Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*[1]

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Abstract—The seven-spotted lady beetle, *Coccinella septempunctata* L., was first reported in Manitoba in 1988. The effect of this introduced species on the relative abundance of the more common native coccinellines was determined from D-Vac Insect Net® and sweepnet samples in alfalfa in 1983–2001, by sweepnet and visual sampling in field crops and other vegetation in 1989–2001, and by transect sampling of aggregations of coccinellines in spring and autumn on the shore of Lake Manitoba from 1989 to 2001. The trends of annual changes in the abundance of six species in southern Manitoba were similar, whether based on the mean density per 200 sweeps in alfalfa or on their relative abundance in alfalfa, on other vegetation, and in aggregations on the beach. Before 1988, *Hippodamia tredecempunctata tibialis* (Say), *Coccinella transversoguttata richardsonii* Brown, and *Hippodamia convergens* Guerin were the most abundant species, followed by *Hippodamia parenthesis* (Say) and *Coccinella trifasciata perplexa* Mulsant. By 1992, *C. septempunctata* had become the dominant species, but *H. tredecempunctata* has since been the dominant species in most collections. The relative abundance of *C. transversoguttata*, *H. convergens*, *H. parenthesis*, and *C. trifasciata* has decreased since the establishment of *C. septempunctata*. The decline in abundance of these species seems to be caused by their competitive displacement by *C. septempunctata*. Their displacement also might be a contributing factor in the slight increase in abundance of *H. tredecempunctata* because *C. septempunctata* may compete less directly with this species than with other native coccinellines.

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Résumé—La coccinelle à sept points, *Coccinella septempunctata* L., a été vue pour la première fois au Manitoba en 1988. Les effets de cette espèce introduite sur l'abondance relative des espèces les plus communes de Coccinellinae indigènes ont été déterminés à partir d'échantillons recueillis à l'aspirateur D-Vac[MD] et au filet fauchoir dans de champs de luzerne en 1983–2001, au filet fauchoir et par échantillonnage visuel en 1989–2001 dans des cultures et d'autre végétation en 1989–2001 et par échantillonnage des regroupements de Coccinellinae le long de transects au printemps et en automne sur les rives du lac Manitoba. Les variations annuelles de l'abondance suivent les mêmes tendances chez six espèces du sud du Manitoba, que ces tendances soient estimées à partir de la densité moyenne des récoltes calculée sur 200 coups de filet dans de la luzerne ou de l'abondance relative dans la luzerne, dans d'autre végétation et dans les regroupements sur la plage. Avant 1988, *Hippodamia tredecempunctata tibialis* (Say), *Coccinella transversoguttata richardsonii* Brown et *Hippodamia convergens* Guerin étaient les espèces les plus abondantes,

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suivies d'*Hippodamia parenthesis* (Say) et de *Coccinella trifasciata perplexa* Mulsant. En 1992, *C. septempunctata* était devenue l'espèce la plus abondante, mais depuis ce temps, *H. tredecempunctata* domine dans la plupart des échantillons. L'abondance relative de *C. transversoguttata*, *H. convergens*, *H. parenthesis* et *C. trifasciata* a diminué depuis l'établissement de *C. septempunctata*. La diminution de l'abondance de ces espèces semble attribuable à leur remplacement par compétition par *C. septempunctata*. Ce remplacement peut aussi être en partie responsable de la légère augmentation de l'abondance d'*H. tredecempunctata*, parce que *C. septempunctata* fait une compétition moins directe à cette espèce qu'aux autres.

[Traduit par la Rédaction]

Introduction

The seven-spotted lady beetle, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), herewithin referred to as C7, is an Eurasian species that has been established in North America (Quebec, Canada, and New Jersey, United States of America) since 1973 (Angalet and Jacques 1975; Larochelle 1979). It spread rapidly, aided by releases by the United States Department of Agriculture for the biocontrol of aphids. It was established in several eastern states by 1979 (Angalet *et al.* 1979) and in Minnesota by 1987 (Schaefer *et al.* 1987). C7 first appeared in Manitoba in 1988 (Matheson 1989), and rapidly spread throughout the grassland and parkland areas of Manitoba and Saskatchewan (Turnock *et al.* 1990). The early detection of C7 presented an opportunity to document the impact of this exotic species on native coccinellines of southern Manitoba.

The coccinellid fauna of Manitoba includes 66 species in 28 genera, including 2 introduced species (Belicěk 1976; Gordon 1985; Bousquet 1990; Wise *et al.* 2002). In Manitoba, Batulla and Robinson (1983) listed the prey used by selected native coccinellines but little is known of their habitat preferences, life histories, or abundance. An estimate of the relative abundance of some native coccinellines prior to the arrival of C7 was made from a collection on a Lake Manitoba beach in 1978 (Turnock and Turnock 1981).

