INFLUENCE OF GREENHOUSE MICROCLIMATE ON *NEOSEIULUS (AMBLYSEIUS) CUCUMERIS* (ACARI: PHYTOSEIIDAE) PREDATION ON *FRANKLINIELLA OCCIDENTALIS* (THYSANOPTERA: THRIPIDAE) AND OVIPOSITION ON GREENHOUSE CUCUMBER

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Abstract   *J. ent. Soc. Ont.* 136: 71–83

The influence of leaf boundary layer vapor pressure deficit (VPD) and leaf temperature on the predation rate by *Neoseiulus (Amblyseius) cucumeris* (Oudemans) (Acari: Phytoseiidae) on *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) and on the oviposition rate by *N. cucumeris* on cucumber leaves were determined for greenhouse cucumber grown under semi-commercial production conditions. Vapor pressure deficit did not affect either the predation or oviposition rates by *N. cucumeris*. Examination of ambient and boundary layer VPDs revealed that it was difficult to produce substantial changes in boundary layer VPD in high-gutter greenhouses. Therefore, the relatively steady state of humid conditions at the leaf boundary layer resulted in no significant differences in predation and oviposition rates despite changes in ambient VPD. However, leaf temperature did influence the predation and oviposition rates by *N. cucumeris*: both rates increased at the higher temperature. This suggests that establishing seasonal release rates should result in increased efficiency of this predator during the cooler periods of the year.

Introduction

The predatory mite *Neoseiulus (Amblyseius) cucumeris* (Oudemans) (Acari: Phytoseiidae) is an important biological control agent used to control *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) on greenhouse cucumbers worldwide (Ramakers and O'Neill 1999; Shipp and Ramakers 2004). *Neoseiulus cucumeris* feeds primarily on first instar *F. occidentalis*, and adult female mites have been reported in

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laboratory trials at 25-26°C to reach a predation plateau of between 4.4 and 6.9 first instars per day on cucumber leaf disks (Shipp and Whitfield 1991; van Houten et al. 1995a; 1995b). However, the predation rate of the nymphal stages of *N. cucumeris* on *F. occidentalis* is more complex and often depends on the presence of an adult *N. cucumeris* to assist in killing the larger prey host or to share a killed first instar (Cloutier and Johnson 1993). Control of *F. occidentalis* at the recommended rates for release of *N. cucumeris* is often not achieved until 5-6 weeks after the mites are released into the greenhouse (Shipp et al. 1996).

Improving the predation efficiency of *N. cucumeris* should result in faster, more effective control of *F. occidentalis* populations. Abiotic conditions such as temperature and humidity influence the rate of predation by mites (Stenseth 1979; Ball 1980; Everson 1980; Hardman and Rogers 1991). Higher temperatures are believed to cause greater predation rates as a result of the increased energy demand of the predator, which translates behaviorally into hunger and its associated activities, such as foraging (Everson 1980). Laboratory evidence indicates that vapor pressure deficit (VPD) (i.e., the difference between saturate and actual water vapor pressure at a specific air temperature) affects predation rates as well. Stenseth (1979) reported that *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) provides more effective control of *Tetranychus urticae* (Koch) (Acari: Tetranychidae) at higher temperatures and humidities (27°C and 70-85% RH). The predation rate by *N. cucumeris* on *F. occidentalis* was strongly influenced by VPD in laboratory trials (Shipp et al. 1996). A quadratic model fitted to the predation responses of adult *N. cucumeris* on first instar *F. occidentalis* over a VPD range of 0.4-3.94 kPa showed that the greatest predation rates occurred at either end of the VPD range.

The efficacy of a biological control agent also depends on its ability to reproduce in its environment. Several factors can affect the ovipositional behaviour of predatory mites. A mated *N. cucumeris* can oviposit 1.3 to 2.5 eggs per day depending on plant host, climate, and food (Castagnoli and Simoni 1990; Castagnoli and Liguori 1991; van Houten et al. 1995a; 1995b).

