Delphastus catalinae and Coleomegilla maculata lengi (Coleoptera: Coccinellidae) as biological control agents of the greenhouse whitefly, Trialeurodes vaporariorum (Homoptera: Aleyrodidae)

Éric Lucas,* Claude Labrecque and Daniel Coderre
Département des Sciences Biologiques, Université du Québec à Montréal, CP 8888 Succ 'Centre-ville', Montréal, Québec, Canada H3C 3P8

Abstract: Predation efficacy and compatibility of the predatory lady beetles *Coleomegilla maculata lengi* Timberlake and *Delphastus catalinae* (Horn) against the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) were studied in laboratory on glabrous fuchsia (*Fuchsia hybrida* Voss cv Lena Corolla) and pubescent poinsettia plants (*Euphorbia pulcherrima* Willd ex Klotzch cv Dark Red Annette Hegg). On glabrous plants (fuchsia), fourth-instar and adults of *C maculata* were the most efficient, both against whitefly eggs and pupae. On pubescent plants (poinsettia), the larger stages of *C maculata* were negatively affected and less efficient than adults of *D catalinae*. The presence of plant structure did not affect the voracity of either predator species. Finally, the simultaneous use of both predator species generated inter-specific competition. These results provide recommendations for biological control of whitefly in horticultural greenhouses.
© 2004 Society of Chemical Industry

1 INTRODUCTION

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) is one of the main pests of greenhouses around the world.[1,2] The whitefly is resistant to an array of chemical pesticides[3,4] including insect growth regulators.[5] In vegetable greenhouses, the parasitoids *Encarsia formosa* Gahan and *Eretmocerus* spp[6–8] and the mirid bugs *Macrolophus caliginosus* (Wagner) and *Dicyphus hesperus* Knight[2,9] are successfully used to control the pest all season long. In greenhouses for ornamental production, even low densities of whiteflies are judged unacceptable and their control may require massive releases of natural enemies.

Because of their voracity, coccinellids may be good candidates for whitefly control in these conditions.[10] The lady beetle, *Delphastus catalinae* (Horn) [formerly *D pusillus* (LeConte)] is one of the main predators of whiteflies in citrus orchards in Florida[11–13] and in cassava in Colombia.[14] This minute coccinellid (1.5 mm of length) is a specialized aleurophagous predator commercialized for the control of *Bemisia*

tabaci (Gennadius) and *B argentifolii* (Bellows and Perring). Heinz and Parrella[15] demonstrated that the introduction of this coccinellid successfully controlled *B argentifolii* populations.

The twelve-spotted lady beetle, *Coleomegilla maculata lengi* Timberlake is a medium size coccinellid (about 6–7 mm) present in North America, South America and Northern Europe. The predator is one of the dominant species in several crops including maize,[16] wheat,[17] potato[18] and orchards.[19,20] Its polyphagous habits[10] improve field survival during periods of whitefly scarcity, and allow successful rearing on a liver diet.[21] Furthermore, it can attack several other greenhouse pest species including the green peach aphid, *Myzus persicae* (Sulzer),[22–24] the two-spotted spider mite *Tetranychus urticae* Koch[25] and eggs of several lepidopteran species.[26,27] Previous observations by Dysart[28] and Link and Costa[29] demonstrated that *C maculata* also attacked and consumed *Trialeurodes abutilonea* (Haldeman) and *B tabaci*.

Several physical characteristics of ornamental plants including height, plant structure and pubescence may have an impact on biological control of whiteflies. The presence of trichomes especially affects, mechanically or chemically, locomotion, foraging behavior, attachment to the plant and oviposition of phytophagous and predaceous insects.[30–33] For example, whiteflies laid significantly more eggs on pubescent cultivars of soybean and cotton than on glabrous ones.[34,35] Plant morphology and architecture also significantly influenced efficiency against natural enemies.[36–40]

In this study, we examine and compare the potential of the two coccinellid predators against greenhouse whiteflies. It constitutes the first evaluation of the twelve-spotted lady beetle against *T vaporariorum*. We predicted that, according to its larger size, *C maculata* may be more efficient than *D catalinae*. In the laboratory, we examined the predation efficacy of the two predators on glabrous fuchsia and pubescent pointsettia. The simultaneous utilization of both species for the biological control of the greenhouse whitefly was also evaluated.

