ELSEVIER

Seasonal activity of the spider mite predators *Stethorus punctillum* (Coleoptera: Coccinellidae) and *Neoseiulus fallacis* (Acarina: Phytoseiidae) in raspberry, two predators of *Tetranychus mcdanieli* (Acarina: Tetranychidae)

Michèle Roy [a,*], Jacques Brodeur [b], Conrad Cloutier [c]

[a] *Direction des services technologiques, Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, 2700 rue Einstein, Sainte-Foy, Que., Canada G1P 3W8*
[b] *Centre de Recherche en Horticulture, Département de Phytologie, Université Laval, Sainte-Foy, Que., Canada G1K 7P4*
[c] *Centre de Recherche en Horticulture, Département de Biologie, Université Laval, Sainte-Foy, Que., Canada G1K 7P4*

Abstract

Colonization of raspberry *Rubus idaeus* L. fields by the Mcdaniel spider mite *Tetranychus mcdanieli* McGregor and two of its predators *Stethorus punctillum* Weise and *Neoseiulus fallacis* (Garman) was studied in Québec in 1995 and 1996 in three sites, to determine predator seasonal synchrony with prey, and compare their impact in pesticide-managed and pesticide-free fields. The potential role of weeds as reservoirs of spider mites and predators was also examined by sampling the ground cover. In both types of fields and in both years, *N. fallacis* established very early on raspberry and was closely synchronized with *T. mcdanieli.* In contrast, *S. punctillum* was absent in pyrethroid and organophosphate insecticide-managed raspberry, and its arrival was delayed by ≈1 month in pesticide-free systems, suggesting that only the summer generations colonize raspberry by immigrating from overwintering habitats. At all sites and in both years, there was a relationship between the estimated impact of *N. fallacis* and *S. punctillum* and spider mite abundance, greater impact of the predators being associated with lower tetranychid abundance. The effects of insecticides in spring were not as dramatic as for *S. punctillum*, but greatly reduced *N. fallacis* populations and lowered their impact compared to the pesticide-free systems. Despite some species including *Potentilla norvegica* clearly being suitable for spider mites, weeds in the ground cover did not appear to influence the colonization or abundance of spider mites, nor synchrony or impact of *N. fallacis* and *S. punctillum*. We suggest that *N. fallacis* and *S. punctillum* are complementary predators of mites in the raspberry fields in Québec. Because of its sustained activity throughout the season and its early synchrony with the predominant *T. mcdanieli*, *N. fallacis* is a critical factor to spider mite population regulation in this system, while *S. punctillum* appears later as a mobile and voracious predator capable of substantial impact during summer when *Tetranychus urticae* joins *T. mcdanieli* in this system.
© 2005 Elsevier Inc. All rights reserved.

Keywords: *Tetranychus mcdanieli*; *Neoseiulus fallacis*; *Stethorus punctillum*; Temperature; Seasonal ecology; Predator–prey synchrony; Biological control

1. Introduction

Spider mites (Acarina: Tetranychidae) are important pests of crop plants including red raspberry, *Rubus idaeus* L. (Charles et al., 1990; Gordon et al., 1990; Mariéthoz et al., 1994; Roy et al., 1999; Shanks et al., 1992). Two important groups of predators are predatory mites (Acarina: Phytoseiidae) and coccinellid beetles of the genus *Stethorus* (Coleoptera: Coccinellidae), both of which have been reported as regulator agents of tetranychid pests on red raspberry

* Corresponding author. Fax: +1 418 646 6806.
E-mail address: michele.roy@mapaq.gouv.qc.ca (M. Roy).

(Baillod et al., 1996; Charles et al., 1985; Congdon et al., 1993; Dondale, 1968; Raworth, 1989; Roy et al., 1999; Wood et al., 1994). Spider mite biological control has been implemented with success on various perennial crop systems based on conservation and augmentation of phytoseiids and *Stethorus* spp. (reviewed by Helle and Sabelis, 1985; Nyrop et al., 1998), suggesting that a similar approach could be implemented in raspberry crop systems (Baillod et al., 1996; Charles et al., 1990; Congdon et al., 1993; Wood et al., 1994).

In a previous exploratory study of spider mites and their natural enemies on red raspberry (Roy et al., 1999), we found the McDaniel spider mite, *Tetranychus mcdanieli* McGregor, to be the most important pest in raspberry fields in Québec, with the two-spotted spider mite, *Tetranychus urticae* (Koch), less common and occurring at lower densities later in the season than *T. mcdanieli*. Among the guild of insect and mite predators, the indigenous phytoseiid *Neoseiulus fallacis* (Garman) was the most abundant species in commercial fields managed with pesticides, while the introduced coccinellid *Stethorus punctillum* Weise was also common in pesticide-free fields, but rare or absent in commercial fields managed with pesticides and on wild raspberry bushes. Based on population density data collected over two seasons at two sites, predators did not correlate with spider mite populations (Roy et al., 1999). In particular, the tetranychids were abundant in untreated fields despite coccinellid and phytoseiid predation, suggesting their low potential for spider mite control at a desirable level in Québec. Hypothetically, the cool spring conditions generally prevailing in this region could result in seasonal asynchrony between tetranychid pests and their natural enemies (Tauber et al., 1986), as it is well established that natural enemies must be active in the early stages of herbivore population development, in order to have a regulatory impact (Van Driesche and Bellows, 1996).

Seasonal asynchrony can either be due to lack of temporal or spatial occurrence. Temporal asynchrony may result from differences in temperature thresholds between herbivorous pests and their natural enemies, allowing pests to escape regulation early in the season and to reach damaging levels (Campbell et al., 1974; Hodek and Honek, 1996; Obrycki and Tauber, 1981). In a direct comparison of temperature-dependent development of *S. punctillum* and its prey *T. mcdanieli* (Roy et al., 2002), we found no evidence of significant discrepancy between low-temperature thresholds. However, even with potential temporal synchrony, spatial asynchrony in spring could still limit natural enemy impact by introducing a migratory delay before predation, which could be important when the natural enemy overwinters away from its foraging and breeding habitats. According to Hodek and Honek (1996) coccinellid efficiency in field crops in the spring mainly depends on proximity with hibernation

sites. We do not have data pertaining to *N. fallacis* synchrony with *T. mcdanieli* in raspberry in Québec, however, it is noteworthy to mention that delay in natural regulation for some phytoseiid–spider mite associations is described, which have been attributed to differential overwintering mortality between prey and predator (Hu et al., 1996; Overmeer, 1985).

This 2-year field study had as its primary objective to develop more specific knowledge of the factors limiting natural biological control of spider mites in raspberry crop systems in Québec, with particular emphasis on the seasonal ecology of *T. mcdanieli* as the primary tetranychid pest, and *N. fallacis* and *S. punctillum* as its principal arthropod natural enemies. We documented early spring colonization of cultivated raspberry by spider mites and their predators over two field seasons, and in three sites. We also determined the season-long patterns of abundance of spider mites and their predators in relation to raspberry phenology, in both pesticide-managed and pesticide-free raspberry systems. Weed plants in the ground cover of fields were also sampled throughout the season to explore their potential as reservoirs for spider mites and predators.

