

AN ABSTRACT OF THE DISSERTATION OF

Chuleui Jung for the degree of Doctor of Philosophy in Entomology presented on
January 11, 2001. Title: Ambulatory and Aerial Dispersal Among Specialist and
Generalist Phytoseiid Mites

Abstract approval.

Redacted for Privacy

Brian A. Croft

Specialist and generalist phytoseiid mites are widely used for biological control of spider mites. Understanding dispersal attributes of these mites is important to implementing more stable, cost-efficient integrated pest management. In this regard, we studied dispersal of phytoseiid mites from a local ambulatory phase of movement within a prey patch to a longer-range phase that includes emigration (aerial take-off and dispersal distance) and immigration to a new plant.

Specialist phytoseiids showed higher ambulatory and aerial dispersal than generalist species. Somewhat different dispersal strategies were seen between *Neoseiulus fallacis* (more specialized predator) and *N. californicus* (more generalized predator): The most important difference was earlier and continuous dispersal of *N. californicus* from a prey patch. Cues from spider mite infestation suppressed the dispersal rates for specialists, but either increased or did not change the dispersal rates for generalist phytoseiids.

Aerodynamic calculations support the hypothesis that *Phytoseiulus persimilis* may not require a standing take-off behavior to become airborne. However, with less vertical profile, a mite may become airborne more by standing erect (*N. fallacis*), than a species that does not show standing take-off (*N. californicus*). Jumping behavior by *P. persimilis* was observed for the first time among Phytoseiidae.

Falling speed ranged from 0.4 to 0.73 m/s for 13 phytoseiid species and 0.79 to 0.81 for two-spotted spider mite. These values were quite similar to theoretical estimates for specialist phytoseiids, but less for generalists. From falling speed estimates and other morphological data, it was possible to predict aerial dispersal distance of phytoseiids using analytical models.

After landing on bare soil following aerial dispersal, high mortality of *N. fallacis* was observed in the field during summer. Distance from the landing point to target plants showed negative log linear relationships. Soil surfaces and management actions influenced survival and recovery. Environmental conditions greatly affected survival of the predator. We speculated that phytoseiids that fell on ground were moving to the target plants via both ambulatory and aerial means.

©Copyright by Chuleui Jung

2001

All Rights Reserved

**Ambulatory and Aerial Dispersal Among Specialist and Generalist Phytoseiid
Mites**

by

Chuleui Jung

A Dissertation

Submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Doctor of Philosophy

Presented January 11, 2001

Commencement June 2001

Doctor of Philosophy dissertation of Chuleui Jung presented on January 11, 2001

Approved:

Redacted for Privacy

Major Professor, representing Entomology

Redacted for Privacy

Head of Department of Entomology

Redacted for Privacy

Dean of Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Redacted for Privacy

Chuleui Jung, Author

ACKNOWLEDGEMENTS

Dr. Brian A. Croft deserves special acknowledgement for his supports and guidance during my studies. Further more, he has shown me how to conduct research, publish scientific papers and function as a scientist in many ways. My other committee members, Drs. Joe Beatty, Ken Johnson, Jack DeAngeles, and Phil Rossignol were very generous with their time and comments. I would also thank our group of Len Coop, Hans Luh, Peter Schausberger, Paul Pratt, Dan Slone, Diedre Prischmann, and Scott Blackwood for assistance and companionship. I appreciate Drs. Krantz, Jepson, and Bajwa for their kindness and help, Tae-Hwan Kim and Dr Berry's lab for willingness to support my requests. I thank many Korean students and all other entomology members for making my stay in Corvallis enjoyable. I am in debt to the Korean government for initial support of my studies. Finally, I appreciate my parents in Cheju and Choe-ga in Suwon, Korea for their encouragement and patience. I express a deep appreciation to my wife, Yoonsuk Min and kids, Sunghoo and Sungyoon for their love, endurance and companionship.

CONTRIBUTION OF AUTHORS

Brian A. Croft was involved in the design, analysis and writing of each chapter of this dissertation. Chapter 5 was used with permission from Kluwer Academic Publishers. The original publication is:

Jung, C. and B. A. Croft. 2000. Survival and plant-prey finding by *Neoseiulus fallacis* (Acari: Phytoseiidae) on soil substrates after aerial dispersal. Exp. Appl. Acarol. 24: 579-596.

TABLE OF CONTENTS

	<u>Page</u>
 CHAPTER 1	
INTRODUCTION.....	1
 CHAPTER 2	
AMBULATORY AND AERIAL DISPERSAL AMONG SPECIALIST AND GENERALIST PREDATORY MITES (ACARI: PHYTOSEIIDAE).....	6
ABSTRACT.....	7
INTRODUCTION.....	8
MATERIALS AND METHOD	9
RESULTS.....	14
DISCUSSION.....	22
REFERENCES.....	28
 CHAPTER 3	
AERODYNAMIC ASPECTS OF DISPERSAL TAKE-OFF BEHAVIOR AMONG THE PHYTOSEIID MITES, <i>Phytoseiulus persimilis</i> , <i>Neoseiulus fallacis</i> AND <i>N. californicus</i>	34
ABSTRACT.....	35
INTRODUCTION.....	36
MATERIALS AND METHOD.....	38
RESULTS.....	40
DISCUSSION.....	43
REFERENCES.....	49

TABLE OF CONTENTS (CONTINUED)

	Page
 CHAPTER 4	
AERIAL DISPERSAL OF PHYTOSEIID MITES (ACARI: PHYTOSEIIDAE): ESTIMATING FALLING SPEED AND DISPERSAL DISTANCE OF ADULT FEMALES.....	52
ABSTRACT.....	53
INTRODUCTION.....	54
MATERIALS AND METHOD	56
RESULTS.....	61
DISCUSSION.....	69
REFERENCES.....	76
 CHAPTER 5	
SURVIVAL AND PLANT-PREY FINDING BY <i>Neoseiulus fallacis</i> (ACARI: PHYTOSEIIDAE) ON SOIL SUBSTRATES AFTER AERIAL DISPERSAL.....	82
ABSTRACT.....	83
INTRODUCTION.....	84
MATERIALS AND METHOD.....	86
RESULTS.....	92
DISCUSSION.....	102
REFERENCES.....	108
 CHAPTER 6	
CONCLUSIONS.....	114
BIBLIOGRAPHY.....	118

LIST OF FIGURES

<u>Fig.</u>	<u>Page</u>
1.1. Conceptual description of spider mite and phytoseiid interactions and dispersal.	4
2.1. Walking patterns (walking speed, net speed and turning coefficient) of five phytoseiid mites after starvation of 2, 6, 12 and 24 hr	16
2.2. Activity levels of five phytoseiid mites measured on a smooth lima bean leaf (a) and a hairy hazelnut leaf (b) relative to the starvation of 2, 6, 12 and 24 hr.	17
2.3. Aerial dispersal rates of five phytoseiid mites measured in the wind tunnel (wind speed 1.4 m/s).	21
3.1. Vertical velocity profiles for a free stream wind speed (4 m/s) at 10 (broken line) and 30 mm (continuous line) from the leading edge of a flat surface and scaled illustrations of 3 phytoseiid mites in walking and standing posture (from the left, Nf or Nc in walking posture, Nf in standing posture and Pp in walking posture).....	42
3.2. Trajectories of horizontal displacement from the mechanical pencil rod, 30 mm above the surface (a: <i>N. fallacis</i> , b: <i>N. californicus</i> , and c: <i>P. persimilis</i>).	44
4.1. Average falling speeds (m/s) measured vs. theoretically estimated.....	64
4.2. Cumulative dispersal distances measured vs. simulated from wind tunnel studies; single line refers to GJ model output and dotted line does to OL model output.	66
4.3. Distance distribution of aerial dispersal, measured vs. simulated in greenhouse settings:(a), dispersal of <i>N. fallacis</i> and <i>P. persimilis</i> , and (b), that of <i>N. fallacis</i> and <i>N. californicus</i>	67
4.4. Distance distribution of aerial dispersal, measured vs. simulated in the field conditions with <i>N. fallacis</i> (a) and <i>G. occidentalis</i> and <i>T. pyri</i> (b).	68
5.1. Distance dependant recovery of <i>N. fallacis</i> (Log (% recovery+1) + SE) under field (F1, F2, F3) and greenhouse (G1, G2, G3) conditions.....	93

LIST OF FIGURES (CONTINUED)

<u>Fig.</u>	<u>Page</u>
5.2. Effects of soil surface types (a: upper graph, ANOVA, df=3,10, P<0.095) and management practices (b: lower graph, ANOVA, df=3,10, P<0.02) on recovery of <i>N. fallacis</i> (mean % $\pm$ SE) in receiver plant units with prey mites (<i>T. urticae</i>) in the field.....	94
5.3. Mortality prediction model of <i>N. fallacis</i> held without food and water (degree-day baseline temperature = 4 °C: $Mortality = (0.026 - 0.00022 \times RH (\%)) \times DD$ (GLM, $R^2=0.87$).....	97
5.4. Variation of recovery (mean % $\pm$ SE) at 0.22 m distance on fine soil under different environmental settings. Estimates based on random chance, temperature-humidity-dependent mortality and emigration rate from released leaf-pack.....	99
5.5. Direction-dependant recovery of <i>N. fallacis</i> on receiver plants with <i>T. urticae</i> in a field study (a: upper graph) and environmental conditions during study periods (b: lower graph). Environmental measurements are ambient temperature (Temp), relative humidity (R.H.), and frequency of eastward winds (Wind to East), and wind speeds exceeding 5 m/s (WS>5).....	100
5.6. Cumulative recovery pattern (mean % $\pm$ SD) of <i>N. fallacis</i> to receiver plant units with <i>T. urticae</i> after predator releases at 0.22 m distance on fine soil in the field and greenhouse.....	101

LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1. Diffusion coefficient (D) and mean travel distances (r) of phytoseiid mites on a patch of lima bean plants infested with TSSM and pollen; measured at day 1, 3 and 5 after predator release.....	18
2.2. Some parameters of local dynamics of TSSM and phytoseiid mites (<i>Neoseiulus fallacis</i> vs <i>N. californicus</i>); I: interaction time, D: time of the first dispersal, f: fraction of predator dispersal before prey extinction, T: total number of predator dispersal, SD: standard deviation.....	18
2.3. Effect of previous TSSM infestation on aerial take-off of phytoseiid mites (24 hr starved) under the wind tunnel (1.3 m/s).	20
3.1. Vertical profiles; <i>H1</i> : height of leg, <i>H2</i> : height of body, distance from the surface to the dorsum, <i>A</i> : cross-section area of predatory mites in walking vs. standing posture, and aerodynamic parameters; <i>V</i> : wind speed at the corresponding height, <i>Re</i> : Reynolds number, <i>Cd</i> : drag coefficient and <i>Fm</i> : drag force.....	41
4.1. Parameters used in the falling speed estimation (Eq. 1) of mite species.....	58
4.2. Falling speed measurements and weight of well-fed and starved mites (n=20).....	63
4.3. Hypothetical distribution of wind speeds and dispersal potentials in simplified cropping systems based on 8 m/s wind speed at reference height, 10 m.....	73
5.1. Environmental conditions under which each experiment was performed in the Field (F) and in the greenhouse (G).....	98

Ambulatory and Aerial Dispersal Among Specialist and Generalist Phytoseiid Mites

CHAPTER 1

INTRODUCTION

Phytoseiid mites are widely used as biological control agents of spider mites (Helle and Sabelis 1985). Four life-style type groups of phytoseiids have been proposed based on diet range and ecological traits (McMurtry and Croft 1997). Type I species are obligate specialist predators of spider mites and include species such as *Phytoseiulus persimilis* Athias-Henriot and *P. macropilis* (Banks). Type II species are specialist predators of spider mites but they also feed on other mites and a few insects. *Neoseiulus fallacis* (Garman), and *Galendromus occidentalis* (Nesbitt) are Type II species. Type III species are generalist predators of mites, insects and pollens and include *Typhlodromus pyri* Scheuten, *Kampimodromus aberrans* (Oudemans) and *Amblyseius andersoni* Chant. Type IV species prefer pollens as diet, but also feed on mites and insects. Species in the genus *Euseius* are type IV.

Spider mite biological control systems that include specialist type predators often undergo boom and burst cycles, but they provide quick control of spider mite outbreaks (Nachman 1988). On the other hand, spider mite-generalist phytoseiids systems show less fluctuation, and provide slower and more limited control of spider mite outbreaks (Walde et al. 1992). However, for ecological and human-

related reasons, spider mite-phytoseiid systems are unstable and thus efficient dispersal mechanisms have evolved for these mites to find plant and prey resources and escape local and regional extinction.

Dispersal is an adaptive process that permits individuals to spread and escape unfavorable conditions, and to colonize new habitats (Price 1984). Dispersal influences persistence, distribution, and abundance, and determines gene flow in a population. Pesticide resistance features in many pests and natural enemies in agricultural settings are affected by the degree of dispersal (Dunley and Croft 1992). Also, dispersal influences community structure, such as multi-species prey-predator interactions. Understanding dispersal of phytoseiids is important to implementation of biological control and more broadly, to efficient and cost-effective integrated pest management in agriculture.

Phytoseiid mites have evolved two main modes of dispersal (Johnson and Croft 1976, Sabelis and Dicke 1985); short distance ambulatory movement within a prey patch (or plant) and long distance aerial movement between prey patches (or plants). The latter is mainly passive and by wind, but some active take-off behaviors have been reported (Sabelis and Afman 1994). Figure 1.1 describes the conceptual framework of phytoseiid mite dispersal ranging from local interaction, to emigration and immigration via the air. At a local level, prey-predator interaction and ambulatory movements are important. As prey food levels decline and with starvation and onset of wind, aerial take-off of phytoseiids occurs. Air currents transport mites a certain distance and deposit them. To date, no control of landing

by airborne phytoseiids has been reported. Thus, if an airborne mite does not land on a plant or spider mite colony, they may undergo ambulatory searching or redispersal through the air.

The overall goal of this dissertation was to understand phytoseiids dispersal as described in Figure 1. Specific objectives or questions were: How do phytoseiids interact with spider mites in patches and disperse ambulatorially? What aerodynamic constraints and behaviors are involved in aerial take-off for more long-range dispersal? After aerial take-off, how far can phytoseiids move in air and what factors influence the distance dispersed? Are active, within air behaviors possible that control distance and direction of movement? After landing from aerial dispersal and depending on where they land, how well do phytoseiids survive and how do they find their plant/prey hosts thereafter?

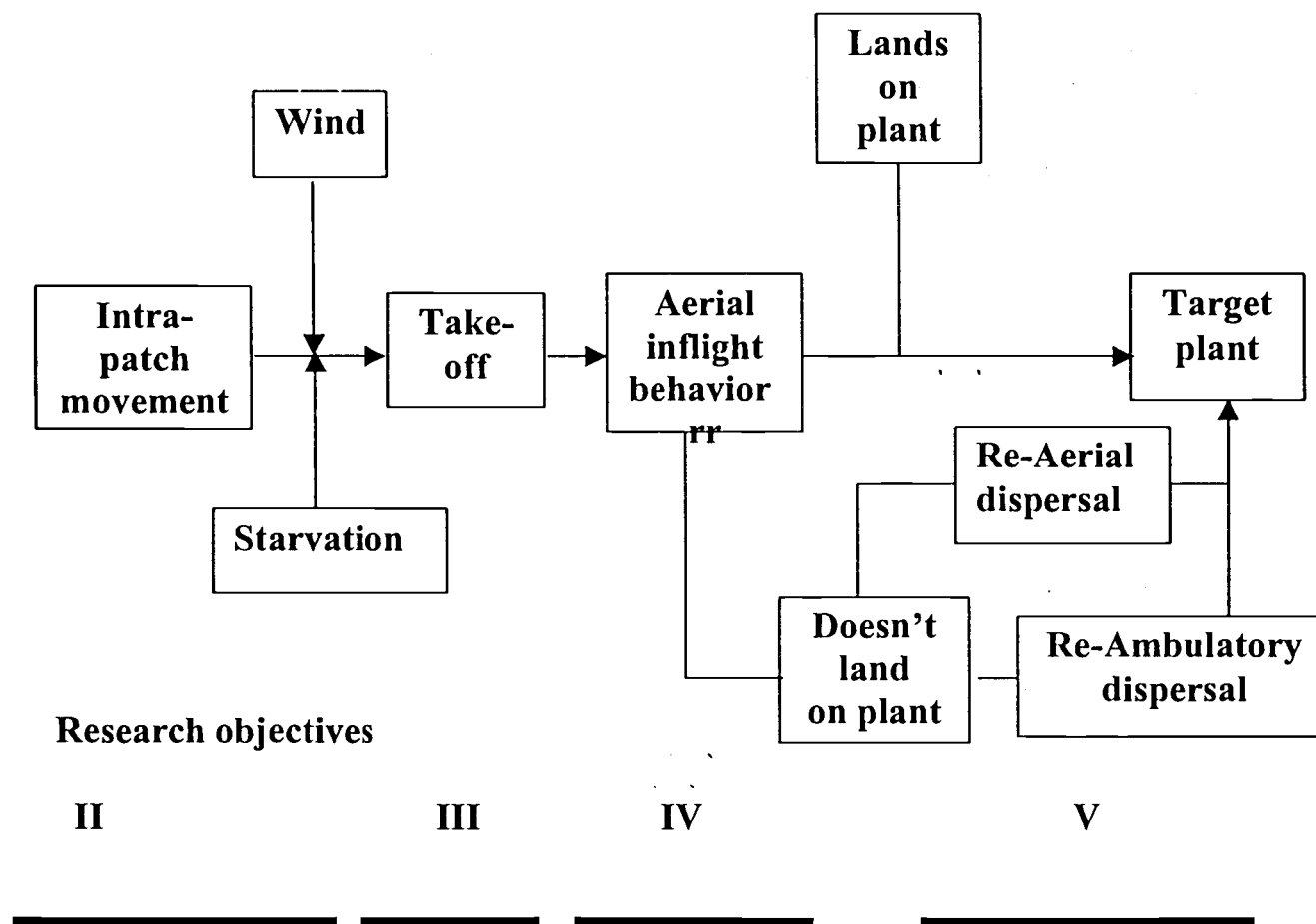


Fig. 1.1. Conceptual description of spider mite and phytoseiid interaction and dispersal. The corresponding chapter in the dissertation to each research objective is shown at the bottom.

REFERENCES

- Dunley, J. E., and B. A. Croft. 1992. Dispersal and gene flow of pesticide resistance traits in phytoseiid and tetranychid mites. *Exp. Appl. Acarol.* 14 313-326.
- Helle, W., and M. W. Sabelis [eds.]. 1985. Spider mites. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.
- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). *Annals of the Entomological Society of America* 69 1019-1023.
- McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. *Ann. Rev. Entomol.* 42 291-321.
- Nachman, G. 1988. Regional persistence of locally unstable predator/prey populations. *Exp. & Appl. Acarol.* 5 293-318.
- Price, P. W. 1984. *Insect ecology*. John Wiley & Sons, New York.
- Sabelis, M. W., and M. Dicke. 1985. Long-range dispersal and searching behaviour, pp. 141-157. *In* W. Helle and M. W. Sabelis [eds.], *Spider mites. Their biology, natural enemies and control*. Elsevier, Amsterdam.
- Walde, S. J., J. P. Nyrop, and J. M. Hardman. 1992. Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Exp. Appl. Acarol.* 14 261-292.

CHAPTER 2

AMBULATORY AND AERIAL DISPERSAL AMONG SPECIALIST AND GENERALIST PREDATORY MITES (ACARI: PHYTOSEIIDAE)

Chuleui Jung and Brian A. Croft

Prepared for Environmental Entomology

ABSTRACT

Predator-prey systems having a specialist predator often are over-exploitive, unstable and transient while similar systems with a generalist predator show less fluctuation, more stability and regulation at lower densities. These population dynamics also result in different dispersal patterns between specialist and generalists predators. In this regard, ambulatory and aerial dispersal were studied among five predaceous phytoseiid mites having different degrees of predation specialization: (*Phytoseiulus persimilis* Athias-Henriot, Specialist I; *Neoseiulus fallacis* (Garman) Specialist II; *N. californicus* Chant, Specialist II/Generalist III; *Kampimodromus aberrans*, Generalist III; and *Euseius finlandicus*, Generalist IV). In general, specialist species had higher walking activity and aerial dispersal than generalist species. Somewhat different dispersal strategies were seen between *N. fallacis* and *N. californicus*: Dispersal from a prey (two-spotted spider mite, *Tetranychus urticae* Koch) patch was earlier for the more generalized *N. californicus*, and *N. fallacis* (more specialized phytoseiid) did not disperse until almost all prey were eliminated. Both dispersed aerially at similar rates. Cues from spider mite infestations decreased dispersal of specialist phytoseiids, but either acted to increase or not affect dispersal of generalist phytoseiid species.

KEYWORDS: Walking speed, diffusion coefficient, aerial take-off, infochemicals.

INTRODUCTION

Dispersal is an important life history component that permits individuals to spread and escape from unfavorable conditions, and colonize new habitats (Price 1984).

Dispersal influences persistence, distribution and abundance of populations (Dingle 1996); it also affects gene flow (e.g. evolution of pesticide resistance in agriculture, Dunley and Croft 1992). Dispersal of predaceous mites is important to persistence of many acarine predator-prey systems (Huffaker et al. 1963, Nachman 1988, van de Klashorst 1992).

Predaceous phytoseiid mites are used as biological control agents of spider mites and insects in many crops (Helle and Sabelis 1985). Four life-style types of phytoseiids have been proposed based on diet range and ecological traits; they range from obligate specialists (Type I) that feed mostly on web-spinning spider mites to generalists (Type IV) that use many foods, but prefer pollens (McMurtry and Croft 1997, see also McMurtry and Rodriguez 1987).

Spider mite biological control systems having specialist predators are more transient than those having generalist predators: spider mites distribute in patches, and predators overexploit these aggregations of prey and then emigrate or die of starvation, thus leaving plants unprotected. Predator-prey dynamics often go through boom-burst cycles in these cases (Bernstein 1984, Nachman 1987a,b, van de Klashorst 1992). Conversely, spider mite-generalist phytoseiid systems show less fluctuation, and slower and more limited control of spider mite outbreaks

(McMurtry 1992, Walde et al. 1992). Thus, different dispersal patterns occur between specialist and generalist phytoseiids (Levin et al. 1984, Dunley and Croft 1990, McMurtry 1992, Hewitt and Butlin 1997).

We examined some factors influencing ambulatory and aerial dispersal of five phytoseiid species ranging from Type I to Type IV (McMurtry and Croft 1997). For ambulatory dispersal, walking patterns and activity were measured in the laboratory, and diffusion coefficients (D) were assessed in a greenhouse study. We determined whether there are different strategies of dispersal between specialist and generalist predators in a local predator-prey interaction. For aerial dispersal, rates after different exposure times to a constant wind speed and effects of spider mite infestations were evaluated. Different capacities to disperse are discussed relative to foraging and local and regional population dynamics.

MATERIALS AND METHOD

Mites: Laboratory strains of 5 phytoseiid species and one tetranychid mite, two-spotted spider mite, *Tetranychus urticae* Koch (TSSM) were tested. Only the adult female stage was used because it is the primary dispersing stage and of great importance to population dynamics aspects (Johnson and Croft 1976, Boykin and Campbell 1984, Sabelis and Dicke 1985). Laboratory cultures of phytoseiids were maintained by feeding them on *T. urticae*, (*Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus fallacis* (Garman) and *N. californicus* McGregor), and birch pollen,

Betula pendula Roth (*Kampimodromus aberrans* (Oudemans) and *Euseius finlandicus* (Oudemans)). These species span from a Type I specialists to a Type IV generalists (McMurtry and Croft 1997). *P. persimilis* is a Type I, obligate specialist predator of spider mites, *N. fallacis* and *N. californicus* are Type II, specialist predator of spider mites, although *N. californicus* is more of a generalist than *N. fallacis* (Croft et al. 1997). *K. aberrans* is a Type III generalist that feeds on pollens, other mites, and insects, and *E. finlandicus* is Type IV generalist, that mostly feeds on pollen. Hereafter, these species are referred to as Pp, Nf, Nc, Ka, and Ef.

Ambulatory dispersal

Walking pattern and activity: All five phytoseiids were evaluated for walking speed, net-speed, turning coefficient and activity level. Mixed-aged adult females were held without food for 2, 6, 12, and 24 hr (n=15 per each treatment) on each lima bean leaf (*Phaseolus lunatus* L.) bordered with wet tissue under 24 ± 1.2 °C and held under continuous dark (refer as the standard method of starvation in this study). An adult female predatory mite was placed on the center of a cardboard arena (dia. 40 cm) bordered with sticky material (Tanglefoot®, Grand Rapids, MI) at 24 ± 1.2 °C and 70 ± 10 % RH. Walking path was tracked for 1-1.5 min on a grid under cool light. Walking speeds (total length of the walking path over time) and net speeds (distance from the origin over time) were measured. Turning coefficient was the ratio of net speed divided by walking speed (Bernstein 1983). Ten

individuals from each starvation treatment per each species were evaluated.

Activity level was determined as the number of mites moving divided by number of mites ($n=15$) in each starvation arena (2, 6, 12 and 24 hr). Observations were made for 2 min, 3 times per treatment under cool light on either a smooth lima bean (*P. lunatus*) or a hairy filbert leaf (*Corylus avellana*). Data were analyzed by ANOVA-LSD (Ramsey and Schafer 1997) using SAS 6.2.

Diffusion coefficients: Pp, Nf, Nc and Ef were evaluated for the mean travel distance (r) and diffusion coefficients (D) on lima bean plant patches. Experiments were conducted in a greenhouse at $26:21 (\pm 5) ^\circ\text{C}$ (L:D), photoperiod of 16:8 (L:D) and $75\pm 10\%$ RH. A square plot (1 m dia.) of lima bean plants (160 ± 8.2 plants with 2 leaves per plant, 3 wk old) had 23 ± 7.5 mobile TSSM per leaf and birch pollen spread evenly. Thus, food was in excess for all species. Leaves were continuously overlapped. 100 adult females predator mites per species were placed in the center of each plot (4 replicates per species) and sampled 20 leaves along a diagonal transect with a optic visor (10X) at 1, 3 and 5 days after predator release. Mean travel distances were compared by ANOVA-LSD and diffusion coefficients were calculated according to Shigesada and Kawasaki (1997).

Local dynamics of spider mite-phytoseiid (Nf vs. Nc) interactions: *Neoseiulus californicus* has more ambulatory movement between prey patches than Nf (Pratt et al. 1998) and a different overall dispersal strategy between these two species was

expected. We expected Nf to emigrate between patches at a point near prey extinction and Nc to show an earlier, more constant dispersal between patches during an interaction period (e.g. milker-killer strategy, Van Baalen and Sabelis 1995, Pels and Sabelis 1999), but we expected Nf to aeri ally disperse more rapidly than Nc (Pratt et al. 1998). Local patch dynamics of either Nf or Nc with TSSM were studied in a two-leaf system of lima bean. The first two leaves that attach oppositely on the stem were removed from the stem. A piece of paper towel was placed on top of a water saturated foam pad, and leaves were placed ventral side up on the paper towel. The edge of each leaf was sealed with wet tissue paper and adhesive (Tanglefoot®), thus allowing mites to move between leaves only via the petiole. For each pair of leaves, one was considered an interaction arena of TSSM and predator, the other, a receiver arena for immigrating predators. Six young TSSM females were placed in each interaction arena. After 2 d, two adult female predatory mites were placed in a TSSM-colonized arena (6 replicates per species). In each receiver arena, eggs of TSSM were replaced periodically as a food for predators that dispersed from an interaction arena. TSSM and predators in an interaction arena were assessed daily until all predators dispersed or died. Predators dispersed into a receiver arena were removed after counting. Mites caught in adhesive along the edge of an interaction arena were counted as dispersed. The interaction time that was defined as days between predator introduction and prey elimination, time of the first dispersal, fraction of predator dispersal before prey

extinction, and total number of predator dispersed were compared with Student's t-test (Ramsey and Schafer 1997).