2 MATERIALS AND METHODS

2.1 Insect material

Delphastus catalinae were obtained from a commercial rearing facility (Applied Bionomics, Vancouver, BC). Once in the laboratory, they were reared on *T vaporariorum* eggs. *Coleomegilla maculata* individuals came from permanent rearing on an artificial liver-based diet. Rearing originated from field-collected insects around Montreal (Canada) and new material was taken from the field each year. Both coccinellids were reared at 24 ($\pm$1) °C, 70% RH and a 16:8 h light:dark photoperiod. *Trialeurodes vaporariorum* eggs and pupae were reared in greenhouses at the beginning of spring, on poinsettia (*Euphorbia pulcherrima* Willd ex Klotzch cv Dark Red Annette Hegg) and fuchsia (*Fuchsia hybrida* Voss cv Lena Corolla) plants.

2.2 Predation on glabrous fuchsia

All the experiments were done under laboratory controlled conditions as in Section 2.1. The first test compared the voracity of *C maculata* and *D catalinae* on whitefly eggs and pupae. Whitefly egg predation was assessed by testing adults and second and fourth instar of *C maculate*, and adult *D catalinae*. The experimental setup consisted of a Petri dish (9 cm diameter) covered with a moistened filter paper. A fuchsia (glabrous) leaf infested with 500 *T vaporariorum* eggs was overturned and put on the filter paper. The exact number of eggs was obtained by cutting the leaf. This process minimized egg manipulation and allowed the eggs to maintain their natural upright position. Before the test, eggs were examined under a stereo microscope in order to remove aborted or damaged eggs. Controls without predators were used in order to evaluate counting errors. Twenty replicates were carried out.

Pupal predation used the same experimental set-up. Three predator treatments were tested: adult and fourth-instar *C maculata*, and adult *D catalinae*. Eighty *T vaporariorum* pupae were individually transferred onto a clean fuchsia leaf. Damaged pupae and also pupae closed to adult emergence were withdrawn. Twenty-one replicates were carried out.

The experiment started with the introduction of a 24-h starved individual predator in the Petri dish. After 6 h, the predator was removed and each Petri dish was stored at 4 °C for 1 h to avoid hatching of the eggs or emergence of the pupae. Predation was then assessed by using a stereo microscope. Pupae were examined to detect all signs of predation. The number of predated eggs or pupae was counted. For each prey type (eggs or pupae) the number of prey consumed was compared using a one-way ANOVA followed by a LSD Fisher's protected post-hoc test.[41] Predator-free controls were carried out in order to evaluate counting errors. All analyses were performed with SuperAnova®.[42]

2.3 Effect of pubescence

In order to evaluate the predation efficiency on a pubescent plant, an experiment was done on poinsettia seedlings. The experimental set-up and conditions were similar to those in the previous experiment, except that a pointsettia leaf with 500 *T vaporariorum* eggs was cut instead of a fuchsia leaf. Three predatory treatments were tested: adult and second-instar *C maculata* and adult *D catalinae*. Twenty replicates were carried out. Data were compared by a one-way ANOVA.

In order to evaluate the effects of pubescence on coccinellid voracity, results obtained with eggs on glabrous fuchsia were compared to the same treatment on pubescent poinsettia. The comparison was done separately for *C maculata* adults, *C maculata* second instar and *D catalinae* adults using one-way analyses of variances.

2.4 Effect of plant structure

Predator voracity was compared in presence and absence of plant structure. A Petri dish (9.0 cm diameter) with a moistened paper was used as a set-up without vertical structure. A caged poinsettia seedling was used as a vertical structure. The seedling, with three equal-sized and undamaged leaves, was fixed with Plasticine in a hole pierced in the bottom of a plastic container (8.1 cm high × 15.0 cm diameter). This container was then placed into a second plastic container with water which soaked the seedling roots. The set-up was hermetically sealed by a plastic lid with a meshed opening (muslin) to allow ventilation. A poinsettia leaf was cut in order to present 500 *T vaporariorum* eggs and put either on the moistened paper in the Petri dish, or on the superior leaf of the seedling in the cage. A coccinellid predator starved for 24 h was introduced at the beginning of the experiment. Two treatments were carried out: (1) one adult of *C maculata* and (2) one

adult of *D catalinae*. The experiment was replicated twenty times. Experimental conditions were similar to those described in Section 2.3. The number of prey consumed was compared using a one-way ANOVA.