In the past, the majority of studies examining the influence of temperature and humidity on predation and oviposition rates were conducted in controlled environment chambers in order to precisely control the climatic parameters being investigated. However, insects and mites usually spend most of their time within the boundary layer of plant leaves (i.e., 0.5-5.0 mm from the leaf surface depending on wind speed, leaf shape, size, and hairiness), which can have temperature and humidity conditions that are quite different from greenhouse ambient conditions (Nobel 1974; Ferro and Southwick 1984). Ferro et al. (1979) showed that leaf temperatures on apple trees could reach 25°C on cool, clear days while ambient air temperature was only 15°C. Conversely, on hot sunny days when the air temperature was 39°C, leaf temperature was only 26°C. The changes between greenhouse macroclimate and microclimate at the plant surface are not as great as in the field situation since the climate in the greenhouse can be controlled using computerized climate control systems. However, the macroclimate in the greenhouse can be very different from the microclimate at the phyllopane (leaf surface) due to thermal, concentration, and velocity boundary layers that can result in steep gradients in temperature, VPD, and CO_2 (Jewett and Jarvis 2001). Boulard et al. (2002), in studying the influence of tomato leaf boundary layer climate on the implications of microbial control of whiteflies, found that relative humidity measured at 5 mm from the leaf surface in a tomato greenhouse could be 20-30% greater than ambient

measurements. The objectives of the present study were to determine the influence of boundary layer VPD and leaf temperature on the rate of predation by *N. cucumeris* on *F. occidentalis*, and on the oviposition rate by *N. cucumeris* on greenhouse cucumber.

Methods

Experimental treatments

Trials were conducted at the Greenhouse and Processing Crops Research Centre, Harrow, Ontario on greenhouse cucumber (*Cucumis sativus* L.) (cv. Bodega) in three glasshouse compartments (7x13 m) from May 2000 to September 2001. A planting density of 1.5 plants/m^2 (seven double rows with 10 plants/row/compartment) was used for all trials. The outside rows and end plants for each row served as guard plants and were not used in any measurements. The Harrow Fertigation Manager (Climate Control Systems Inc., Leamington, ON) was used to irrigate and fertilize the plants according to commercial recommendations (Ontario Ministry of Agriculture and Food 2001).

Three ranges of ambient VPD treatments were evaluated at each of two ambient temperatures regimes to simulate winter crop production conditions (21˚C day and 20˚C night) and summer conditions (25˚C day and 22˚C night) as measured at top canopy height (2.2 m). It was not possible to use exactly the same ambient VPD values for the range of humidity treatments for the summer and winter trials because greenhouse ambient VPD is directly affected by outside humidity conditions. However, the differences among ambient VPD treatment values at the top canopy among the three greenhouses for the summer and winter trials were essentially similar (0.26-0.65 kPa) over all trials. The three VPD treatments were achieved by randomly assigning one of three humidity settings to each of the three greenhouses that were set at the same temperature regime (summer or winter production conditions). Thus, each trial consisted of three greenhouses at the same ambient temperature (21 or 25˚C), but with each greenhouse at a different humidity. The trials were replicated over time. An Argus Greenhouse Climate Management System (Argus Control System Ltd., White Rock, BC) was used to maintain set point temperature and humidity conditions at the top canopy height.

All predation trials were conducted on the undersurface of leaves at two heights in the canopy (middle: 1.5 m, top: 2.2 m) and oviposition trials were conducted at one height in the canopy (middle: 1.5 m). VPD values at middle canopy were always higher than at top canopy. This relationship is common in greenhouse vegetables due to the lower light intensity and wind velocity within the canopy and has been shown for both low and high-gutter greenhouses (Jewett and Jarvis 2001; Zhang and Shipp 2002). At mid-canopy height in each greenhouse, ambient temperature and humidity were measured with a Hycal temperature/humidity probe (Hycal Co., El Monte, CA). Leaf temperatures were monitored using infra-red thermocouple (IRt) sensors (Omega, Laval, PQ), that were placed 1-2 cm from the leaf surface. These climate parameters (ambient temperature and humidity, and leaf surface temperature) in combination with the greenhouse cucumber plant surface climate model (PSCLIMATE) developed by Zhang et al. (2002), were used to calculate ambient and boundary layer VPDs.