In this paper, we report on the density and relative abundance of the most common coccinellids collected with sweepnets in fields of alfalfa in the Red River Valley of Manitoba (1987–2001), and their relative abundance in southern Manitoba in samples (D-Vac®, sweepnet, visual) from various crops and other vegetative habitats (1983–2001), and in collections from aggregations of lady beetles on the shore of Lake Manitoba (1989–2001). We shall examine changes in the relative abundance of these species relative to the type of sampling, habitat, season, and year of sampling. From these data, we will evaluate the impact of C7 on the abundance of native coccinellids in Manitoba.

Methods

Sampling coccinellid communities to determine species abundance is difficult, and all methods are subject to biases (Hodek and Honěk 1996). Three approaches were used: sweepnet or visual-count sampling in annual crops and weeds and in perennial herbaceous plants and shrubs, and transect sampling of beetle aggregations on the shore of Lake Manitoba. Sampling with a sweepnet is mostly limited to the upper stratum of the plants being sampled. Visual counts, which can cover the whole plant, were used in herbaceous habitats (*e.g.*, flower beds, experimental plots) where the damage caused by sweepnets was unacceptable and on the accessible portions of trees and shrubs. The sampling methods may be biased by daily and seasonal changes in coccinellid activity, either by the beetles' vertical movements within vegetation or by movements among

different types of vegetation. Beetle aggregations on beaches can be sampled only when the wind direction brings the beetles ashore and when minimum temperatures are low enough to delay their subsequent flight from the beach. The species composition of such aggregations in spring and autumn may be biased by interspecific differences in the timing of flight activity over the lake and in the temperature threshold for flight from the beach.

The temperature requirements for development differ among some coccinellids (LaMana and Miller 1996). Hence, the annual total number of degree-days over 5°C, from 1 April to 31 July (the usual period for reproduction of the overwintering generation), was taken from the meteorological records for Glenlea (49°38′N, 97°00′W) from 1983 to 2001 to see if temperature could explain changes in relative abundance of any of the species. Glenlea is central to the area where the majority of sweepnet and visual-count sampling was conducted.

Sampling from vegetation

Adult lady beetles in southern Manitoba move in late April or early May from overwintering sites to plants infested with prey. The overwintering adults can usually be found feeding and ovipositing on prey-infested vegetation until mid- to late July, after which new generation adults become common. The new adults are then found on vegetation until they move to sites to overwinter. There is usually one generation per year in Manitoba.

Sweepnet sampling was the most used method because of the high correlation between the density estimated by absolute sampling and that estimated by sweepnet sampling (Ellington *et al.* 1984; Arefin and Ivliev 1988). Most samples from agricultural crops used 200 sweeps per field to maintain a high likelihood of sampling the majority of species in the habitat (Elliott and Kieckhefer 1990). The earliest collections (1983–1985) are from fields of alfalfa [*Medicago* spp. (Leguminosae)] in the Red River Valley (49°–51°N, 96°–98°W) (Matheson 1988). A D-Vac Insect Net® was used, with 1000 contacts in four fields in 1983, 3000 contacts in three fields in 1984, and 7250 contacts in four fields in 1985. In surveys of alfalfa fields in the Red River Valley to detect the appearance of C7 in Manitoba, 20–80 sweeps per field were taken in 18 fields in 1987 and in 35 fields in 1988. In 1989 and 1990, collections of 200 sweeps per field of alfalfa or canola [*Brassica napus* L. (Cruciferae)] were used in a study of *Lygus* spp. (Hemiptera: Miridae) (Timlick *et al.* 1993). Since 1989, collections of 200 or more sweeps per field have been made in several crops. In smaller patches of vegetation, 50 or more sweeps were taken, depending on the size of the patch. The visual-count method, in which the full height of the plant was examined (Iperti *et al.* 1988), was used in some spring cereal fields and for ornamental plants, and visual counts were also taken from trees and shrubs by examining leaves and stems observable from the ground.

Early (May–July) sweepnet samples were of the overwintering generation of lady beetles and were mainly from alfalfa and winter annuals such as wild mustard [*Sinapsis arvensis* L. (Cruciferae)] and stinkweed [*Thlapsi arvense* L. (Cruciferae)]. Later samples (August, September) were of the new generation and were from perennial weeds and native plants, forage legumes (alfalfa, clover) and grasses, and from annual cereals (spring wheat, canary grass, barley), canola, oilseed flax, buckwheat, shrubs, small trees, and summer annuals (flowers, vegetables).