2.5 Use of both predator species

In this experiment, both predators were used together. The experimental conditions and set-up were similar to those of the previous experiment with a caged poinsettia seedling (Section 2.4). Two adult coccinellids, one *D catalinae* and one *C maculata* were introduced onto the seedling at the beginning of the experiment. Twenty replicates were carried out. A theoretical value (representing a non-interaction situation) was calculated with the results obtained in the preceding experiment on poinsettia seedlings. The theoretical consumption corresponded to the sum of the consumption of one adult *D catalinae* and the consumption of one adult *C maculata* found in the preceding experiment. This theoretical value was calculated for each replicate and then compared to the observed predation by the two predators using a one-way ANOVA.

3 RESULTS

In all the tests, counting error was less than 1.5%.

3.1 Predation on glabrous fuchsia

Egg consumption on fuchsia differed significantly among the different predators ($F_{3,76} = 2.95$, $P = 0.0382$) (Fig 1). The fourth-instar *C maculata* was the more voracious stage, consuming 214.8 eggs, followed by adult *C maculata* with 186.3 (87% of the fourth-instar consumption) and by second-instar *C maculata* with 145 eggs (68%). Both fourth-instar and adults had a significantly higher consumption (respectively LSD, $P = 0.007$ and $P = 0.033$) than adults of *D catalinae* with only 87.3 eggs eaten (41% of the fourth-instar consumption). *Coleomegilla maculata* consumed entirely the egg while *D catalinae* sucked completely the egg leaving a standing membrane.

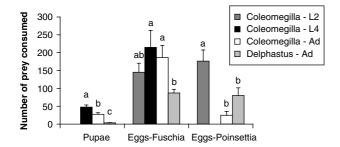When consuming whitefly pupae on fuchsia, the voracity of the different predator stages differed ($F_{2,60} = 25.64$, $P = 0.001$) (Fig 1). All the predator treatments were significantly different (LSD, $P < 0.05$). Fourth-instar *C maculata* were again the more voracious stages, consuming 47.5 pupae during 6 h, whereas adults consumed about 27.5 pupae (this is 52% of larval consumption). *Delphastus catalinae* consumed only 3.7 pupae, this is 8% of the fourth-instar *C maculata* consumption. Both stages of *C maculata* generally ate the entire pupae or occasionally consumed portions of the pupal underside. *Delphastus catalinae* extracted the internal fluids of the pupae entirely or in part.

3.2 Effect of pubescence

Egg consumption on the pubescent poinsettia also differed according to the predator type ($F_{2,57} = 11.42$, $P = 0.0001$) (Fig 1). Second-instar *C maculata* had the maximal consumption with 176.4 eggs eaten, significantly more than adult *D catalinae* with 80.1 eggs eaten (45% of the second-instar consumption) (LSD, $P = 0.004$), and also significantly more than adults *C maculata* with 24.8 eggs (14%) (LSD $P = 0.0001$).

Adult *C maculata* saw a 7-fold reduction in their consumption on the pubescent poinsettia compared to the glabrous fuchsia ($F_{1,38} = 20.59$, $P = 0.0001$) (Table 1). By contrast, whitefly egg consumption was similar on both plants for the second-instar *C maculata* ($F_{1,38} = 0.61$, $P = 0.440$) and for *D catalinae* adult ($F_{1,38} = 0.09$, $P = 0.7632$). The predators had the same characteristic foraging behavior on both plant types, beginning with an extensive search (long linear paths, fast speed); and once a prey was consumed, exhibiting intensive search (increase in angular speed, decrease in linear speed), as observed elsewhere.[43,44]

3.3 Effect of plant structure

Plant structure did not affect the predation efficiency on whitefly eggs of either adult *C maculata* ($F_{1,38} = 0.33$, $P = 0.5685$) or of adult *D catalinae* ($F_{1,38} = 0.55$, $P = 0.4618$) (Table 1). Egg consumption was higher for *D catalinae* than *C maculata*, both on plant structure (5.6-fold increase) and in Petri dishes (3-fold increase). The two predator species had very different foraging behaviors. When put on the seedling, *D catalinae* had a slow displacement and localized its prey a short while later. This lady beetle spent the majority of its time on the seedling. By contrast, *C maculata* thoroughly explored the experimental set-up after its introduction, before resting.