2. Material and methods

In 1995 and 1996, field studies were carried out at three sites in agricultural communities located near Québec City (46°59′N 71°29′W), Québec, Canada: St. Laurent, Île d'Orléans; St. Jean, Île d'Orléans; and Deschambault. The St. Laurent site was a 1 ha commercial field of cultivar Killarney managed with two to three fungicide treatments to control diseases including anthracnose *Elsinoe veneta* (Burkholder) Jenk. and gray mold *Botrytis cinerea* Pers. ExFr; and three to four insecticide treatments to control the tarnished plant bug *Lygus lineolaris* (Palisot de Beauvois), the strawberry bud weevil *Anthonomus signatus* Say, and the raspberry beetle *Byturus unicolor* Say. The St. Jean site was a 1 ha field of early-season cultivars, mainly Killarney, undergoing conventional management practices with the exception of chemical pesticides, which were excluded. The Deschambault site was 1 ha of Killarney located on the experimental farm of the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec. Management practices in this site were similar to the St. Jean site with no pesticide application; however, weeds were excluded by mechanical control supplemented by hand weeding.

In 1995 and 1996, at the St. Jean and St. Laurent sites, ground cover sampling under the raspberry canopy started, respectively, on April 29 and April 30 and ended, respectively, on August 29 and September 2, except at the St. Jean site in 1995 where ground cover sampling ended on May 25, when the grower decided to exclude

all weeds for the rest of the season. No ground cover sampling took place at the weed-free Deschambault site. Ground cover sampling was performed once or twice a week, in five randomly positioned quadrats (30 × 30 cm). For each dicotyledonous weed, five leaves were collected to determine ground cover colonization by spider mites and their predators. Grass weeds were not considered because preliminary work revealed no spider mites on grassy plants (M. Roy et al., unpublished).

At all sites, on a weekly basis, from April 29 to May 19 in 1995 and from April 30 to May 20 in 1996, 10 raspberry fruiting canes were randomly selected for assessment of spring colonization by spider mites and predators. Thirty buds per cane were sampled from the dormant stage to the green-leaf-tip stage. Raspberry foliage sampling was also performed once or twice a week as follows. At each sampling date after foliage expansion, 50 mature leaflets per site were collected at random. Killarney leaves have three leaflets of which the terminal one was sampled, being the most representative of spider mite distribution (Mariéthoz et al., 1994). From the beginning of sampling until harvest, leaflets were taken from the median portion of fruiting canes, 1.0–1.5 m above ground. After harvest, leaflets were collected in the central portion of primocanes, whose leaves have five leaflets.

Weeds, raspberry buds, and leaflets were individually placed in plastic bags, kept in an insulated cooler with ice, and brought to the laboratory where they were stored at 4 °C for up to 3 days. *Tetranychus urticae*, *T. mcdanieli*, *N. fallacis*, and *S. punctillum* were identified under a stereomicroscope and their density was recorded per weed leaf, or per raspberry bud or leaflet. Following Nyrop et al. (1994), a maximum of 20 phytoseiids were mounted on slides and identified to species using Chant and Hansell's (1971) key.

Adults of *S. punctillum* fly away or drop when disturbed while foraging on plants (Felland et al., 1995) and thus were sampled by trapping. At each site, 16 yellow sticky boards Pherocon (Zoecon, Palo Alto, CA) made of two panels fixed back to back with sticky sides facing outwards (each 20.5 × 14.6 cm) were placed on stakes at random, 50 cm above plant canopy. Trapping continued from the end of April to the end of September, traps being renewed weekly. Boards were sorted in the laboratory to determine counts of *S. punctillum*.

Temperature data were obtained from the Environment Canada weather station at the Québec City airport (30, 42, and 40 km from the St. Laurent, St. Jean, and Deschambault sites). Raspberry phenological development was also monitored.
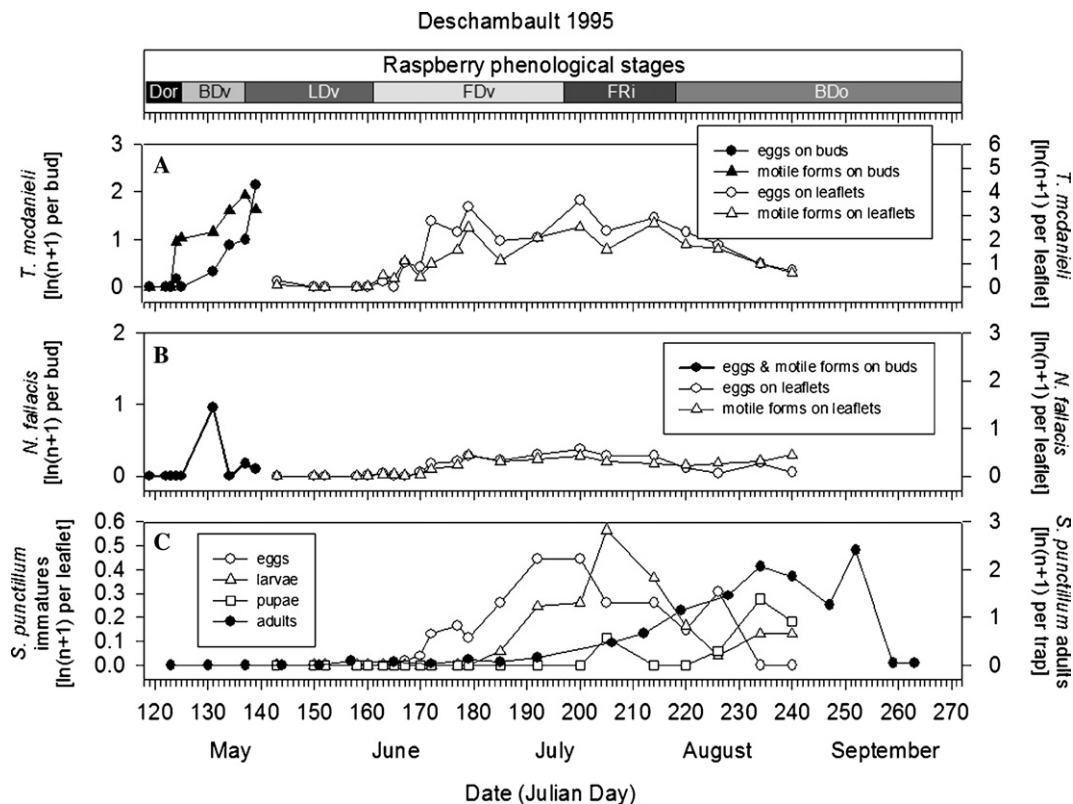

Fig. 1. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the Deschambault site during the 1995 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy).

3. Results

Colonization of raspberry by *T. mcdanieli* and *N. fallacis* occurred at the earliest possible time in spring in contrast to *S. punctillum*. In 1995, at Deschambault and St. Jean (pesticide-free plots), overwintering females of *T. mcdanieli* began colonizing canes at bud break in early May (Figs. 1A and 2A). During leaf development, ⩽2 *T. mcdanieli* eggs per motile forms were detected per leaflet. Spider mite density increased rapidly during flowering and fruiting and declined afterwards. *T. urticae* was not detected on buds in spring, but was observed on leaflets from mid-June on, at densities near 20% those of *T. mcdanieli* at Deschambault and St. Jean, respectively (data not shown). At both sites, *N. fallacis* overwintered females were first found on buds shortly after *T. mcdanieli* (Figs. 1B and 2B), while *S. punctillum* adults were captured 4–5 weeks after mites were first observed (Figs. 1C and 2C). *N. fallacis* reproduction started almost immediately after raspberry colonization (data not shown), while the first *S. punctillum* eggs were found on leaflets 10 and 13 days after the first adults were trapped at Deschambault and St. Jean, respectively. Thereafter, both predators remained present throughout the season.