Aerial dispersal

Aerial dispersal rate: Pp, Nf, Nc, Ka and Ef were used to measure proportions of mites that aerially dispersed from a standard platform. A leaflet (15 mm x 15 mm) attached to a lima bean plant stem was the platform. The stem was inserted into a test tube with water, and fixed by placing foam around the stem to prevent contact with the tube wall. Using this design, walking out of the platform was not possible. An adult female was placed on each platform 20 min before introduction to a wind tunnel (0.6 x 0.6 x 1 m, Jung and Croft 2000; wind speed @ 1.3 ± 0.04 m/s; 25 ± 2.1 °C; and 50 ± 4.6 % RH). Treatments were starvation of 0, 1, or 2 days, and wind for 3 or 12 continuous hours. For each treatment, 30-90 replicates were run. Dispersal was determined by the absence of a mite on the platform in the tunnel. Dispersal rates among species and among treatments within a species were analyzed by Chi-square (Ramsey and Schafer 1997). After finding a low dispersal rate for Ef (see results), dispersal of 7-day starved females was assessed.

Effect of previous spider mite infestation on dispersal: Take-off suppression by chemical cues from spider mite infested plants has been reported for Pp (Sabelis and Afman 1994). In our studies, we tested whether suppression would occur for phytoseiid species of other life style types. Dispersal platforms were made as

described above but with lima bean leaves that were grown in an isolated place from spider mites. On each platform, 20 adult female TSSM were allowed to infest for 1 d. and then every mite and associates were brushed off one hour prior to the test. One-day starved adult female phytoseiids of mixed ages were used. Dispersal rates from never-infested and previously infested platforms were compared within and between species (Z-statistics, Ramsey and Schafer 1997).

RESULTS

Ambulatory dispersal

Walking pattern and activity: Walking paths of specialist phytoseiids were more circular and more complex than walking paths of generalists (Fig. 2.1). There was a trend of higher walking speed in specialist phytoseiids than generalist phytoseiids (Fig. 2.1, $P_p > N_f > N_c > E_f > K_a$, ANOVA, $df=4, 49$, $P < 0.001$) for all starvation times. Turning coefficients showed a reverse order to walking speed ($K_a > E_f > N_c > N_f > P_p$, ANOVA, $df=4, 49$, $P < 0.01, 0.001, 0.02, 0.005$, respectively at starvation of 2, 6, 12 and 24 h). Within a species, starvation period did not affect walking patterns much. However, a few exceptions were (ANOVA, $df=3, 39$, $P < 0.05$ respectively) a higher walking speed and net speed at 12 hr starvation in *Ef*, higher walking speeds at 12 and 24 hr starvation in *Ka*, and a change in turning coefficient from high to low in *Nf* as the starvation increased. There was no significant difference of net walking speed among species. This was mostly

because of the way that net walking speed was calculated (see methods). The differences in net speed were higher in specialist than generalist species and showed a similar trend to walking speed results (see Fig. 2.1, walking pattern, ANOVA, $df=4, 49$, $P<0.001$ for all starvation treatments). While the pattern of a higher activity in specialists than generalists was also seen on a hairy leaf, activity generally was lower on the hairy filbert leaf than on the smooth bean leaf (Fig. 2.2).

Diffusion coefficients (Table 2.1): Mean travel distances (r) increased as the time after predator release increased, but diffusion coefficients (D) became stable after day 3 for the specialist Pp and Nf. In contrast, mean travel distance did not increase much after day 3 for the generalist, Ef, and the diffusion coefficient kept decreasing as time from predator introduction increased. In Nc, travel distance and diffusion coefficient kept increasing as time from predator introduction increased.

Local dynamics of spider mite-phytoseiid (Nf vs Nc) interaction (Table 2.2):

Interaction time did not differ (9.5 and 10.17 d, respectively) for Nf and Nc (T-test, $df=6$, $P>0.5$). However, the first dispersal occurred earlier and more continuously for Nc than Nf (6.0 vs. 8.5 d, T-test, $df=6$, $P=0.005$). The fraction of predator dispersal before prey extinction from an interaction arena was larger for Nc (0.32 vs. 0.15, T-test, $df=6$, $P=0.1$). Total number of predator dispersed from an

interaction arena was slightly higher in Nc than Nf (25.5 vs 19.5, T-test, $df=6$, $P=0.07$).

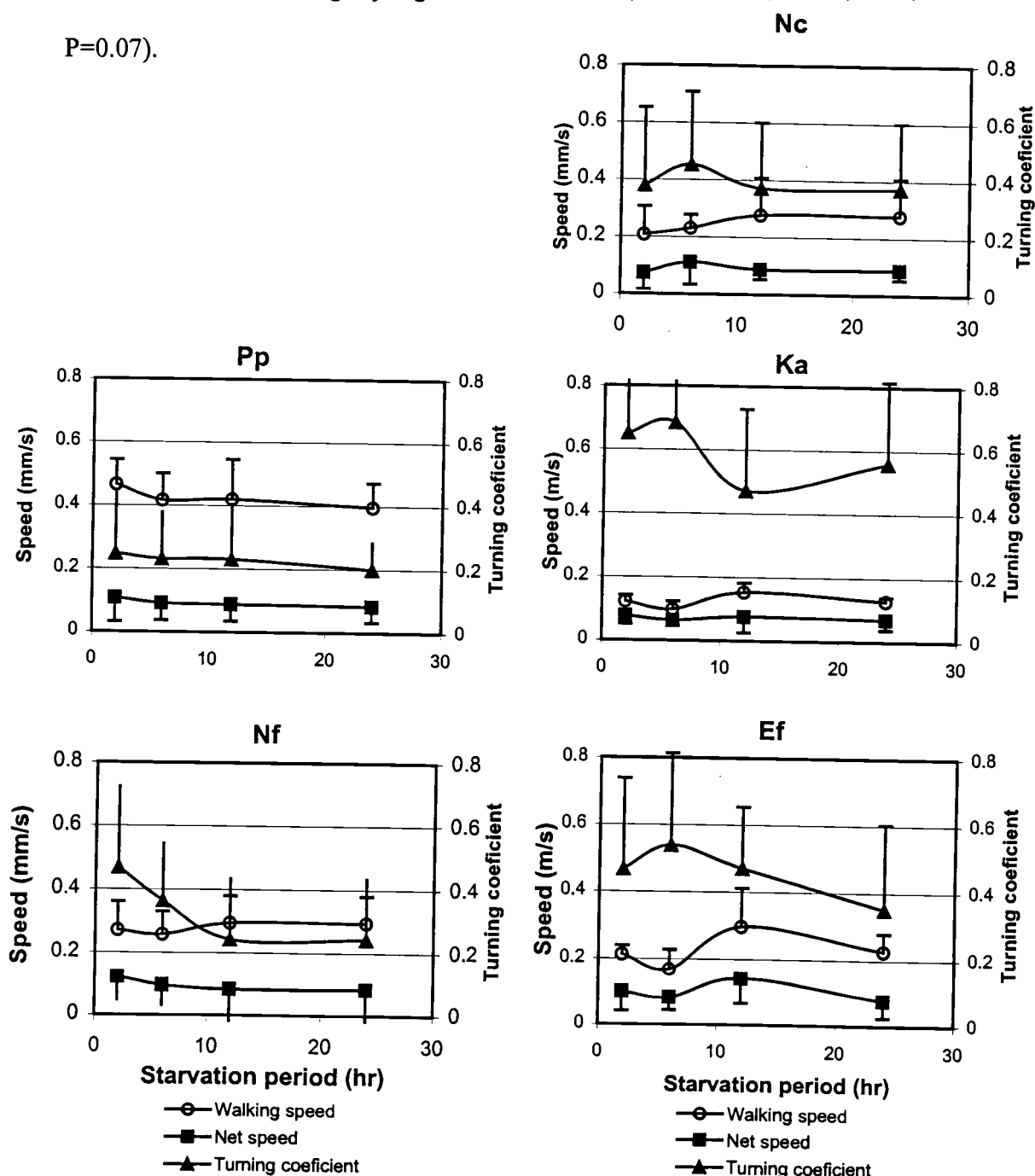
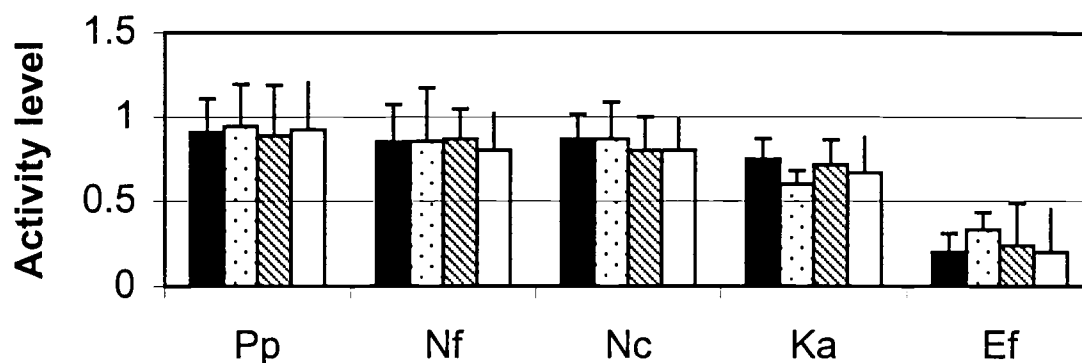


Fig. 2.1. Walking patterns (walking speed, net speed and turning coefficient) of five phytoseiid mites relative to the starvation of 2, 6, 12 and 24 hr. Patterns distinguish specialist predators of TSSM (Pp: *Phytoseiulus persimilis*, Nf: *Neoseiulus fallacis*) and generalist predators (Nc: *N. californicus*, Ka: *Kampimodromus abberans*, and Ef: *Euseius finlandicus*).

a) on a smooth lima bean leaf



b) on a hairy filbert leaf

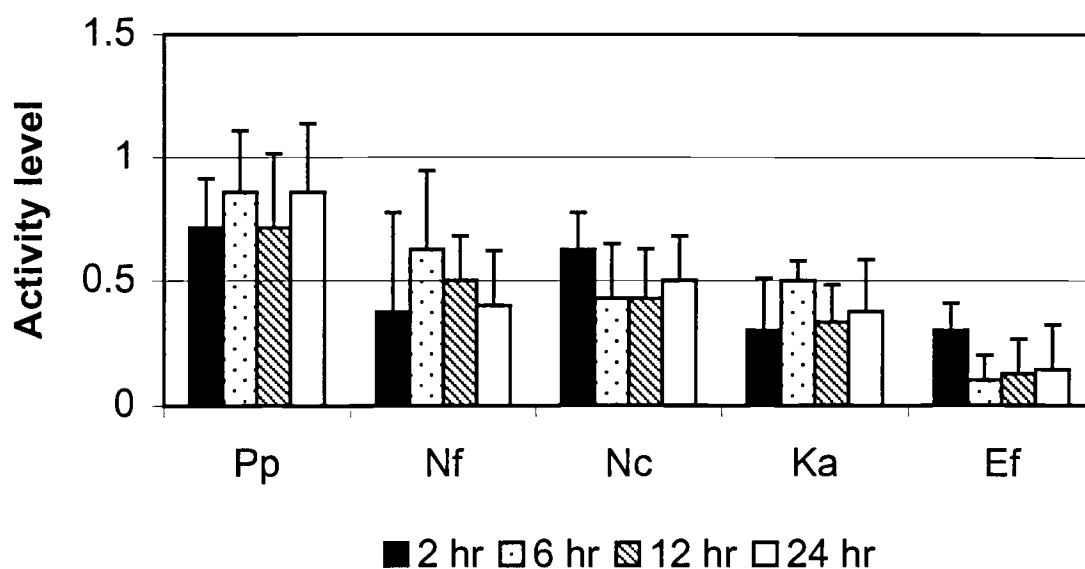


Fig. 2.2. Activity levels of five phytoseiid mites measured on a smooth lima bean leaf (a) and a hairy hazelnut leaf (b) relative to the starvation of 2, 6, 12 and 24 hr. Pp: *Phytoseiulus persimilis*, Nf: *Neoseiulus fallacis*, Nc: *N. californicus*, Ka: *Kampimodromus abberans*, and Ef: *Euseius finlandicus*.

Table 2.1. Diffusion coefficient (D) and mean travel distances (r) of phytoseiid mites on a patch of lima bean plants infested with TSSM and pollen measured at day 1, 3 and 5 following predator release

	D (cm ² /d)			r (cm)		
	Day 1	Day 3	Day 5	Day 1	Day 3	Day 5
Pp	10.6	16.2	15.6	5.6 ± 4.01	13.9 ± 1.99	16.4 ± 8.06
Nf	2.8	10.4	9.6	3.2 ± 1.31	10.8 ± 3.38	13.4 ± 4.21
Nc	5.6	12.6	14.0	4.7 ± 0.28	12.1 ± 2.59	16.7 ± 1.35
Ef	8.3	7.1	4.5	5.1 ± 3.39	8.2 ± 3.56	8.4 ± 3.86

* ANOVA test of travel distance among species at day 1, 3 and 5 showed no significant difference (df=3,15; P=0.65, 0.16 and 0.13 respectively)

Table 2.2. Some parameters of local dynamics of TSSM and phytoseiid *mites* (*Neoseiulus fallacis* vs *N. californicus*); I: interaction time (d), D: time of first dispersal (d), f: fraction of predator dispersal before prey extinction, Q: total number of predator dispersed, and SD: standard deviation

	<i>N. fallacis</i>		<i>N. californicus</i>		P *
	Mean	S.D.	Mean	SD	
I	9.5	1.64	10.17	1.47	0.57
D	8.5	0.84	6.0	0.89	0.005
F	0.15	0.20	0.32	0.13	0.1
Q	19.5	5.95	25.5	4.41	0.07

*: Student's t-test, n = 6 each.

Aerial dispersal

Aerial dispersal rate (Fig. 2.3): Specialists showed higher aerial dispersal rates than generalists ($P_p > N_f > N_c > K_a > E_f$, Chi-square test, $P < 0.01$ for each starvation level and wind exposure time). As duration of wind exposure increased from 3 to 12 hr, dispersal rate increased (Chi-square, $P < 0.01$, 0.01, and 0.05 for 0, 1 and 2 d starvation period, respectively) but with the same trend of higher dispersal in specialists. For P_p , dispersal rate increased as starvation time increased for 3 starvation levels ($P < 0.001$). In N_f , N_c and K_a , dispersal increased from 0 to 1 d starvation ($P < 0.01$), but not from 1 to 2 d starvation ($P > 0.1$). E_f showed consistently the lowest dispersal rate, which did not change relative to starvation (Chi-square, $P > 0.4$). Dispersal rates of 7-day starved E_f were 0.14 and 0.2 respectively under 3 and 12 h wind exposure, and did not differ from dispersal rates of shorter starvation (0, 1, and 2 d) (Chi-square, $P > 0.45$).

Effect of previous spider mite infestation (Table 2.3): Previous infestation of spider mites significantly suppressed aerial dispersal in specialists ($P_p > N_f > N_c$). There was no change in dispersal rate in the generalist K_a when leaves were infested or not infested with prey mites. Interestingly dispersal rate increased for E_f on leaves infested with spider mites.

Table 2.3. Effect of previous TSSM infestation on aerial take-off of phytoseiid mites (24 hr starved) under the wind tunnel (1.3 m/s). Twenty adult female TSSM per dispersal arena were held for 1 day and brushed off 1 hr prior to the test

	Clean leaf arena		TSSM infested arena	
	N	Dispersal rate	n	Dispersal rate
Pp	38	0.63	30	0.27 *
Nf	92	0.47	26	0.27 *
Nc	40	0.48	28	0.32 *
Ka	30	0.40	30	0.40 ns
Ef	30	0.07	30	0.27 **

*: Significant suppression of dispersal (Z-test, $P < 0.0001$)

**: Significant increase of dispersal (Z-test, $P < 0.0001$)

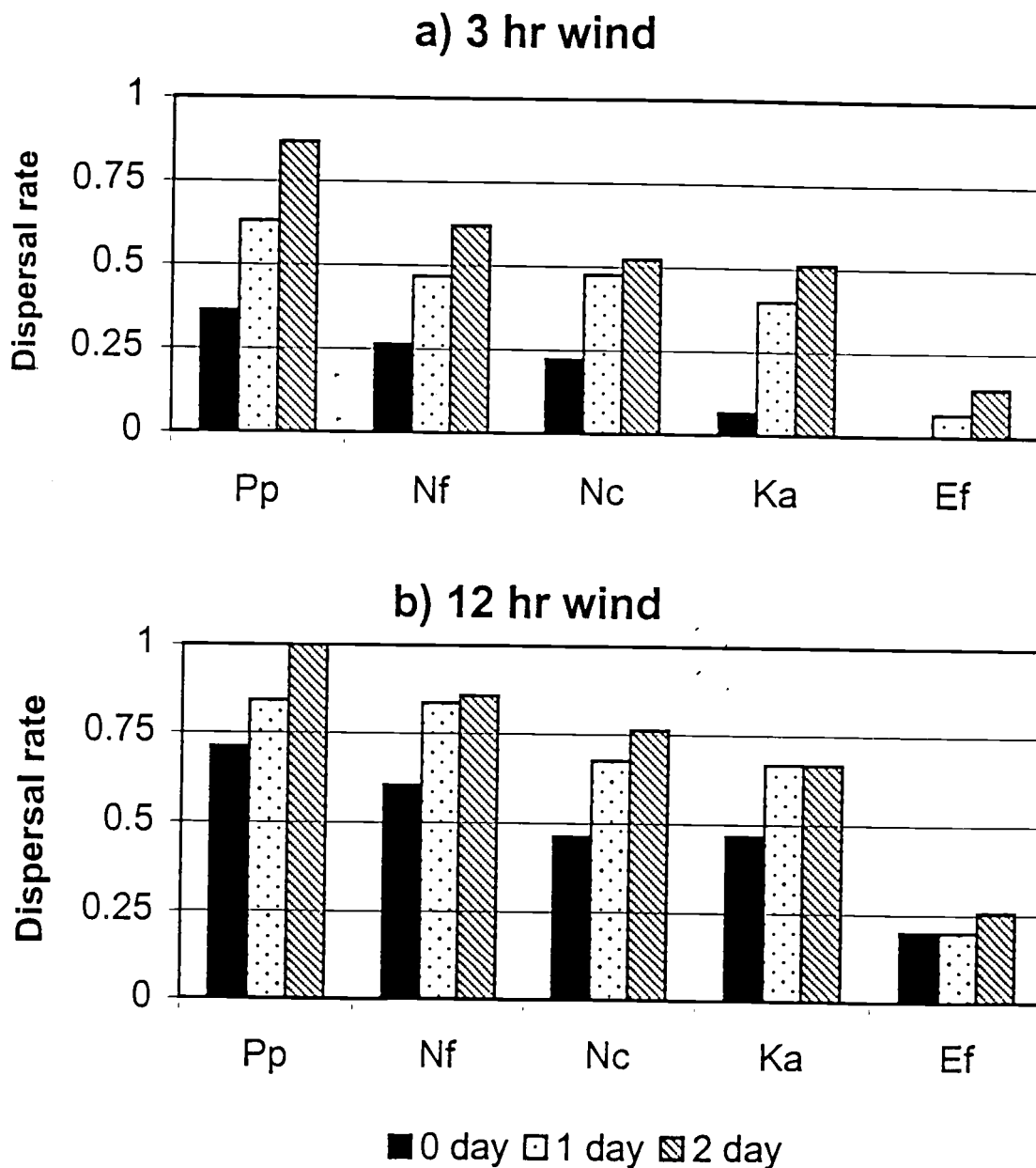


Fig. 2.3. Aerial dispersal rates of five phytoseiid mites measured in wind tunnel (wind speed 1.4 m/s). Treatments were the starvation of 0, 1 and 2 day and periods of wind exposure (a: 3 hr and b: 12 hr). Pp: *Phytoseiulus persimilis*, Nf: *Neoseiulus fallacis*, Nc: *N. californicus*, Ka: *Kampimodromus abberans*, and Ef: *Euseius finlandicus*.

DISCUSSION

We report a consistent pattern of higher activity and ambulatory and aerial dispersal among specialist than generalist phytoseiids and confirmed different dispersal strategies between Nf and Nc. While local ambulatory dispersal from a prey patch occurred earlier for the more generalized *N. californicus*, for the more specialized *N. fallacis* ambulatory dispersal did not occur until most prey were eliminated. Cues from infestation of *T. urticae* acted as arrestants for specialists, but either as neutral or repellent factors for generalist phytoseiids. Other specific aspects of ambulatory and aerial dispersal are noted below.

Walking dispersal

Walking speed estimates were similar to studies by Bernstein (1983) for Pp and Berry and Holtzer (1990) for Nf. However, linear walking pattern (Bernstein 1983) of specialist predators was not observed within 24 h starvation. Bernstein (1983) suggested that as mites starved, they left plants by taking a more linear path (high turning coefficient), and avoided plants already colonized where prey could be declining. Instead in this study specialist predators showed constantly complex and circular walking patterns with higher activity level, as they became hungrier. A generalist predator showed less activity, lower walking speed, but higher turning coefficient (more linear path). This implies different tactics of ambulatory movement for specialists vs. generalists. Spider mites are transient, patchily

distributed food sources, and the efficient location of these patches is critical for population development of specialist phytoseiids (Sabelis and Dicke 1985, Nachman 1987a, b). In contrast, generalists feed on mites, insects, pollens and even plant juice (McMurtry and Rodriguez 1987, McMurtry 1992). They have higher rates of intraguild predation (Schausberger and Croft 1999) and tolerance to starvation (lower metabolism, Croft et al. 1996), thus active searching for foods may not be the foremost purpose for ambulatory movement. Possibly, predation from macropredators or other disturbances may be more important to these species. When physically disturbed, generalists quickly move away, but if left undisturbed they are less prone to leave a resting position (McMurtry 1992, Croft et al. 1995). Diffusion coefficients measured on lima beans support the inference of a rapid disturbance response by generalist (e.g. Ef) but a more limited overall diffusion than specialists. Ef quickly moved out from the epicenter right after release but then little thereafter. Specialists, Pp and Nf showed a gradual increase in travel distance. The use of diffusion coefficients may be of limited value in diffusion models because this value could depend on habitat continuity, presence or abundance of food, period of experimentation and other environmental variables. Large variations of diffusion coefficients are noted in greenhouse tests (0.0003-0.0016 m²/d herein, 0.0003-0.0011 m²/d for Nf and Nc (Pratt et al. 1998), and 0.14 m²/d for *Galendromus occidentalis* (Nesbitt) (Rabbinge and Hoy 1980)). A high value from a field study (3-3.4 m²/d from Croft and Coop 1998) probably reflects some aerial dispersal in strawberry fields. However, a high value for *G. occidentalis* that

generally has lower walking speed than other specialist phytoseiids is less easy to explain (Rabbinge and Hoy 1980).

Interestingly, different strategies of local dispersal were found between Nf and Nc thus confirming a trend of longer travel distance of Nc than Nf (Pratt et al. 1998). Because Nf and Nc have similar predation, developmental and population growth rates when feeding on TSSM (Croft et al. 1997, Pratt et al. 1998, Pratt et al. 1999), the different strategies of dispersal found here may reflect a real difference between a more specialist and more generalist species (i.e., milker vs. killer strategies, see Van Baalen and Sabelis 1995). Some Nc started to disperse from patches early in an interaction, whereas Nf rarely dispersed until prey mites were almost eliminated at the local level. Thus, Nc may produce more offspring by reducing predation at local patch levels resulting from early dispersal of adult females. Also, walking of Nc path was more linear than Nf. Thus, a higher diffusion coefficient in Nc than in Nf at some spatial scale might be expected. However, because of energy cost for ambulation and risks involved, biological control efficiencies for each strategy could differ appreciably (Croft et al. 1997).

Aerial dispersal

The pattern of aerial dispersal was similar to the pattern of ambulatory dispersal: Specialists showed higher rates than generalists; also, longer wind exposure resulted in more dispersal. Starvation effects on aerial dispersal differed. Dispersal of Pp, an obligate specialist on TSSM, increased as starvation time

increased. However, dispersal of Nf, Nc and Ka only increased as starvation changed from 0-1 day, but not from 1 to 2 day in 12 hr wind exposure. No aerial dispersal-starvation relationship was seen for Ef, a species that showed the lowest overall aerial dispersal rate. These results refute the conclusion that dispersal primarily depends on food or starvation for all phytoseiids (Johnson and Croft 1976, Dover et al. 1979, Sabelis and Afman 1984). Even 7 d starved Ef showed a similar rate of dispersal to 1 d starved mites. These results indicate that for some, dispersal rate may be more evolutionary fixed and less affected by short-term conditions (Cohen and Motro 1989, Crespi and Taylor 1990, Ronce et al. 1999). Since adaptation depends on genetic flexibility and selection pressure (Dingle 1996), specialists exposed to fluctuating predator-prey dynamics and repeated local extinctions may have been selected for efficient dispersal mechanisms that mimic the movement of their main prey (van de Klashorst et al. 1992, Margolies 1995, Pels and Sabelis 1999). Alternately, less specific spider mites-associated predators (Nf, Nc and Ka) may balance energy more for ambulatory and aerial dispersal. Depended on where they land, aerial dispersal may be followed by ambulatory searching or redispersal phase, and such redispersing mites may require energy reserves to locate prey or a host plant (Jung and Croft 2000). Slow metabolism, tolerance to starvation, broad diet range, and low walking and searching efficiency in generalists may contrast to efficient searching abilities and tendencies to readily venture off to find aggregated prey in specialists.

Use of an excised leaflet as a dispersal platform may inadequately represent nature, but standard methods are needed to study dispersal among species that are as diverse in this regard as generalist-specialist phytoseiids (McMurtry and Croft 1997). As compared to a ringed leaf arena with sticky material or an artificial media (glass/plastic), an excised leaf with stem may be a compromise between standardization and relevance in the field. Also, some phytoseiids show frequent leaf edge walking when prey mites are scarce (Berry and Holtzer 1990), this would seemingly affect becoming airborne and would be missing from tests with artificial barriers that constrain mites.

Use of herbivore-induced plant volatiles by arthropod predators or parasitoids for foraging has been reported (Roland 1990, Vet and Dicke 1992). Also, cues from prey feeding attract phytoseiids associated with spider mites over short distances (Schmidt 1976, Hislop and Prokopy 1981, Hoy and Smilanick 1981, Sabelis et al. 1984). Can phytoseiids detect prey sources or mite-damaged plants and control take-off? Sabelis and Afman (1994) reported suppression of aerial take-off in *Pp* from spider mite infested plants. We questioned whether similar responses would occur with other phytoseiids. In our study, previous TSSM infestations affected dispersal differently for specialists vs. generalists. Dispersal was decreased for specialists, but was increased for *Ef* or did not change for *Ka*. Some *Euseius* species (generalist phytoseiids) have been reported as having difficulties in foraging on the complex and sticky web of spider mites, often resulting in death by starvation (McMurtry and Rodriguez 1987). Were these

altered dispersal rates directly caused by cues directly from spider mites or were plant responses also involved? We could not separate these factors in our tests, but since the leaf was brushed to remove mites, physical damage from either spider mite feeding and/or brushing could have been involved. The directions of response (attract and repel) suggest chemical cues were affecting dispersal and may infer that phytoseiids can control take-off, to some degree.