3.4 Use of both predator species

Egg consumption in the multi-specific treatment (42.73 (±4.55)) was significantly lower than the theoretical result (57.75 (±5.24)) obtained by one individual of each species ($F_{1,38} = 4.69$, $P = 0.0366$). No behavioral interference among the individuals has been observed.

4 DISCUSSION

Our prediction that *C maculata* would be more efficient than *D catalinae* was not verified. *Coleomegilla maculata*

Figure 1. Number (±SE) of whitefly eggs and pupae consumed during 6 h by *Coleomegilla maculata* adults and larvae and *Delphastus catalinae* adults on fuchsia (glabrous) and poinsettia (pubescent) seedlings. Different letters indicate a significant difference in predator consumption for the same prey (ANOVA, $P < 0.05$).

Table 1. Effect of plant pubescence and plant structure on whitefly eggs consumption by *Coleomegilla maculata* and *Delphastus catalinae*

Predator species-stage[a]	Number of whitefly eggs consumed[b]				
	Mean	SE	Mean	SE	
Effect of pubescence					
	Poinsettia (pubescent)		Fuchsia (glabrous)		
Coleomegilla-L2	176.4	31.1	145.1	25.5	ns
Coleomegilla-Ad	24.8	11.0	186.3	33.9	*
Delphastus-Ad	80.1	21.5	87.3	10.4	ns
Effect of plant structure					
	No plant structure (Petri dish)		Plant structure (Pointsettia)		
Coleomegilla-Ad	24.8	11.0	17.5	6.4	ns
Delphastus-Ad	80.0	21.5	98.1	11.1	ns

[a] L2 = second instar, Ad = adult.
[b] An asterisk indicates a significant difference between means on the same line (ANOVA, $P < 0.05$), ns = non significant.

was more efficient on glabrous fuchsia whereas *D catalinae* was more efficient on pubescent poinsettia. Factors determining their respective efficiencies were mainly their size and the presence or absence of trichomes.

In the absence of trichomes, the larger species, *C maculata*, was more efficient than the smaller *D catalinae*, and among the different stages of *C maculata*, the fourth-instar larvae were the most voracious. The mean biomass of *C maculata* adult (16.4 ($\pm$0.5)mg) is more than thirty times greater than the mean biomass of *D catalinae* adult (0.53 ($\pm$0.1)mg). Body size is a determinant factor usually correlated (positively or negatively) with several ecological characteristics, including locomotory abilities, home range, susceptibility to extraguild, intraguild or intra-specific predation, metabolic and ingestion rate.[45–49] In Coccinellidae, the voracity is usually maximum in larger species and during the fourth larval and adult stages.[50] Thus, in the case of inundative release of predatory biological control agents on glabrous plants, the largest and most voracious stages/species may be the most appropriate agents to use.

The other predominant factor is the presence or absence of trichomes. Adults of *C maculata* showed a reduction of 7-fold in their consumption when trichomes were present. In this case, body size also may be very important since, smaller individuals like second-instar *C maculata* or adult *D catalinae* were not adversely affected. Since adult *D catalinae* consumption did not decrease in the presence of trichomes, body shape may not be a predominant factor concerning trichome susceptibility. If further studies confirm that larger life stages are more affected by the presence of trichomes, it can mean that larger natural enemies may be at a disadvantage in systems with pubescent plants. The literature indicated that whiteflies laid significantly more eggs on hirsute and pubescent cultivars of soybean and cotton than on glabrous ones.[34,35] Obrycki and Tauber[51] observed that adult coccinellids were evenly distributed among potato cultivars with differing levels of pubescence, but

eggs were more abundant on plants with high trichome density. This suggests a higher level of egg predation on less pubescent plants. Several studies described how plant pubescence adversely affected the foraging behavior of chrysopid, syrphid, and coccinellid species, including *C maculata, Adalia bipunctata* (L), *Coccinella septempunctata* L, *C transversoguttata* Faldermann and *Hippodamia convergens* Guerin-Meneville.[30–32] On tobacco, a high density of trichomes reduced the searching speed of *H convergens* larvae[36] and increased their probability of being captured by glandular trichomes.[52]