At St. Jean and St. Laurent, characterized by a weedy ground cover, *T. mcdanieli* was found at high densities on rosaceous weeds, especially *Potentilla* spp. (Table 1). Other weeds including *Asclepias syriaca* L., *Erigeron strigosus* Mùhl., *Malva neglecta* Wallr., *Barbarea vulgaris* R. Br., and *Capsella bursa-pastoris* L. also supported high mite densities, but those species were uncommon. Other species supported low *T. mcdanieli* populations, while others (six at St. Jean and eight at St. Laurent) including *Vicia cracca* L. and *Polygonum convolvulus* L. did not support *T. mcdanieli*, despite being very common (data not shown). The presence of weeds did not appear to affect raspberry colonization by *T. mcdanieli*, as indicated by comparing colonization patterns at St. Jean vs Deschambault (Figs. 1A and 2A). *N. fallacis* on weeds was closely related to the presence of *T. mcdanieli* (Table 1) while no *S. punctillum* was found on weeds.

Spider mite colonization under the chemical pesticide management regime at St. Laurent in 1995 did not differ from the pesticide-free sites, with first occurrence of *T. mcdanieli* occurring at bud break (Fig. 3A), and of *T. urticae* at the end of May (data not shown). However, overwintering *T. mcdanieli* females on buds in early May were 2.0 and 1.9 times more abundant at St. Laurent, than Deschambault and St. Jean, respectively (Figs. 1A, 2A, and 3A). Similarly, densities of *T. mcdanieli* motiles on leaflets from late May to late August were 8.3 and 16.4 times greater at St. Laurent than Deschambault and
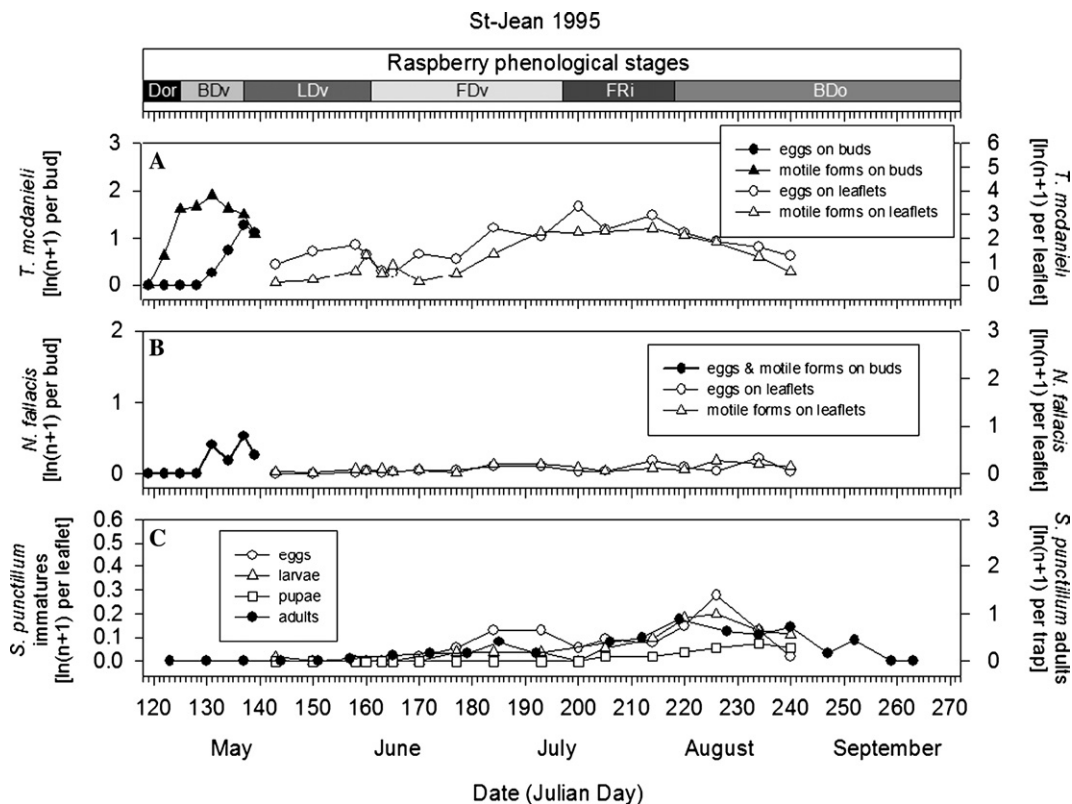

Fig. 2. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the St. Jean site during the 1995 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy).

Table 1
Average density (per 30×30 cm quadrat) of *T. mcdanieli* and *N. fallacis* on weed leaves at the St. Jean and St. Laurent sites, Québec, in 1995; weeds are sorted according to their frequency of occurrence within quadrats; no *S. punctillum* was found on weeds in this study

Weed species	Weed frequency	Family	T. mcdanieli		N. fallacis	
			Motile forms	Eggs	Motile forms	Eggs
St. Jean site[a]						
Stellaria media (L.) Cyrill.	0.67	Caryophyllaceae	0.0	1.0	0.0	0.0
E. strigosus Mühl.	0.67	Compositae	1.0	0.0	0.0	0.0
Solidago rugosa Mill.	0.67	Compositae	2.0	0.0	0.0	0.0
Veronica agrestis L.	0.67	Scorphulariaceae	1.0	0.0	0.0	0.0
Chrysanthemum leucanthenum L.	2.00	Compositae	0.0	4.0	0.0	0.0
B. vulgaris R. Br.	3.33	Cruciferae	32.0	9.2	1.6	1.2
M. neglecta Wallr.	4.00	Malvaceae	12.5	42.8	1.2	0.5
Taraxacum officinale Weber	5.33	Compositae	5.5	0.0	0.0	0.0
Potentilla norvegica L.	5.33	Rosaceae	25.4	60.4	2.8	1.9
St. Laurent site[b]						
Malva moschata L.	0.67	Malvaceae	6.0	13.0	1.0	2.0
A. syriaca L.	1.33	Asclepiadaceae	24.0	84.0	3.5	0.0
E. strigosus Mühl.	1.33	Compositae	20.5	19.5	5.5	8.0
C. bursa-pastoris L.	1.33	Cruciferae	22.0	23.0	0.0	0.0
Potentilla recta L.	1.33	Rosaceae	2.0	1.0	2.0	0.0
M. neglecta Wallr.	3.33	Malvaceae	13.6	8.2	0.0	0.0
Fragaria virginiana Duchesne	3.33	Rosaceae	112.8	77.0	1.4	0.4
Trifolium agarium L.	4.00	Leguminosae	1.2	0.2	0.0	0.0
T. officinale Weber	6.67	Compositae	0.4	0.0	0.0	0.0
B. vulgaris R. Br.	8.00	Cruciferae	2.7	2.6	0.1	0.0
Potentilla intermedia L.	8.00	Rosaceae	43.1	90.5	1.4	0.8
P. norvegica L.	26.00	Rosaceae	37.3	64.9	2.6	2.8

[a] At this site spider mites were present on 9 out of 15 weed species; weeds on which no spider mites were found were *Hieracum* sp., *Oxalis stricta* L., *Rumex longifolius* DC., *Ranunculus reptans* L., *Galium* sp., and *Erysimum cheiranthoides* L.