Predation trials with *Neoseiulus cucumeris*

        A single, 1-2 day old, mated female mite and 15 first instar *F. occidentalis* were placed on the undersurface of a cucumber leaf in a plexiglass clip cage (0.7x4.0 cm) (Fig. 1). The cage had thrips-proof screening on one end on the lower surface of the leaf and a padded plastic plate on the top of the leaf. A fold back clip was used to hold together both pieces of the cage. To ensure that all test mites were at the same age, eggs of *N. cucumeris* were collected by sifting commercially purchased cultures of Thripex-plus (Koppert Canada, Leamington, ON) using a fine mesh screen. Eggs that passed through the screen were collected on the bottom of a 9 cm Petri dish and were placed using a moistened camel's hair brush on the ventral side of a kidney bean (*Phaseolus vulgaris* L.) leaf. The leaf was then floated on distilled water on the bottom of a 14 cm Petri dish to maintain a high humidity and to prevent the mites from leaving the leaf. The leaf was held in the centre of the dish by placing TangleFoot (Adhesive Pest Management and Tree Protection Products, Grand Rapids, MI) between the leaf and the bottom of the dish. Cohorts of 30 eggs were placed beneath a small piece of leaf (20 mm^2) that was placed at the centre of each larger leaf. The dishes were incubated at $25 \pm 1^{\circ}$C and L12:D12. The mites were fed frozen first and second instar *F. occidentalis* daily and were transferred to a new leaf after each molt. Adults appeared approximately 5-6 days after hatching. To ensure mating and starvation, the mites
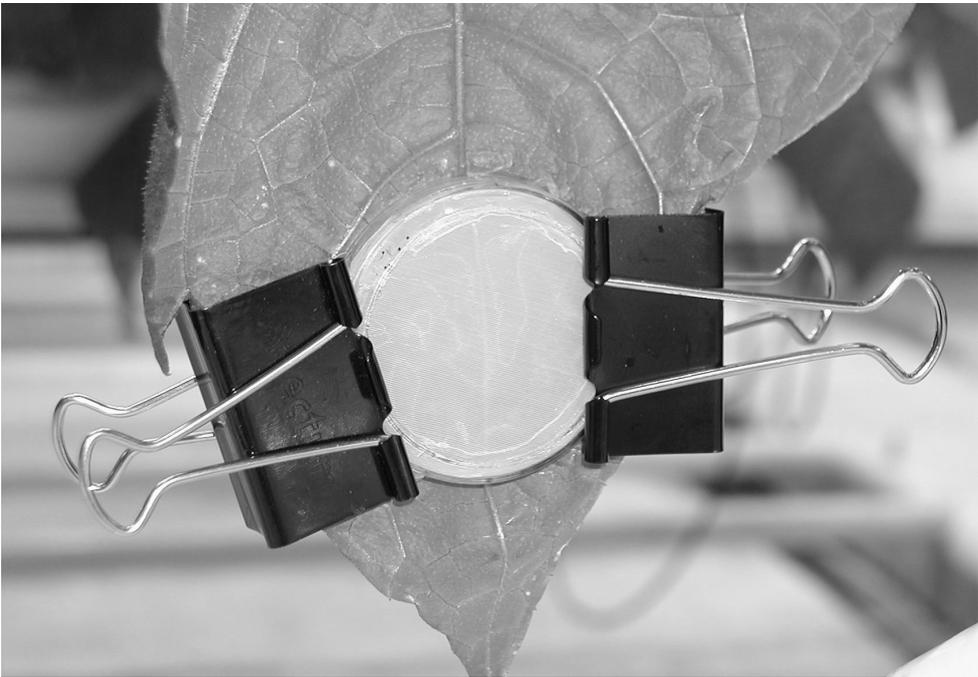

FIGURE 1. Screen leaf cage used in the predation and oviposition trials as viewed on the undersurface of a cucumber leaf.

were placed in a vial (1 female: 1 male) without food for 24 h before a trial.

First instar *F. occidentalis* were used in the predation trials, as this is the preferred prey stage for *N. cucumeris* (Shipp and Whitfield 1991). To obtain first instars, adult *F. occidentalis* were placed on the ventral side of kidney bean leaves that were placed on a piece of filter paper and cotton, saturated with distilled water, on the bottom of a 9 cm Petri dish. A Petri dish cover with thrips-proof screening on one end was placed over the Petri dish and secured with a large, fold-back clip to confine the *F. occidentalis*. The Petri dish was placed in a controlled environmental chamber at $27 \pm 1°C$ and 80% RH. The adults were removed after 24 h and first instar *F. occidentalis* were removed with a moistened camel's hair brush approximately 3-4 days later.