REFERENCES

- Bernstein, C. 1983. Some aspects of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) dispersal behaviour. *Entomophaga* 28: 185-198.
- Bernstein, C. 1984. Prey and predator emigration responses in the acarine system *Tetranychus urticae*-*Phytoseiulus persimilis*. *Oecologia* 61: 134-142.
- Berry, J. S., and T. O. Holtzer. 1990. Ambulatory dispersal behavior of *Neoseiulus fallacis* (Acarina: Phytoseiidae) in relation to prey density and temperature. *Exp. Appl. Acarol* 8: 253-279.
- Boykin, L. S., and W. V. Campbell. 1984. Wind dispersal of the Two-spotted spider mite (Acari: Tetranychidae) in North Carolina peanut fields. *Environ. Entomol.* 13: 221-227.
- Cohen, D., and U. Motro. 1989. More on optimal rates of dispersal: taking into account the cost of the dispersal mechanism. *Am. Nat.* 134: 659-663.
- Crespi, B. J., and P. D. Taylor. 1990. Dispersal rates under variable patch density. *Am. Nat.* 135: 48-62.
- Croft, B. A., and L. B. Coop. 1998. Heat units, release rate, prey density, and plant age effects on dispersal by *Neoseiulus fallacis* (Acari: Phytoseiidae) after inoculation into strawberry. *J. Econ. Entomol.* 91: 94-100.
- Croft, B. A., and M. B. Croft. 1993. Larval survival and feeding by immature *Metaseiulus occidentalis*, *Neoseiulus fallacis*, *Amblyseius andersoni* and *Typhlodromus pyri* on life stage groups of *Tetranychus urticae* Koch and phytoseiid larvae. *Exp. Appl. Acarol.* 17: 685-693.
- Croft, B. A., S. S. Kim, and D. I. Kim. 1995. Leaf residency and interleaf movement of four Phytoseiid mites (Acari: Phytoseiidae) on apple. *Environ. Entomol.* 24: 1344-1351.

- Croft, B. A., S. S. Kim, and D. I. Kim. 1996. Intra- and interspecific predation on four life stage groups by the adult females of *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacis* and *Amblyseius andersoni*. Exp. Appl. Acarol. 20: 435-444.
- Croft, B. A., L. N. Monetti, and P. D. Pratt. 1997. Comparative life histories and predation types: Are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) similar Type II selective predators of spider mites? Environ. Entomol. 27: 531-538.
- Dingle, H. 1996. Migration. The biology of life on the move. Oxford University Press, Oxford.
- Dover, M. J., B. A. Croft, S. M. Welch, and R. L. Tummala. 1979. Biological control of *Panonychus ulmi* (Acarina: Tetranychidae) by *Amblyseius fallacis* (Acarina:Phytoseiidae) on apple: a Prey-Predator Model. Environ. Entomol. 8: 282-292.
- Dunley, J. E., and B. A. Croft. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). Exp. Appl. Acarol. 10: 137-149.
- Dunley, J. E., and B. A. Croft. 1992. Dispersal and gene flow of pesticide resistance traits in phytoseiid and tetranychid mites. Exp. Appl. Acarol. 14: 313-326.
- Helle, W., and M. W. Sabelis [eds.]. 1985. Spider mites. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.
- Hewitt, G. M., and R. K. Butlin. 1997. Causes and consequences of population structure, pp. 350-372. In J. R. Krebs and N. B. Davies [eds.], Behavioural ecology, Fourth ed. Blackwell Science, London.
- Hislop, R. G., and R. J. Prokopy. 1981. Mite predator responses to prey and predator-emitted stimuli. J. Chem. Ecol. 7: 895-904.

- Hoy, M. A., and J. M. Smilanick. 1981. Non-random prey location by the phytoseiid predator *Metaseiulus occidentalis*: differential responses to several spider mite species. *Entomol. Exp. Appl.* 26: 291-300.
- Huffaker, C. B., K. S. Shea, and S. G. Herman. 1963. Experimental studies on predation: Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34: 305-329.
- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 69: 1019-1023.
- Johnson, D. T., and B. A. Croft. 1981. Dispersal of *Amblyseius fallacis* (Acarina: Phytoseiidae) in an apple Ecosystem. *Environ. Entomol.* 10: 313-319.
- Jung, C., and B. A. Croft. 2000a. Survival and plant-prey finding by *Neoseiulus fallacis* (Acari: Phytoseiidae) on soil substrates after aerial dispersal. *Exp. Appl. Acarol.* 24 579-596.
- Jung, C., and B. A. Croft. 2000b. Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): Estimating falling speed and dispersal distance of adult females. *Oikos* submitted.
- Jung, C., and B. A. Croft. 2001. Aerodynamic aspects of dispersal take-off behavior among the phytoseiid mites, *Phytoseiulus persimilis*, *Neoseiulus fallacis* and *N. californicus*. (in prep.)
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patch environments. *Theor. Popul. Biol.* 26: 165-191.
- Margolies, D. C. 1995. Evidence of selection on spider mites dispersal rates in relation to habitat persistence in agroecosystem. *Ent. Exp. Appl.* 76: 105-108.

- McMurtry, J. A. 1992. Dynamics and potential impact of generalist phytoseiids in agroecosystems and possibilities for establishment of exotic species. *Exp. Appl. Acarol.* 14: 371-382.
- McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. *Ann. Rev. Entomol.* 42: 291-321.
- McMurtry, J. A., and J. G. Rodriguez. 1987. Nutritional ecology of phytoseiid mites, pp. 609-644. *In* F. S. Jr. and J. G. Rodriguez [eds.], *Nutritional ecology of insects, mites, spiders and related invertebrates*. John Wiley & Sons, New York.
- Nachman, G. 1987a. Systems analysis of acarine predator-prey interactions. I. A stochastic simulation model of spatial processes. *J. Anim. Ecol.* 56: 247-265.
- Nachman, G. 1987b. 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.
- Pels, B., and M. W. Sabelis. 1999. Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. *Oikos* 86: 573-583.
- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within- and Between-Plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in simulated bean and apple plant systems. *Environ. Entomol.* 27: 148-153.
- Pratt, P. D., P. Schausberger, and B. A. Croft. 1999. Prey-food types of *Neoseiulus fallacis* (Acari: Phytoseiidae) and literature versus experimentally derived prey-food estimates for five phytoseiid species. *Exp. Appl. Acarol.* 23: 551-565.

- Price, P. W. 1984. Insect ecology. John Wiley & Sons, New York.
- Rabbinge, R., and M. A. Hoy. 1980. A population model for Two-spotted spider mite *Tetranychus urticae* and its predator *Metaseiulus occidentalis*. Ent. Exp. Appl. 28: 64-81.
- Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, New York.
- Roland, J. 1990. Parasitoid aggregation: Chemical ecology and population dynamics, pp. 185-211. In M. Mackauer, L. E. Ehler and J. Roland [eds.], Critical issues in biological control. Intercept, Andover, Hants, UK.
- Ronce, O., F. Perret, and I. Olivieri. 2000. Evolutionary stable dispersal rates does not always increase with local extinction rates. Am. Nat. 155: 485-496.
- Sabelis, M. W., and B. P. Afman. 1994. Synomone-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. Exp. Appl. Acarol. 18: 711-721.
- Sabelis, M. W., and M. Dicke. 1985. Long-range dispersal and searching behaviour, pp. 141-157. In W. Helle and M. W. Sabelis [eds.], Spider mites. Their biology, natural enemies and control. Elsevier, Amsterdam.
- Sabelis, M. W., J. E. Vermaat, and A. Groeneveld. 1984. Arrestment responses of the predatory mite, *Phytoseiulus persimilis*, to steep odour gradients of a kairomene. Physiological Entomology 9: 437-446.
- Schausberger, P., and B. A. Croft. 1999. Predation on and discrimination between con- and heterospecific eggs among specialist and generalist phytoseiid mites (Acari: Phytoseiidae). Environ. Entomol. 28: 523-528.
- Schausberger, P., and B. A. Croft. 2000. Cannibalism and intraguild predation among phytoseiid mites: are aggressiveness and prey preference related to diet specialization? Exp. Appl. Acarol.

- Schmidt, G. 1976. The influence of traces left by prey animals on the searching behaviour and success of *Phytoseiulus persimilis* A. & H. (Acarina: Phytoseiidae). *Z. Angew. Entomol.* 82: 216-218.
- Shigesada, N., and K. Kawasaki. 1997. Biological invasion: theory and practice. Oxford Univ. Press, New York.
- Van Baalen, M., and M. W. Sabelis. 1995. The milker-killer dilemma in spatially structured predator-prey interactions. *Oikos* 74: 391-400.
- van de Klashorst, G., J. L. Readshaw, M. S. Sabelis, and R. Lingeman. 1992. A demonstration of asynchronous local cycles in an acarine predator-prey system. *Exp. Appl. Acarol.* 14: 185-199.
- Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141-172.
- Walde, S. J., J. P. Nyrop, and J. M. Hardman. 1992. Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Exp. Appl. Acarol.* 14: 261-292.

CHAPTER 3

AERODYNAMIC ASPECTS OF DISPERSAL TAKE-OFF BEHAVIOR AMONG THE PHYTOSEIID MITES, *Phytoseiulus* *persimilis*, *Neoseiulus fallacis* AND *N. californicus*

Chuleui Jung and Brian A. Croft

ABSTRACT

Some wingless arthropods have evolved take-off behaviors that enable them to become airborne. We examined aerodynamic attributes of dispersal relative to the body size and standing vs. walking postures for three phytoseiids that were suspected to have different take-off behaviors and dispersal abilities, *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus fallacis* (Garman) and *N. californicus* (McGregor). The average vertical profile of Pp was significantly higher than that of Nf and Nc when in the walking position. The body height of Nf in the standing posture was significantly greater than that of Nf and Pp in the walking position. Cross-section areas also showed similar patterns of difference. Nf in the standing posture would have more than twice the drag force than in the walking posture because of higher fluid momentum in the boundary layer. However, Pp in the walking position would have similar drag to Nf in the standing posture because of a higher vertical profile and larger size. We report the ‘jumping behavior’ of *P. persimilis*, a first among the Phytoseiidae (Acari). Aspects of jumping behavior relative to aerial dispersal are discussed.

Keywords: Drag force, Force of attachment, Boundary layer, Jumping behavior.

INTRODUCTION

Dispersal is an adaptive process that permits individual organisms to escape unfavorable conditions and colonize new habitats (Price, 1984). Winged arthropods disperse actively by flight, whereas some wingless species have evolved take-off behaviors that enable them to become airborne. Described take-off behaviors (Brandenburg and Kennedy 1982, Washburn and Washburn 1983, Margolies and Kennedy 1985, Weyman 1993) include one type that involves standing erect and facing downwind. This behavior occurs among scale insects (Stephens and Alyer 1987, Washburn and Washburn 1983), spider mites (Smithly and Kennedy 1985), and some phytoseiid mites (e.g., *Neoseiulus fallacis* (Garman) (Johnson and Croft 1976) and *Galendromus occidentalis* (Nesbitt) (Hoy 1982).

Recently, some have questioned whether an aerial take-off behavior is an essential component of dispersal because some highly dispersive phytoseiids do not show such behaviors (Sabelis and Afman 1994). Even with added information on biotic/abiotic conditions that affect dispersal, factors that mechanically constrain take-off have not been studied to any extent. Fluid mechanics (aerodynamics) that affect take-off of a mite from a surface boundary layer are important: Wind blowing parallel to the surface decreases as height decreases, creating less wind at the boundary layer. Thickness of the laminar boundary layer increases, as distance from the leading edge increases to where flow becomes unstable and forms a turbulent layer. Organisms within a boundary layer experience differential wind

speeds depending on their size and behavior. Take-off of a mite occurs when drag overcomes force of attachment to a surface.

We hypothesized that species with high vertical profiles may not require other behaviors to gain momentum for take off, but species with lower vertical profiles may have evolved behaviors such as standing erect for this purpose. We examined the aerodynamic attributes of dispersal for three phytoseiids that were suspected to have different take-off behaviors and dispersal abilities, *Phytoseiulus persimilis* Athias and Henriot, *Neoseiulus fallacis* (Garman) and *N. californicus* (McGregor) (hereafter also referred to as Pp, Nf and Nc). *P. persimilis* has a high tendency to disperse ambulatorially and aurally, but it does not show any known take-off behavior (Sabelis and Afman 1994, Jung and Croft 2001). *N. fallacis* also has a high tendency to aurally disperse and frequently shows a take-off behavior (standing posture) in air currents (Johnson and Croft 1976, 1981), but its ambulatory dispersal distance is more confined than that of *N. californicus* when with prey (Pratt et al. 1998). *N. californicus* has lesser tendency to disperse aurally than *N. fallacis* (Pratt et al. 1998) and as yet, no take-off behavior has been seen for this species. We measured profiles, weights and cross-sectional areas and calculated fluid dynamics for each species. In tests of pre-takeoff behavior in almost still air, we observed ‘jumping behavior’ in one species. Thereafter, we measured horizontal displacement of each species in still air from a 30 mm high stand and projected effects that such behaviors might have on dispersal under more natural conditions.

MATERIALS AND METHOD

Measurements: vertical height and cross-sectional area

Using stop motion pictures taken by a CD video camera (CV-730 series, EmCall Scientific Inc. San Diego) mounted on a binocular microscope (20X), we measured vertical height and cross-section area of each species in the walking posture (n=10 each) and *N. fallacis* in a standing posture (n=1). Starved adult females (24 hr) were used because they are the stage that most frequently disperses aerially (Johnson and Croft 1976, Sabelis and Afman 1994, Jung and Croft 2001). Aspects of vertical height that were measured were leg height (distance from surface to bottom of abdomen) and body height (sum of leg height and vertical thickness of idiosoma for mites in walking posture, and sum of leg height and longitudinal length of idiosoma for a mite in standing posture). In calculating cross-section area, we assumed that mites always faced directly away from the wind (Johnson and Croft 1976).

Boundary layer and drag force

Assuming laminar flow on a smooth surface, wind speed profile was estimated at 10 and 30 mm away from the leading edge by the Blasius approximation (Curle 1962; pp 20) for a free stream velocity of 4 m/s. At this wind speed, frequent aerial dispersal and specific dispersal behaviors have been seen (Johnson and Croft 1973,

Sabelis and Afman 1984). Thickness of boundary layer (δ) relative to increasing distance from the leading edge was estimated (Monteith and Unsworth 1997) where x is the distance from the leading edge, and Re is the Reynolds number at x . Within the boundary layer, drag force (Fm) was calculated using Reynolds number (Re) and drag coefficient (Cd) parameters from the above measurements. Reynolds numbers (Re , Curle 1962) were estimated for walking (Pp, Nf, Nc) and standing (Nf). The drag coefficient (Cd) over this Re ($1 < Re < 400$) range was determined assuming a spheroid shape (Monteith and Unsworth 1997), where, V is a wind speed corresponding to height of mite (H), and ν is kinematic viscosity of dry air (20°C). Drag forces (Fm) on a smooth surface was calculated (Monteith and Unsworth 1997), where, A is cross-sectional area of mites, ρ is the density of the air (1.204 kgm^{-3}), and V is the corresponding wind speed at the apex height of each posture.

$$\delta = x \times 1.72 \times Re_x^{-0.5}$$

$$Re = (V \times H) / \nu$$

$$Cd = (24 / Re)(1 + 0.17 \times Re^{0.66})$$

$$Fm = Cd \times 0.5 \times \rho \times V^2 \times A$$

Horizontal displacement of mites

During preliminary dispersal studies, a behavior called “jumping” was observed in Pp. To evaluate take-off and trajectories of displacement, individual females of each species were held under almost still (unmeasurable) air conditions and at $24 \pm 1.2^\circ\text{C}$ and $70\% \pm 10\%$ RH. An individual mite was placed near the tip of a 0.5 mm

dia. rod using a single haired camel-hair brush. Thereafter, the tip of the rod and mite were observed for take-off behavior and subsequent landing position on a flat surface 3 cm below the rod tip. As each mite fell, its initial landing location was recorded and the mite was removed from the landing arena. Distances displaced from the vertical axis point directly below the rod tip were calculated and distances were analyzed by ANOVA, LSD (Ramsey and Schafer 1997).

RESULTS

The average vertical profile of Pp in the walking position was significantly higher than the average vertical profile of Nf and Nc in walking position (Table 3.1, ANOVA, $df=2,29$, $F=31.24$ and 40.64 , $P<0.001$ for leg height and body height, respectively). The apex of the body height of Nf in the standing posture was significantly greater than the apex of the body height of Pp in the walking position (Table 3.1, T-test, $P<0.001$). Cross-sectional areas of bodies for each mite also showed the same patterns of difference (Table 3.1).

Wind speed decreases as distance from surface decreases from a vertical point that defines boundary layer thickness (Fig. 3.1). Boundary layer thickness increases as the distance from the leading edge increases until a critical point where air movement becomes turbulent. So, wind velocity gradient relative to height become greater as the distance from the leading edge decreases (Fig. 3.1).

Table 3.1 shows the Reynolds number, drag coefficient and drag forces of Pp, Nf and Nc when in walking and Nf in standing postures. Nf in the standing posture would have more than twice the drag force than in walking posture because of more fluid momentum in the boundary layer. However, Pp in the walking position would have similar drag to Nf in the standing posture because of a higher vertical profile and a larger size.

Table 3.1. Vertical profiles; *H1*: height of leg, *H2*: height of body, distance from the surface to the dorsum, *A*: cross-section area of predatory mites, and aerodynamic parameters; *V*: wind speed at the corresponding height, *Re*: Reynolds number, *Cd*: drag coefficient and *Fm*: drag force

Species	Posture	<i>H1</i> mm	<i>H2</i> mm	<i>A</i> ⁴ mm ²	<i>V</i> m/s	<i>Re</i>	<i>Cd</i>	<i>Fm</i> 10 ⁻⁸ N
Pp	Walking	0.138 a ¹	0.38 a	0.137	1.30	32	2	27.9
Nf	Standing	0.121* ²	0.45 ** ³	0.144	1.41	40.9	1.74	30.0
Nf	Walking	0.101 b	0.27 b	0.086	0.92	16.1	3.07	13.5
Nc	Walking	0.093 b	0.26 b	0.088	0.88	14.9	3.23	13.3

¹: means with different letter within a column represent significant difference (ANOVA, df=2, 29, ea. P<0.001)

²: Difference of *H1* between standing and walking posture in Nf (T-test, P<0.05)

³: Difference of *H2* between standing and walking posture in Nf, and standing Nf vs. walking Pp (T-test, ea. P<0.05)

⁴: Partial data from Croft et al., 1999

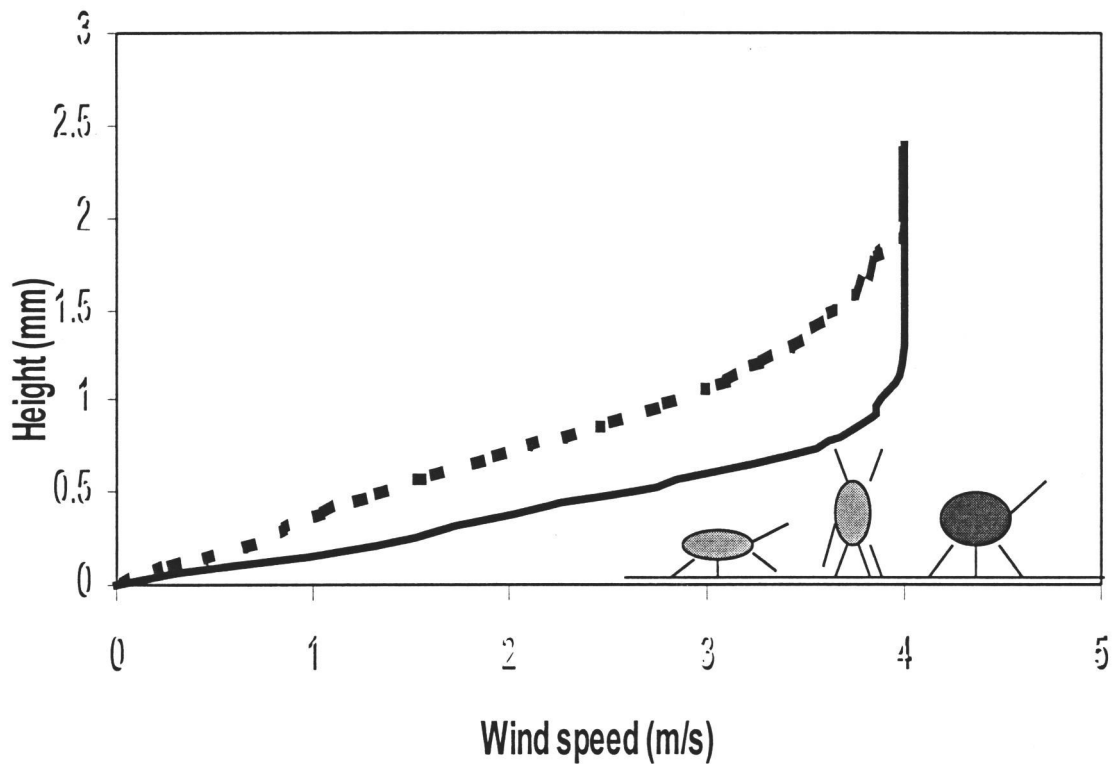


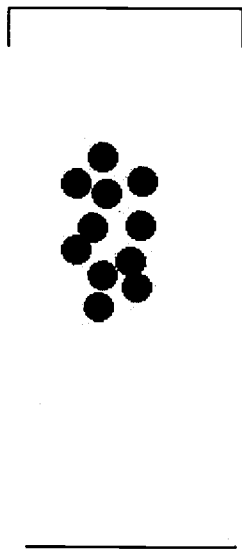
Fig. 3.1. Vertical velocity profiles for a free stream wind speed (4 m/s) at 10 (broken line) and 30 mm (continuous line) from the leading edge of a flat surface and scaled illustrations of 3 phytoseiid mites in walking and standing posture (from the left, Nf or Nc in walking posture, Nf in standing posture and Pp in walking posture).

Distance displacement of mites measured 30 mm below the tip of the mechanical pencil rod showed a single modality and normal-like distribution with mean distances of 5.4 ± 2.01 mm and 6.01 ± 2.85 mm for adult female Nf and Nc, respectively (Fig. 3.2). In tests, neither Nc or Nf were observed to display any standing behavior nor any other take-off behavior on the rod tip. However, for adult females of Pp, there was a bi-modal distribution of mean distance displaced (5.8 ± 2.89 and 28.2 ± 4.05 mm; Fig. 3.2). Mean distance displaced significantly differed between it and the other two species (four data means; ANOVA, $df=3,36$, $F=121.7$, $P<0.0001$). Some adult females of Pp on the rod were seen to crouch, extend themselves and then release into the air whereas others did not show this same behavioral sequence.

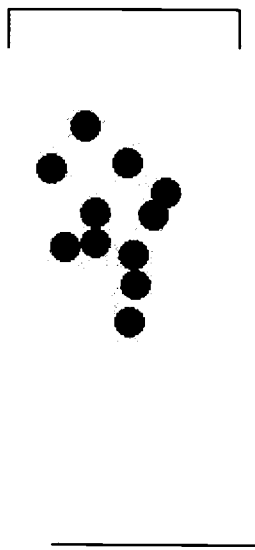
DISCUSSION

Aerial take-off occurs when drag on a mite is sufficient to overcome force of attachment to a substrate. Assuming that attachment force was equal among species (which may not be so), our calculations suggest that a species with a more vertical profile (e.g. Pp), may not require a standing behavior to achieve enough momentum to become airborne, but those with a less vertical profile (e.g. Nf), may benefit from standing, and become highly dispersive. With Nc, its limited vertical profile and lack of upright posture may account for its more limited aerial dispersal ability relative to Nf (Pratt et al. 1998, Croft et al. 1997) and presumably to Pp.

a) *N. fallacis*



b) *N. californicus*



c) *P. persimilis*

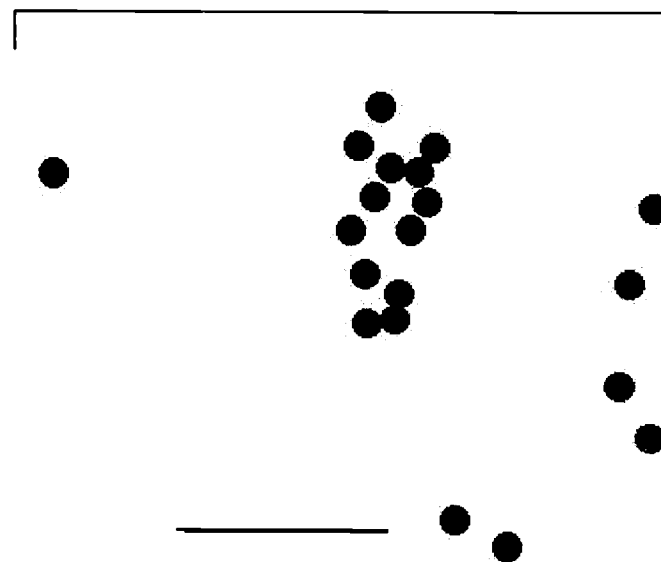


Fig. 3.2. Trajectories of horizontal displacement from the mechanical pencil rod, 30 mm above the surface (a: *N. fallacis*, b: *N. californicus*, and c: *P. persimilis*). Lower bars represent the scale of 20 mm.

The quantitative relationships and results of this study may not exactly reflect conditions as they occur in nature. Drag and attachment force may depend on mite's condition with respect to wind, surface topography and position on a plant. Also air currents in nature are more complex and violent than the laminar flow of the laboratory. However, qualitative aspects of our results would not be invalidated with more realistic parameter estimates.

Drag is positively correlated with mite size and wind speed at height H . Boundary layer would be thicker on a hairy leaf than on a smooth leaf, thus providing more space of reduced wind, and less take-off. A thicker boundary layer would occur on under- vs. upper-sides of leaves since, in most plants, undersides have more trichomes, hairs, ribs, veins and domatia (Walter and O'Dowd 1992a, b). Grace and Wilson (1976) demonstrated using a *Populus* leaf held parallel to laminar airflow, that winds of the upper surface were similar to a theoretical boundary structure model, but at the lower surface, distorted wind profiles produced a thicker boundary layer and more shelter. So individuals on an underside of a leaf would have less inducement for take off than on the upper. Many generalist predators that have lower dispersal rates (Dunley and Croft 1990, Jung and Croft 2001) are more often associated with domatia on leaf undersides than are specialists that have higher dispersal rates (Walter and O'Dowd 1992a, b). Movement of a mite to a leaf upper-side also may increase aerial take-off. Higher frequency of Nf (a specialist) on the upper-sides of leaves than Nc (more generalist) (Jung and Croft 2001), suggests that this mechanism alone could confer

a differential dispersal rate to these two very closely related species. The horizontal position of mites on a leaf can influence take-off. If near a leading leaf edge, a mite will experience more wind and dispersal than when further inward from a leaf edge. High frequency of edge walking in *Nf* (Berry and Holtzer 1990) could lead to increased aerial take-off as well.

Force of attachment may depend on physical powers of grasping, levels of physiological starvation and/or any active behavioral component of take-off. The force required for 50% aerial take-off of *Pp* on an upper-side of apple leaf was estimated at 4×10^{-8} N, based on Sabelis and Afman (1994). When compared to force required to detach spores of *Helminthosporium maydis* from infected maize leaves (ca. 1×10^{-7} N, Aylor 1975), *Pp* becomes airborne at much lower wind speeds than the passively dispersing spore. Active control over take-off has been established in several phytoseiid species (Sabelis and Afman 1994, Jung and Croft 2001). The standing behavior of *Nf* (Johnson and Croft 1976) may either lessen grasp or increase drag or both. Dispersal rates increased as starvation increased for some phytoseiids (Johnson and Croft 1976, Sabelis and Afman 1994, Jung and Croft 2001)

Jumping is a mechanism to enhance dispersal in many mites such as *Zetorchestes falzonii* (Acari: Oribatida) (Krisper 1990, 1991), *Upodes* (Acari: Prostigmata) (Walter and Proctor 1997) and *Saltiseius* (Acari: Mesostigmata: Salticidae, N. F.) (Walter 2000), but ours is the first report among phytoseiids. For the former two species, four pairs of legs are involved in jumping outward. We

observed jumping only for Pp, although it was tested for all three species. When Pp jumps, only 3 pairs of legs are involved in a driving motion away from a substrate and the first pair of legs is in a waving position. Jumping and lateral movement was distinct from passive dislodgment and dropping as indicated by direction and distance moved. The horizontal distance that jumping Pp were displaced from 30 mm height was about 30 mm. This was about 5 times the passive dislodgement distance and 50 times the body length of Pp. According to a dispersal model based on falling speed (Jung and Croft 2000), for Pp to be displaced that far by wind alone, would require 2m/s wind speed. Our observations of Pp jumping occurred in almost still air (see further description below).