[b] At this site spider mites were present on 12 out of 20 weeds; weeds on which no spider mites were found were *Silene cucubalus* Wibel., *Cichorium intybus* L., *Solidago rugosa* Mill., *Galium* sp., *Galeopsis tetrahit* L., *V. cracca* L., *P. convolvulus* L., and *C. leucanthenum* L.

St. Jean, respectively. Severe spider mite infestation (>50 motile forms per leaflet) in June at St. Laurent caused bronzing of primocane leaves, and high densities persisted until the end of July and then declined below 10 motiles per leaflet. Densities of *T. urticae* followed a similar trend and were five times higher than recorded at the pesticide-free sites (data not shown). Colonization of buds and leaflets by *N. fallacis* at St. Laurent followed a trend similar to pesticide-free sites, but was characterized by higher predator densities (Fig. 3B). *S. punctillum* was absent from the St. Laurent raspberry system (Fig. 3C).

Our study indicates that both predators contributed to reduce *T. mcdanieli* populations based on the observed density trends (Table 2). To estimate the impact of each predator, we used predator/prey ratios in combination with assumptions based on our data and published results. Thus for *N. fallacis*, we assumed that its impact on spider mite populations was low if the predator/prey ratio during the season was less than 1/100; moderate if the ratio was 1/10 to 1/100, and high for a ratio greater than 1/10. These impact levels are similar to those reported for phytoseiids used for biocontrol of spider mites on greenhouse crops and field crops such as strawberry (Janssen and Sabelis, 1992), taking into account data on *N. fallacis* predation rates (Dover et al.,

1979). Similarly for *S. punctillum*, we assumed that its impact was low if the predator/prey ratio was less than 1/1000; moderate if between 1/100 and 1/1000, and high if greater than 1/100. Thus, we assumed that on a per capita basis, the impact of *S. punctillum* on spider mites was 10 times greater than *N. fallacis*. These assumptions are conservative based on extrapolations from *Stethorus loxtoni/T. urticae* (Richardson, 1977), and *Stethorus picipes/Oligonychus punicae* (Hirst) ratio data (Tanigoshi, 1973). Our assumptions also incorporate predation rate data of *S. punctillum* on *T. mcdanieli* (M. Roy, unpublished data), and those of Houck (1980) for the association *S. picipes–T. urticae*.

In 1996, patterns of spider mite colonization were similar to the previous year, but *T. mcdanieli* densities on raspberry buds and leaflets were about half those of 1995 (Figs. 4A, 5A, and 6A). Similarly, the density of *T. urticae* was 18 times less than 1995, and both spider mite species were also found at lower densities on weeds (data not shown). In contrast, *N. fallacis* densities on raspberry (Figs. 4B, 5B, and 6B) and weeds (not shown) were similar to those observed in 1995. Trends in *S. punctillum* densities in 1996 were not consistent among immature life stages and adults. Immature stages on leaflets were 2.7 times more abundant in 1996 than 1995, but 2.4 times fewer beetles were trapped (Figs. 4C and 5C). As in 1995,
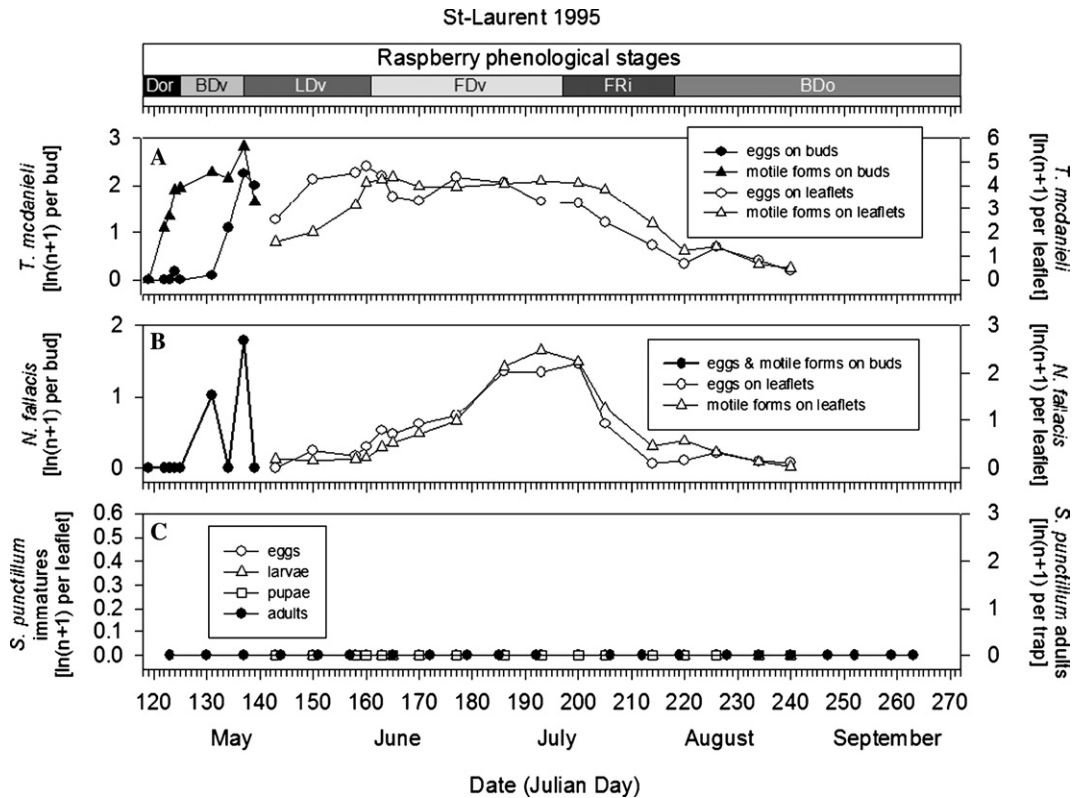
Fig. 3. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the St. Laurent site during the 1995 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy); insecticide treatments were applied on May 31, June 23, July 3, and July 10.

Table 2
Summary of raspberry colonization by *T. mcdanieli*, *N. fallacis*, and *S. punctillum* at two pesticide-free (Deschambault and St. Jean) and one treated (St. Laurent) sites in Québec, along with discrete quantitative seasonal estimates of prey abundance and predator impact (expressed as predator to prey ratio)

Site	Year	Bud break[a]	*T. mcdanieli*		*N. fallacis*		*S. punctillum*	
			Colonization date[b]	Prey abundance[c]	Synchrony[d]	Predator impact[e]	Synchrony	Predator impact[f]
Deschambault	1995	124	124	Moderate	+7	Moderate	+33	Moderate to high
	1996	129	129	Low	+5	High to moderate	+36	High
St. Jean	1995	121	122	Moderate	+9	Low to moderate	+35	Moderate to high
	1996	125	126	Low	+5	High to moderate	+32	High
St. Laurent	1995	121	122	High	+9	Low to moderate	Absent	None
	1996	128	129	Moderate	0	Moderate to high	Absent	None

[a] Julian date of bud break.
[b] Julian date of first spider mite record.
[c] Number per leaflet (low = less than 10; moderate = between 11 and 50; high = more than 50).
[d] Delay in days since colonization by *T. mcdanieli*.
[e] Seasonal trend in *N. fallacis* to spider mite prey ratio (low = less than 1/1000; moderate = between 1/100 and 1/1000; high = more than 1/100).
[f] Seasonal trend in *S. punctillum* to spider mite prey ratio (low = less than 1/100; moderate = between 1/10 and 1/100; high = more than 1/10).