Glandular trichomes increased larval *C maculata* mortality and reduced *Helicoverpa zea* (Boddie) egg consumption on tomatoes.[53] On potato plants, intraguild predation by *C maculata* on *Aphidoletes aphidimyza* (Rondani) eggs was also reduced when trichome density increased.[33] Furthermore, small, first-instar *C maculata* were more efficient in capturing eggs of *A aphidimyza* than large, fourth-instar coccinellids at high trichome density, agreeing with the hypothesis that larger individuals may be more affected than smaller ones. Despite our interesting results on pubescent plants, a previous study by Heinz and Parrella[54] showed that *D catalinae* (formerly *D pusillus*) oviposition and consumption of *B argentifolii* nymphs and eggs were higher on less pubescent poinsettia cultivar (Annette Hegg Brilliant Diamond). Also, on two cultivars of *Gerbera jamesonii* Bolus, the parasitoid *E formosa* was not affected by trichome density except at high whitefly density, where parasitism was lower on the cultivar with the higher hair density.[55]

In this study, the presence of a plant structure did not affect the efficacy of predation by adults of either species. While tests in Petri dishes evaluate the maximum consumption of the predator, tests on vertical plant structure likely provide results closer to the real efficacy in the field. A previous study[56] showed that the voracity of *C maculata* on *Leptinotarsa decemlineata* (Say) eggs was similar on a plant structure (four-leaf potato stem, *Solanum tuberosum* L) and in a Petri dish were similar. *Coleomegilla maculata*

is commonly observed on potato plants in the field, predating CPB eggs despite the presence of trichomes. However, in both studies, the experimental set-ups were different from the situation *in situ*. Carter *et al*[37] has shown that coccinellid larvae can be affected by the plant structure. Otherwise, the two predator species may be affected differently by the presence of the plant structures, according to their respective size and foraging behaviors. The slow *D catalinae* stayed almost the whole time on the seedling, whereas the rapid *C maculata* thoroughly visited the experimental set-up after its introduction. These results need to be confirmed in greenhouses on larger seedlings of different species.

Despite significant differences in both species ecology (prey specificity, size, mobility, etc), interspecific competition was recorded between the two coccinellids. Further studies involving larval stages, on different plant types, in the presence of different prey types, should be conducted to confirm these results. Nevertheless, the great difference in size among the two species should favor intraguild predation, mainly among larval stages and then limit the efficacy of such a combination.[57,58] That releases of *D catalinae* failed to control whitefly population in field-grown cotton and study observations suggested that intraguild predation by the local predator fauna may have been responsible for the failure of the program.[59] However, in greenhouses, such local fauna are absent. Moreover, possible compatibility may exist with other natural enemies such as parasitoids. Fourth-instar and adult female *D catalinae* avoided fourth-instar *B tabaci* parasitized by the endoparasitoids *Encarsia transvena* (Timberlake) and *Eretmocerus* sp in a laboratory study.[60] In an experiment including *D catalinae* and two parasitoids, *E formosa* and *E pergandiella* Howard, releases of the coccinellid in combination with one or both of the parasitoids provided the greatest levels of whitefly control.[61]

Finally, the results of this study provide preliminary recommendations for biological control of whiteflies in horticultural greenhouses. The selection of the biological control agent in an inundative program should depend on plant species and cultivars. On glabrous plants, *C maculata* may be a suitable auxiliary, more efficient than *D catalinae* since its voracity is higher. In this case, older larval instars and adults may have the strongest short-term impact. On pubescent plants, the situation should be rather different. Large stages would be inefficient and *D catalinae* or younger larval instars of *C maculata* should be more appropriate candidates. Since interspecific competition was recorded, the simultaneous use of both coccinellid species should be avoided. These preliminary results have to be confirmed with different levels of whitefly density over a longer period. Furthermore, in order to assess the real potential of these predators as biological control agents of the whitefly, their efficacy and their acceptability should be tested in a commercial greenhouse system.