The predation trials were conducted for 24 h, after which the cage and leaf area inside the cage were removed and examined using a dissecting microscope (50X magnification) for the number of dead and live thrips. A thrips was considered dead, if it was shriveled or did not move when touched with a probe. The status of the mite (live or dead) also was noted and any cages in which the mite was dead were not included in the data analysis. For each trial, a leaf cage was also set up with 15 first instar thrips and no predatory mites at each canopy height for each VPD treatment to determine the survival rate of *F. occidentalis* over the 24 h predation period. Predation trials were replicated six to nine times for each temperature and VPD treatment over the summer and winter crop production periods with two to four cages per plant height (middle and top canopy) in each trial. For each predation trial, middle and top canopy leaf cages were paired together on the same plant. Different cucumber plants were used for each pairing and for each trial.

Oviposition trials with *Neoseiulus cucumeris*

A single 1-2 day old, mated female *N. cucumeris* which was starved for 24 h was transferred to the undersurface of a cucumber leaf at middle canopy in each of the treatment greenhouses. The same cages as those used in the predation trials were set up with one *N. cucumeris* per cage per treatment. Frozen second instar *F. occidentalis*, in excess of what a mite would consume (>10 thrips/mite/day), were placed in the cage as food. Every 24 h for 7 days, the leaf and cage were examined using a dissecting microscope (50X magnification), and the number of oviposited eggs and status of the mites (live, dead, or missing) was recorded. For examination of the leaf cage, the leaf area around the cage was cut and the cage and excised leaf area were returned to the laboratory for observation. After checking the leaf and cage, the cage and mite were placed on a new leaf in the same greenhouse. Cages that had missing mites were discarded. This procedure was replicated three times at each temperature and VPD treatment with 8-10 cages per replication.

Data analysis

All count data were square root transformed before analysis; untransformed data are reported in the tables and graphs. The impact of leaf surface temperature, crop canopy height, and leaf boundary layer VPD on the daily predation rate (prey/predator/day) by *N. cucumeris* on *F. occidentalis*, and on the oviposition rate (eggs/female/day) by *N. cucumeris* was analyzed using an ANCOVA. The ANCOVA was conducted with temperature and canopy height as the main factors for the predation trials, with temperature as the main factor for the ovipositional trials, and VPD as the covariate factor for both experiments

(PROC GLM, SAS Institute 1995).

Results and Discussion

Influence of vapor pressure deficit on predation and oviposition rates of *Neoseiulus cucumeris*

Mean (± SE) ambient temperatures and corresponding leaf boundary layer VPDs and leaf temperatures for the predation and oviposition trials are presented in Table 1. The survival rate for first instar *F. occidentalis* that were placed in the control leaf cages was always greater than 97.5%, indicating essentially zero mortality of the first instars when *N. cucumeris* was not present in the leaf cages. ANCOVA showed that the predation rate of *N. cucumeris* at the top and middle canopy heights was not significantly different ($F_{1,81}$= 1.76, P= 0.19) (Table 2). The mean numbers of first instar *F. occidentalis* killed by *N. cucumeris* were not significantly affected by the leaf boundary layer VPDs ($F_{1,81}$= 1.42, P= 0.24) (Table 2). All first and second order interactions were also not significant.

Previous studies found that mite predation rates can be affected by different air humidity regimes (Mori and Chant 1966a; Shipp et al. 1996; Rott and Ponsonby 2000). At high VPDs (low humidities), mites become dehydrated and as a result, feed more to compensate for this loss of water (Boudreaux 1958). Mori and Chant (1966b) found that the predatory mite, *P. persimilis*, and its prey, *T. urticae*, are more active at higher VPDs which results in more frequent encounters between predator and prey and thus higher rates of predation. However, Shipp et al. (1996) reported that first instars of *F. occidentalis* were less active at high VPDs, while *N. cucumeris* remained active. *Neoseiulus cucumeris* ceased moving after 12 h at VPDs ≥ 2.12 kPa. In the present study, leaf surface VPDs were always low (< 0.69 kPa) and thus, the mites or thrips were not exposed to dehydrating water stress conditions. In addition, the thrips could obtain water by feeding on the cucumber leaves.

The results from Shipp et al. (1996) indicated that even over the limited VPD range tested in the present greenhouse trials, predation rates should have increased with decreased VPD. In the controlled environmental chamber trials, temperature and VPD were constant, but in the greenhouse trials, VPDs fluctuated slightly (up to ± 7%). Kramer and Hain (1989) and van Houten and van Lier (1995) reported that mite survival increased when mites were exposed to fluctuating versus constant humidity conditions. Also, due to reduced air movement in the cage compared to an open leaf, the boundary layer in the leaf cages may be slightly greater than would be predicted using the PSCLIMATE model to determine VPD at the leaf surface. However, the basic premise for air movement in a boundary layer is "still" air.