At present, we do not know how frequently jumping occurs, what initiates it, or how it is related to dispersal. Crouching (Sabelis and Afman 1994) is commonly seen when Pp is exposed to air currents. But take-off occurs in a very brief moment (Jung, personal observation). Thus, jumping may have been overlooked unless great attention is paid to lift-off. However, if jumping were associated with aerial dispersal, it would help Pp escape the boundary layer of air. Also, jumping may compensate for lack of a standing take-off posture.

Also, we have indication that some wind may be needed before Pp will exhibit jumping behavior. In the laboratory having heating and cold air ducts, some small air movement could be seen using a smoke bomb, but none could be detected with a wind-monitoring device (minimum 0.3m/s. precision within 3%). However, in a closed room with no airflow ducts and no detectable wind, a lower

rate of jumping behavior was observed (Jung, unpublished data). Studies between air currents and jumping may elucidate how these factors are related

Our results may indicate the possible adaptive value of standing for aerial take-off for Nf; Pp when walking has as much drag as standing Nf. However, the evolutionary value of standing cannot be inferred by mechanistic analyses. More detailed behavioral analyses of take-off are needed. Also, it is unresolved just why standing is so common in many wingless arthropods when an organism could readily move to the upwind edge of the leaf where boundary layer is small (Sabelis and Afman 1994).

REFERENCES

- Aylor, D. E. 1975. Force required to detach conidia of *Helminthosporium maydis*. Plant Pathology 55: 99-101.
- Berry, J. S., and T. O. Holtzer. 1990. Ambulatory dispersal behavior of *Neoseiulus fallacis* (Acarina: Phytoseiidae) in relation to prey density and temperature. Exp. Appl. Acarol 8: 253-279.
- Brandenburg, R. L., and G. G. Kennedy. 1982. Intercrop relationships and spider mite dispersal in a corn/peanut agro-ecosystem. Entomol. Exp. Appl. 32: 269-276.
- Croft, B. A., H.-K. Luh, and P. Schausberger. 1999. Larval size relative to larval feeding, cannibalism of larvae, egg or adult female size and larval-adult setal patterns among 13 phytoseiid mite species. Exp. Appl. Acarol. 23: 1-12.
- Croft, B. A., L. N. Monetti, and P. D. Pratt. 1997. Comparative life histories and predation types: Are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) similar Type II selective predators of spider mites? Environ. Entomol. 27: 531-538.
- Curle, N. 1962. The boundary layer equations. Oxford, London.
- Dunley, J. E., and B. A. Croft. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). Exp. Appl. Acarol. 10: 137-149.
- Grace, J., and J. Wilson. 1976. The boundary layer over a *Populus* leaf. J. Exp. Bot. 27: 231-241.
- Hoy, M. A. 1982. Aerial dispersal and field efficacy of a genetically improved strain of the spider mite predator *Metaseiulus occidentalis*. Entomol. Exp. Appl. 32: 205-212.

- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). *Annals of the Entomological Society of America* 69: 1019-1023.
- Johnson, D. T., and B. A. Croft. 1981. Dispersal of *Amblyseius fallacis* (Acarina: Phytoseiidae) in an apple Ecosystem. *Environ. Entomol.* 10: 313-319.
- Jung, C., and B. A. Croft. 2000. Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): Estimating falling speed and dispersal distance of adult females. *Oikos* submitted .
- Jung, C., and B. A. Croft. 2001. Ambulatory and aerial dispersal among specialist and generalist predatory mites (Acari: Phytoseiidae). *Environ. Entomol.* (in prep.).
- Krisper, G. 1990. The jump of the mite-Genus *Zetorchestes* (Acarida, Oribatida). *Zool. Jb. Anat.* 120: 289-312.
- Krisper, G. 1991. The saltatory capacity of an oribatid mite, pp. 397-398. *In* R. Schuster and P. W. Murphy [eds.], *The acari : reproduction, development, and life history strategies*. Chapman & Hall, London.
- Monteith, J. L., and M. H. Unsworth. 1990. *Principles of environmental physics*. Chapman and Hall, New York.
- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within- and Between-Plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in simulated bean and apple plant systems. *Environ. Entomol.* 27: 148-153.
- Price, P. W. 1984. *Insect ecology*. John Wiley & Sons, New York.

- Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, New York.
- Sabelis, M. W., and B. P. Afman. 1994. Synomone-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. Exp. Appl. Acarol. 18: 711-721.
- Smitley, D. R., and G. G. Kennedy. 1985. Photo-oriented aerial dispersal behavior of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface. Ann. Entomol. Soc. Am. 78: 609-614.
- Stephens, G. R., and D. E. Aylor. 1978. Aerial dispersal of Red Pine Scale, *Matsucoccus resinosae* (Homoptera: Margarodidae). Environ. Entomol. 7: 556-563.
- Walter, D. E. 2000. A jumping mesostigmatan mite, *Saltiseius hunteri* N. G., N. Sp. (Acari: Mesostigmata: Trigynaspida: Saltiseiidae, N. Fam.) from Australia. Internat. J. Acarol. 26 25-31.
- Walter, D. E., and D. J. O'Dowd. 1992a. Leaf morphology and predators: Effect of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). Environ. Entomol. 21: 478-484.
- Walter, D. E., and D. J. O'Dowd. 1992b. Leaves with domatia have more mites. Ecology 73: 1514-1518.
- Walter, D. E., and H. C. Proctor. 1999. Mites. Ecology, evolution and behavior. CABI publishing, New York.
- Washburn, J. O., and L. Washburn. 1983. Active aerial dispersal of minute wingless arthropods: Exploitation of boundary-layer velocity gradients. Science 23: 1088-1089.
- Weyman, G. S. 1993. A review of the possible causative factors and significance of ballooning in spiders. Ethol. Ecol. Evol. 5: 279-291.

CHAPTER 4

AERIAL DISPERSAL OF PHYTOSEIID MITES (ACARI: PHYTOSEIIDAE): ESTIMATING FALLING SPEED AND DISPERSAL DISTANCE OF ADULT FEMALES

Chuleui Jung and Brian A. Croft

Submitted to OIKOS, August 2000.

ABSTRACT

Aerial dispersal is important to immigration and redistribution of phytoseiid mites that often can provide biological control of spider mite pests. Falling speed of a mite and wind largely determine dispersal distance of such a passively blown organism. A diffusion model of wind-blown phytoseiids could provide insight into their dispersal. To this end, we measured morphologies, body weights and falling speeds of adult females of 13 phytoseiid and one tetranychid mite species. These data were then incorporated into seed dispersal models (Greene and Johnson 1989, Okubo and Levin 1989) and results were compared to mite dispersal distances in wind tunnel, greenhouse and field.

Weights of phytoseiid species ranged from 5.25-21.7 μg ; starved mites weighed less than fed mites. Geometric diameters (dg) of idiosomas were correlated to weights. Falling speeds for phytoseiids were 0.39-0.73 m/s, and less than for *T. urticae* (0.79 m/s) in still air. In some species, active mites had slower falling speeds than inactive (anesthetized) mites indicating that behavior influenced falling. Starved mites had significantly slower falling speeds than fed mites and dispersed farther. Equation-based estimates of falling speed were close to measured ones (2-8% deviation) for some species. There were significant relationships between falling speed and body weight and morphological traits. Greene and Johnson's seed dispersal model (1989) provided better fits to dispersal of mites in the wind tunnel, greenhouse and field studies than Okubo and Levin's (1989)

model. Limits of models in describing mite dispersal distance and applications to IPM are discussed.

INTRODUCTION

Adaptations for dispersal by organisms are universal and may result in behaviors that are hazardous to individuals. Dispersal, however, is advantageous and essential to population persistence, either in unstable or stable environments (Hassell et al. 1991, Turchin 1997). Dispersal of predaceous mites is important to redistribution and persistence of prey (spider mites)-predator interactions (Huffaker et al. 1963, Takafuji 1977), even though local extinctions of either may occur (Nachman 1988, Sabelis et al. 1991). For biological control of spider mites, aerial dispersal of predatory mites is a major means of colonization from nearby habitats and spread over a crop (Johnson and Croft 1981, Hoy et al. 1985, Sabelis and van der Meer 1986, Charles and White 1988, Duso 1989, Dunley and Croft 1990, Klashorst et al. 1992, Janssen et al. 1997, Tixier et al. 1998, 2000).

While there is evidence for behavioral control of take-off for some phytoseiids (Johnson and Croft 1976, 1981, Sabelis and Afman 1994), dispersal *per se* over long distances is mostly passive and aerial. Phytoseiids can travel >100 m on air currents (Johnson and Croft 1981, Dunley and Croft 1990, Hoy et al. 1985), as can 'prey' mite, tetranychids (Brandenburg and Kennedy 1982, Boykin and

Campbell 1984). However, to our knowledge, mites of neither group can control landing (Jung and Croft 2000). Dispersal distances of aerially dispersing mites can be expressed as a probability density curve, the tail of which may be as important as the median to pest control. But estimating the tail of a dispersal-distance curve is difficult because of sampling limitations (Turchin 1998, Jongejans and Schippers 1999). Sampling problems may be overcome by use of mechanistic models of wind dispersal of small particles/organisms (insects: Stephens and Aylor 1978, pathogens: Aylor 1998, seed and pollen: Greene and Johnson 1989, Okubo and Levin 1989, McEvoy and Cox 1987, in general: Pedgley 1982)

To date, no mechanistic model has been applied to aerial dispersal of mites except a ballistic function (Sabelis and Dicke 1985). We used two models that were developed to predict seed and pollen dispersal (Greene and Johnson 1989, Okubo and Levin 1989). These models describe movement downwind and in vertical directions using wind speed, variance of wind speed, height of release, and terminal speed (falling speed). The most species-specific trait is terminal speed. Terminal speed is related to morphology and weight and is estimated either by dropping an organism in still air (Morse and Schmitt 1986, Andersen 1992, Frost 1997), or by an aerodynamic equation (Eq. 1, Gorial and O'Callaghan 1990, Song and Litchfield 1991, Misener and Boiteau 1993).

We measured falling speeds of 13 phytoseiid species and one tetranychid species when fed vs. starved and inactive (anesthetized) vs. active. Observed falling speeds were compared to theoretical estimates based on body size and

morphological data. We also compared model outputs to dispersal data from wind tunnel, greenhouse and field studies.

MATERIALS AND METHOD

Morphology, weight and falling Speed

Mites: Thirteen phytoseiid species and one spider mite, *Tetranychus urticae* Koch, were measured for morphology, weight, and falling speed. We used only adult females because this stage most often undergoes aerial dispersal (Johnson and Croft 1976, Boykin and Campbell 1984, Pratt et al. 1998). Cultures of phytoseiids were fed *T. urticae*, (*Phytoseiulus persimilis* Athias-Henriot, *P. macropilis* (Banks), *Neoseiulus longispinosus* (Evans), *Galendromus occidentalis* Nesbitt, *N. fallacis* (Garman) and *N. californicus* McGregor), birch pollen, *Betula pendula* Roth (*Euseius hibisci* (Chant), *E. finlandicus* (Oudemans) and *Kampimodromus aberrans* (Oudemans)), or both (*Amblyseius andersoni* Chant, *Typhlodromus pyri* Scheuten, *N. cucumeris* (Oudemans) and *Neoseiulus barkeri* Hughes). Hereafter, these species are also referred to as Pp, Pm, Nl, Go, Nf, Nc, Eh, Ef, Ka, Aa, Tp, Ncc and Nb, respectively.

Morphology: Morphological data (Croft et al. 1999) were obtained for 8-10 gravid, well-fed females of each species that were placed in Hoyer's medium on a microscope slide and then in an oven (40-45 °C) for 24 h for clearing of specimens.

Length and width of idiosoma, extended leg length, and setal length of s4 and Z5 (Croft et al. 1999) were measured under a phase-contrast microscope (200X). Setal protection indices based on the proportion overlapping of seta (Sabelis and Bakker 1992) were related to falling speed and dispersal distance.

Weight: Gravid females were weighed using a Perkin Elmer Autobalance (AD-2 Model, reading 0.1 μ g with 3% error range). Individual were held with excess food either for 2 d (fed mites) or without food and water for 1 d (starved mites) at 20-25 °C, 60-70 % R.H. Mites were anesthetized with ethyl ether anhydrous gas, $(CH_3CO_2)_2O$ (Mallinckrodt Baker Inc. Kentucky USA) to prevent movement. Two or five individuals were weighed at once; sample size was 20 per species, and weights per individual were based on small group averages.

Falling speed measurement: Falling speeds were measured in a vertical glass tube (1.2 m l. X 5 cm dia.) at 20 ± 3 °C and 60 ± 5 % RH. Lights were used to observe release of a mite at the upper end and settling at the lower end, but were kept away from the tube to prevent heating. Air movement in the tube was negligible. A single gravid female was held on the tip of a camel-hair brush and released by flipping the brush with the finger over the tube opening. Time of fall was measured with a 1/100s stopwatch (Sportline®, Campbell, CA). Fed inactive vs. fed active and fed active vs. starved active mites were compared within (T-test, $P=0.05$; Ramsey and Schafer 1997), and among species (ANOVA, Tukey's HSD; Ramsey and Schafer 1997). Ethyl ether anhydrous gas was used to inactivate mites.

Falling speed estimation: Aerodynamics is determined by equilibrium conditions when a particle is suspended in air (Gorial and O'Callaghan 1990, Song and Litchfield 1991, Misener and Boiteau 1993). Terminal speed of a particle is obtained by setting gravitational force equal to resistance drag for a spherical particle, but a correction ($\pi/6Z$) is applied to drag coefficient (0.44, Lapple 1956) for irregular particles such as mites;

$$V_t^2 = \frac{4gd_g\rho_p}{(\pi/6Z) \times 3 \times 0.44 \times \rho_a} \quad (\text{Eq. 1})$$

where $Z = \frac{\pi}{6} \left(\frac{d_g}{d_m} \right)^3 (\text{sphericity})$ and $\text{sphericity} = d_g/d_m$.

Following Eq. 1 (parameters in Table 4.1), we calculated falling speeds using idiosoma sizes (Croft et al. 1999) and compared these estimates with actual ones. Since data came from mites mounted on microscope slides, we assumed mite size was flattened by 60% comparing the idiosoma size of live and slide-mounted *N. fallacis* adult females (e.g. idiosoma width of 278.7 vs. 322.9 μm).

Table 4.1. Parameters used in the falling speed estimation (Eq. 1) of mite species

d	Diameter of particle ^a	V _t	Terminal speed of particle (m/s)
d _m	Major diameter	Z	Volume shape factor
d _g	Geometric mean diameter	ρ_a	Specific density of air (kg/m ³) ^b
d _e	Diameter of equivalent sphere	ρ_p	Specific density of particle (kg/m ³) ^c
M	Mass of particle, Kg		

^a: Mites were all assumed having ellipsoidal (lemon-like) shape.

^b: 1.205 Kg/m³ at 20 °C (Vogel 1994)

^c: 1070 kg/m³ (Misener and Boiteau 1993)

Testing seed flux models for mite dispersal

Models: Dispersal distance from a point source depends on falling speed (W_s), release height (H), wind speed (u) and turbulence (σ_x , σ_z). Greene and Johnson (1989) derived their model (Eq. 2; GJ model) from a ballistic function with a logarithmic distribution of wind speed profiles. Okubo and Levin's model (1989; Eq. 3; OL model) is a cross-wind integrated form of a tilted plume model derived from the Gaussian plume model with a gravitational deposition factor of falling speed. With a similar form of expression, the GJ model uses the geometric mean of wind speed (u_g) and the variance of wind speed in the downwind direction (σ_x), but OL model uses the arithmetic mean of wind speed (u) and the variance of wind speed in the vertical direction (σ_z).

$$GJ(x) = \frac{n}{\sqrt{2\pi x \sigma_x}} \exp \left\{ \frac{-(\ln(W_s x / H u_g))^2}{2 \sigma_x^2} \right\} \quad (\text{Eq. 2})$$

$$OL(x) = \frac{n W_s}{\sqrt{2\pi u \sigma_z}} \exp \left\{ \frac{-(H - W_s x / u)^2}{2 \sigma_z^2} \right\} \quad (\text{Eq. 3})$$

These models were tested against mite dispersal data under 3 conditions: horizontal wind tunnel, greenhouse and field.

Wind tunnel tests: Three species (*T. urticae*, *P. persimilis*, *N. fallacis*) were selected because of ease in obtaining large numbers and handling. The wind tunnel (0.6 x 0.6 x 2 m) had a fan (0.6 x 0.6 m) at one end and a coarse mesh filter at the other.

The fan provided an out-going constant air speed; the filter reduced incoming air turbulence. Mites were released into the wind tunnel through a glass tube (1 x 9 cm) at one end of the tunnel. The tube was inserted from the ceiling to eliminate launch effects such as resistance to drag, and threshold wind speed for mite detachment. The tunnel floor had adhesive (Tanglefoot[®], Grand Rapids, MI) to trap dispersing mites. Dispersal distance in the tunnel was measured at 5-cm intervals. Cumulative dispersal curves were compared to model output under $H=0.29$ or 0.36 m, $u=1.8$ m/s, and $\sigma=0.3$. Falling speeds for *P. persimilis*, *T. urticae* and *N. fallacis* (fed vs. starved), respectively, were from earlier experiments (Table 4.2 in Results).

Greenhouse tests: We used parameters for *P. persimilis*, and *N. fallacis* to compare model and actual dispersal data. In a greenhouse of 10 x 4 m, 300 mites of each species were introduced into a line of lima bean plants, *Phaseolus lunatus* L., infested with moderate densities of *T. urticae* (3 pots per species, 20 bean plants per pot, 2 leaves per plant, and >50 spider mites per leaf). Six lines of 8 pots of receiver plants were placed at 1-meter intervals. Each pot was held in a water bath to prevent mite ambulation to or between receiver plants. A fan (0.6 m x 0.6 m) provided continuous wind. Trapped mites from receiver plants were removed every 2 days for 8 days.

We also compared model results against data from an earlier greenhouse study. Pratt et al. (1998) studied dispersal of *N. fallacis* and *N. californicus* under

the same wind conditions and set up as described above. The only difference was Pratt et al. used a 1 x 3 m bench with spider mite-infested potted plants as a producer unit from which phytoseiids dispersed and 3 other benches spaced 1 m apart with similar potted plants as receiver units. For their study, dispersal distribution was integrated at 1-m intervals. Parameters in the models were $H=0.3$ m, $u=2.2$ m/s, and $\sigma=0.6$ and falling speeds were from earlier experiments (Table 4.2 in Results)

Field tests: We used dispersal estimates from 2 studies: Johnson and Croft (1981) assessed dispersal distance of *N. fallacis* from an apple orchard to prey-infested bean plants in an open field and Dunley and Croft (1990) did the same for *G. occidentalis* and *T. pyri* from an apple orchard to potted apple trees. Parameter were $H=5$ m, $u=6$ m/s and $\sigma=2$ (M. Unsworth, pers. comm.) and falling speeds were from earlier experiments (Table 4.2 in Results)

RESULTS

Morphology, weight and falling speed

Weights of 13 phytoseiid species that were fed ranged from 5.25-21.7 μg and fed *T. urticae* was 28.3 μg ; starved mites weighed less than fed mites (Table 4.2). Geometric diameters (dg) of idiosomas were correlated to weights ($R^2=0.91$,

$F_{1,12}=109.2$, $P<0.0001$). Falling speeds for phytoseiids were 0.39-0.73 m/s, which were less than for *T. urticae* (0.79 m/s). In species with high falling speeds (Pp, Pm, Go, Nf, Tp, Aa), active mites had slower falling speeds than inactive (anesthetized) mites (T test, $P<0.05$). Starved mites of some species had slower falling speeds than fed mites (Pp, Pm, Nf, Nc, Aa; T test, $P<0.05$). There was a positive relationship between falling speed and body weight ($R^2=0.46$ and 0.64 , $F_{1,12}=10.4$ and 20.7 , $P<0.001$, for inactive and active mites, respectively). Adding the marginal dorsal protection index (positive), s4 (negative) and Z5 (positive) into the regression, increased R^2 to 0.83 and 0.93 , respectively for falling speeds of inactive and active mites. However, no morphological measurement was significantly correlated to differences in falling speeds of inactive vs. active mites. Falling speeds from the aerodynamic model were 0.63-0.78 m/s for the 13 phytoseiids and 0.81 m/s for *T. urticae*. Estimates were near measured values (2-8% deviation) for 8 of 14 species, but for 5 (Pp, Ncc, Nb, Ef, Eh), the model overestimated the actual by 20-30% and for Ka, ap. 80% (Fig. 4.1). Appendage differences such as setae and legs lengths may have contributed to these differences, but no statistical significance was found when leg size and setal protection indices were included as regression variables.

Table 4.2. Falling speed measurements and weight of well-fed and starved mites (n=20)

Sp ¹	Weight (μ g)		Falling speed (m/s)							
	Well-fed	Starved	Well-fed Inactive		Well-fed Active		Starved Active			
	mean	mean	mean	SD	mean	SD	mean	SD		
Pp	21.7b ²	11.4b	0.62cd	0.058	0.58cdef	* ³ 0.045	0.48c	* ⁴	0.069	
Pm	19.8c	11.0b	0.73ab	0.088	0.66b	* 0.084	0.58a	*	0.078	
Nl	8.54h	5.25f	0.55e	0.066	0.49g	* 0.089	0.48c	ns	0.063	
Go	9.16gh	7.15de	0.65c	0.081	0.57cdef	* 0.068	0.55ab	ns	0.033	
Nf	13.5de	8.70c	0.67bc	0.084	0.62bcd	* 0.070	0.50bc	*	0.059	
Nc	14.0d	8.25cd	0.68bc	0.045	0.65bc	ns 0.061	0.49c	*	0.060	
Tp	10.0gh	7.99cde	0.63cd	0.096	0.54defg	* 0.084	0.51bc	ns	0.034	
Aa	13.8d	11.6b	0.64c	0.059	0.59bcde	* 0.054	0.49bc	*	0.068	
Ncc	11.9ef	9c	0.54e	0.029	0.54defg	ns 0.064	-		-	
Nb	13.4de	10.5cde	0.50e	0.036	0.53efg	ns 0.057	0.48c	*	0.051	
Ka	9.10gh	7.01e	0.39f	0.059	0.39h	ns 0.046	-		-	
Eh	11.9ef	9.2c	0.53e	0.036	0.53efg	ns 0.094	-		-	
Ef	10.4fg	8.80c	0.56de	0.079	0.55defg	ns 0.081	-		-	
Tu	28.3a	23.1a	0.79a	0.081	0.76a	ns 0.095	-		-	
ANOVA										
df	13, 266	13, 266	13, 266		13, 266		8, 171			
F	266.6	279.4	46.6		27.9		7.5			
P	0.0001	0.0001	0.0001		0.0001		0.0001			

¹ : Species Pp: *Phytoseiulus persimilis*, Pm: *P. macropilis*, Nl: *Neoseiulus longispinosus*, Go: *Galendromus occidentalis*, Nf: *N. fallacis*, Nc: *N. californicus*, Tp: *Typhlodromus pyri*, Aa: *Amblyseius andersoni*, Ncc: *N. cucumeris*, Nb: *N. barkeri*, Ka: *Kampimodromus aberrans*, Eh: *Euseius hibisci*, Ef: *E. finlandicus*, Tu: *Tetranychus urticae*

² : Means which are significantly different within column are followed with different letters (ANOVA, Tukey's HSD).

³ : Within each species, falling speed of inactive vs. active were compared by t-test (P=0.05).

⁴ : Within each species, falling speed of well-fed vs. starved were compared by t-test (P=0.05).

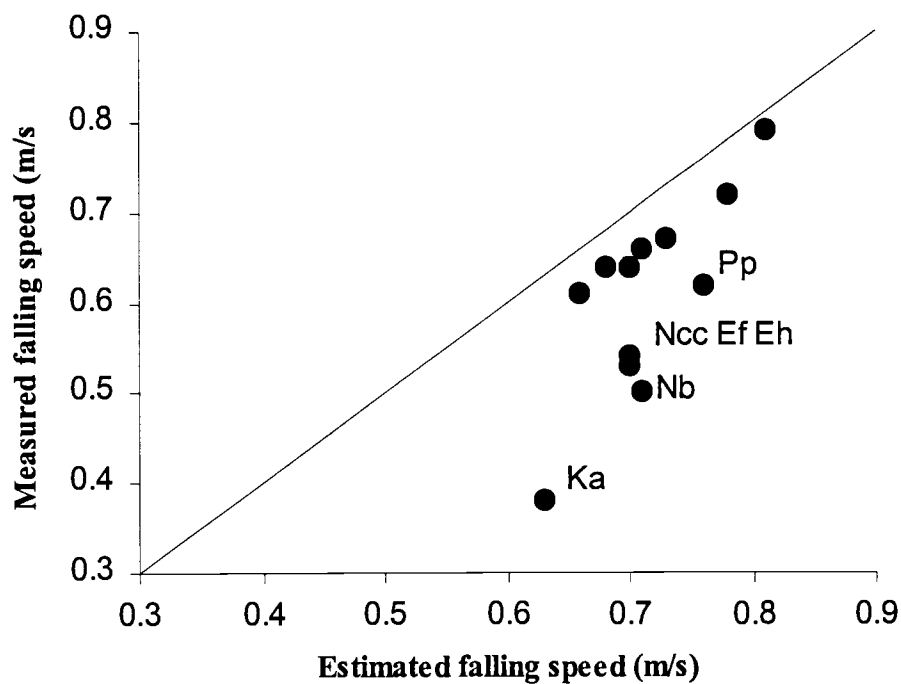


Fig. 4.1. Average falling speeds (m/s) measured vs. theoretically estimated. A 1:1 line facilitates the comparison. Species with large deviation are abbreviated as Pp: *Phytoseiulus persimilis*, Ncc: *Neoseiulus cucumeris*, Nb: *N. barkeri*, Ef: *Euseius filandicus*, Eh: *E. hibisci*, and Ka: *Kampimodromus aberrans*.

Testing seed flux models for mite dispersal

Wind tunnel tests: Cumulative curves for measured and model-based dispersal distances (Fig. 4.2) indicated that the GJ gave a better fit than the OL model. The GJ model slightly overestimated slopes for both *T. urticae* and *P. persimilis* (Fig. 4.2a,b). The medians and tails of the simulated dispersal curves were more distant than those of the measured (Fig. 4.2a,b). However, for *N. fallacis*, the GJ estimates were close to the head, median and tail of observations for fed and starved mites (Fig. 4.2c,d; $W_s=0.62$ and 0.50 , $H=0.36$ and 0.29 , respectively). In contrast, OL model curves differed considerably from the observed, mainly by having lower slopes and intercepts close to the origin.

Greenhouse tests: Dispersal curves of *N. fallacis* and *P. persimilis* were similar in the greenhouse and the GJ model output again behaved better for both species than the OL model (Fig. 4.3a). Pratt et al. (1998) found that *N. fallacis* dispersed farther per dispersal event than *N. californicus*. But neither GL nor OL showed much difference in dispersal distance between these species. Interestingly, the curve of *N. californicus* was more like the GJ output, but the curve of *N. fallacis* was more like the OL output (Fig. 4.3b).

Field tests: For dispersal from apple trees, the GJ model behaved like the observed for *N. fallacis* (Johnson and Croft 1981, Fig. 4.4a), and *T. pyri* and *M. occidentalis* (Dunley and Croft 1990, Fig. 4.4b). But it was difficult to compare the latter 2 species because data were not taken between 10-100 m (Dunley and Croft

1990). However, we doubt that dispersal would have been greatest between 10-100 m as predicted by the OL (Fig. 4.4b).