REFERENCES
1 Gerling D, *Whiteflies: their bionomics, pest status and management*, Intercept Ltd, Andover, UK (1990).
2 Gabarra R and Besri M, Tomatoes, in *Integrated pest and disease management in greenhouse crops*, ed by Albajes R, Lodovica Gullino M, van Lenteren JC and Edad Y, Kluwer Academic Publishers, Dordrecht, pp 420–434 (1999).
3 Elhag EA and Horn DJ, Laboratory selection of greenhouse whitefly for resistance to malathion. *Entomol Exp Appl* **35**:21–26 (1983).
4 Sanderson J and Roush T, Monitoring insecticides in greenhouse whitefly (*Trialeurodes vaporariorum* (West)) with yellow sticky cards. *J Econ Entomol* **85**:634–641 (1992).
5 Gorman K, Hewitt F, Denholm I and Devine GJ, New developments in insecticide resistance in the glasshouse whitefly (*Trialeurodes vaporariorum*) and the two-spotted spider mite (*Tetranychus urticae*) in the UK. *Pest Manag Sci* **58**:123–130 (2002).
6 Gould HJ, Parr WJ, Woodville HC and Simmonds SP, Biological control of glasshouse whitefly (*Trialeurodes vaporariorum*) on cucumbers. *Entomophaga* **20**:285–292 (1975).
7 Parr WJ, Gould HJ, Jessop NH and Ludlam FAB, Progress towards a biological control programme for glasshouse whitefly (*Trialeurodes vaporariorum*) on tomatoes. *Ann Appl Biol* **83**:349–363 (1976).
8 Greenberg SM, Jones WA and Liu TX, Interactions among two species of *Eretmocerus* (Hymenoptera: Aphelinidae), two species of whiteflies (Homoptera: Aleyrodidae), and tomato. *Environ Entomol* **31**:397–402 (2002).
9 McGregor RR, Gillespie DR, Park CG, Quiring DMJ and Foisy MRJ, Potential use of *Dicyphus hesperus* Knight (Heteroptera: Miridae) for biological control of pests of greenhouse tomatoes. *Biol Control* **16**:104–110 (1999).
10 Hodek I, Food relationships, in *Ecology of Coccinellidae*, ed by Hodek I and Honèk A, Kluwer Academic Publishers, Boston, pp 143–238 (1996).
11 Muma MH, Lady beetles (Coccinellidae: Coleoptera) found on citrus in Florida. *Fla Entomol* **38**:117–124 (1955).
12 Fitzpatrick G, Cherry RH and Dowell RV, Short-term effects of three insecticides on predators and parasites of the citrus blackfly. *Environ Entomol* **7**:553–555 (1978).
13 Dowell RV, Fitzpatrick G, Zumstein R, Johnson M and Fiore J, Integrated biological control of citrus blackfly and current Florida citrus spray programmes. *Trop Agric* **63**:301–303 (1986).
14 Gold CS and Altieri MA, The effects of intercropping and mixed varieties of predators and parasitoïds of cassava whiteflies (Homoptera: Aleyrodidae) in Colombia. *Bull Entomol Res* **79**:115–122 (1989).
15 Heinz KM and Parrella MP, Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) infesting *Euphorbia pulcherrima*: evaluations of releases of *Encarsia luteola* (Hymenoptera: Aphelinidae) and *Delphastus pusillus* (Coleoptera: Coccinellidae). *Environ Entomol* **23**:1346–1353 (1994).
16 Coderre D and Tourneur JC, Déclin estival des populations aphidiennes du maïs. *Rev Entomol Quebec* **32**:16–24 (1988).
17 Maredia KM, Gaga SH, Landis DA and Wirth TM, Visual response of *Coccinella septempunctata* (L), *Hippodamia parenthesis* (Say), (Coleoptera: Coccinellidae), and *Chrysoperla*

carnea (Stephens), (Neuroptera: Chrysopidae) to colors. *Biol Control* **2**:253–256 (1992).