The effect of leaf boundary layer VPDs on the number of eggs oviposited daily by *N. cucumeris* was also not significant ($F_{1, 14}$ =1.21, P= 0.29) (Table 3). There is no published information on the effect of VPD on the oviposition rate of predatory mites, although laboratory trials have found that *Tetranychus* spp. have an increased oviposition rate under "dry" conditions (Boudreaux 1958). The range of boundary layer VPDs in our study was probably too narrow to detect any influence of VPD on oviposition rates by *N. cucumeris*.

TABLE 1. Mean (± SE) ambient and corresponding leaf boundary-layer vapor pressure deficits (VPD) and leaf temperatures used in A. *Neoseiulus cucumeris* predation trials; and B. *N. cucumeris* oviposition trials.

Trial	Canopy height	Ambient temp. (°C)	Ambient VPD (kPa) in three greenhouses			Leaf temp. (°C)	Boundary layer VPD (kPa) in three greenhouses		
A	Top	21.0 ± 0.23	0.35 ± 0.020	0.64 ± 0.018	0.96 ± 0.054	20.0 ± 0.38	0.09 ± 0.005	0.25 ± 0.014	0.43 ± 0.030
	Middle	21.6 ± 0.24	0.67 ± 0.035	1.08 ± 0.041	1.32 ± 0.027	20.8 ± 0.24	0.24 ± 0.017	0.42 ± 0.021	0.69 ± 0.015
	Top	24.5 ± 0.50	0.26 ± 0.008	0.52 ± 0.012	0.81 ± 0.017	23.7 ± 0.55	0.13 ± 0.005	0.22 ± 0.010	0.35 ± 0.009
	Middle	24.9 ± 0.48	0.79 ± 0.013	0.98 ± 0.015	1.25 ± 0.029	23.7 ± 0.48	0.27 ± 0.011	0.36 ± 0.009	0.60 ± 0.016
B	Middle	21.6 ± 0.30	0.42 ± 0.003	0.69 ± 0.007	0.84 ± 0.011	20.1 ± 0.26	0.11 ± 0.001	0.28 ± 0.003	0.50 ± 0.002
		25.2 ± 0.54	0.78 ± 0.009	0.99 ± 0.050	1.29 ± 0.006	24.0 ± 0.51	0.31 ± 0.003	0.40 ± 0.002	0.63 ± 0.004

Top = 2.2 m and Middle = 1.5 m. Oviposition trials were only performed at middle canopy.

TABLE 2. ANCOVA for the effect of temperature and canopy height (main factors) and leaf bounder layer VPD (covariate) on the daily predation rate (number of first instar *Frankliniella occidentalis/*female/day) by *Neoseiulus cucumeris.*

Effect	df	F	Probability
Temperature	1	25.87	< 0.0001
Height	1	1.76	n.s.
Temp*Height	1	0.33	n.s.
VPD	1	1.42	n.s.
VPD*Temp	1	0.05	n.s.
VPD*Height	1	1.39	n.s.
VPD*Temp*Height	1	0.67	n.s.
Error	81		

TABLE 3. ANCOVA for the effect of temperature (main factor) and leaf boundry layer VPD (covariate) on the daily oviposition rate (number of eggs/female/day) by *Neoseiulus cucumeris.*

Effect	df	F	Probability
Temperature	1	12.18	0.0036
VPD	1	1.21	n.s.
VPD*Temperature	1	0.18	n.s.
Error	14		

        Examination of VPD data during the trials reveals how stable boundary layer VPD is without extreme changes in the ambient conditions (Table 1). Extreme climate changes are detrimental to greenhouse crop production, and it is believed that the use of high-gutter (4.2-5.4 m) greenhouses have substantially reduced the occurrence of extreme fluctuation in greenhouse climate due to a "buffer" layer of air between the crop and the outside of the greenhouse (Jewett and Jarvis 2001; Hao et al. 2005). Thus, in high-gutter greenhouse vegetable production systems as used in this study, ambient VPDs for recommended commercial production practices (0.4-0.8 kPa [Ontario Ministry of Agriculture and Food 2001]) have a minimal impact on plant boundary layer VPD, which is usually in a range that seems to be too small to have a significant impact on predation or oviposition rates by *N. cucumeris*. However in low-gutter greenhouses (< 2.5 m), especially with side ventilation, boundary layer VPD is much more impacted by ambient VPD and can even approach ambient conditions depending on wind speed (Boulard et al. 2004).

