Huffaker, C. B. 1972. Ecology of tetranychid mites and their natural enemies: a review. III. Biology, ecology and pest status, and host-plant relations of Tetranychids. Hilgardia 41: 343-432

Van Lenteren, J.C. and Woets, J. 1988. Biological and integrated pest control in greenhouses. Ann. Rev. Entomol. 33: 239-269

Van Lenteren, J. C., and de Ponti, O. M. B. 1990. Plant leaf morphology, host-plant resistance and biological control. Symp. Biol. Hung. 39: 365-386

Vet, L. E. M., and Dicke, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annu. Rev. Entomol. 37: 141-172

Walde, S. J. 1991. Patch dynamics of a phytophagous mite population: effect of number of subpopulations. Ecology 72: 1591-1598

Walde, S. J. 1994. Immigration and the dynamics of a predator-prey interaction in biological control. J. Anim. Ecol. 63: 337-346.

Walde, S. J. and Nachman, G. 1999. Dynamics of spatially structured spider mite populations. Pp. 163-189 In B. A. Hawkins and H. V. Cornell (eds.), Theoretical Approaches to Biological Control. Cambridge University Press, Cambridge, UK.

Walter, D. E. and O'Dowd, D. J. 1992. Leaf morphology and predators: effect of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). Environ. Entomol. 21: 478-484.

Weisser, W. W. 1995. Within-plant foraging behaviour of the aphid parasitoid *Aphidius funebris*: plant architecture, host behaviour, and individual variation. Entomol. Exp. Appl. 76: 133-141

Yasuda, H. and Ishikawa, H. 1999. Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. J. Appl. Ent. 123: 474-478

Zhang, Z.-Q., Sanderson, J.P. and Nyrop, J. P. 1991. Foraging time and spatial patterns of predation in experimental populations. A comparative study of three mite predator-prey systems (Acari: Phytoseiidae, Tetranychidae). Oecologia. 90: 185-196

Zhang, Z.-Q. and Sanderson, J. P. 1993. Hunger and age effects on searching behavior of three species of predatory mites (Acari: Phytoseiidae). Can. J. Zool. 71: 1997-2004