S. punctillum was not observed on weeds (data not shown), and at the St. Laurent site (Fig. 6C).

4. Discussion

In all fields the occurence of *N. fallacis* was well synchronized with that of *T. mcdanieli*, with a delay of ca. 1 week, except in St. Laurent where no delay was observed.

In contrast, *S. punctillum*, which was observed only in pesticide-free plots, arrived ≈1 month later than *T. mcdanieli*. In pesticide-free plots, *N. fallacis* densities were lower than in insecticide-treated plots. This can be related to a number of reasons, including availability of alternative food sources such as pollen (Pratt et al., 1999), presence of other arthropods in the system, or competition with *S. punctillum*. Although our previous study (Roy et al., 1999) has shown other arthropods are
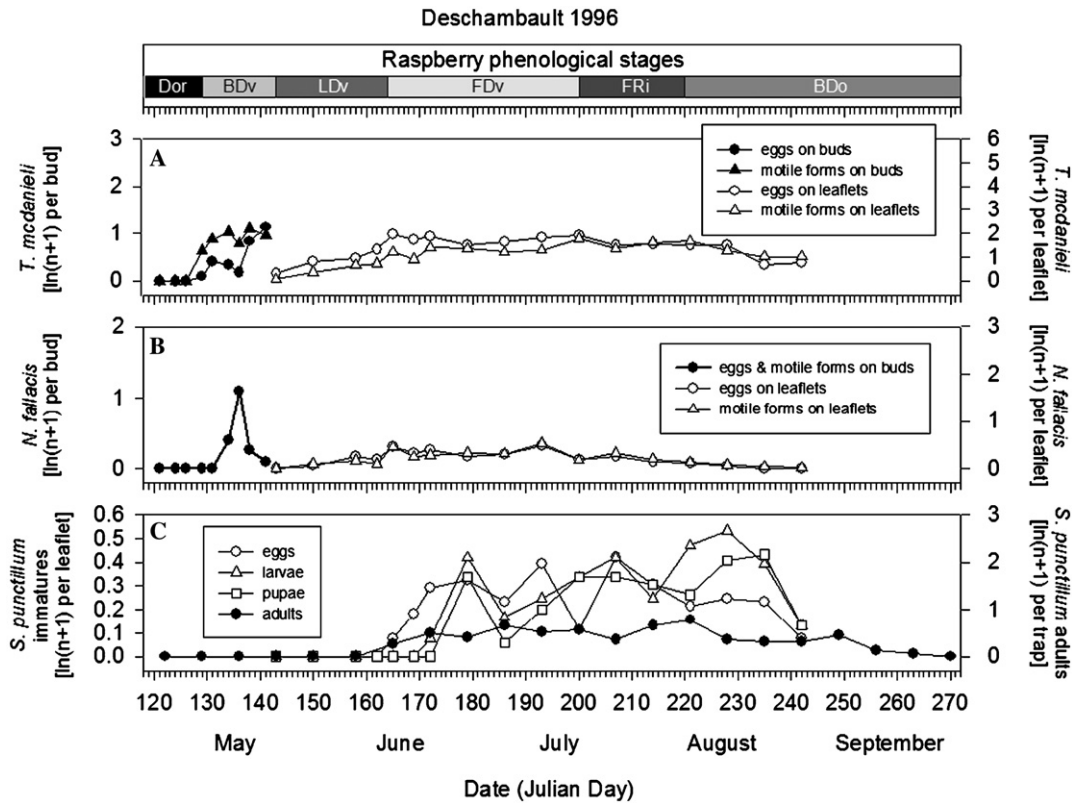
Fig. 4. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the Deschambault site during the 1996 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy).

few in this system, our data do not allow determining the exact reason for these lower densities.

Nevertheless, our data indicate that *N. fallacis* readily responds to increases in spider mite numbers by recruitment and reproduction among prey populations (Nyrop et al., 1998), as shown by its rapid increase following colonization by *T. mcdanieli* (Figs. 1B, 2B, 3B, 4B, 5B, and 6B). *T. mcdanieli* populations generally increased for 3–4 weeks before *S. punctillum* adults were detected in early June and oviposition was not detected until mid-June (Figs. 1C, 2C, 4C, and 5C). This delayed response of the coccinellid to its prey is somewhat surprising, since Congdon et al. (1993) in Washington State reported no delay between *Stethorus punctum picipes* Casey and *T. urticae* on red raspberry. Considering the length of the delay, we suggest that *S. punctillum* in the region of study may have to move into raspberry from remote overwintering sites, possibly from orchards or woodlands as observed for some aphidophagous coccinellids (Hodek and Honek, 1996).

The overwintering habitat, survival, dormancy development, dispersal ability, and foraging behavior of *Stethorus* in general and *S. punctillum* in particular are poorly documented. *Stethorus* sp. was found overwintering under leaf litter in woodlands and orchards (Colburn and Asquith, 1971; Felland et al., 1995; Putnam, 1955).

We regularly sampled leaf litter in raspberry fields, but no overwintering beetles were found (M. Roy, unpublished data). Colburn and Asquith (1971) reported that *S. punctum* adults feed on eggs of the European red mite, *Panonychus ulmi* (Koch), in apple orchards, both prior to overwintering in fall and in spring. Both satiated and starved *S. punctum* females strongly preferred eggs over active stages of *T. urticae* (Houck, 1991). It is likely that *S. punctillum* in Québec overwinters in apple orchards (or similarly protected habitats), and develops during spring on *P. ulmi*, which is common in orchards in southern Québec (Parent and Pilon, 1978; M. Roy, unpublished data). Consequently, it appears that only summer generations of *S. punctillum* colonize raspberry fields. Moreover, *S. punctillum*, native to Europe, may not be well adapted to survive the winter conditions encountered in raspberry fields in Québec, where the ground cover is scarce and the snow cover is relatively shallow compared to woods and orchards where winter survival might be better.