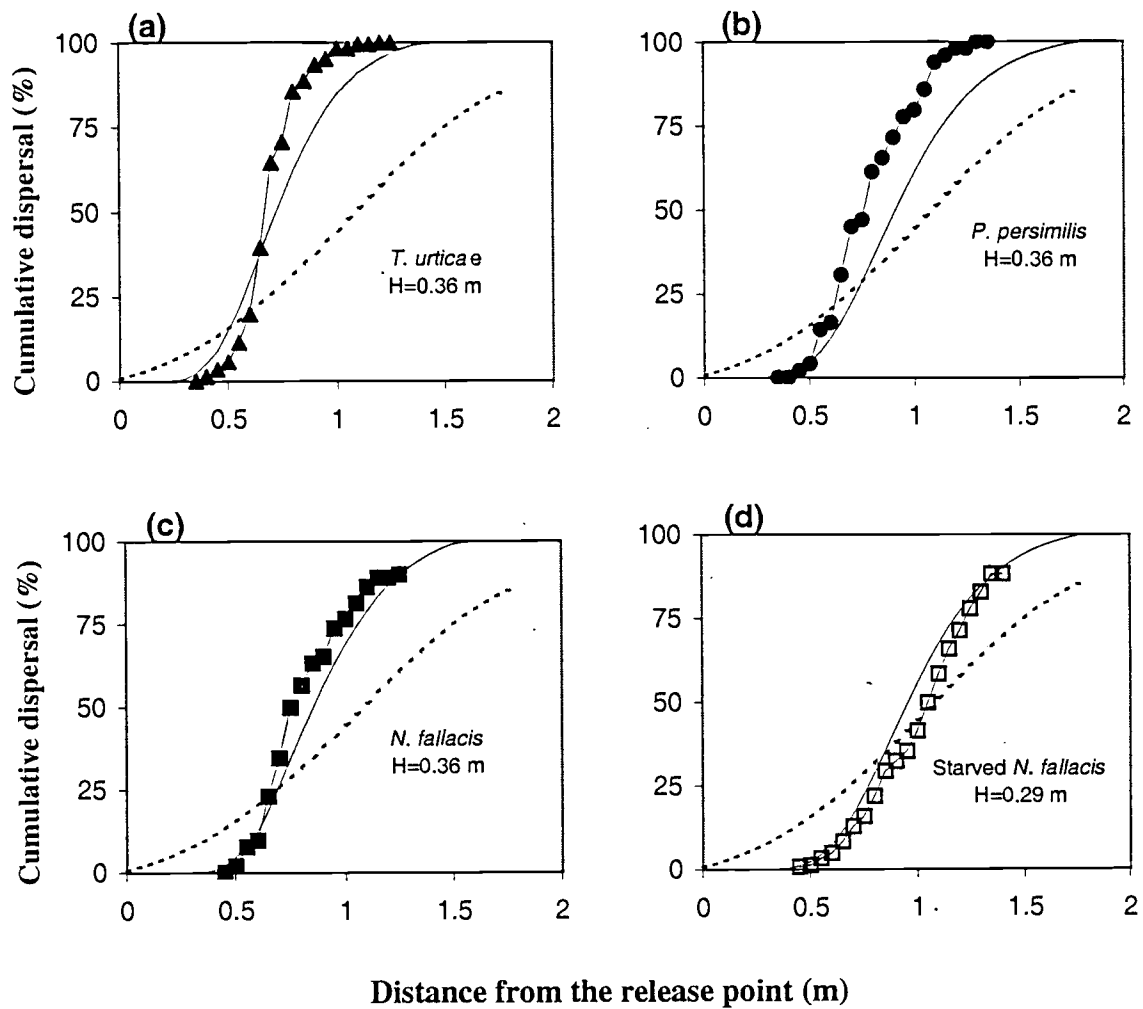


Fig. 4.2. Cumulative dispersal distances measured vs. simulated from wind tunnel studies; continuous lines refer to GJ model outputs and dotted lines do to OL model outputs. Wind parameters were $u=1.8$ m/s and $\sigma=0.3$. Falling speeds for simulation were 0.58, 0.76, 0.62 and 0.50 m/s respectively.

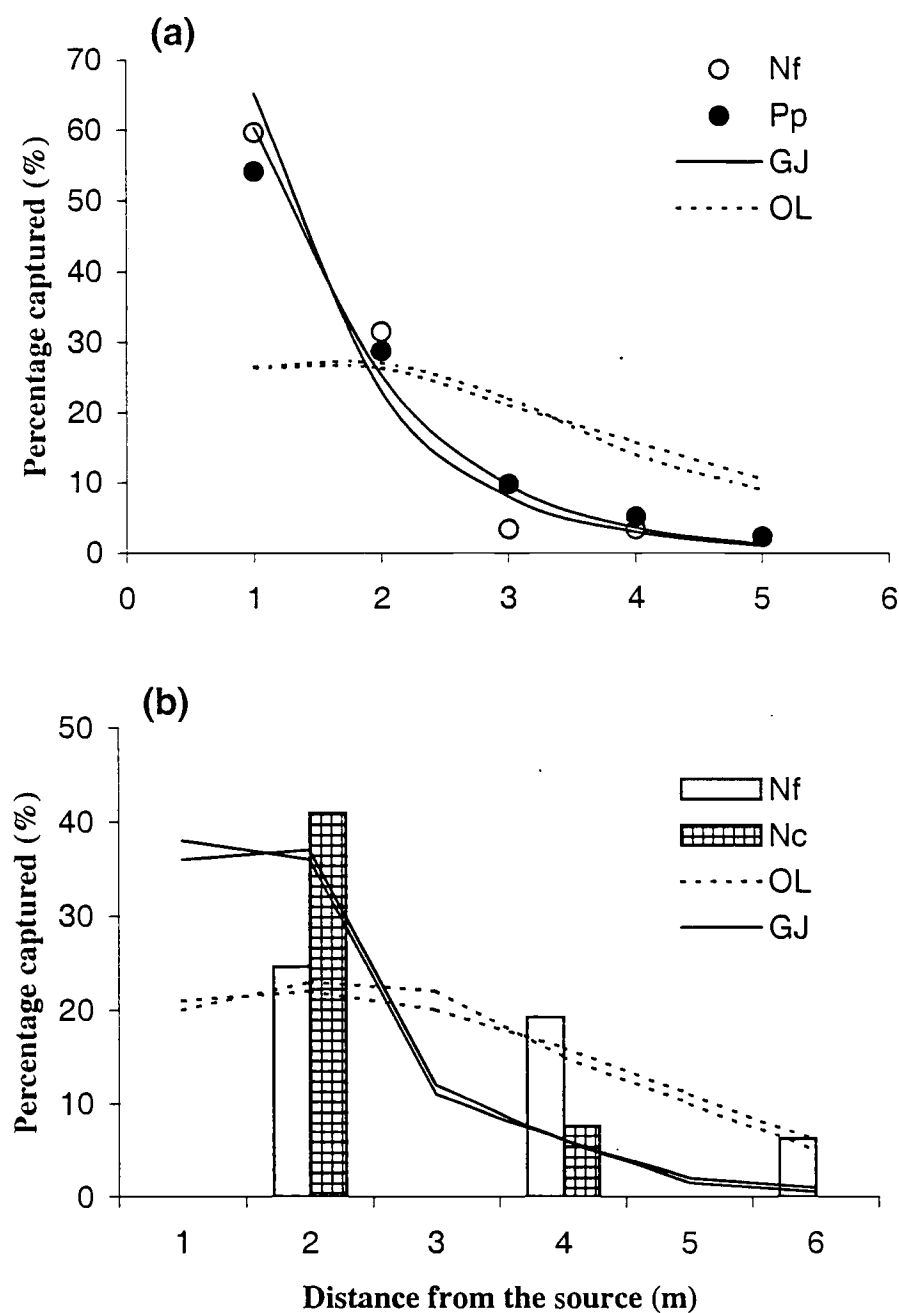


Fig. 4.3. Distance distribution of aerial dispersal, measured vs. simulated in greenhouse settings: (a), dispersal of *N. fallacis* and *P. persimilis*, and (b, modified from Pratt et al. 1998), dispersal of *N. fallacis* and *N. californicus*. Continuous lines refer to GJ model outputs and dotted lines do to OL model outputs. Environmental parameters were $H=0.3$ m, $u=2.2$ m/s, and $\sigma=0.3$.

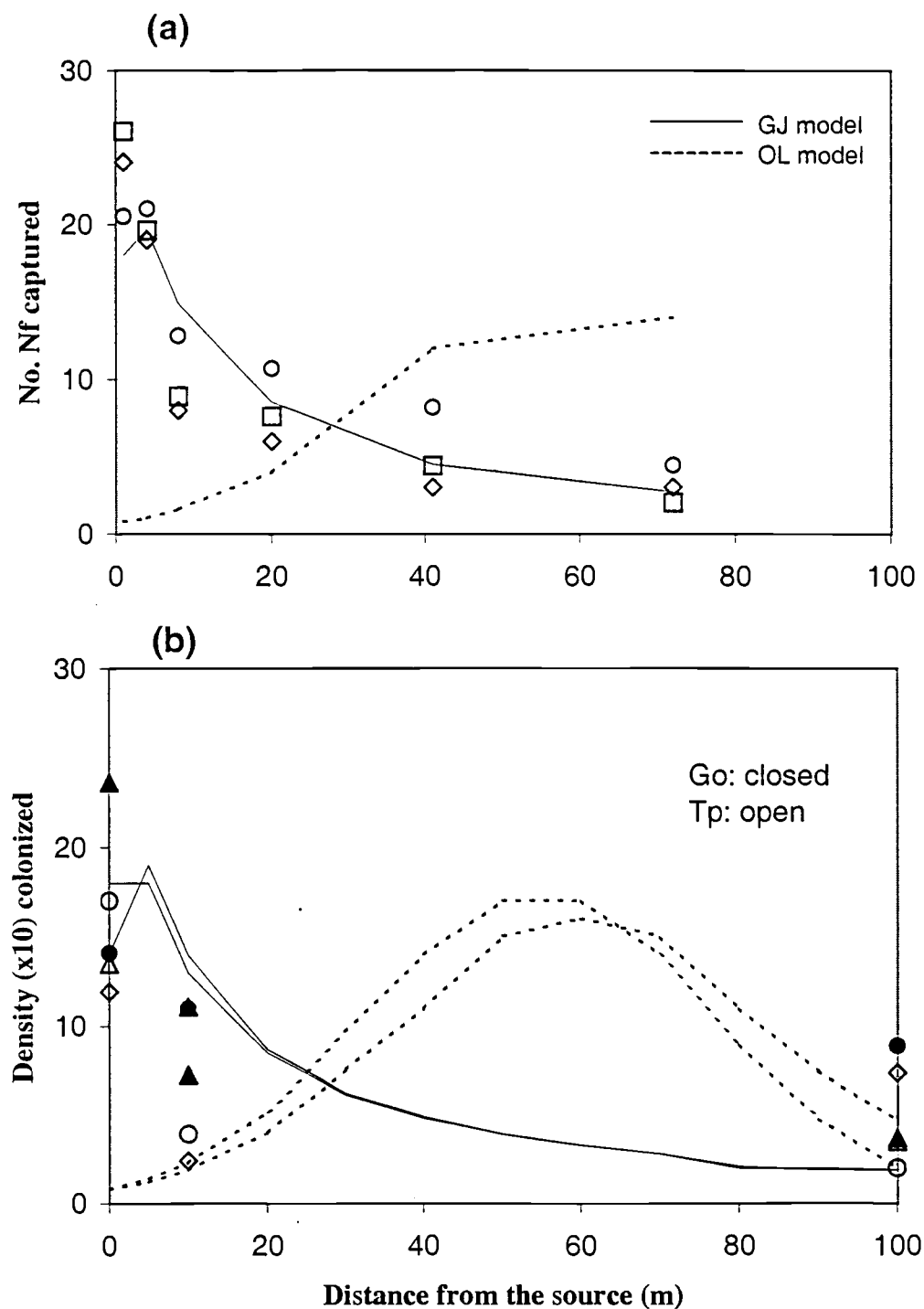


Fig. 4.4. Distance distribution of aerial dispersal, measured vs. simulated in the field conditions with *N. fallacis* (a, modified from Johnson and Croft 1981) and *G. occidentalis* and *T. pyri* (b, modified from Dunley and Croft 1990). Different legends represent different timing of samplings. Environmental parameters for simulation were $H=5$ m, $u=6$ m/s and $\sigma=2$.

DISCUSSION

Morphology, weight and falling speed

Morphological and behavioral adaptations have evolved in small arthropods to facilitate dispersal (Johnson and Croft 1978, Washburn and Washburn 1983, Foster 1997), but identifying such traits is difficult. Simple adaptations should be the most obvious. For example, reduced weights, extension or movement of appendage or setal lengths or setal orientations may cause a mite to remain in air longer than when such traits are lacking. Either by orientation or movements, aerial buoyancy or dropout could be influenced so that the mite may more-or-less control landing as some non-winged scale insects can (Washburn and Washburn 1983).

Body weight estimates varied among species and were similar to values reported by Sabelis (1981; Pp: 24-28, Aa:15-17, *A. bibens*: 10-12, Go: 8-10 μg), but higher than those of McMurtry and Rodriguez (1987; Pp: 16.8, Go: 8.9, Nf: 8.6 μg). Falling speeds also varied among species. Both phytoseiids and *T. urticae* achieved equilibrium falling rates soon after falling began as was observed in similar falling towers of 1.2 or 2.4 m ht. in preliminary tests. For *G. occidentalis*, measured falling speed (0.57 m/s) was slightly higher than that reported by Sabelis and Dicke (1985, 0.5 m/s). Also falling speeds for mites were more than for similar-sized insects (0.27-0.33 m/s for crawlers of scale, Stephens and Aylor 1978, Washburn and Washburn 1983). Body shapes and appendage lengths may account for some differences between mites and insects, but there may be other factors that

influence falling. For example, the eriophyid, *Abacarus hystrix* (Nalepa) lowers falling speed (0.05-0.14 m/s) by producing a wax filament that increases wind friction (Frost 1997).

Falling speed was positively correlated to body weight, the marginal dorsal setal protection index and length of Z5, but negatively correlated to length of s4. Marginal dorsal setae and setae Z5 are parallel to the body, but s4 setae are at a right angle to the body. This may imply that falling of phytoseiids may be anterior-down, not posterior-down as for some scale crawlers (Washburn and Washburn 1983), but actual falling orientation among phytoseiids has not been measured. Differences in falling speed between active vs. inactive mites were greater among specialized feeders on spider mites (ca. 10% in Pp, Pm, Nl, Go, Nf, Tp, Aa) than mostly pollen feeders (ap. 2-3% in Ncc, Nb, Ka, Ef, Eh). Because there was no correlation between the differences of falling speeds (active vs. inactive mites) and morphological traits, we suspected that these differences represented in-air behavioral effects such as when scale insects waving their leg (Washburn and Washburn 1983). Since specialized phytoseiids that feed mostly on spider mites have a higher tendency to disperse than generalist feeders (McMurtry and Croft 1997), such dispersal behaviors may evolve more among the former. Lowering falling speed by any behavioral adaptation increases dispersal distance with an increased drag coefficient (Washburn and Washburn 1983). Also, given that some phytoseiids can detect spider mite infested plants by chemical means (Hislop and Prokopy 1981, Sabelis and Afman 1994), if an aerial dispersing mite would bring

in appendages (i.e. contracting the legs), it might facilitate movement toward ground (landing). Such landing control could enhance prey finding and reduce mortality that phytoseiids sometimes suffer when they fall on bare ground (Janssen 1999, Jung and Croft, 2000). For several phytoseiids, the falling speed of starved mites was less than for fed mites; starved mites also dispersed farther which likely enables them to move to more distant prey patches.

Falling speeds based on an aerodynamic equation were like measured ones for some species. While deviations may be attributed to appendage differences, consistent overestimation of falling rates in Pp, Ncc, Nb, Eh, Ef and Ka may be because an ellipsoid body shape (lemon-like) is assumed in models. Except for Pp, the above-listed species are generalists that feed mostly on pollen. They may not be as vertically distended as species that feed mostly on spider mites, because of less food intake per feeding episode. Assessing falling behaviors by alternative means such as videotaping (Misener and Boiteau 1993) or via vertical wind tunnels (Jongejans and Schippers 1999) may provide more detailed information on falling rates and orientations for these small mites.

Model testing and application

Equation-based mathematical models are alternatives to model data fitting or experimental tests of mite dispersal. As noted, a tail of dispersal distance distribution can be important because reproductive rates of some phytoseiids are so high that only a few females can initiate exponential increase and effective pest

control (Sabelis and Janssen 1994). In this regard, the GJ model behaved more like dispersal curves that came from wind tunnel, greenhouse and field studies than did the OL model. While these models may be too simple for predicting dispersal under greenhouse and field conditions, sensitivity tests indicated that any changes in parameters would have small effects on dispersal distance estimates. The models used herein focused on dispersal from a point source. Dispersal curves from area sources (tree seeds into adjacent clear areas, apple mites into an open field) also decline monotonically, like in Fig. 4.3b (Greene and Johnson 1989). This suggests that the GJ model can be used to explore dispersal distances in the field. Although the OL model has some advantages such as incorporation of vertical turbulence of air currents (σ_z) (Okubo and Levin 1989, Turchin 1998), because of higher falling speeds relative to their size, vertical diffusivity may be less important to dispersal distance of phytoseiid mites than horizontal variation of wind speed. For use of GJ model, wind data can easily be obtained from a standard meteorological site because only the geometric mean of log-distributed wind speeds and downwind variation (σ_x) are required. Furthermore, vertical eddy effects could be plugged into the GJ model as friction velocity (Eq. 4; Greene and Johnson 1989, Monteith and Unsworth 1990);

$$u = (u^*/k) \ln((z-d)/z_0) \quad \text{if } z > d + z_0, \text{ otherwise } u = 0 \quad (\text{Eq. 4})$$

where, u is wind velocity from height z , u^* is friction velocity (or wind speed of interest herein), k is a von Karman constant (0.41), z_0 is a constant roughness length, and d is height of zero plane. In a homogeneous area like a grass- or

cornfield, d and z_0 have been estimated ($d=0.63z$ and $z_0=0.13z$; Monteith and Unsworth 1990). Using these types of inputs to model mite dispersal in a cornfield (assuming field homogeneity and 2 m plant height) and given 8 m/s wind speed at 10 m height, we can estimate friction velocity as 0.93 m/s and effective wind speed as 2.38 m/s (Table 4.3). However, if we are interested in modeling dispersal from apple trees into an open area, parameter d is not necessary. Based on such an approach, Table 4.3 gives estimates of wind speeds and dispersal distance of *N. fallacis* and *T. urticae* in several crops.

Table 4.3. Hypothetical distribution of wind speeds and dispersal potentials in simplified cropping systems based on 8 m/s wind speed at reference height, 10 m

Crop			Wind speed ² (m/s)			Dispersal ³ (m)	
	Profile ¹	Height (m)	U*	U**	σ	<i>N. fallacis</i>	<i>T. urticae</i>
Strawberry	Homo	0.2	0.55	1.41	0.42	0.45-0.72	0.29-0.43
Mint	Homo	0.5	0.65	1.67	0.5	1.5-2.5	0.95-1.7
Corn	Homo	2	0.93	2.38	0.71	8.5-17	5.5-12
Christmas tree	spaced	3	1.01	5.03	1.51	14.5-36	12-34
Apple	spaced	5	1.19	5.97	1.79	19-50	16-48
Hop	spaced	8	1.41	7.21	2.16	26-90	20-85

¹: Homo means homogenous systems, $d=0.63z$, and spaced do spaced systems, $d=0$.

²: From $U=(U^*/K)\ln((z-d)/z_0)$, U^{**} was inversely calculated. σ was assumed as 30% of U^{**}

³: Estimated dispersal distance (50-85 percental) from GJ model based on the falling speed of *N. fallacis*=0.5, *T. urticae*=0.76 m/s (see table 4.2).

In a low profile strawberry field, dispersal is limited to few meters (Croft and Coop 1998). Only a 10-20 m (30 rows of corn) of *T. urticae* dispersal occurred from blackberry (about 2-3 m high) into corn (Brandenburg and Kennedy 1982, Boykin and Campbell 1984). The 70-100 m dispersal of phytoseiids from tall apple trees to a nearby area (Johnson and Croft 1981, Dunley and Croft 1990) may be possible. However, 200 m from almond trees (Hoy et al. 1985) to open fields in a single season is beyond our estimates (Table 4.3). In the last case, multiple dispersal events may have occurred, also turbulent and convectional air movement may be important in determining dispersal distance. The short distance reported for dispersal of *K. aberrans* from woody vegetation (12 m height) to a vineyard (Tixier et al., 2000) suggests need for more information on influences of mite spatial distributions in vegetation and structural effects of plant canopy on mite dispersal.

Limits and further considerations

With a simplified mechanistic mathematical model, we may estimate average dispersal distance of phytoseiids. However, other aspects should be considered for more precise prediction. Even though the adult female most frequently disperses, immatures and adult males also move aurally (Hoy et al. 1985, Duso 1987, Tixier et al 1998, Pels and Sabelis 1999). Effects of immature dispersal could be adding as a stochastic component with weighted age structure relative to falling speed; this would likely spread dispersal curves. Minimum wind speed for take-off or dislodgement could be important. For *N. fallacis*, 0.5 m/s was

needed to initiate dispersal (Johnson and Croft 1976) and actual dispersal was monitored at 0.4 m/s for *P. persimilis* (Pels and Sabelis 1999). Timing and tendency to disperse during spider mite-predator mite interaction needs study within- and between-species (van Baalen and Sabelis 1995). For example, even with similar densities on apple trees, *G. occidentalis* emigrated sooner and farther than *T. pyri* (Dunley and Croft 1990). Pratt et al. (1999) noted different dispersal timings and distances between *N. californicus* and *N. fallacis*. *K. aberrans* was the main phytoseiid immigrating to a vineyard from vegetation where several phytoseiids were present; what factors affected its displacement were unknown (Tixier et al. 1998). Intraspecific variation in dispersal was reported for *P. persimilis* strains (Pels and Sabelis 1999).

Another area that needs evaluation in modeling dispersal of phytoseiids are high-quality meteorological data. Single aerial dispersal events occur over short times (20 sec for dispersing 100 m at 5 m/s wind speed) and narrow daily windows, e.g. early evening (*G. occidentalis*, Hoy et al. 1985; *N. fallacis*, Jung and Croft, 2000), or seasonal periods (Brandenburg and Kennedy 1982, Duso 1987, Charles and White 1988, Tixier et al. 1998). Future models of phytoseiid dispersal should consider ambulatory movement, as well as prey-predator interaction effects. More inclusive models may improve areawide IPM of plant-feeding mites within and between crops (Croft 1999, Kogan et al. 1999).

REFERENCES

- Andersen, M. C. 1991. Mechanistic models for the seed shadows of wind-dispersed plants. *Amer. Nat.* 137: 476-497.
- Andersen, M. C. 1992. An analysis of variability in seed settling velocities of several wind dispersed Asteraceae. *Amer. J. Bot.* 79: 1087-1091.
- Aylor, D. E. 1998. The aerobiology of apple scab. *Plant Disease* 82: 838-849.
- Boykin, L. S., and W. V. Campbell. 1984. Wind dispersal of the Two-spotted spider mite (Acari: Tetranychidae) in North Carolina peanut fields. *Environ. Entomol.* 13: 221-227.
- Brandenburg, R. L., and G. G. Kennedy. 1982. Intercrop relationships and spider mite dispersal in a corn/peanut agro-ecosystem. *Entomol. Exp. Appl.* 32: 269-276.
- Charles, J. G., and V. White. 1988. Airborne dispersal of *Phytoseiulus persimilis* (Acarina: Pytoseiidae) from a raspberry Garden in New Zealand. *Exp. Appl. Acarol.* 5: 47-54.
- Croft, B. A. 1999. Management of spider mite for biological control and pesticide resistance: A case of landscape level IPM for diverse agriculture in the Pacific Northwest (PNW) United States, pp. 27-66. *In* T. Saito and B. A. Croft [eds.], *Implementing spider mite resistance management programs*. Japan Crop Protection Association.
- Croft, B. A., and L. B. Coop. 1998. Heat units, release rate, prey density, and plant age effects on dispersal by *Neoseiulus fallacis* (Acari: Phytoseiidae) after inoculation into strawberry. *J. Econ. Entomol.* 91: 94-100.
- Croft, B. A., H.-K. Luh, and P. Schausberger. 1999. Larval size relative to larval feeding, cannibalism of larvae, egg or adult female size and larval-adult

- setal patterns among 13 phytoseiid mite species. *Exp. Appl. Acarol.* 23: 1-12.
- Dunley, J. E., and B. A. Croft. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). *Exp. Appl. Acarol.* 10: 137-149.
- Duso, C. 1989. Role of the predatory mites *Amblyseius aberrans* (Oud.), *Thphlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acar, Phytoseiidae) in vineyards. I. The effects of single or mixed phytoseiid population releases on spider mite densities (Acar, Tetranychidae). *J. Appl. Ent.* 107: 474-492.
- Frost, W. E. 1997. Polyphenic was production in *Abacarus hystrix* (Acar: Eriophyidae), and implications for migratory fitness. *Physio. Entomol.* 22: 37-46.
- Gorial, B. Y., and J. R. O'Callaghan. 1990. Aerodynamic properties of grain/straw materials. *J. Agric. Engng. Res.* 46: 275-290.
- Greene, D. F., and J. E.A. 1989. A model of wind dispersal of winged or plumed seeds. *Ecol.* 70: 339-347.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269: 578-581.
- Hassel, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353: 255-258.
- Hislop, R. G., and R. J. Prokopy. 1981. Mite predator responses to prey and predator-emitted stimuli. *J. Chem. Ecol.* 7: 895-904.
- Hoy, M. J., J. J. Groot, and H. E. van de Baan. 1985. Influence of aerial dispersal on persistence and spread of pesticide-resistant *Metaseiulus occidentalis* in California almond orchards. *Entomol. Exp. Appl.* 37: 17-31.

- Huffaker, C. B., K. S. Shea, and S. G. Herman. 1963. Experimental studies on predation: Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34: 305-329.
- Janssen, A. 1999. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. *Entomol. Exp. Appl.* 90: 191-198.
- Janssen, A., Van Gool, E., Lingeman, R., Jacas, J. and Van de Klashorst, G. 1997. Metapopulation dynamics of a persisting predator-prey system in the laboratory: time series analysis. *Exp. Appl. Acarol.* 21 415-430.
- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). *Annals of the Entomological Society of America* 69: 1019-1023.
- Johnson, D. T., and B. A. Croft. 1981. Dispersal of *Amblyseius fallacis* (Acarina: Phytoseiidae) in an apple Ecosystem. *Environ. Entomol.* 10: 313-319.
- Jongejans, E., and P. Schippers. 1999. Modeling seed dispersal by wind in herbaceous species. *Oikos* 87: 362-372.
- Jung, C., and B. A. Croft. 2000. Survival and plant-prey finding by *Neoseiulus fallacis* (Acari: Phytoseiidae) on soil substrates after aerial dispersal. *Exp. Appl. Acarol.* 24 :579-596.
- Klashorst, G. v. d., J.L. Readshaw, M.W. Sabelis and R. Lingeman. 1992. A demonstration of asynchronous local cycles in an acarine predator-prey system. *Exp. Appl. Acarol.* 14 185-199.
- Kogan, M., B. A. Croft, and R. F. Sutherst. 1999. Applications of ecology for integrated pest management, pp. 681-738. *In* C. B. Huffaker and A. P. Gutierrez [eds.], *Ecological entomology*, 2nd ed. John Wiley & Sons, INC, New York.