Influence of temperature on predation and oviposition rates of *Neoseiulus cucumeris*

ANCOVA of the predation data showed that the mean number of first instar *F. occidentalis* killed by *N. cucumeris* was significantly influenced by leaf temperature ($F_{1,\,81}$ = 25.87, *P*< 0.0001) (Table 2). A predation rate of 8.5-8.7 thrips/day at 24°C was approximately double the rate at 20°C. The increase in predation rate with increased temperature corresponds with laboratory trials conducted on different leaf surfaces with other predatory mite species (Stenseth 1979; Ball 1980; Everson 1980; Hardman and Rogers 1991). Leaf temperature influences the body temperature of the predatory mite as well as the food conversion rate (Sabelis 1981). Temperature has been shown to affect the rate of gut emptying, the attack rate, and handling time of the prey (Thompson 1978, Everson 1980; Sabelis 1981). Higher temperatures increase the metabolic rate of predators and thereby decrease the digestive pause between prey (Nakamaru 1977). Hungry predators have more successful capture rates, are more active, and search more vigorously for prey (Sandness and McMurtry 1972). Under higher temperatures, *N. cucumeris* is more active than *F. occidentalis* (Shipp et al. 1996; T. Jones, unpublished data) and would probably have more frequent encounters with *F. occidentalis*, resulting in an increased predation rate.

The mean number of eggs oviposited by *N. cucumeris* was also influenced by temperature (Table 3). *Neoseiulus cucumeris* oviposited a significantly greater number of eggs at the higher temperature when compared to the lower temperature range ($F_{1,14}$ = 12.18, *P*= 0.0036) (Table 4). van Houten et al. (1995a) and Gillespie and Ramey (1988) observed oviposition rates of 2.2 and 1.5 eggs/day at 25 and 20°C respectively, for *N. cucumeris*. This relationship is the result of proportionately decreased digestion time and increased predation rate at higher temperatures. The increased predation at higher temperatures provides the mite with the increased energy required for the higher egg production.

TABLE 4. Number of first instar *Frankliniella occidentalis* (mean ± SE) killed over a 24 h period by *Neoseiulus cucumeris* and the number of eggs laid by female *N. cucumeris* at two leaf temperatures.

Leaf temperature (°C)	Canopy height	Predation rate (prey/day)	n[1]	Oviposition rate (eggs/female/day)	n[2]
24	Top	8.5 ± 0.30 a	21	--	
	Mid	8.7 ± 0.46 a	19	2.14 ± 0.05 a	9
20	Top	4.3 ± 0.26 b	25	--	
	Mid	4.4 ± 0.24 b	24	1.37 ± 0.05 b	9

[1] Number of replicates over time with two to four cage observations each trial per greenhouse.
  The initial prey density is 15 thrips per cage.
[2] Number of replicates over time with eight to ten cage observations each trial.
  Within each column, means followed by different letters are significantly different at *P*< 0.05.

Previous studies investigating the interactions between climate (temperature and humidity) and predation and oviposition rates by greenhouse predatory mites were all conducted under controlled conditions in the laboratory. It is important to test these relationships under conditions that are more similar to commercial production conditions to ensure that the relationships are still valid. The present experiment is the first study to evaluate the influence of leaf temperature and boundary layer VPD on predation and oviposition rates by *N. cucumeris* on a greenhouse crop (cucumber) under semi-commercial production conditions. Under high-gutter greenhouse production conditions, boundary layer VPD varied very little from 0.1-0.7 kPa. At this range, VPD did not have a significant impact on predation or oviposition rates by *N. cucumeris*. The range for leaf boundary layer VPD can be much greater under low-gutter greenhouse production conditions, especially with side ventilation (Boulard et al. 2004). Leaf temperature did have a significant impact on predation and oviposition rates by *N. cucumeris*.