At all sites and in both years, the abundance of *N. fallacis* and *S. punctillum* appears to be negatively related to spider mite abundance, larger predator impact estimates being associated with lower spider mite densities (Table 2). In the early part of both seasons, *N. fallacis* clearly had more impact in both pesticide-free systems than at
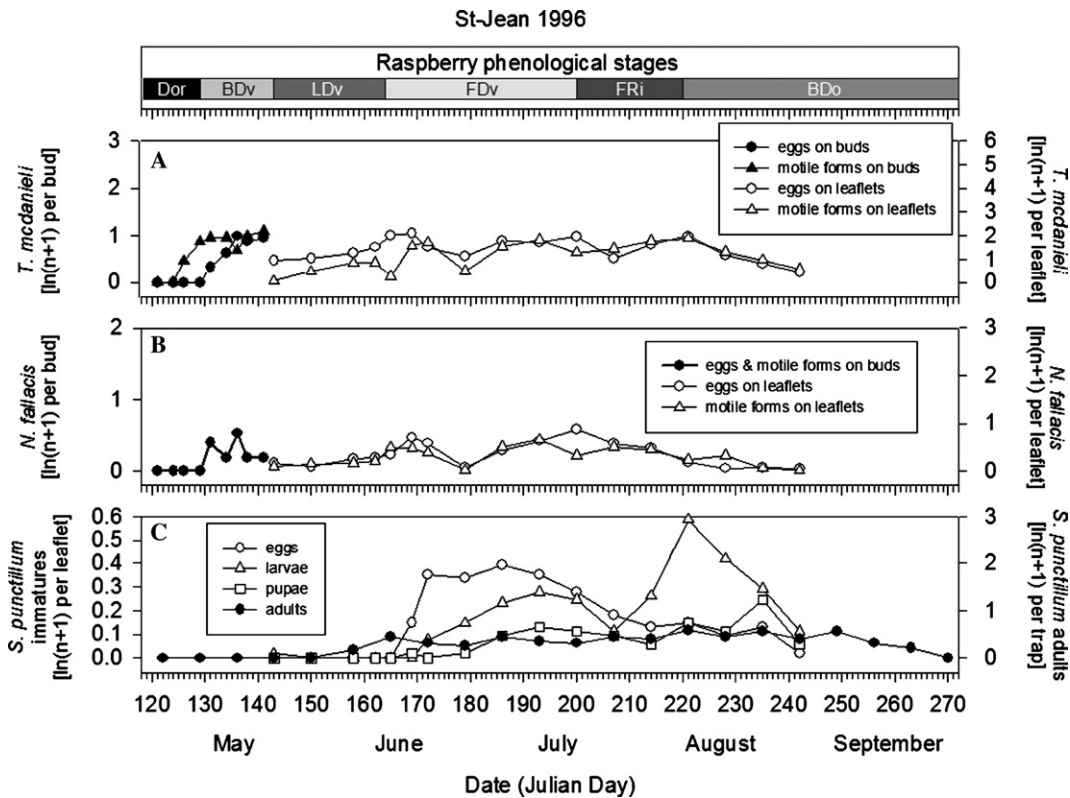
Fig. 5. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the St. Jean site during the 1996 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy).

St. Laurent, a pattern associated with significantly less spider mites in these systems than St. Laurent. The same can be said of the combined impacts of both predators.

These results corroborate our previous survey (Roy et al., 1999) of *N. fallacis* and *S. punctillum* in pesticide-free and commercial raspberry in the same region. In St. Laurent, synthetic pyrethroids and organophosphates were applied to control strawberry bud weevil in May and tarnished plant bug in June. These spring treatments apparently reduced *N. fallacis* populations and lowered its impact compared to the untreated systems (Table 2). *N. fallacis* did not develop large populations until mid-June which in 1995 was too late to provide satisfactory spider mite control as indicated by leaf damage and lowered yield and fruit quality (M. Roy, unpublished data). The sustained presence of *N. fallacis* at St. Laurent throughout the season suggests partial resistance to organophosphates and pyrethroids, which has been documented from other strains and sites (Croft, 1990; This-tlewood, 1991). The effects of pesticides on *S. punctillum* were more dramatic than *N. fallacis* as shown by its overall absence at the St. Laurent site. This agrees with insecticides being slightly, to highly toxic to *Stethorus* spp. (Asquith and Hull, 1973; Bartlett, 1963; Caron et al., 1999; Edwards and Hodgson, 1973; Hull et al., 1985; James, 2003; Shanks et al., 1992; Walters, 1976). Pyrethroids are known to be extremely toxic to coccinellids

and have already been implicated in spider mite infestations on red raspberries in Washington State (Shanks et al., 1992).

Weeds in the raspberry fields did not appear to play a major role as spider mite or predator reservoirs. Despite species like *P. norvegica* clearly being suitable to both spider mites and *N. fallacis*, weeds did not influence the timing of colonization of raspberries or the abundance of spider mites, nor *N. fallacis* synchrony and impact. In apple orchards, ground cover similarly had no effect on *N. fallacis* dynamics (Nyrop et al., 1994). Two potential non-exclusive factors could explain *S. punctillum* absence in the raspberry ground cover. First, trichomes on some weed plants may be antagonistic to *S. punctillum* (Putnam, 1955; Rott and Ponsonby, 2000; Roy et al., 1999). Some weeds supporting relatively high *T. mcdanieli* densities (e.g., *P. norvegica*) are much more pubescent than raspberry. Second, according to Majerus (1994) herbaceous plants are not exploited by *S. punctillum*, which seems to be mainly adapted to hunt spider mite prey on broad-leaved deciduous trees and shrubs. Although more specific data would be necessary to reach a definitive conclusion, the apparently low impact of weed management observed here might be partly explained by the relatively low proportion of the overall host plant resource for this spider mite–predator system, which is accounted for by the weed cover compared to raspberry canes.
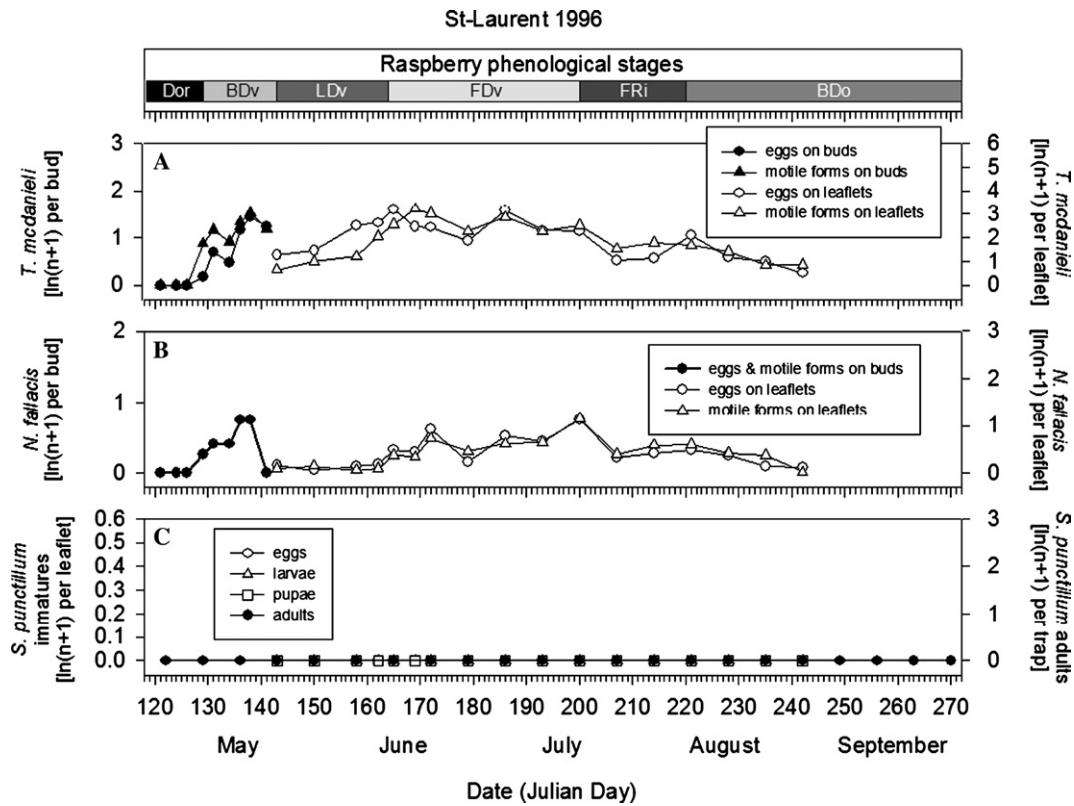
Fig. 6. Seasonal fluctuations of: (A) *T. mcdanieli*, (B) *N. fallacis*, and (C) *S. punctillum* densities on raspberry at the St. Laurent site during the 1996 growing season; top panel shows raspberry phenological stages (Dor = dormancy; BDv = bud development; LDv = leaf development; FDv = flower and fruit development; FRi = fruit ripening; BDo = beginning of dormancy); insecticide treatments were applied on June 9, July 7, and July 14.