- Lapple, C. E. 1956. Fluid and particle mechanics. Univ. Delaware Press.
- McEvoy, P. E., and C. S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. Ecology 68: 2006-2015.
- McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. Ann. Rev. Entomol. 42: 291-321.
- McMurtry, J. A., and J. G. Rodriguez. 1987. Nutritional ecology of phytoseiid mites, pp. 609-644. In F. S. Jr. and J. G. Rodriguez [eds.], Nutritional ecology of insects, mites, spiders and related invertebrates. John Wiley & Sons, New York.
- Misener, G. C., and G. Boiteau. 1993. Suspension velocity of the Colorado Potato Beetle in free fall. Amer. Potato J. 70: 309-316.
- Monteith, J. L., and M. H. Unsworth. 1990. Principles of environmental physics. Campman and Hall, Inc., London.
- Morse, D. H., and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. Oecol. 67: 372-379.
- Nachman, G. 1988. Regional persistence of locally unstable predator/prey populations. Exp. Appl. Acarol. 5: 293-318.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecol. 70: 329-338.
- Pedgley, D. 1982. Windborne pests and diseases: meteorology of airborne organisms. John Wiley & Sons.
- Pels, B., and M. W. Sabelis. 1999. Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. Oikos 86: 573-583.

- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within- and Between-Plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in simulated bean and apple plant systems. *Environ. Entomol.* 27: 148-153.
- Ramsey, F. L., and D. W. Schafer. 1997. *The statistical sleuth*. Duxbury Press, New York.
- Sabelis, M. W. 1981. Biological control of two-spotted spider mites using phytoseiid predators. Agricultural research reports 910 pudoc, Wageningen.
- Sabelis, M. W., and B. P. Afman. 1994. Synomone-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. *Exp. Appl. Acarol.* 18: 711-721.
- Sabelis, M. W., and F. M. Bakker. 1992. How predatory mites cope with the web of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp. Appl. Acarol.* 16: 203-225.
- Sabelis, M. W., and M. Dicke. 1985. Long-range dispersal and searching behaviour, pp. 141-157. *In* W. Helle and M. W. Sabelis [eds.], *Spider mites. Their biology, natural enemies and control*. Elsevier, Amsterdam.
- Sabelis, M. W., and J. van der Meer. 1986. Local dynamics of the interaction between predatory mites and two-spotted spider mites, pp. 322-344. *In* J. A. J. Metz and O. Diekmann [eds.], *Dynamics of Physiologically Structured Populations. Lecture Notes in Biomathematics 68*. Springer-Verlag. pp 322-344
- 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.

- Song, H., and J. B. Litchfield. 1991. Predicting method of terminal velocity for grains. *Transactions of the ASAE* 34: 225-230.
- Stephens, G. R., and D. E. Aylor. 1978. Aerial dispersal of Red Pine Scale, *Matsucoccus resinosae* (Homoptera: Margarodidae). *Environ. Entomol.* 7: 556-563.
- 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.
- Tixier, M.-S., S. Kreiter, and P. Auger. 2000. Colonization of vineyards by phytoseiid mites: their dispersal patterns in the plot and their fate. *Exp. Appl. Acarol.* 24: 191-211.
- Tixier, M.-S., S. Kreiter, P. Auger, and M. Weber. 1998. Colonization of Languedoc vineyards by phytoseiid mites (Acari: Phytoseiidae): influence of wind and crop environment. *Exp. Appl. Acarol.* 22: 523-542.
- Turchin, P. 1998. Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants. Sinauer Ass. Inc., Sunderland, MA.
- van Baalen, M., and M. W. Sabelis. 1995. The milker-killer dilemma in spatially structured predator-prey interactions. *Oikos* 74: 391-400.
- Vogel, S. 1994. Life in moving fluids. Princeton Univ. Press.
- Washburn, J. O., and L. Washburn. 1983. Active aerial dispersal of minute wingless arthropods: Exploitation of boundary-layer velocity gradients. *Science* 23: 1088-1089.

Chapter 5

SURVIVAL AND PLANT-PREY FINDING BY *Neoseiulus fallacis* (ACARI: PHYTOSEIIDAE) ON SOIL SUBSTRATES AFTER AERIAL DISPERSAL

Chuleui Jung and Brian A. Croft

Published in Volume 24 of Experimental and Applied Acarology, 2000, pp. 579-596

Used with kind permission from Kluwer Academic Publishers.

ABSTRACT

In a greenhouse and in an open field, aspects of aerial and ambulatory dispersal of the phytoseiid mite, *Neoseiulus fallacis* (Garman) were studied with a focus on events that would occur after aerially dispersing mites had landed on soil or associated substrates. We measured recovery of predators on lima bean plants (*Phaseolus lunatus* L.) that were infested with the two-spotted spider mite, *Tetranychus urticae* Koch. Factors thought to affect movement and colonization were distance to a receiver unit from a release (landing) point, intervening soil surfaces such as clods, gravel, fine soil and grass, and management of soil surfaces such as mulching, watering or both. In the field, the effect of distance (0.11 – 1.76 m) from a landing point to a receiver unit was significant, with a negative log linear relationship. Soil surfaces such as clods and management actions such as watering with mulching allowed for more capture of predators on bean plants with prey than did other treatments. Environmental conditions greatly affected survival of *N. fallacis*. Predators in the field that were present on bare soil suffered high mortality (ca. 90%) at fluctuating daytime conditions of $26.4 \pm 4.8^{\circ}\text{C}$ and $56 \pm 13.4\%$ R.H. Predators only suffered 10% mortality in the greenhouse under the same setting, but under more controlled and favorable environmental conditions. Effects of environmental conditions, mode of dispersal and implications to biological control are discussed.

INTRODUCTION

Phytoseiid mites are widely used for biological control of spider mites in greenhouse, field, and orchard crops (Helle and Sabelis, 1985; McMurtry and Croft, 1997). Depending on the temporal and spatial scale of assessment, prey-predator interactions of tetranychid and phytoseiid mites are highly unstable and last only a few generation cycles (Nachman, 1987; Sabelis et al., 1991). This is, in part, because spider mites tend to overexploit a plant food source and then disperse to new plants, whereas predators may take some time to find a spider mite colony and then to reduce it to a low level. Thus, after extinction of local prey source, emigration of a predatory mite usually occurs (Bernstein, 1983; Pels and Sabelis, 1999). Dispersal of both mites plays an important role in metapopulation dynamics and persistence of biological control (Nachman, 1987; Sabelis et al., 1991; Strong et al., 1999). The clumped distribution of spider mite and their abilities to disperse widely confer a high selection on evolution of efficient dispersal and prey finding mechanisms on specialized phytoseiid mite species that feed mostly on spider mites (Sabelis and Dicke, 1985).

Johnson and Croft (1976, 1981) first reported aerial dispersal of a phytoseiid mite *Neoseiulus fallacis* (Garman) under various conditions of temperature and starvation. Aerial dispersal is the main mechanism of colonization by phytoseiids from surrounding vegetation into an agroecosystem and spreading over a large area (Brandenburg and Kennedy, 1982; Dunley and Croft, 1990; Pratt

et al., 1998; Tixier et al., 1998). When predaceous mites disperse passively through the air, they probably have little control of where they land. Unless they land on a suitable target, they may have to aerially disperse again or search by walking for nearby spider mite colonies. During these activities, they may suffer high mortality if conditions are not favorable. For example, poor survival of *N. fallacis* that fell on the ground was observed during mid-summer in strawberry fields (Coop and Croft, 1995; Croft and Coop, 1998).

Species of phytoseiids that require high humidity for optimum development and reproduction are especially vulnerable to hot, dry conditions (Croft et al., 1993). With *N. fallacis*, it is important to understand the fate of mites that disperse from plants and fall to the ground. In Oregon where this species is widely used for biological control of spider mites, ambient temperatures often exceed 35°C and relative humidity is about 30-50 % during mid- to late- summer. Conditions at the soil microhabitat level may be even more extreme. Under these conditions, not being on a plant or a protective place can be critical to survival of the predator (Croft and Croft, 1993). There have been many studies on phytoseiid dispersal (Hoy, 1982; Field and Hoy, 1985; Sabelis and Afman, 1994; Strong and Croft, 1996; Tixier et al., 1998). But few have included investigations of survival on soil or colonization of new plants in the field from ground substrates (Raworth et al., 1994; Janssen, 1999).

We studied survival of and colonization of plants infested with *Tetranychus urticae* Koch by *N. fallacis* under conditions that aerial dispersing mites might

encounter when they fall to the ground. In the field, effects of several treatments on predator survival and colonization of plants were investigated: (1) distance to a receiver plant unit from a center release point, (2) soil surface types such as clods, gravel, fine soil and grass on colonization success, and (3) management practices such as mulching or watering and both. In the greenhouse, similar experiments were conducted for comparisons with field observations. Also in the laboratory under starvation conditions, survival of *N. fallacis* was measured under different temperature and relative humidity combinations.

MATERIALS AND METHODS

Standard experimental setting

The *N. fallacis* source population that was used for this study came from peppermint (*Mentha piperita* L.) plants collected throughout central Oregon, USA (Morris, 1998). *N. fallacis* were reared on lima bean plants, *Phaseolus lunatus* L., that were infested with *T. urticae* at 26:21 (± 5) °C (D: N), photoperiod 16:8 h (L: D), and 75 (± 10)% R.H. Lima bean plants containing infestations of *T. urticae* (>50/leaf) were used as receiver units to measure dispersal and colonization by predatory mites. A receiver unit, 3-4 wks after seed germination, was 8 bean plants with a total of 16 leaves in a plastic pot (10 x 10 x 10 cm). From a central release point, 4 receiver units were placed in the field out in each direction (E., W., S., N.)

at 0.22 m distance except for in distance treatments. Every treatment had 4 replicates unless otherwise stated. . A leaf-pack of 20 bean leaves harboring 300 ± 42.3 adult female *N. fallacis* was placed at each central release point. Released mites were semi-starved and in a similar physiological state to those that would be dispersing naturally. Preliminary studies showed that predatory mites left rapidly as the leaf-pack desiccated (24 hr after release, $25 \pm 19.1\%$ of predatory mites were remaining on the released leaf-pack and $1.3 \pm 1.4\%$ after 48 hr). Some nymphs, larvae and eggs of *N. fallacis* were present on released leaves. However, these life-stages were thought to have dispersed little in this study because they are very susceptible to dry condition and are much less likely to move from plant to plant than adult female *N. fallacis* (C. Jung, unpublished data). Releases of predator were made early in the day when temperature and humidity conditions were favorable to survival of predatory mites ($15.2 \pm 2.2^{\circ}\text{C}$ and $93 \pm 5.9\%$ R.H.). Receiver units were checked for any newly arrived *N. fallacis* with an optic visor at 10X magnification every morning at a fixed time for 5 days. Every *N. fallacis* that was found was removed from the receiver unit.

Field studies

Field studies were carried out in the Oregon State University (OSU) Botany Research Farm, Corvallis, OR. A preliminary assessment with sentinel plants, which were lima bean plants infested with *T. urticae* (Kogan et al. 1999),

confirmed that no predaceous mites were present in the study field. This field was a well-tilled loamy soil without any vegetation.

Distance (F1, F2, F3): After a dispersing mite has landed near or on a target plant or on the bare ground, it has to search for a site where it can survive and colonize. Although there have been extensive studies on phytoseiid interactions with prey-induced plant volatiles (Hislop and Prokopy, 1981; Sabelis and van de Baan, 1983; Sabelis and Dicke, 1985), it is unclear to what extent *N. fallacis* can respond to olfactory cues from plants and what mechanisms of plant host finding are involved. To evaluate different distances from a release (or landing) point to a receiver plant on survival and recovery of *N. fallacis*, 2 trials (F1, F3) of 4 treatments (0.22, 0.44, 0.88, and 1.76 m) were applied with 4 replicates, resulting in 16 plots per trial. A second trial (F2) of 4 distance treatments (0.11, 0.22, 0.44, and 0.88) was investigated with 3 replicates. All trials were conducted on a fine soil surface. Each plot was randomly located in the field (50 x 65 m) with enough space (> 6 m) between plots to ensure that there was no interaction with other test plots. During all tests, soil moisture content in the study field did not exceed 5%.

Ground surface types (F4): Ground surface types that were tested were fine soil, clod soil, gravel-covered, and turf grass. We hypothesized that dispersing mites would suffer different mortality depending on the type of substrate that they landed upon. For the fine soil treatment, soil lumps were removed by sifting. In clod plots,

lumps of soil ($\approx$ 5-10 cm diameter) were gathered to create an uneven profile. Gravel (2-3 cm diameter) was placed evenly and thoroughly over a flat soil. Turf grass was mowed to 5-10 cm high and was completely dry due to the lack of irrigation for several weeks.

Management practices (F5): Environmental manipulation and management may conserve natural enemies and thereby enhance biological control (Strong and Croft, 1995; Nyrop et al., 1998). Under the hot, dry conditions, effects of soil surface and water treatments on recovery of *N. fallacis* on receiver units were evaluated. Treatments were no watering on bare soil, no watering with mulching, watering on bare soil, and watering with mulching. Well-dried grass materials were placed in sufficient quantity to cover soil in mulching treatments. Every morning, water was lightly sprayed to moisten soil (2 liters per plot) in plots with water treatments.

Greenhouse studies

Distance (G1, G2, G3): In these studies, environmental conditions were held relatively constant over time and no appreciable winds occurred. General experimental settings were the same as in field studies, but receiver units were checked for predators every 12 hr. Effects on predator survival of several conditions of distances to host plant, temperature-humidity and soil moisture combinations were compared. Because of space limitation, distance treatments were only 0.11, 0.22, and 0.44 m in these studies. Environmental conditions for

tests were soil moisture either at $<5\%$ or $\approx 25\%$ and temperature-humidity at either $22 \pm 0.6^\circ\text{C}$, $65 \pm 5\%$ R.H. or $30 \pm 0.6^\circ\text{C}$, $40 \pm 5\%$ R.H., respectively.

Laboratory studies

Temperature-humidity-dependent mortality: In the laboratory, the combined effects of relative humidity and temperature on survival of gravid adult female *N. fallacis* were measured without provisioned food and water. Stock cultures of predators were maintained at $25 \pm 5^\circ\text{C}$ and $\approx 70\%$ R.H. in a rearing unit modified from that of McMurtry and Scriven (1964). Mixed life stages of *T. urticae* were fed to predators regularly. All predators tested were randomly selected from populations of well-fed adult females (mixed ages) and individuals were transferred into plexiglass cells (Schausberger, 1998). Cells consisted of holes with a diameter of 1.5 cm drilled into rectangular pieces of plexiglass (8 cm x 3.5 cm x 0.3 cm) and closed at the bottom by a fine nylon mesh. Cells were placed into humidity chambers constructed from plastic boxes. Wire supports served as rests for plexiglass cells above salt solutions. Combined effects of temperature (12, 20, 28, $35 (\pm 1)^\circ\text{C}$) and relative humidity ($\approx 45, 75, 100\%$) on survival of *N. fallacis* were evaluated. Relative humidities in boxes were maintained by saturated solutions of MgCl_2 (45%), NaCl (75%), and distilled water (100%) (Croft et al., 1993). Mortality levels were checked every 12 hr for 7 days and, after that, every 24 hr for a maximum of 22 days.

Relation to Environmental Conditions: Records of average daily temperature and relative humidity were used to investigate the relationship between environmental conditions and recovery of *N. fallacis* at the standard setting of 0.22 m distance and on fine soil. Results were compared with probability estimates based on random chance recovery. Probabilities were calculated as the proportional area occupied by receiver units to the circumference in each distance sector. This estimate then was used with data on distance-independent mortality, emigration rate from released leaf-pack (0.75 for 1st day and 0.25 for 2nd day), and temperature-humidity dependant mortality from laboratory test. From distance tests, directional effect of recovery was then analyzed with environmental data (wind speed, wind direction, air temperature and relative humidity). Also, cumulative recovery patterns were compared from the field and greenhouse data. Environmental data were taken from a nearby weather station (Oregon State University Field Station at Hyslop Farm near Corvallis, OR). Drapek (1993) previously found low variation of these measurements from this field station when compared to similar data from a nearby large field in the Willamette Valley.

Statistical Analysis: In field and greenhouse tests, cumulative percent recovery over 5 days was analyzed for treatment effect by analysis of variance (ANOVA) with a least significant difference (LSD) test (Ramsey and Schafer, 1996). To assess recovery of predators relative to distance from release points, a general linear model (GLM) was used (Ramsey and Schafer, 1996). Varying distance

effects were also compared using probability estimates. From the laboratory mortality data, a degree-day mortality model of temperature effects was created with 3 different relative humidity components. A baseline temperature for the degree-day calculation was approximated from the GLM analysis.

RESULTS

Field studies

Distance: The effect of distances from release point to receiver unit on recovery was significant (GLM, distance, $P < 0.0001$). There was a negative log linear relationship between these variables when same-sized receiver units were used (Fig. 5.1). Three trials conducted under different environmental conditions showed different recovery levels (GLM, trial, $P < 0.0001$), but the same rate of recovery relative to distance (no interaction term, GLM, distance x trial, $P > 0.82$) (Fig. 5.1). Compared to probability estimates, no distance-dependant mortality was observed, but released mites were affected greatly by environmental factors and a 40-90% overall mortality was seen in all test.

Ground surface types: Soil surface types had marginally significant effects on survival and recovery on receiver units (ANOVA, $df=3,10$, $P < 0.095$) (Fig. 5.2). The clod surface provided the highest recovery of predators, $\approx 12\%$, and the gravel,

the lowest (Fig. 5.2). Fine dry soil and dry grass treatments were intermediate in recovery compared to clod and gravel substrates (Fig. 5.2a).

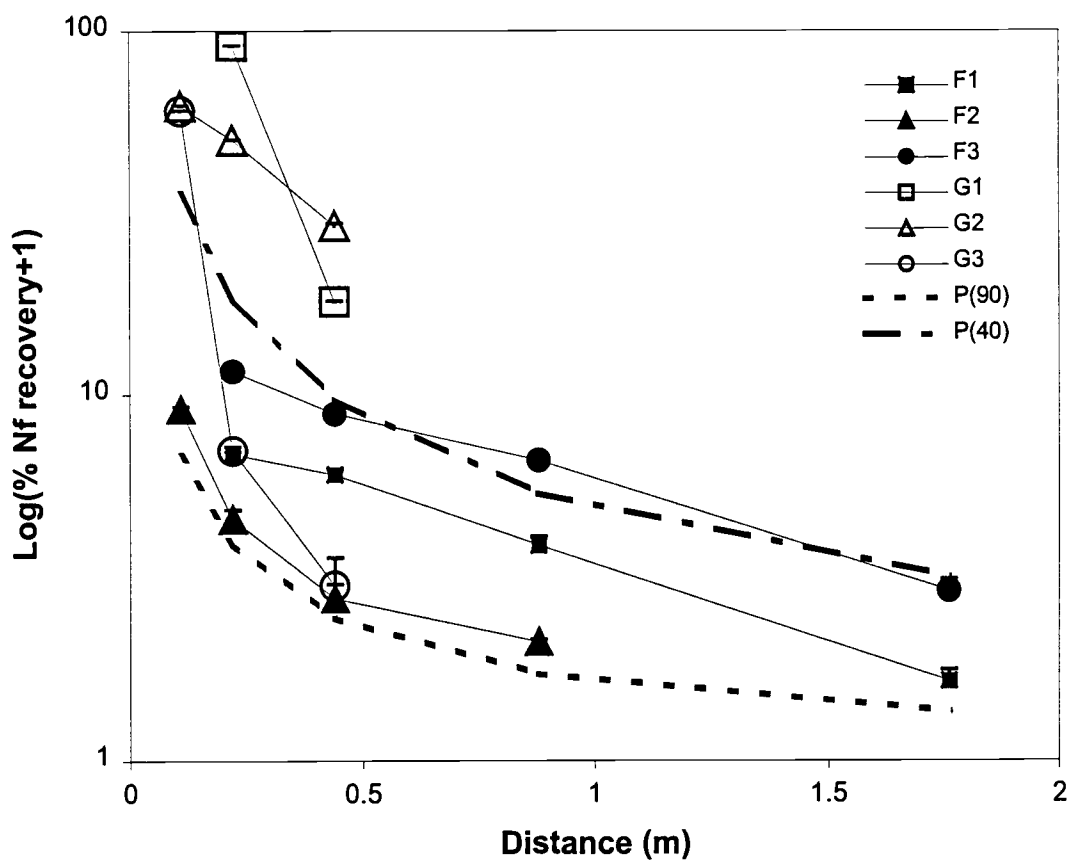


Fig. 5.1. Distance dependant recovery of *N. fallacis* ($\text{Log}(\% \text{ recovery} + 1) + \text{SE}$) under field (F1, F2, F3) and greenhouse (G1, G2, G3) conditions. Probability (P) of *N. fallacis* to reach receiver units by random chance and with no distance-dependent mortality. Overall mortality was applied as 90% and 40% in P(90) and P(40), respectively.

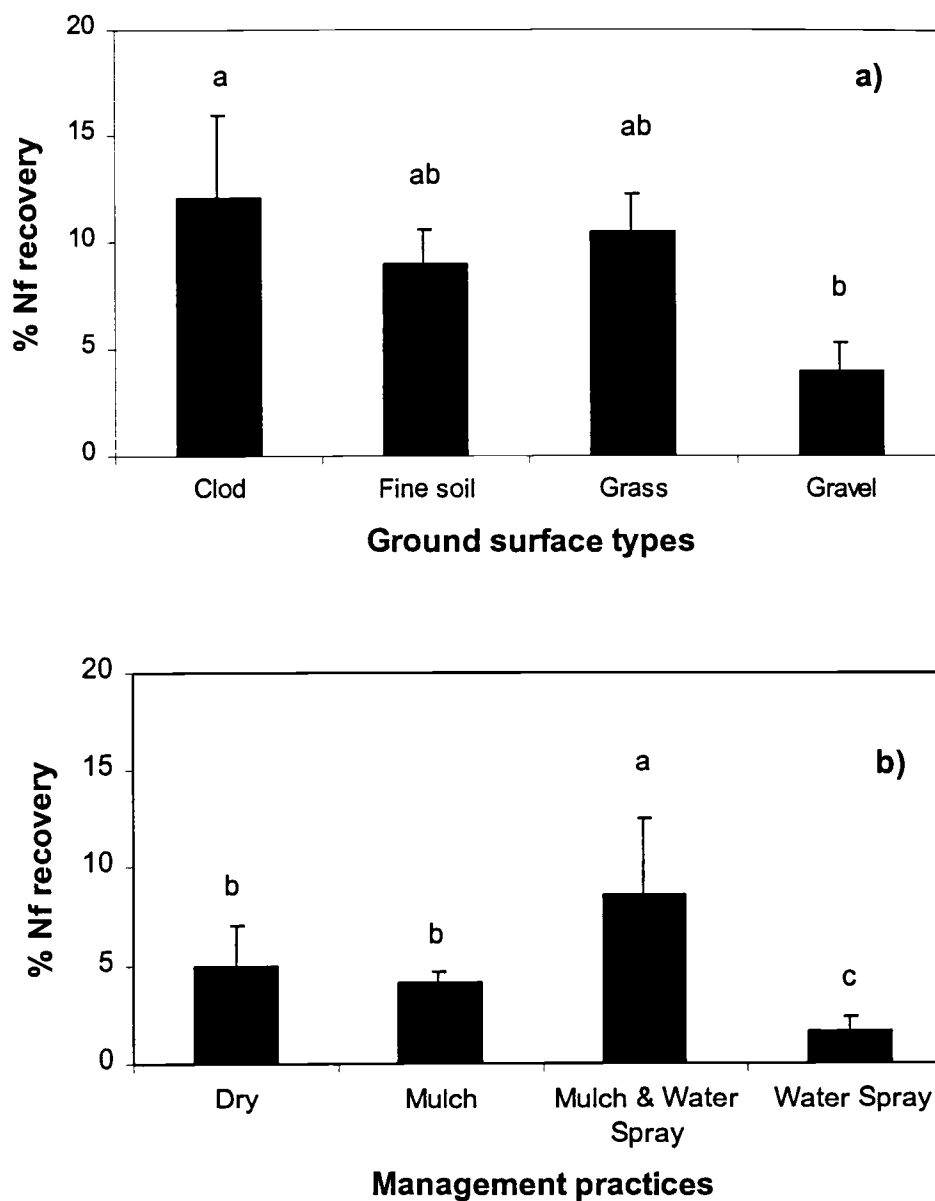


Fig. 5.2. Effects of soil surface types (a: upper graph, ANOVA, $df=3,10$, $P<0.095$) and management practices (b: lower graph, ANOVA, $df=3,10$, $P<0.02$) on recovery of *N. fallacis* (mean % $\pm$ SE) in receiver plant units with prey mites (*T. urticae*) in the field.

Management practices: Management practices differentially influenced survival and recovery of predatory mites (ANOVA, $df=3,10$, $P<0.020$). Watering with mulching seemed to provide both shelter and a humid environment and this treatment resulted in the highest recovery (Fig. 5.2b). Watering on bare soil was worst for the survival of mites on the ground. No watering on bare soil and no watering with mulching did not differ in their effects on predators; both resulted in intermediate *N. fallacis* recovery.

Greenhouse studies

Distance: Recovery of predaceous mites was variable and highly dependent on conditions of the experiment. Under warm, humid ambient conditions with dry soil, $90 \pm 7.48\%$ of released predators were recovered on receiver units at 0.22 m. In contrast, only about 60% were recovered under hot, less humid conditions, even at 0.11m (Fig. 5.1). In latter case, the effect of soil moisture content was not significant at 0.11 m (ANOVA, $df=1,7$, $P>0.05$), but at 0.22 and 0.44 m, recovery was significantly higher in moderately wet soil than in dry soil (ea. ANOVA, $df=1,7$, $P<0.05$) (Table 5.1). Also, recovery was drastically decreased under hot, dry air and dry soil as distance increased (Fig. 5.1).

Laboratory studies

Temperature- humidity-dependent mortality: The bivariate prediction model for mortality of *N. fallacis* when starved (baseline temp. = 4 °C) showed that for each

three level of humidity treatments, mortality increased linearly as degree-days increased (Fig. 5.3). Also an increase in relative humidity lowered the slope (decreased the mortality rate) of the regression model.

Relation to Environmental Conditions: Recovery of released *N. fallacis* at the standard distance on fine soil was largely influenced by the environmental conditions under which the test was performed (Fig. 5.4). Probability estimates that accounted for random chance, temperature-humidity-dependent mortality and emigration rate from released leaf-pack were higher when compared to the observed. However, the patterns that were predicted generally agreed with the observed data from field and greenhouse studies (correlation, $r=0.6$) when the G1 and G2 results were excluded from the comparison. In G1 and G2, environmental conditions were relatively favorable for *N. fallacis* survival and recovery of predators was much higher than other treatments, 90 and 49%, respectively (Fig. 5.4). However, variation of the observed was much larger than that of predicted. From field distance tests, recovery was consistently the highest in eastern receiver units (ANOVA, $df=3, 44$, $P<0.0001$). About 95% of all mites were captured in this directional plot (Fig. 5.5a). Relatively higher wind speeds ($>5\text{m/s}$) were coincident with the eastward direction in late afternoon (Fig. 5.5b). This was about the time that harsh environmental conditions changed to being more favorable for survival of *N. fallacis* (Fig. 5.5b). In the greenhouse where there were no winds, however, there was no directional effect (ANOVA, $df=3, 28$, $P>0.8$). Recovery rate gradually

increased in the greenhouse tests, but a gradually decreasing pattern was shown in the field (Fig. 5.6).