In summary, the current introduction rates of *N. cucumeris* for *F. occidentalis* do not consider greenhouse climatic or plant surface microclimatic conditions when recommendations are made to growers. Usually an introduction rate is recommended depending on the crop and/or the level of thrips infestation, irrespective of the time of year. This study demonstrated that plant surface microclimate can have a significant impact on the effectiveness of predatory mites. Leaf surface temperatures of cucumber plants were different from ambient air temperatures, but were within about $1 \pm 0.5°C$ of ambient temperature (Table 1). Greenhouse climate is accurately controlled using computerized climate control systems and can be maintained within narrow limits ($\pm 1°C$) within commercial greenhouses. The 24 h temperature regimes used in our study corresponds to climate conditions in greenhouse cucumber crops during the winter and summer in Ontario. However, similar seasonal differences occur for other greenhouse cucumber production areas in temperate climate regions.

Based on the results from this study, *N. cucumeris* will provide the most effective control of *F. occidentalis* when conditions are near the higher end of recommended production temperatures for cucumbers (17-25°C (Ontario Ministry of Agriculture and Food 2001)). Growers often state that thrips control during the winter months is not as effective as during summer, or that it takes too long (Shipp, unpublished data). Therefore, during winter conditions when temperatures are lower, growers should introduce mites more frequently into the greenhouse. Increased knowledge and understanding of greenhouse climate and plant surface microclimate, and their effect on insect and mite biology/behaviour will result in improved effectiveness of biological control programs for greenhouse crops.

Acknowledgements

References

Ball, J. C. 1980. Development, fecundity, and prey consumption of four species of predacious mites (Phytoseiidae) at two constant temperatures. Environmental Entomology 9: 298-303.

Boudreaux, H. B. 1958. The effect of relative humidity on egg-laying, hatching, and survival in various spider mites. Journal of Insect Physiology 2: 65-72.

Boulard, T., M. Mermier, J. Fargues, N. Smits, M. Rougier, and J.C. Roy. 2002. Tomato leaf boundary layer climate: implications for microbiological whitefly control in greenhouses. Agriculture and Forest Meteorology 110: 159-176.

Boulard, T., H. Fatnassi, J. C. Roy, J. Lagier, J. Fargues, N. Smits, M. Rougier, and B. Jeannequin. 2004. Effect of greenhouse ventilation on humidity of inside air and in leaf boundary-layer. Agriculture and Forest Meteorology 125: 225-239.

Castagnoli, M. and S. Simoni. 1990. Biological observations and life table parameters of *Amblyseius cucumeris* (Oudemans) (Acarina: Phytoseiidae) reared on different diets. Redia 73: 569-583.

Castagnoli, M. and M. Liguori. 1991. Laboratory observations on duration of copulation and egg production of three Phytoseiid species fed on pollen. pp. 231-239 *In* The Acari: Reproduction, Development and Life History Strategies. Schuster R. and Murphy P.W. (eds.) Chapman and Hall, London. 554 pp.

Cloutier, C. and S. G. Johnson. 1993. Interaction between life stages in a phytoseiid predator: western flower thrips prey killed by adults as food for photonymphs of *Amblyseius cucumeris*. Experimental and Applied Acarology 17: 441-449.

Everson, P. 1980. The relative activity and functional response of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) and *Tetranychus urticae* (Acarina: Tetranychidae): The effect of temperature. The Canadian Entomologist 112: 17-24.

Ferro, D, R. B. Chapman, and D. R. Penman. 1979. Observations on insect microclimate and insect pest management. Environmental Entomology 8: 1000-1003.

Ferro, D. N. and E. E. Southwick. 1984. Microclimate of small arthropods: estimating humidity within the leaf boundary layer. Environmental Entomology 13: 926-929.

Gillespie, D. R. and C. A. Ramey. 1988. Life history and cold storage of *Amblyseius cucumeris* (Acarina: Phytoseiidae). Journal of Entomological Society of British Columbia 85: 71-76.

Hao, X., T. Jewett, J. Zheng, and S. Khosla. 2005. Microclimate and energy consumption in commercial, hot-water and steam heated greenhouses for tomato production. Acta Horticulturae 691: 171-178.

Hardman, J. M. and M. L. Rogers. 1991. Effects of temperature and prey density on survival, development, and feeding rates of immature *Typhlodromus pyri* (Acari: Phytoseiidae). Environmental Entomology 20: 1089-1096.

Jewett, T. J. and W. R. Jarvis. 2001. Management of the greenhouse microclimate in relation to disease control: a review. Agronomie 21: 351-366.