18 Boiteau G, The significance of predators and cultural methods, in *Potato pest management in Canada; Lutte contre les parasites de la pomme de terre au Canada*, ed by Boiteau G, Singh R and Parry R, Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec, Sainte-Foy, pp 201–223 (1987).

19 Putman WL, Occurence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Canad Entomol* **96**:1149–1155 (1964).

20 Chouinard G, *Bilan des observations phytosanitaires 1999 du Réseau-pommier*, Ministère de l'Agriculture, des Pêcheries and de l'Alimentation du Québec, Réseau d'avertissements phytosanitaires, Québec (2000).

21 Gagné I and Coderre D, Cold storage of *Coleomegilla maculata* larvae. *Biocontrol Sci Technol* **11**:361–369 (2001).

22 Gurney B and Hussey NW, Evaluation of some coccinellid species for the biological control of aphids in protected cropping. *Ann Appl Biol* **65**:451–458 (1970).

23 Mack TP and Smilowitz Z, Development of a green peach aphid natural enemy sampling procedure. *Environ Entomol* **9**:440–445 (1980).

24 Mack TP and Smilowitz Z, Using temperature-mediated functional response Models to predict the impact of *Coleomegilla maculata* (DeGeer) adults and 3rd-instar larvae on green peach aphids. *Environ Entomol* **11**:46–52 (1982).

25 van Lenteren JC and Woets J, Biological and integrated pest control in greenhouses. *Annu Rev Entomol* **33**:239–269 (1988).

26 Szumkowski W, Observations on Coccinellidae. I Coccinellidae as Predators of Lepidopterous Eggs and Larvae in Venezuela. *Trans Ninth Int Congr Entomol* **1**:778–781 (1952).

27 Warren LO and Tadic M, Biological Observations on *Coleomegilla maculata* and its role as a Predator of the Fall Webworm. *J Econ Entomol* **60**:1492–1496 (1967).

28 Dysart R, Natural enemies of the banded-wing whitefly, *Trialeurodes abutilonea* (Hemiptera: Aleurodidae). *Ann Entomol Soc Am* **59**:28–33 (1959).

29 Link D and Costa EC, Ocorrência de inimagos naturais da Mosca Branca, *Bemisia tabaci* (Gennadius, 1889), Na cultura da soja. *Centro Ciências Rurais* **10**:111–113 (1980).

30 Norris DM and Kogan M, Biochemical and morphological bases of resistance, in *Breeding plants resistant to insects*, ed by Maxwell FG and Jennings PR, John Wiley and Sons, Toronto, pp 23–62 (1980).

31 Obrycki JJ and Tauber MJ, Natural enemy activity on glandular pubescent potato plants in the greenhouse: an unreliable predictor of effects in the field. *Environ Entomol* **13**:679–683 (1984).

32 Hodek I and Honèk A, Distribution in habitats, in *Ecology of Coccinellidae*, ed by Hodek I and Honèk A, Kluwer Academic Publishers, Boston, pp 95–142 (1996).

33 Lucas E and Brodeur J, Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Environ Entomol* **28**:622–627 (1999).

34 Butler GD Jr, Henneberry TJ and Wilson FD, *Bemisia tabaci* (Homoptera: Aleyrodidae) on cotton: adult activity and cultivar oviposition preference. *J Econ Entomol* **79**:350–354 (1986).

35 McAuslane HJ, Influence of leaf pubescence on oviposional preference of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on soybean. *Environ Entomol* **25**:834–841 (1996).

36 Elsey KD, Influence of plant host on searching speed of two predators. *Entomophaga* **19**:3–6 (1974).

37 Carter MC, Sutherland D and Dixon AFG, Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* **63**:394–397 (1984).

38 Grevstad FS and Klepetka BW, The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* **92**:399–404 (1992).

39 Messina FJ, Jones TA and Nielson DC, Host-plant effects on the efficacy of two predators attacking Russian wheat aphids (Homoptera: Aphididae). *Environ Entomol* **26**:1398–1404 (1997).