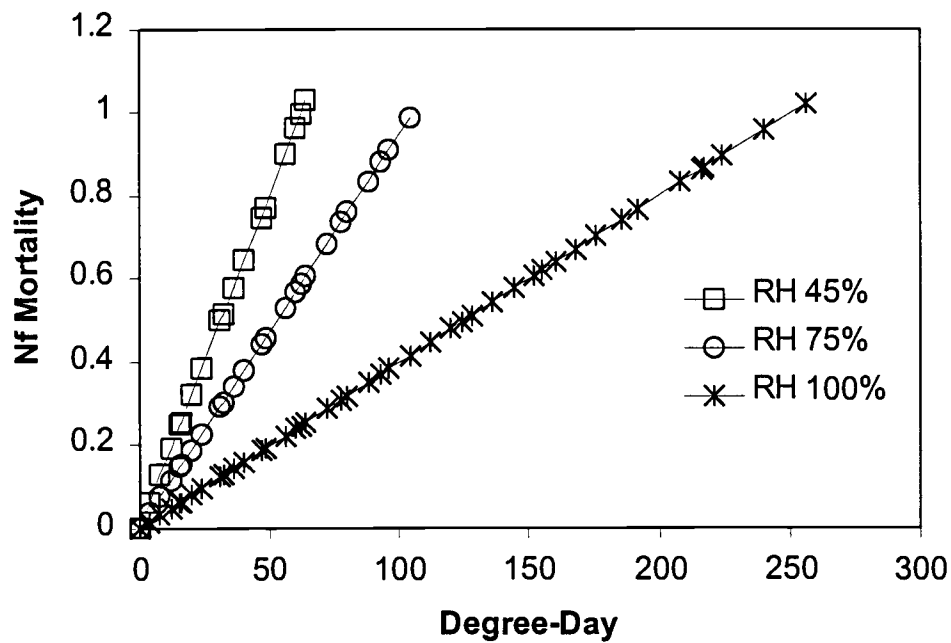


Fig. 5.3. Mortality prediction model of *N. fallacis* held without food and water (degree-day baseline temperature = 4 °C: $Mortality = (0.026 - 0.00022 \times RH (\%)) \times DD$ (GLM, $R^2 = 0.87$).

Table 1. Environmental conditions under which each experiment was performed in the Field (F) and in the greenhouse (G)

Treatment		Conditions		
		Soil	Temperature (°C) ¹	RH (%) ²
F1	Distance	Dry ³	27.7	47.35
F2	Distance	Dry	30.23	52.45
F3	Distance	Dry	26.56	48.29
F4	Ground surface type	Dry	24.85	52.45
F5	Management Practice	Dry	30.8	48.29
G1	Distance	Dry	22	65
G2	Distance	Humid ⁴	30	40
G3	Distance	dry	30	40

¹: Average of daily mean temperature

²: Average of daytime relative humidity (8 am-10 pm)

³: Soil moisture content <5 %

⁴: Soil moisture content ≈20 %

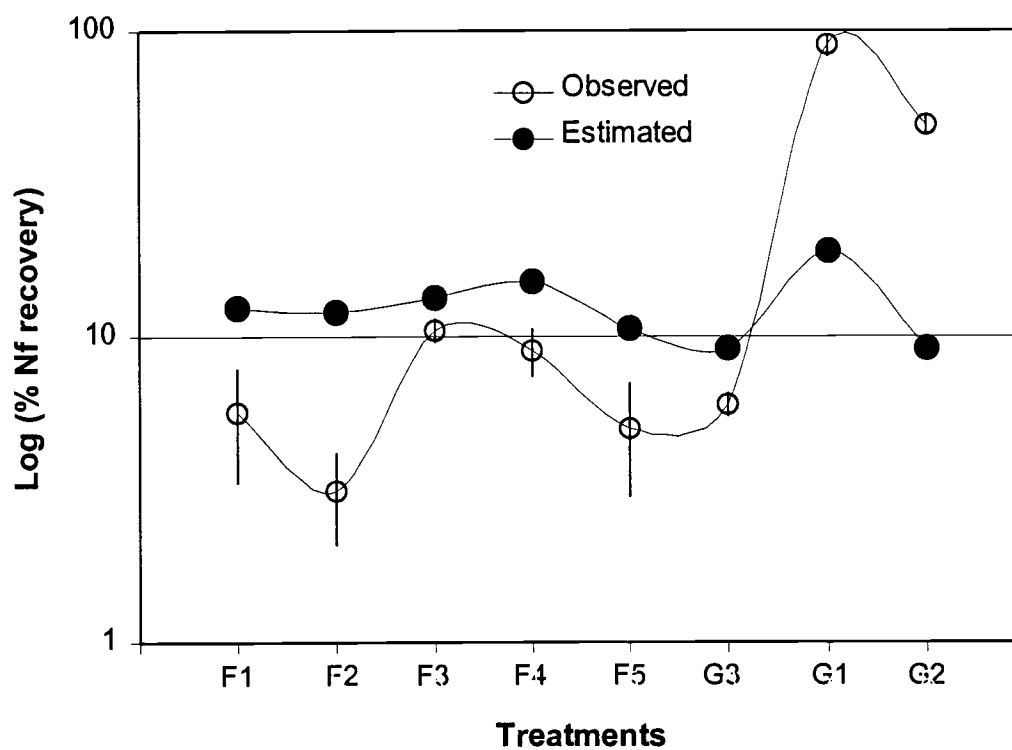


Fig. 5.4. Variation of recovery (mean % $\pm$ SE) at 0.22 m distance on fine soil under different environmental settings. Estimates based on random chance, temperature-humidity-dependent mortality and emigration rate from released leaf-pack.

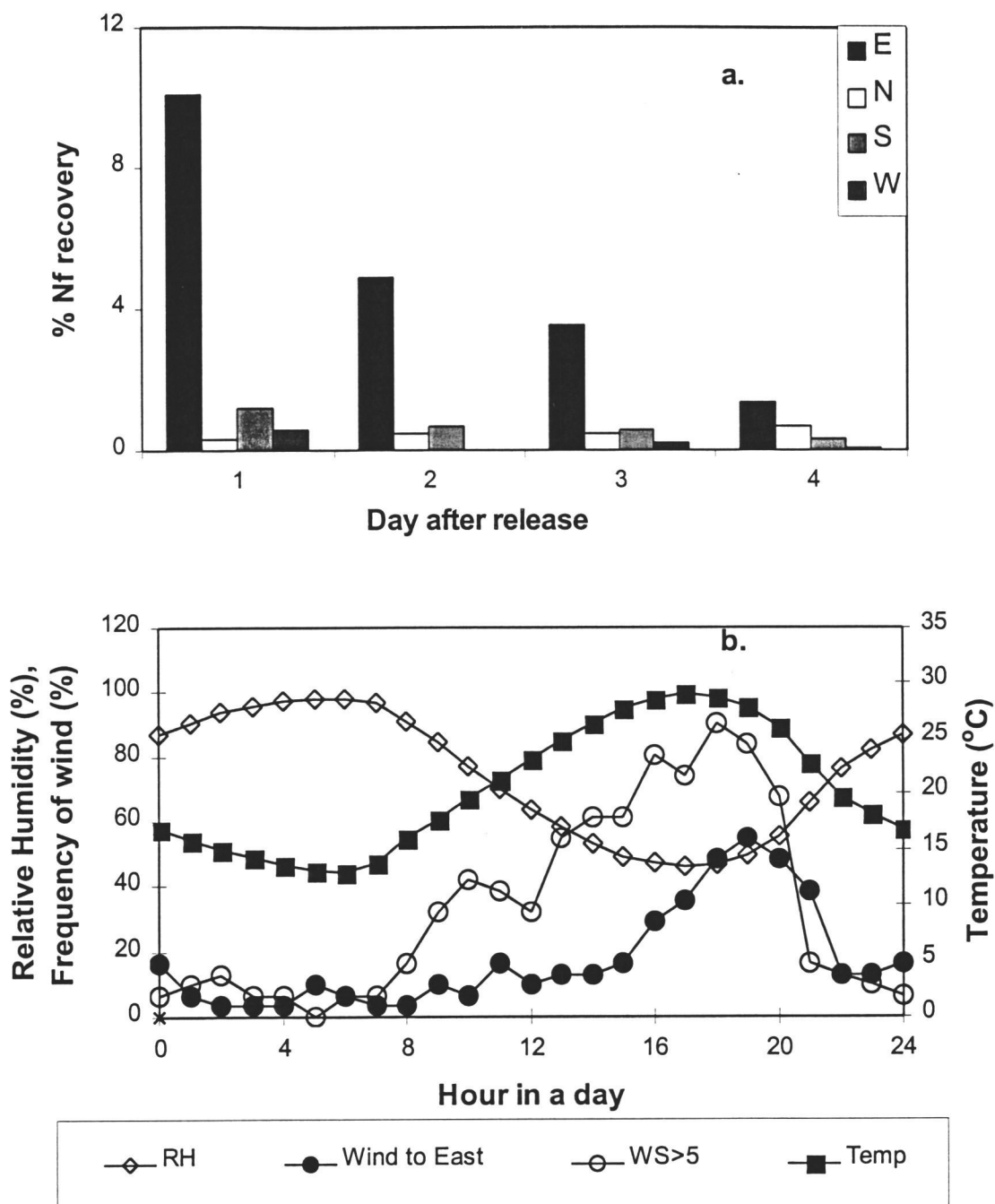


Fig. 5.5. Direction-dependant recovery of *N. fallacis* on receiver plants with *T. urticae* in a field study (a: upper graph) and environmental conditions during study periods (b: lower graph). Environmental measurements are ambient temperature (Temp), relative humidity (R.H.), and frequency of eastward winds (Wind to East), and wind speeds exceeding 5 m/s (WS>5).

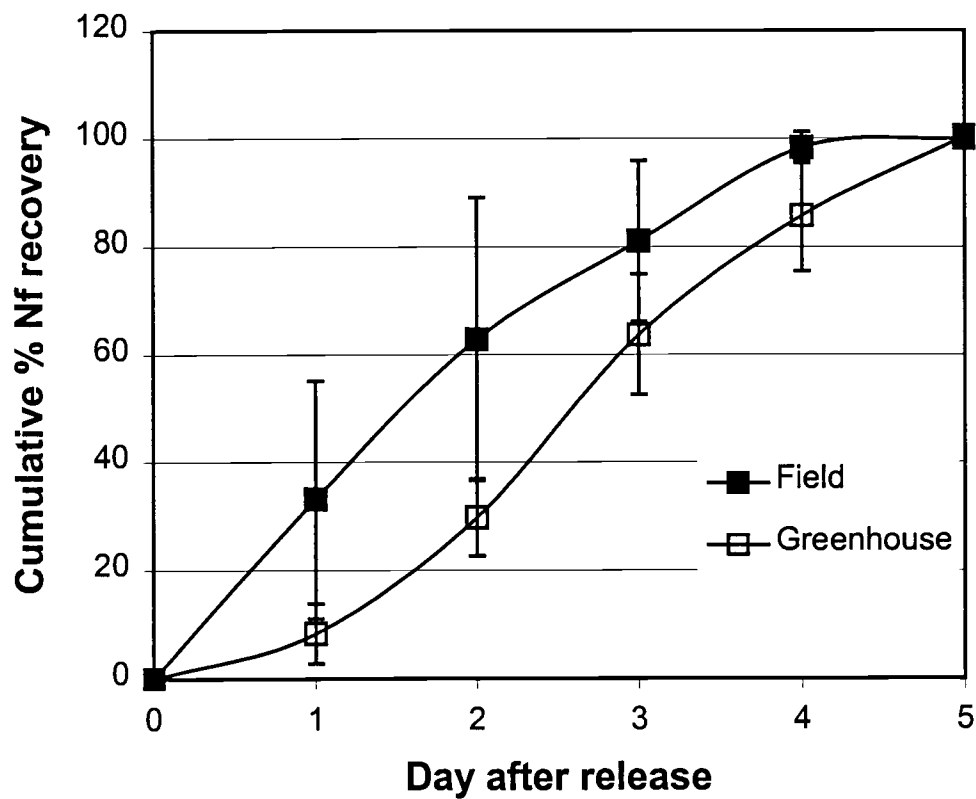


Fig. 5.6. Cumulative recovery pattern (mean $\pm$ SD) of *N. fallacis* to receiver plant units with *T. urticae* after predator releases at 0.22 m distance on fine soil in the field and greenhouse.

DISCUSSION

Effect of different factors and primary means of dispersal

Recovery of *N. fallacis* on receiver host plants with prey mites was variable and greatly influenced by environmental conditions. Recovery was low (only 10%) on receiver plants in the field when mites were placed on soil under hot and dry conditions and the most mites were captured downwind. These data could reflect either an aerial dispersal or a downwind ambulation. We favored the former explanation (see below). In contrast, recovery of predators in the greenhouse was as high as 90% when conditions were highly favorable and the receiver units were close to the release site (0.11 m). No directional effect on recovery was seen when wind was not present. These contrasting results raised questions about the primary mode of predator dispersal and host plant/prey finding of *N. fallacis*.

Production of volatiles by bean plants that were infested with *T. urticae* would be a primary cue for predators to move directionally by ambulation (Hislop and Prokopy, 1981; Sabelis and van de Baan, 1983; Sabelis and Dicke, 1985). However, several other factors could have been involved. Negative photo-orientation of ambulating *P. persimilis* (Bernstein, 1983) and spider mites (Smitley and Kennedy, 1985; Margolies, 1987) have been reported. *N. fallacis* is negatively phototactic and during late afternoon, this factor could have affected capture. Another explanation may be that *N. fallacis* walks downwind to avoid extremes of heat and wind. Sabelis and van der Weel (1993), however, found that starved *P.*

persimilis walked upwind regardless of prey stimuli, and predators that were well-fed walked downwind only without chemical stimuli. Janssen (1999) suspected natural light intensity effect on the direction of NNW for *P. persimilis* in a greenhouse study. Just how these factors might confer a directional component to ambulatory movement needs further investigation with *N. fallacies* and phytoseiids in general.

While ambulatory movement over soil seemed to occur in greenhouse tests, *N. fallacis* appears to have much greater difficulty or spends more time traversing soil than plants (Berry and Holtzer, 1990, 1991). For example, recovery at 0.44 m distance was 2-30% and it took 3 days for 50% recovery even at 0.11 m (Fig. 6). This compares to just minutes to hours to cover these distances on plants held under similar environmental conditions and with the same species (Berry and Holtzer, 1990) or with *Phytoseiulus persimilis* (Janssen, 1999). This slower movement on soil could be because of surface irregularities, greater surface area per unit distance and/or a different walking capacity in *N. fallacis* as compared to *P. persimilis*. Even under about the same temperature and humidity conditions, increased soil moisture provided for increased recovery of *N. fallacies*, probably by lessening desiccation and starvation. Another explanation could be that under more moderate temperatures and humidities, *N. fallacis* changed walking with more turning and increased possibility to find a plant with prey (Penman and Chapman, 1980).

While we think that some ambulatory movement to receiver plants occurred in our field studies, we speculate that *N. fallacis* primarily used aerial means to disperse from ground to receiver plants. In the field, air currents often increased in late afternoon and early evening, especially on days that are hot and dry and not favorable for dispersal or survival of predators apart from plants. Results that lent support to this speculation were the low rates of recovery in field tests, even at 0.11 m distance. This lack of recovery indicates that continuous releases of volatiles from prey-infested plants were not a major factor limiting dispersal. Rather, dispersal seemed to occur more discontinuously. During the extremes of mid-day, *N. fallacis* may stay in protected areas on plants or on ground in more moist, shadowed areas, but start moving when conditions become more favorable. As seen in weather data, in late afternoon- early evening, temperatures, humidity conditions, and wind intensity changed to favor survival of *N. fallacis* and we speculate that this caused mites to disperse, survive and mostly to be recovered in eastern receiver units. Hoy et al. (1985) similarly reported greatest dispersal of predatory mite *Galendromus* (= *Metaseiulus*) *occidentalis* at 4-10 pm when relative humidity started to increase and temperature decreased, yet wind speeds were still relatively high.

Considering the level of 90% recovery of predators in greenhouse tests, we considered that 2 factors of our experimental design might have been affected results. First, recoveries may have been higher than normally occurs among naturally dispersing *N. fallacis* because some cannibalism of immature stages may

have occurred while predators were still on leaf packs (Schausberger and Croft, 2000). However, this effect on survival would only have occurred under favorable environmental conditions. Under extreme environmental conditions, immature life stages of the predator would have quickly died and would have provide little if any additional food to dispersing adult female mites. Another factor that may have influenced colonization of plants was that predators might have been less attracted to a receiver plant once it was colonized earlier by the species (Janssen et al. 1997). This factor was discounted as having much effect in field studies, because proportions of colonized units were relatively low and this relatively specialized predator of spider mites does not seem to be greatly limited in colonizing plants that were previously occupied by individuals of the species (Pratt, 1999).

Ground surface types and Management practices

Ground substrates and management practices seemed to have some effects on survival and recovery of *N. fallacis*. Soil surface with higher vertical profiles and more spatial complexity allowed for better recovery. This may be, in part, due to more shadowed and sheltered areas where mites were less exposed to the sun and wind, and thus individuals suffered less humidity loss. Also, the heightened platforms of clods and grass may have enhanced aerial redispersal after landing. In gravel plots, low recovery may due to the physical property of gravel. Gravel absorbs heat that would be highly detrimental to *N. fallacis*. From the management treatments, direct water spray to bare ground was deleterious to *N. fallacis* survival,

probably because mites drowned. Watering on mulch resulted in the highest recovery among management treatments. Apparently plant residues provided protected places and higher humidity for *N. fallacis*. These results suggest that manipulation of plant residues may be used to conserve predaceous mites in crops such as strawberry and hop (Strong and Croft, 1995) where mulching of vegetation is common (Coop and Croft, 1995).

Implication on biological control

Because our studies were limited in time and space, treatments could have been affected by prevailing weather. Also, treatments such as in soil surface types and management practices may have not represented the variability of real field conditions. Even with these limitations, some implications of our studies to biological control can be drawn. Effective and persistent biological control can be achieved by maintaining predaceous mites in close proximity to spider mites on a crop (Nyrop et al., 1998). As we have shown, *N. fallacis* suffer high mortality if they do not land on a target plant (with prey) after dispersal. Thus, in augmentation, care must be taken when releasing predators. Improper placement of predators out of a target plant/patch may result in poor pest control because of increased mortality of predator. In conservation, understanding the life history of the predaceous mite is important. For example, *N. fallacis* requires a humid environment (Croft et al., 1993) and seems to be most effective in low herbaceous crops where relatively high humidity is maintained, but less effective in taller

plants (Strong and Croft, 1995; Nyrop et al., 1998; Kogan et al., 1999). If biological control depends more on natural predator immigration from surrounding natural vegetation such as occurs in vineyards (Boller et al., 1988; Tixier et al., 1998), habitat management will insure better survival of invaders. Survival of immigrating mites from the surrounding vegetation is conducive to early-season population build up on many crops (Ferro and McNeil, 1998). Usually the physiological condition of an invading individual is poor because dispersal is initiated after local resources have been exploited (Johnson and Croft, 1976, 1979; Hoy, 1982; Field and Hoy, 1985; Pratt et al., 1998; Pels and Sabelis, 1999). Hungry individuals after aerial dispersal quickly die if they do not find food. Use of ground cover, mulching and changing planting methods and/or modification of cultural practices may enhance survival of predatory mites on the ground (Flexner et al., 1991). Also, in hops, a "landing pad" of foliage was demonstrated to enhance survival of aerially dispersing *N. fallacis* (Strong et al., 1999). Further research is needed to test the survival and recovery of dispersing mites in real field situations at larger scales and landing distribution of aerially dispersing mites relative to vegetation spatial patterns and structure.

REFERENCES

- Bernstein, C. 1983. Some aspects of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) dispersal behaviour. *Entomophaga* 28: 185-198.
- Berry, J. S., and T. O. Holtzer. 1990. Ambulatory dispersal behavior of *Neoseiulus fallacis* (Acarina: Phytoseiidae) in relation to prey density and temperature. *Exp. Appl. Acarol* 8: 253-279.
- Berry, J. S., T. O. Holtzer, and J. M. Norman. 1991. Experiments using a simulation model of the Banks grass mite (Acarina: Tetranychidae) and the predatory mite, Nf (Acarina: Phytoseiidae) in a corn microenvironment. *Environ. Entomol.* 20: 1174-1178.
- Boller, E. F., U. Remund, and M. P. Candolfi. 1988. Hedges as potential sources of *Typhlodromus pyri*, predatory mite in vineyards of northern Switzerland. *Entomophaga* 33: 247-255.
- Brandenburg, R. L., and G. G. Kennedy. 1982. Intercrop relationships and spider mite dispersal in a corn/peanut agro-ecosystem. *Entomol. Exp. Appl.* 32: 269-276.
- Coop, L. B., and B. A. Croft. 1995. *Neoseiulus fallacis*: dispersal and biological control of *Tetranychus urticae* following minimal inoculations into a strawberry field. *Exp. Appl. Acarol.* 19: 31-43.
- Croft, B. A., and L. B. Coop. 1998. Heat units, release rate, prey density, and plant age effects on dispersal by *Neoseiulus fallacis* (Acari: Phytoseiidae) after inoculation into strawberry. *J. Econ. Entomol.* 91: 94-100.
- Croft, B. A., and M. B. Croft. 1993. Larval survival and feeding by immature *Metaseiulus occidentalis*, *Neoseiulus fallacis*, *Amblyseius andersoni* and *Typhlodromus pyri* on life stage groups of *Tetranychus urticae* Koch and phytoseiid larvae. *Exp. Appl. Acarol.* 17: 685-693.

- Croft, B. A., R. H. Messing, J. E. Dunley, and W. B. Strong. 1993. Effects of humidity on eggs and immatures of *Neoseiulus fallacis*, *Amblyseius andersoni*, *Metaseiulus occidentalis* and *Typhlodromus pyri* (Phytoseiidae): implications for biological control on apple, caneberry, strawberry and hop. *Exp. Appl. Acarol.* 17: 451-459.
- Drapek, R. J. 1993. Use of a geographic information system to modify pheromone trap-based predictions of *Helicoverpa zea* (Boddie) damages, pp. 158, Entomology. Oregon St. Univ., Corvallis.
- Dunley, J. E., and B. A. Croft. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). *Exp. Appl. Acarol.* 10: 137-149.
- Ferro, D. N., and J. N. McMeil. 1998. Habitat enhancement and conservation of natural enemies of insects, pp. 123-132. *In* P. Barbosa [ed.], Conservation biological control. Academic press, San Diego.
- Field, R. P., and M. A. Hoy. 1985. Diapause behavior of genetically improved strain of the spider mite predator *Metaseiulus occidentalis* (Acarina: Phytoseiidae). *Entomol. Exp. Appl.* 38: 113-120.
- Flexner, J. L., P. H. Westigard, P. Gonzalves, and R. Hilton. 1991. The effect of groundcover and herbicide treatment on twospotted spider mite density and dispersal in southern Oregon pear orchards. *Entomol. Exp. Appl.* 60: 111-123.
- Helle, W., and M. W. Sabelis [eds.]. 1985. Spider mites. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.
- Hislop, R. G., and R. J. Prokopy. 1981. Mite predator responses to prey and predator-emitted stimuli. *J. Chem. Ecol.* 7: 895-904.
- Hoy, M. A. 1982. Aerial dispersal and field efficacy of a genetically improved strain of the spider mite predator *Metaseiulus occidentalis*. *Entomol. Exp. Appl.* 32: 205-212.

- Hoy, M. J., J. J. Groot, and H. E. van de Baan. 1985. Influence of aerial dispersal on persistence and spread of pesticide-resistant *Metaseiulus occidentalis* in California almond orchards. *Entomol. Exp. Appl.* 37: 17-31.
- Janssen, A. 1999. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. *Entomol. Exp. Appl.* 90: 191-198.
- Janssen, A., J. Bruin, G. Jacobs, R. Schraag, and M. W. Sabelis. 1997. Predators use volatiles to avoid prey patches with conspecifics. *J. Anim. Ecol.* 66: 223-232.
- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). *Annals of the Entomological Society of America* 69: 1019-1023.
- Johnson, D. T., and B. A. Croft. 1979. Factors affecting the dispersal of *Amblyseius fallacis* in an apple tree ecosystem, pp. 477-483. *In* J. G. Rodriguez [ed.], *Recent advances in Acarology*. Academy Press, New York.
- Johnson, D. T., and B. A. Croft. 1981. Dispersal of *Amblyseius fallacis* (Acarina: Phytoseiidae) in an apple Ecosystem. *Environ. Entomol.* 10: 313-319.
- Kogan, M., B. A. Croft, and R. F. Sutherst. 1999. Applications of ecology for integrated pest management, pp. 681-738. *In* C. B. Huffaker and A. P. Gutierrez [eds.], *Ecological entomology*, 2nd ed. John Wiley & Sons, INC, New York.
- Margolies, D. C. 1987. Conditions eliciting aerial dispersal behavior in Banks Grass Mite, *Oligonychus pratensis* (Acari: Tetranychidae). *Environ. Entomol.* 16: 928-932.
- McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. *Ann. Rev. Entomol.* 42: 291-321.

- McMurtry, J. A., and G. T. Scriven. 1965. Insectary production of phytoseiid mites. *J. Eco. Ent.* 58: 282-285.
- Morris, M. A. 1998. Biological control of *Tetranychus urticae* (Koch) on peppermint by *Neoseiulus fallacis* (Garman): Density relationships, overwintering, habitat manipulation and pesticide effects, pp. 79, Entomology. Oregon St. Univ., Corvallis.
- Nachman, G. 1987. Systems analysis of acarine predator-prey interactions. I. A stochastic simulation model of spatial processes. *J. Anim. Ecol.* 56: 247-265.
- Nyrop, J., G. English-Loeb, and A. Roda. 1998. Conservation biological control of spider mites in perennial cropping systems, pp. 307-333. *In* P. Barbosa [ed.], Conservation biological control. Academic press, San Diego.
- Pels, B., and M. W. Sabelis. 1999. Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. *Oikos* 86: 573-583.
- Penman, D. R., and R. B. Chapman. 1980. Effect of temperature and humidity on the locomotory activity of *Tetranychus urticae* (Acari: Tetranychidae), *Typhlodromus occidentalis* and *Amblyseius fallacis* (Acarina: Phytoseiidae). *Acta Ecologica* 1 2353-269.
- Pratt, P. D. 1999. Biological control of spider mites by the predatory mite *Neoseiulus fallacis* (Acari: Phytoseiidae) in ornamental nursery plant systems, pp. 150, Entomology. Oregon St. Univ., Corvallis.
- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within- and Between-Plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in simulated bean and apple plant systems. *Environ. Entomol.* 27: 148-153.
- Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, New York.

- Raworth, D. A., G. Fauvel, and P. Auger. 1994. Location, reproduction and movement of *Neoseiulus californicus* (Acari: Phytoseiidae) during the autumn, winter and spring in orchards in the south of France. *Exp. Appl. Acarol.* 18: 593-602.
- Sabelis, M. W., and B. P. Afman. 1994. Synomone-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. *Exp. Appl. Acarol.* 18: 711-721.
- Sabelis, M. W., and H. E. v. d. Baan. 1983. Location of distant spider mite colonies by phytoseiid predators: Demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Ent. Exp. appl.* 33: 303-314.
- Sabelis, M. W., and M. Dicke. 1985. Long-range dispersal and searching behaviour, pp. 141-157. *In* W. Helle and M. W. Sabelis [eds.], *Spider mites. Their biology, natural enemies and control*. Elsevier, Amsterdam.
- 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., and J. J. v. d. Weel. 1993. Anemotactic response of the preatory mite, *Phytoseiulus persimilis* Athias-henriot, and their role in prey finding. *Exp. Appl. Acarol.* 17: 521-529.
- Schausberger, P. 1998. The influence of relative humidity on egg hatch in *Euseius finlandicus*, *Typhlodromus phylli* and *Kampimodromus aberrans* (Acari, Phytoseiidae). *J. Appl. Ent.* 122: 497-500.
- Schausberger, P., and B. A. Croft. 2000. Intraguild predation and cannibalism among generalist and specialist phytoseiid mites: nutritional benefits. *Ecol. Entomol.* (in print)
- Smitley, D. R., and G. G. Kennedy. 1985. Photo-oriented aerial dispersal behavior of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface. *Ann. Entomol. Soc. Am.* 78: 609-614.