The results of this field study in combination with our previous research on this system (Roy et al., 1999, 2003a,b) provide support to the view of complementary impacts of *N. fallacis* and *S. punctillum* on spider mite populations in raspberry fields in Québec, a system characterized by the marked predominance of *T. mcdanieli* over *T. urticae* as the tetranychid pest. *N. fallacis* clearly emerges as the most important regulating factor of *T. mcdanieli* on opening foliage in early spring, while *S. punctillum* seems to be a delayed-response, high prey density predator, able to impact spider mite populations over the long term and mainly in the summer. Our previous studies of *S. punctillum* and *T. mcdanieli* temperature-dependence suggested that despite similar low-temperature thresholds for development and potential for spring synchrony (Roy et al., 2002), the coccinellid is unable to match spider mite population growth under cool spring temperatures, based solely on development and reproductive rates. However, because of high voracity and high mobility, rapid recruitment at prey patches remains a major attribute of *S. punctillum*, which probably accounts for its significant impact once it establishes in raspberry fields.

Many studies tend to separately address the impact of coccinellids and phytoseiids as biological control agents of spider mites, despite recognition that both are signifi-

cant components of spider mite predator guilds on crop plants. In perennial crops like raspberry, *N. fallacis* is generally considered to be capable of keeping spider mite populations below economic thresholds through conservation and augmentation (Nyrop et al., 1998). In contrast, *Stethorus* spp. in similar strategies generally appears to have yielded unpredictable results (reviewed by Hagen et al., 1999). We suggest that a more efficient biological control strategy in raspberry could be developed by better integration of the combined potentials of phytoseiids and *Stethorus* coccinellids as spider mite predators. In particular, more understanding of their potential for additive or synergistic interactions is needed, in order to engineer season-long effective control, especially in systems such as in Québec where a spider mite complex dominated by a resident species well adapted to the local climate (Roy et al., 2002, 2003a,b) is involved. Interestingly, Tanigoshi (1973) was able to observe that on avocado the phytoseiid *Typhlodromus floridanus* Muma and the coccinellid *S. picipes* together more effectively suppressed the tetranychid *O. punicae* (Hirst) than either predator acting alone.

Susceptibility to chemical pesticides does appear to be a serious constraint on the successful conservation of both kinds of spider mite predators. Although insecticide treatments against key insect pests appear to be

necessary on commercial raspberry fields in Québec, registration of insecticides less harmful to *N. fallacis* and especially *S. punctillum* should be prioritized as a basis for developing an effective control program where the integration of natural predators is a primary objective. Finally, a better understanding of *S. punctillum* overwintering ecology also appears essential to allow early season impact of the coccinellid on spider mites, possibly by strategic habitat manipulation or augmentative releases.

Acknowledgments

References

Asquith, D., Hull, L.A., 1973. *Stethorus punctum* and pest-population responses to pesticide treatments on apple trees. J. Econ. Entomol. 66, 1197–1203.

Baillod, M., Antonin, P., Mittaz, C., Terrettaz, R., 1996. Lutte biologique contre l'acarien jaune commun, *Tetranychus urticae* Koch, en cultures de framboisiers. Rev. Suisse Vitic. Arboric. Hortic. 28, 153–155.

Bartlett, B.R., 1963. The contact toxicity of some pesticide residues to hymenopterous and coccinellid predators. J. Econ. Entomol. 56, 694–698.

Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., Mackauer, M., 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11, 431–438.

Caron, J., Laverdière, L., Roy, M., 1999. Guide De Lutte Intégrée Contre Les Tétranyques Dans La Production De La Framboise. Horti-Protection, Breakeyville, Québec, Canada.

Chant, D.A., Hansell, R.I.C., 1971. The genus *Amblyseius* (Acarina, Phytoseiidae) in Canada and Alaska. Can. J. Zool. 49, 703–758.

Charles, J.G., Collyer, E., White, V., 1985. Integrated control of *Tetranychus urticae* with *Phytoseiulus persimilis* and *Stethorus bifidus* in commercial raspberry gardens. New Zealand J. Exp. Agric. 13, 385–393.

Charles, J.G., Thomas, W.P., Workman, P.J., 1990. Control of *Tetranychus urticae* (Acari, Tetranychidae) in New Zealand berryfruit crops. In: Bostanian, N.J., Wilson, L.T., Dennehy, T.J. (Eds.), Monitoring and Integrated Management of Arthropod Pests of Small Fruit Crops. Intercept, Andover, UK, pp. 207–220.

Colburn, R., Asquith, D., 1971. Observations on the morphology and biology of the ladybird beetle *Stethorus punctum*. Ann. Entomol. Soc. Am. 64, 1217–1221.

Congdon, B.D., Shanks Jr., C.H., Antonelli, A.L., 1993. Population interaction between *Stethorus punctum picipes* (Coleoptera, Coccinellidae) and *Tetranychus urticae* (Acari, Tetranychidae) in red raspberries at low predator and prey densities. Environ. Entomol. 22, 1302–1307.

Croft, B.A., 1990. Arthropod Biological Control Agents and Pesticides. Wiley, New York, USA.

Dondale, C.D., 1968. A model outbreak of the mite *Tetranychus mcdanieli* McGregor in Ontario. Proc. Entomol. Soc. Ontario 100, 29–45.

Dover, M.J., Croft, B.A., Welch, S.M., Tummala, R.L., 1979. Biological control of *Panonychus ulmi* (Acarina, Tetranychidae) by *Amblyseius fallacis* (Acarina, Phytoseiidae) on apple, a prey–predator model. Environ. Entomol. 8, 282–292.

Edwards, B.A.B., Hodgson, P.J, 1973. The toxicity of commonly used orchard chemicals to *Stethorus nigripes* (Coleoptera, Coccinellidae). J. Aust. Entomol. Soc. 12, 222–224.

Felland, C.M., Biddinger, D.J., Hull, L.A., 1995. Overwintering emergence and trapping of adult *Stethorus punctum punctum* (Coleoptera, Coccinellidae) in Pennsylvania apple orchards. Environ. Entomol. 24, 110–115.