40 Clark TL and Messina FJ, Foraging behavior of lacewing larvae (Neuroptera: Chrysopidae) on plants with divergent architectures. *J Insect Behav* **11**:303–317 (1998).

41 Sokal RR and Rohlf FJ, *Biometry; the principles and practice of statistics in biological research*, 2nd edn, WH Freeman and Company, New York (1981).

42 Abacus Concepts Inc, *Superanova*, Bonita Avenue, Berkeley, CA (1989).

43 Dixon AFG, An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L). *J Anim Ecol* **39**:739–751 (1959).

44 Podoler H and Henen J, Foraging behavior of two species of the genus *Chilocorus* (Coleoptera: Coccinellidae): a comparative study. *Phytoparasitica* **14**:11–23 (1986).

45 Calder WA, *Size, function and life history*, Harvard University Press, Cambridge, MA (1984).

46 Peters RH, *The ecological implications of body size*, Cambridge University Press, Cambridge, UK (1983).

47 Sabelis MW, Predatory arthropods, in *Natural enemies, the population biology of predators, parasites and diseases*, ed by Crawley MJ, Blackwell Scientific Publications, Oxford, pp 225–265 (1992).

48 Polis GA, Myers CA and Holt RD, The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annu Rev Ecol Syst* **20**:297–330 (1989).

49 Polis GA, The evolution and dynamics of intraspecific predation. *Annu Rev Ecol Syst* **12**:225–251 (1981).

50 Iablokoff-Khnzorian SM, *Les coccinelles; Coléoptères—Coccinellidae*, Société Nouvelle des Éditions Boubée, Paris (1982).

51 Obrycki JJ and Tauber MJ, Seasonal occurence and relative abundance of aphid predators and parasitoids on pubescent potato plants. *Canad Entomol* **117**:1231–1237 (1985).

52 Belcher DW and Thurston R, Inhibition of movement of larvae of the convergent lady beetle by leaf trichomes of tobacco. *Environ Entomol* **11**:91–94 (1982).

53 Barbour JD, Farrar RR Jr and Kennedy GG, Interaction of *Manduca sexta* resistance in tomato with insect predators of *Helicoverpa zea*. *Entomol Exp Appl* **68**:143–155 (1993).

54 Heinz KM and Parrella MP, Poinsettia (*Euphorbia pulcherrima* Willd ex Koltz) cultivar-mediated differences in performance of five natural enemies of *Bemisia argentifolii* Bellows and Perring, n sp (Homoptera: Aleyrodidae). *Biol Control* **4**:305–318 (1994).

55 Sütterlin S and van Lenteren JC, Pre- and post-landing response of the parasitoid *Encarsia formosa* to whitefly hosts on *Gerbera jamesonii*. *Entomol Exp Appl* **96**:299–307 (2000).

56 Giroux S, Duchesne RM and Coderre D, Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): comparative effectiveness of predator developmental stages and effect of temperature. *Environ Entomol* **24**:748–754 (1995).

57 Lucas E, Coderre D and Brodeur J, Instar-specific defense of *Coleomegilla maculata lengi* (Coccinellidae): influence on attack success of the intraguild predator *Chrysoperla rufilabris* (Chrysopidae). *Entomophaga* **42**:3–12 (1997).

58 Lucas E, Coderre D and Brodeur J, Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* **79**:1084–1092 (1998).

59 Heinz KM, Brazzle JR, Parrella MP and Pickett CH, Field evaluations of augmentative releases of *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) for suppression of *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae) infesting corn. *Biol Control* **16**:241–251 (1999).

60 Hoelmer KA, Osborne LS and Yokomi RK, Interactions of the whitefly predator *Delphastus pusillus* (Coleoptera: Coccinellidae) with parasitized sweetpotato whitefly (Homoptera: Aleyrodidae). *Environ Entomol* **23**:136–139 (1994).

61 Heinz KM and Nelson JM, Interspecific interactions among natural enemies of *Bemisia* in an inundative biological control program. *Biol Control* **6**:384–393 (1996).