- Strong, W. B., and B. A. Croft. 1995. Inoculative release of phytoseiid mites (Acarina: Phytoseiidae) into the reapidly expanding canopy of hops for control of *Tetranychus urticae* (Acarina: Tetranychidae). Environ. Entomol. 24: 446-453.
- Strong, W. B., D. H. Slone, and B. A. Croft. 1999. Hops as a metapopulation landscape for tetranychid-phytoseiid interactions: perspectives of intra- and interplant dispersal. Exp. Appl. Acarol. 23: 581-597.
- Tixier, M.-S., S. Kreiter, P. Auger, and M. Weber. 1998. Colonization of Languedoc vineyards by phytoseiid mites (Acari: Phytoseiidae): influence of wind and crop environment. Exp. Appl. Acarol. 22: 523-542.

CHAPTER 6

CONCLUSIONS

The objectives of this study were to understand phytoseiid mite dispersal at levels of local interaction via ambulatory movement and more long distance emigration (aerial take-off and dispersal distance) and immigration to new plant/prey patches (Fig. 1 see page 4 in Introduction).

At the local level, ambulatory dispersal was studied among five species with varying degrees of predation specialization. Overall, specialists had higher walking activity and aerial dispersal than generalists. Different dispersal strategies were seen between *N. fallacis* and *N. californicus*: Dispersal from a prey *T. urticae* patch was earlier in the generalist *N. californicus*, the specialist *N. fallacis* did not disperse until almost all prey were eliminated but both mites aerially dispersed at similar rates. Cues from spider mites infestations acted as arrestants for specialist predators, but either as neutrals or repellents for generalist predators.

Some wingless species have evolved take-off behaviors that enable them to become airborne. We examined aerodynamic attributes of dispersal relative to the body size and standing vs. walking postures for three phytoseiids. The average vertical profile of Pp in the walking position was higher than those of Nf and Nc when in the walking position. The body height of Nf in the standing posture was greater than the body height of Pp when in the walking position. Cross-section

areas also showed these patterns of difference. Nf in the standing posture would have more than twice the drag force than in walking posture because of more fluid momentum in the boundary layer. However, Pp in the walking position would have similar drag to Nf in the standing posture because of a higher vertical profile and larger size. We report the “jumping behavior” of *P. persimilis* relative to aerial dispersal and discuss its possible impact on dispersal.

Dispersal distance is important to immigration and redistribution of phytoseiid mites. Falling speed of a mite and wind largely determine dispersal distance of such a passively blown organism. A diffusion model of wind-blown phytoseiids could provide insight into dispersal. To this end, we measured morphologies, body weights and falling speeds of adult females. These data were then incorporated into seed dispersal models (Greene and Johnson 1989, Okubo and Levin 1989) and results were compared to mite dispersal distances in a wind tunnel, greenhouse and field. Weights of 13 phytoseiids ranged from 5.25-21.7 μg ; starved mites weighed less than fed mites. Falling speeds for phytoseiids were 0.39-0.73 m/s, and less than for *T. urticae* (0.79 m/s). In some species, active mites had slower falling speeds than inactive (anesthetized) mites implying that behavior influenced falling. Starved mites had significantly slower falling speeds than fed mites and dispersed farther. Equation-based estimates of falling speed were close to measured ones (2-8% deviation) for some species, especially specialists. Greene and Johnson’s seed dispersal model (1989) provided better fits to dispersal of mites

in the wind tunnel, greenhouse and field studies than Okubo and Levin's (1989) model.

In a greenhouse and in an open field, aspects of aerial and ambulatory dispersal of *N. fallacis* were studied with a focus on events that would occur after aerially dispersing mites landed on soil or associated substrates. Factors thought to affect movement and colonization were distance to a receiver unit (host plant) from a release (landing) point, intervening soil surfaces such as clods, gravel, fine soil and grass, and management of soil surfaces such as mulching, watering or both. In the field, effect of distance (0.11 – 1.76 m) from a landing point to a receiver unit had a negative log linear relationship. Soil surfaces such as clods and management actions such as watering with mulching allowed more capture of predators on plants with prey than did other treatments. Environmental conditions greatly affected survival of the predator. Predators in the field on bare soil suffered high mortality (ca. 90%) at fluctuating day conditions of $26.4 \pm 4.8^{\circ}\text{C}$ and $56 \pm 13.4\%$ R.H. Predators only suffered 10% mortality in the greenhouse under the same arrangement of plants and releases, but under more favorable environmental conditions. We speculated that phytoseiids that fell on ground were moving to the target plants with prey via both ambulatory and aerial means.

In the future, better understanding of spider mite and phytoseiid mite dispersal features may enhance ability to manage biological control system for pest mites. Most biological control or IPM has focused on local or within-farm level spatial scales. Since dispersal capabilities of spider mites and some phytoseiids are

great and extend across farm management boundaries, more emphasis on area-wide aspects may be possible. For such larger scale population dynamics and management, metapopulation models and GIS capabilities should be considered (Kogan et al. 1998).

BIBLIOGRAPHY

- Andersen, M. C. 1991. Mechanistic models for the seed shadows of wind-dispersed plants. *Amer. Nat.* 137: 476-497.
- Andersen, M. C. 1992. An analysis of variability in seed settling velocities of several wind dispersed Asteraceae. *Amer. J. Bot.* 79: 1087-1091.
- Aylor, D. E. 1975. Force required to detach conidia of *Helminthosporium maydis*. *Plant Pathology* 55: 99-101.
- Aylor, D. E. 1998. The aerobiology of apple scab. *Plant Disease* 82: 838-849.
- Bernstein, C. 1983. Some aspects of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) dispersal behaviour. *Entomophaga* 28: 185-198.
- Bernstein, C. 1984. Prey and predator emigration responses in the acarine system *Tetranychus urticae*-*Phytoseiulus persimilis*. *Oecologia* 61: 134-142.
- Berry, J. S., and T. O. Holtzer. 1990. Ambulatory dispersal behavior of *Neoseiulus fallacis* (Acarina: Phytoseiidae) in relation to prey density and temperature. *Exp. Appl. Acarol* 8: 253-279.
- Berry, J. S., T. O. Holtzer, and J. M. Norman. 1991. Experiments using a simulation model of the Banks grass mite (Acarina: Tetranychidae) and the predatory mite, *Neoseiulus fallacis* (Acarina: Phytoseiidae) in a corn microenvironment. *Environ. Entomol.* 20: 1174-1178.
- Boller, E. F., U. Remund, and M. P. Candolfi. 1988. Hedges as potential sources of *Typhlodromus pyri*, predatory mite in vineyards of northern Switzerland. *Entomophaga* 33: 247-255.

- Boykin, L. S., and W. V. Campbell. 1984. Wind dispersal of the Two-spotted spider mite (Acari: Tetranychidae) in North Carolina peanut fields. *Environ. Entomol.* 13: 221-227.
- Brandenburg, R. L., and G. G. Kennedy. 1982. Intercrop relationships and spider mite dispersal in a corn/peanut agro-ecosystem. *Entomol. Exp. Appl.* 32: 269-276.
- Brandenburg, R. L., and G. G. Kennedy. 1987. Ecological and agricultural consideration in the management of twospotted spider mite (*Tetranychus urticae* Koch), pp. 185-236, *Agricultural zoology reviews*. Intercept Ltd, Wimborne.
- Charles, J. G., and V. White. 1988. Airborne dispersal of *Phytoseiulus persimilis* (Acari: Phytoseiidae) from a raspberry Garden in New Zealand. *Exp. Appl. Acarol.* 5: 47-54.
- Cohen, D., and U. Motro. 1989. More on optimal rates of dispersal: taking into account the cost of the dispersal mechanism. *Am. Nat.* 134: 659-663.
- Coop, L. B., and B. A. Croft. 1995. *Neoseiulus fallacis*: dispersal and biological control of *Tetranychus urticae* following minimal inoculations into a strawberry field. *Exp. Appl. Acarol.* 19: 31-43.
- Crespi, B. J., and P. D. Taylor. 1990. Dispersal rates under variable patch density. *Am. Nat.* 135: 48-62.
- Croft, B. A. 1999. Management of spider mite for biological control and pesticide resistance: A case of landscape level IPM for diverse agriculture in the Pacific Northwest (PNW) United States, pp. 27-66. *In* T. Saito and B. A. Croft [eds.], *Implementing spider mite resistance management programs*. Japan Crop Protection Association.
- Croft, B. A., and L. B. Coop. 1998. Heat units, release rate, prey density, and plant age effects on dispersal by *Neoseiulus fallacis* (Acari: Phytoseiidae) after inoculation into strawberry. *J. Econ. Entomol.* 91: 94-100.

- Croft, B. A., and M. B. Croft. 1993. Larval survival and feeding by immature *Metaseiulus occidentalis*, *Neoseiulus fallacis*, *Amblyseius andersoni* and *Typhlodromus pyri* on life stage groups of *Tetranychus urticae* Koch and phytoseiid larvae. *Exp. Appl. Acarol.* 17: 685-693.
- Croft, B. A., S. S. Kim, and D. I. Kim. 1995. Leaf residency and interleaf movement of four Phytoseiid mites (Acari: Phytoseiidae) on apple. *Environ. Entomol.* 24: 1344-1351.
- Croft, B. A., S. S. Kim, and D. I. Kim. 1996. Intra- and interspecific predation on four life stage groups by the adult females of *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacis* and *Amblyseius andersoni*. *Exp. Appl. Acarol.* 20: 435-444.
- Croft, B. A., H.-K. Luh, and P. Schausberger. 1999. Larval size relative to larval feeding, cannibalism of larvae, egg or adult female size and larval-adult setal patterns among 13 phytoseiid mite species. *Exp. Appl. Acarol.* 23: 1-12.
- Croft, B. A., R. H. Messing, J. E. Dunley, and W. B. Strong. 1993. Effects of humidity on eggs and immatures of *Neoseiulus fallacis*, *Amblyseius andersoni*, *Metaseiulus occidentalis* and *Typhlodromus pyri* (Phytoseiidae): implications for biological control on apple, caneberry, strawberry and hop. *Exp. Appl. Acarol.* 17: 451-459.
- Croft, B. A., L. N. Monetti, and P. D. Pratt. 1997. Comparative life histories and predation types: Are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) similar Type II selective predators of spider mites? *Environ. Entomol.* 27: 531-538.
- Curle, N. 1962. The boundary layer equations. Oxford, London.
- Dingle, H. 1996. Migration. The biology of life on the move. Oxford University Press, Oxford.

- Dover, M. J., B. A. Croft, S. M. Welch, and R. L. Tummala. 1979. Biological control of *Panonychus ulmi* (Acarina: Tetranychidae) by *Amblyseius fallacis* (Acarina: Phytoseiidae) on apple: a Prey-Predator Model. *Environ. Entomol.* 8: 282-292.
- Drapek, R. J. 1993. Use of a geographic information system to modify pheromone trap-based predictions of *Helicoverpa zea* (Boddie) damages, pp. 158, *Entomology*. Oregon St. Univ., Corvallis.
- Dunley, J. E., and B. A. Croft. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). *Exp.-Appl. Acarol.* 10: 137-149.
- Dunley, J. E., and B. A. Croft. 1992. Dispersal and gene flow of pesticide resistance traits in phytoseiid and tetranychid mites. *Exp. Appl. Acarol.* 14: 313-326.
- Duso, C. 1989. Role of the predatory mites *Amblyseius aberrans* (Oud.), *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acari, Phytoseiidae) in vineyards. I. The effects of single or mixed phytoseiid population releases on spider mite densities (Acari, Tetranychidae). *J. Appl. Ent.* 107: 474-492.
- Ferro, D. N., and J. N. McMeil. 1998. Habitat enhancement and conservation of natural enemies of insects, pp. 123-132. *In* P. Barbosa [ed.], *Conservation biological control*. Academic press, San Diego.
- Field, R. P., and M. A. Hoy. 1985. Diapause behavior of genetically improved strain of the spider mite predator *Metaseiulus occidentalis* (Acarina: Phytoseiidae). *Entomol. Exp. Appl.* 38: 113-120.
- Flexner, J. L., P. H. Westigard, P. Gonzalves, and R. Hilton. 1991. The effect of groundcover and herbicide treatment on twospotted spider mite density and dispersal in southern Oregon pear orchards. *Entomol. Exp. Appl.* 60: 111-123.

- Frost, W. E. 1997. Polyphenic was production in *Abacarus hystrix* (Acari: Eriophyidae), and implications for migratory fitness. *Physio. Entomol.* 22: 37-46.
- Gorial, B. Y., and J. R. O'Callaghan. 1990. Aerodynamic properties of grain/straw materials. *J. Agric. Engng. Res.* 46: 275-290.
- Grace, J., and J. Wilson. 1976. The boundary layer over a *Populus* leaf. *J. Exp. Bot.* 27: 231-241.
- Greene, D. F., and J. E.A. 1989. A model of wind dispersal of winged or plumed seeds. *Ecol.* 70: 339-347.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269: 578-581.
- Hassel, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353: 255-258.
- Helle, W., and M. W. Sabelis [eds.]. 1985a. Spider mites. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.
- Helle, W., and M. W. Sabelis [eds.]. 1985b. Spider mites. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.
- Hewitt, G. M., and R. K. Butlin. 1997. Causes and consequences of population structure, pp. 350-372. *In* J. R. Krebs and N. B. Davies [eds.], *Behavioural ecology*, Fourth ed. Blackwell Science, London.
- Hislop, R. G., and R. J. Prokopy. 1981. Mite predator responses to prey and predator-emitted stimuli. *J. Chem. Ecol.* 7: 895-904.

- Hoy, M. A. 1982. Aerial dispersal and field efficacy of a genetically improved strain of the spider mite predator *Metaseiulus occidentalis*. Entomol. Exp. Appl. 32: 205-212.
- Hoy, M. A., and J. M. Smilanick. 1981. Non-random prey location by the phytoseiid predator *Metaseiulus occidentalis*: differential responses to several spider mite species. Entomol. Exp. Appl. 26: 291-300.
- Hoy, M. J., J. J. Groot, and H. E. van de Baan. 1985. Influence of aerial dispersal on persistence and spread of pesticide-resistant *Metaseiulus occidentalis* in California almond orchards. Entomol. Exp. Appl. 37: 17-31.
- Huffaker, C. B., K. S. Shea, and S. G. Herman. 1963. Experimental studies on predation: Complex dispersion and levels of food in an acarine predator-prey interaction. Hilgardia 34: 305-329.
- Janssen, A. 1999. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. Entomol. Exp. Appl. 90: 191-198.
- Janssen, A., Van Gool, E., Lingeman, R., Jacas, J. and Van de Klashorst, G. 1997. Metapopulation dynamics of a persisting predator-prey system in the laboratory: time series analysis. Exp. Appl. Acarol. 21 415-430.
- Janssen, A., J. Bruin, G. Jacobs, R. Schraag, and M. W. Sabelis. 1997. Predators use volatiles to avoid prey patches with conspecifics. J. Anim. Ecol. 66: 223-232.
- Johnson, D. T., and B. A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). Annals of the Entomological Society of America 69: 1019-1023.
- Johnson, D. T., and B. A. Croft. 1979. Factors affecting the dispersal of *Amblyseius fallacis* in an apple tree ecosystem, pp. 477-483. In J. G. Rodriguez [ed.], Recent advances in Acarology. Academy Press, New York.

- Johnson, D. T., and B. A. Croft. 1981. Dispersal of *Amblyseius fallacis* (Acarina: Phytoseiidae) in an apple Ecosystem. *Environ. Entomol.* 10: 313-319.
- Jongejans, E., and P. Schippers. 1999. Modeling seed dispersal by wind in herbaceous species. *Oikos* 87: 362-372.
- Jung, C., and B. A. Croft. 2000a. Survival and plant-prey finding by *Neoseiulus fallacis* (Acari: Phytoseiidae) on soil substrates after aerial dispersal. *Exp. Appl. Acarol.* 24: 579-596.
- Jung, C., and B. A. Croft. 2000b. Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): Estimating falling speed and dispersal distance of adult females. *Oikos* submitted.
- Jung, C., and B. A. Croft. 2001a. Aerodynamic aspects of dispersal take-off behavior among the phytoseiid mites, *Phytoseiulus persimilis*, *Neoseiulus fallacis* and *N. californicus* (in prep).
- Jung, C., and B. A. Croft. 2001b. Ambulatory and aerial dispersal among specialist and generalist predatory mites (Acari: Phytoseiidae). *Environ. Entomol* (in prep).
- Klashorst, G. v. d., J.L. Readshaw, M.W. Sabelis and R. Lingeman. 1992. A demonstration of asynchronous local cycles in an acarine predator-prey system. *Exp. Appl. Acarol.* 14 185-199
- Kogan, M., B. A. Croft, and R. F. Sutherst. 1999. Applications of ecology for integrated pest management, pp. 681-738. *In* C. B. Huffaker and A. P. Gutierrez [eds.], *Ecological entomology*, 2nd ed. John Wiley & Sons, INC, New York.
- Krisper, G. 1990. The jump of the mite-Genus *Zetorchestes* (Acarida, Oribatida). *Zool. Jb. Anat.* 120: 289-312.

- Krisper, G. 1991. The saltatory capacity of an oribatid mite, pp. 397-398. *In* R. Schuster and P. W. Murphy [eds.], *The acari : reproduction, development, and life history strategies*. Chapman & Hall, London.
- Lapple, C. E. 1956. *Fluid and particle mechanics*. Univ. Delaware Press.
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patch environments. *Theor. Popul. Biol.* 26: 165-191.
- Margolies, D. C. 1987. Conditions eliciting aerial dispersal behavior in Banks Grass Mite, *Oligonychus pratensis* (Acari: Tetranychidae). *Environ. Entomol.* 16: 928-932.
- Margolies, D. C. 1995. Evidence of selection on spider mites dispersal rates in relation to habitat persistence in agroecosystem. *Ent. Exp. Appl.* 76: 105-108.
- McEvoy, P. E., and C. S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. *Ecology* 68: 2006-2015.
- McMurtry, J. A. 1992. Dynamics and potential impact of generalist phytoseiids in agroecosystems and possibilities for establishment of exotic species. *Exp. Appl. Acarol.* 14: 371-382.
- McMurtry, J. A., and B. A. Croft. 1997. Life-styles of phytoseiid mites and their roles in biological control. *Ann. Rev. Entomol.* 42: 291-321.
- McMurtry, J. A., and J. G. Rodriguez. 1987. Nutritional ecology of phytoseiid mites, pp. 609-644. *In* F. S. Jr. and J. G. Rodriguez [eds.], *Nutritional ecology of insects, mites, spiders and related invertebrates*. John Wiley & Sons, New York.
- McMurtry, J. A., and G. T. Scriven. 1965. Insectary production of phytoseiid mites. *J. Eco. Ent.* 58: 282-285.

- Misener, G. C., and G. Boiteau. 1993. Suspension velocity of the Colorado Potato Beetle in free fall. *Amer. Potato J.* 70: 309-316.
- Monteith, J. L., and M. H. Unsworth. 1990. Principles of environmental physics. Campman and Hall, Inc., London.
- Morris, M. A. 1998. Biological control of *Tetranychus urticae* (Koch) on peppermint by *Neoseiulus fallacis* (Garman): Density relationships, overwintering, habitat manipulation and pesticide effects, pp. 79, Entomology. Oregon St. Univ., Corvallis.
- Morse, D. H., and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. *Oecol.* 67: 372-379.
- Nachman, G. 1987a. Systems analysis of acarine predator-prey interactions. I. A stochastic simulation model of spatial processes. *J. Anim. Ecol.* 56: 247-265.
- Nachman, G. 1987b. 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.
- Nyrop, J., G. English-Loeb, and A. Roda. 1998. Conservation biological control of spider mites in perennial cropping systems, pp. 307-333. *In* P. Barbosa [ed.], Conservation biological control. Academic press, San Diego.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecol.* 70: 329-338.

- Pedgley, D. 1982. Windborne pests and diseases: meteorology of airborne organisms. John Wiley & Sons.
- Pels, B., and M. W. Sabelis. 1999. Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. *Oikos* 86: 573-583.
- Penman, D. R., and R. B. Chapman. 1980. Effect of temperature and humidity on the locomotory activity of *Tetranychus urticae* (Acari: Tetranychidae), *Typhlodromus occidentalis* and *Amblyseius fallacis* (Acarina: Phytoseiidae). *Acta Ecologica* 1: 253-269.
- Pratt, P. D. 1999. Biological control of spider mites by the predatory mite *Neoseiulus fallacis* (Acari: Phytoseiidae) in ornamental nursery plant systems, pp. 150, Entomology. Oregon St. Univ., Corvallis.
- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within- and Between-Plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) in simulated bean and apple plant systems. *Environ. Entomol.* 27: 148-153.
- Pratt, P. D., P. Schausberger, and B. A. Croft. 1999. Prey-food types of *Neoseiulus fallacis* (Acari: Phytoseiidae) and literature versus experimentally derived prey-food estimates for five phytoseiid species. *Exp. Appl. Acarol.* 23: 551-565.
- Price, P. W. 1984. Insect ecology. John Wiley & Sons, New York.
- Rabbinge, R., and M. A. Hoy. 1980. A population model for Two-spotted spider mite *Tetranychus urticae* and its predator *Metaseiulus occidentalis*. *Ent. Exp. Appl.* 28: 64-81.
- Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth. Duxbury Press, New York.

- Raworth, D. A., G. Fauvel, and P. Auger. 1994. Location, reproduction and movement of *Neoseiulus californicus* (Acari: Phytoseiidae) during the autumn, winter and spring in orchards in the south of France. *Exp. Appl. Acarol.* 18: 593-602.
- Roland, J. 1990. Parasitoid aggregation: Chemical ecology and population dynamics, pp. 185-211. *In* M. Mackauer, L. E. Ehler and J. Roland [eds.], *Critical issues in biological control*. Intercept, Andover, Hants, UK.
- Ronce, O., F. Perret, and I. Olivieri. 2000. Evolutionary stable dispersal rates does not always increase with local extinction rates. *Am. Nat.* 155: 485-496.
- Sabelis, M. W. 1981. Biological control of two-spotted spider mites using phytoseiid predators. *Agricultural research reports 910 pudoc*, Wageningen.
- Sabelis, M. W., and B. P. Afman. 1994. Synomone-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. *Exp. & Appl. Acarol.* 18: 711-721.
- Sabelis, M. W., and H. E. v. d. Baan. 1983. Location of distant spider mite colonies by phytoseiid predators: Demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Ent. Exp. appl.* 33: 303-314.
- Sabelis, M. W., and F. M. Bakker. 1992. How predatory mites cope with the web of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp. Appl. Acarol.* 16: 203-225.
- Sabelis, M. W., and M. Dicke. 1985. Long-range dispersal and searching behaviour, pp. 141-157. *In* W. Helle and M. W. Sabelis [eds.], *Spider mites. Their biology, natural enemies and control*. Elsevier, Amsterdam.
- Sabelis, M. W., and J. van der Meer. 1986. Local dynamics of the interaction between predatory mites and two-spotted spider mites, pp. 322-344. *In* J. A. J. Metz and O. Diekmann [eds.], *Dynamics of Physiologically Structured Populations. Lecture Notes in Biomathematics 68*. Springer-Verlag, pp. 322-344.

- 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., J. E. Vermaat, and A. Groeneveld. 1984. Arrestment responses of the predatory mite, *Phytoseiulus persimilis*, to steep odour gradients of a kairomene. *Physiological Entomology* 9: 437-446.
- Sabelis, M. W., and J. J. v. d. Weel. 1993. Anemotactic response of the predatory mite, *Phytoseiulus persimilis* Athias-henriot, and their role in prey finding. *Exp. Appl. Acarol.* 17: 521-529.
- Schausberger, P. 1998. The influence of relative humidity on egg hatch in *Euseius finlandicus*, *Typhlodromus phyri* and *Kampimodromus aberrans* (Acari, Phytoseiidae). *J. Appl. Ent.* 122: 497-500.
- Schausberger, P., and B. A. Croft. 1999. Predation on and discrimination between con- and heterospecific eggs among specialist and generalist phytoseiid mites (Acari: Phytoseiidae). *Environ. Entomol.* 28: 523-528.
- Schausberger, P., and B. A. Croft. 2000. Intraguild predation and cannibalism among generalist and specialist phytoseiid mites: nutritional benefits. *Ecol. Entomol.* (in print).
- Schmidt, G. 1976. The influence of traces left by prey animals on the searching behaviour and success of *Phytoseiulus persimilis* A. & H. (Acarina: Phytoseiidae). *Z. Angew. Entomol.* 82: 216-218.
- Shigesada, N., and K. Kawasaki. 1997. Biological invasion: theory and practice. Oxford Univ. Press, New York.
- Smitley, D. R., and G. G. Kennedy. 1985. Photo-oriented aerial dispersal behavior of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface. *Ann. Entomol. Soc. Am.* 78: 609-614.

- Song, H., and J. B. Litchfield. 1991. Predicting method of terminal velocity for grains. *Transactions of the ASAE* 34: 225-230.
- Stephens, G. R., and D. E. Aylor. 1978. Aerial dispersal of Red Pine Scale, *Matsucoccus resinosae* (Homoptera: Margarodidae). *Environ. Entomol.* 7: 556-563.
- Strong, W. B., and B. A. Croft. 1995. Inoculative release of phytoseiid mites (Acarina: Phytoseiidae) into the reapidly expanding canopy of hops for control of *Tetranychus urticae* (Acarina: Tetranychidae). *Environ. Entomol.* 24: 446-453.
- Strong, W. B., D. H. Slone, and B. A. Croft. 1999. Hops as a metapopulation landscape for tetranychid-phytoseiid interactions: perspectives of intra- and interplant dispersal. *Exp. Appl. Acarol.* 23: 581-597.
- 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.
- Tixier, M.-S., S. Kreiter, and P. Auger. 2000. Colonization of vineyards by phytoseiid mites: their dispersal patterns in the plot and their fate. *Exp. Appl. Acarol.* 24: 191-211.
- Tixier, M.-S., S. Kreiter, P. Auger, and M. Weber. 1998. Colonization of Languedoc vineyards by phytoseiid mites (Acari: Phytoseiidae): influence of wind and crop environment. *Exp. Appl. Acarol.* 22: 523-542.
- Turchin, P. 1998. Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants. Sinauer Ass. Inc., Sunderland, MA.

- Van Baalen, M., and M. W. Sabelis. 1995. The milker-killer dilemma in spatially structured predator-prey interactions. *Oikos* 74: 391-400.
- van de Klashorst, G., J. L. Readshaw, M. S. Sabelis, and R. Lingeman. 1992. A demonstration of asynchronous local cycles in an acarine predator-prey system. *Exp. Appl. Acarol.* 14: 185-199.
- Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141-172.
- Vogel, S. 1994. *Life in moving fluids*. Princeton Univ. Press.
- Walde, S. J., J. P. Nyrop, and J. M. Hardman. 1992. Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Exp. Appl. Acarol.* 14: 261-292.
- Walter, D. E. 2000. A jumping mesostigmatan mite, *Saltiseius hunteri* N. G., N. Sp. (Acari: Mesostigmata: Trigynaspida: Saltiseiidae, N. Fam.) from Australia. *Internat. J. Acarol.* 26 25-31.
- Walter, D. E., and D. J. O'Dowd. 1992a. Leaf morphology and predators: Effect of leaf domatia on the abundance of predatory mites (Acari: Phytoseiidae). *Environ. Entomol.* 21: 478-484.
- Walter, D. E., and D. J. O'Dowd. 1992b. Leaves with domatia have more mites. *Ecology* 73: 1514-1518.
- Walter, D. E., and H. C. Proctor. 1999. *Mites. Ecology, evolution and behavior*. CABI publishing, New York
- Washburn, J. O., and L. Washburn. 1983. Active aerial dispersal of minute wingless arthropods: Exploitation of boundary-layer velocity gradients. *Science* 23: 1088-1089.
- Weyman, G. S. 1993. A review of the possible causative factors and significance of ballooning in spiders. *Ethol. Ecol. Evol.* 5: 279-291.