Gordon, S.C., Woodford, J.A.T., Barrie, I.A., 1990. Monitoring pests of red raspberry in the United Kingdom and the possible implementation of an integrated pest management system. In: Bostanian, N.J., Wilson, L.T., Dennehy, T.J. (Eds.), Monitoring and Integrated Management of Arthropod Pests of Small Fruit Crops. Intercept, Andover, UK, pp. 1–26.

Hagen, K.S., Mills, N.J., Gordh, G., McMurtry, J.A., 1999. Terrestrial arthropod predators of insect and mite pests. In: Bellows, T.S., Fisher, T.W. (Eds.), Handbook of Biological Control. Academic Press, San Diego, California, USA, pp. 383–503.

Helle, W., Sabelis, M.W., 1985. World Crop Pests, Spider Mites, Their Biology, Natural Enemies and Control, 1B. Elsevier, Amsterdam, The Netherlands.

Hodek, I., Honek, A., 1996. Effectiveness and utilization. In: Hodek, I., Honek, A. (Eds.), Ecology of Coccinellidae. Kluwer Academic, Dordrecht, The Netherlands, pp. 351–390.

Houck, M.A., 1980. Predatory behavior of *Stethorus punctum* (Coleoptera, Coccinellidae) in response to the prey *Panonychus ulmi* and *Tetranychus urticae* (Acarina, Tetranychidae). PhD thesis, Pennsylvania State University, University Park, Pennsylvania, USA.

Houck, M.A., 1991. Time and resource partitioning in *Stethorus punctum* (Coleoptera, Coccinellidae). Environ. Entomol. 20, 494–497.

Hu, X.P., Prokopy, R.J., Mason, J., 1996. Populations of predatory and pest mites in first-level and second-level commercial apple orchard blocks in Massachusetts. J. Appl. Entomol. 120, 47–51.

Hull, L.A., Beers, E.H., Meagher Jr., L., 1985. Impact of selective use of the synthetic pyrethroid fenvalerate on apple pests and natural enemies in large-orchard trials. J. Econ. Entomol. 78, 163–168.

James, D.G., 2003. Pesticide susceptibility of two coccinellids (*Stethorus punctillum picipes* and *Harmonia axiridis*) important in biological control of mites and aphids in Washington hops. Biocontrol Sci. Technol. 13, 253–259.

Janssen, A., Sabelis, M.W., 1992. Phytoseiid life-histories, local predator–prey dynamics, and strategies for control of tetranychid mites. Exp. Appl. Acarol. 14, 233–250.

Majerus, M.E.N., 1994. Ladybirds. HarperCollins, London, UK.

Mariéthoz, J., Baillod, M., Linder, C., Antonin, P., Mittaz, C., 1994. Distribution, méthodes de contrôle et stratégies de lutte chimique et biologique contre l'acarien jaune, *Tetranychus urticae* Koch, dans les cultures de framboisiers. Rev. Suisse Vitic. Arboric. Hortic. 26, 315–321.

Nyrop, J.P., Minns, J.C., Herring, C.P., 1994. Influence of ground cover on dynamics of *Amblyseius fallacis* Garman (Acarina, Phytoseiidae) in New York apple orchards. Agric. Ecosys. Environ. 50, 61–72.

Nyrop, J.P., English-Loeb, G., Roda, A., 1998. Conservation biological control of spider mites in perennial cropping systems. In: Barbosa, P. (Ed.), Conservation Biological Control. Academic Press, San Diego, California, USA, pp. 307–333.

Obrycki, J.J., Tauber, M.J., 1981. Phenology of three coccinellid species thermal requirements for development. Ann. Entomol. Soc. Am. 74, 31–36.

Overmeer, W.P.J., 1985. Diapause. In: Helle, W., Sabelis, M.W. (Eds.), World Crop Pests, Spider Mites, Their Biology, Natural Enemies and Control, 1B. Elsevier, Amsterdam, The Netherlands, pp. 95–102.

Parent, B., Pilon, J.G., 1978. Écologie et dynamique des populations naturelles du tétranyque rouge du pommier, *Panonychus ulmi* (Koch), (Acarina, Tetranychidae), dans le sud-ouest du Québec. Mém. Soc. Entomol. Québec 5, 1–106.

Pratt, P.D., Schausberger, P., Croft, B.A., 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.

Putnam, W.L., 1955. Bionomics of *Stethorus punctillum* Weise (Coleoptera, Coccinellidae) in Ontario. Can. Entomol. 87, 9–33.

Raworth, D.A., 1989. Towards the establishment of an economic threshold for the twospotted spider mite, *Tetranychus urticae* (Acari, Tetranychidae) on red raspberry, *Rubus idaeus*. Act. Hortic. 262, 223–226.

Richardson, N.L. 1977. The biology of *Stethorus loxtoni* Britton and Lee (Coleoptera, Coccinellidae) and its potential as a predator of *Tetranychus urticae* Koch (Acarina, Tetranychidae) in California. Ph. D. thesis, University of California, Berkeley, California, USA.

Rott, A.S., Ponsonby, D.J., 2000. The effects of temperature, relative humidity and host plant on the behaviour of *Stethorus punctillum* Weise (Coleoptera, Coccinellidae) as a predator of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari, Tetranychidae). Biocontrol 45, 155–164.

Roy, M., Brodeur, J., Cloutier, C., 1999. Seasonal abundance of spider mites and their predators on red raspberry in Québec. Environ. Entomol. 28, 735–747.

Roy, M., Brodeur, J., Cloutier, C., 2002. Relationships between temperature and developmental rate of *Stethorus punctillum* (Coleoptera, Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina, Tetranychidae). Environ. Entomol. 31, 177–187.

Roy, M., Brodeur, J., Cloutier, C., 2003a. Effect of temperature on intrinsic rate of natural increase (r_{m}) of a coccinellid and its spider mite prey. Biocontrol 48, 57–72.

Roy, M., Brodeur, J., Cloutier, C., 2003b. Temperature and sex allocation in a spider mite. Oecologia. 128, 36–43.

Shanks Jr., C.H., Antonelli, A.L., Congdon, B.D., 1992. Effect of pesticides on twospotted spider mite (Acari, Tetranychidae) populations on red raspberries in Western Washington. Agric. Ecosys. Environ. 38, 159–165.

Tanigoshi, L.K. 1973. Studies of the dynamic of predation of *Stethorus picipes* Coleoptera, Coccinellidae) and *Typhlodromus floridanus* on the prey *Oligonychus punicae* (Acarina, Phytoseiidae, Tetranychidae). PhD thesis, University of California, Riverside, California, USA.

Tauber, M.J., Tauber, C.A., Masaki, S., 1986. Seasonal Adaptations of Insects. Oxford University Press, New York, USA.

Thistlewood, H.M.A., 1991. A survey of predatory mites in Ontario apple orchards with diverse pesticide programs. Can. Entomol. 123, 1163–1174.

Van Driesche, R.G., Bellows Jr., T.S., 1996. Biological Control. Chapman and Hall, New York, USA.

Walters, P.J., 1976. Susceptibility of the *Stethorus* spp (Coleoptera, Coccinellidae) to selected chemicals used in New South Wales apple orchards. J. Aust. Entomol. Soc. 15, 49–52.

Wood, L., Raworth, D.A., Mackauer, M., 1994. Biological control of the twopotted spider mite in raspberries with the predator mite, *Phytoseiulus persimilis*. J. Entomol. Soc. Br. Columbia 91, 59–61.