Kramer, D. A. and F. P. Hain. 1989. Effect of constant- and variable-humidity and temperature regimes on the survival and developmental periods of *Oligonychus ununguis* (Acarina: Tetranychidae) and *Neoseiulus fallacis* (Acarina: Phytoseiidae). Environmental Entomology 18: 741-746.

Mori, H. and D. A. Chant. 1966a. The influence of prey density, relative humidity, and starvation on the predaceous behaviour of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). Canadian Journal of Zoology 44: 483-491.

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

Nakamura, K. 1977. A model for the functional response of a predator to varying prey densities; Based on the feeding ecology of wolf spiders. Bulletin of National Institute of Agricultural Science (C) 31: 29-89.

Nobel, P. S. 1974. Introduction to Biophysical Plant Physiology. W. H. Freeman and Company, San Francisco. 448 pp.

Ontario Ministry of Agriculture and Food. 2001. Growing Greenhouse Vegetables. Ontario Ministry of Agriculture and Food, Publication Number 371. Queen's Printer, Toronto, Ontario, Canada. 116 pp.

Ramakers, P. M. J. and T. M. O'Neill. 1999. Implementation of IPM: Case Studies - Cucurbits. pp. 435-453 *In* Integrated Pest and Disease Management in Greenhouse Crops. Albajes R., M. Lodovica Gullino, J. C. van Lenteren, and Y. Elad (eds.) Kluwer Academic Publishers, London. 545 pp.

Rott, A. S. and D. J. Ponsonby. 2000. Improving the control of *Tetranychus urticae* on edible glasshouse crops using a specialist coccinellid (*Stethorus punctillum* Weise) and a generalist mite (*Amblyseius californicus* McGregor) as biocontrol agents. Biocontrol Science and Technology 10: 487-498.

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

Sandness, J. N. and J. A. McMurtry. 1972. Prey consumption behavior of *Amblyseius largoensis* in relation to hunger. The Canadian Entomologist 104: 461-470.

SAS Institute, 1995. *SAS/STAT* users guide. SAS Institute. Cary, NC. 1606 pp.

Shipp, J. L. and G. H. Whitfield. 1991. Functional response of the predatory mite, *Amblyseius cucumeris* (Acari: Phytoseiidae), on western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). Environmental Entomology 20: 694-699.

Shipp, J. L., K. I. Ward, and T. J. Gillespie. 1996. Influence of temperature and vapor pressure deficit on the rate of predation by the predatory mite, *Amblyseius cucumeris*, on *Frankliniella occidentalis*. Entomologia Experimentalis et Applicata 78: 31-38.

Shipp, J. L. and P. M. J. Ramakers. 2004. Biological control of thrips on vegetable crops. pp. 265-276 *In* Biocontrol in protected culture. Heinz K. M., R. G. Van Driesche, and M. P. Parrella (eds.) Ball Publishing, Batavia, Illinois. 552 pp.

Stenseth, C. 1979. Effect of temperature and humidity on the development of *Phytoseiulus persimilis* and its ability to regulate populations of *Tetranychus urticae* (Acarina: Phytoseiidae, Tetranychidae). Entomophaga 24: 311-317.

Thompson, D. J. 1978. Towards a realistic predator-prey model: The effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. Journal of Animal Ecology 47: 757-767.

van Houten, Y. M. and A. M. M. van Lier. 1995. Influence of temperature and humidity on

the survival of eggs of the thrips predator *Amblyseius cucumeris*. Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent 60/3a: 879-884.

van Houten, Y. M., P. C. J. van Rijn, L. K. Tanigoshi, P. van Stratum, and J. Bruin. 1995a. Preselection of predatory mites to improve year-round biological control of western flower thrips in greenhouse crops. Entomologia Experimentalis et Applicata 74: 225-234.

van Houten, Y. M., P. van Stratum, J. Bruin, and A. Veerman. 1995b. Selection for non-diapause in *Amblyseius cucumeris* and *Amblyseius barkeri* and exploration of the effectiveness of strains for thrips control. Entomologia Experimentalis et Applicata 77: 289-295.

Zhang, Y, T. J. Jewett, and J. L. Shipp. 2002. A dynamic model to estimate in-canopy and leaf surface microclimate of greenhouse cucumber crops. Transactions of American Society of Agricultural Engineers 45: 179-192.

Zhang, Y. and J. L. Shipp. 2002. Manipulating plant moisture conditions using greenhouse high-pressure fogging. HorTechnology 12: 261-267.