The numbers of coccinellines collected annually ranged from 41 to 502 among the years 1983, 1984, 1987, and 1988 to large numbers (951–4178) in the other years. In all cases, the samples were placed in containers and brought to the laboratory where the coccinellines were identified following Beliček (1976) and Gordon (1985).

The effect of the type of vegetation or habitat on the relative abundance and community diversity of the more abundant species was examined for all samples after 1988, and for samples collected on alfalfa before and during 1988, using the Shannon–Weaver index of community diversity (Honěk and Rejmánek 1982). This index was used because of its moderate sensitivity to sample size (Magurran 1988).

This diversity of sampling methods and habitats provided a broad view of the occurrence of coccinellids in southern Manitoba, but it restricted analyses to comparisons of the relative abundance of the species over the years. However, a subset of these data, from sweepnet sampling of alfalfa fields in the Red River Valley for the years 1987–2001 (except 1997 and 2000), could be analysed to provide a density estimate (no. of beetles per 200 sweeps) for each species and year as well as their relative abundance. The number of alfalfa fields sampled was 18–39 in 1987–1990 and 1992–1993, and 3–9 in the other years. A total of 20–80 sweeps per field were taken in 1987 and 1988, and 200 or more in other years. The density, the mean number of beetles, and the standard error were calculated for each species and year. The annual mean densities of C7 fell into three periods: (1) 1987–1990, <1 C7 per 200 sweeps; (2) 1991–1992, >7 C7 per 200 sweeps; and (3) 1993–2001, <7 C7 per 200 sweeps. To compare mean density per field in the different time periods, a generalized linear model was fitted to the data using the SAS procedure Genmod (SAS Institute Inc 2000). The distribution was a negative binomial with a separate mean for each period and a common dispersion parameter. Observations were weighted by the number of sweeps.

Aggregations on beaches

Movement of large numbers of lady beetles in the autumn from their summer habitats to overwintering sites and the reverse movement in the spring are common features of coccinellids (Hodek and Honěk 1996; Kuznetsov 1997). During such movements the beetles may fall into water and be washed ashore. Large concentrations of lady beetles have been observed on the shores of lakes and oceans in Europe and North America (Lee 1980), and locally on the shores of Lake Winnipeg and Lake Manitoba (Lee 1980; Turnock and Turnock 1981), particularly on the south shore of Lake Manitoba at the Delta Marsh Field Station (University of Manitoba) (50°11′N, 98°23′W). This shore is a north-facing sand beach with a forested barrier beach ridge formed by the reworking of alluvial sand deposits. The lake level is stabilized by a control dam at Fairford River, the only outlet (Kenkel 1986), and the beach varies in width from approximately 5 to 14 m, depending mainly upon wind direction. We made arrangements with the Station staff to notify us when they observed concentrations of lady beetles on the beach.

Lady beetles on the beach were sampled only in the morning, when the beetles were quiescent. The Delta Beach faces north and is shaded by trees on the beach ridge, which delay warming in the mornings. If temperatures rose quickly and the beetles began to fly, no samples were taken or sampling ceased because the different species showed different temperature thresholds for flight. Samples consisted of all lady beetles found in a transect, 1.0 or 0.5 m wide (depending on beetle density), extending at a right angle from the edge of the water to the beach ridge. On a few occasions, two or three separate transects 10 m apart were sampled to determine if the relative abundance of coccinellids varied along the beach. Beetles were usually massed on organic debris at the high-water mark and on driftwood or other items protruding from the sand. Rarely, some beetles were found on the low shrubs at the top of the sand beach. The lady beetles in each transect were placed in containers, and the numbers of living and dead beetles of each species were recorded.

To determine if a single transect was adequate to estimate the relative abundance of coccinellids in beach aggregations, all the beetles in each of three transects 10 m

TABLE 1. Relative abundance of the five most abundant native coccinellid species in collections in southern Manitoba from alfalfa before the arrival of *Coccinella septempunctata* (C7) in 1988, and from alfalfa, other vegetative habitats, and a beach in 1988–2001.

Habitat	No. of years	Relative abundance by species: No. of insects	C7	H13	CT	HC	HP	C3	H′
Alfalfa									
1983–1987	4	1 047	0	0.585	0.253	0.082	0.051	0.013	0.495
1988–2001	11	6 426	0.202	0.541	0.093	0.050	0.077	0.029	0.575
Canola	10	4 018	0.408	0.509	0.056	0.021	0.006	0	0.427
Winter crucifers	7	4 206	0.104	0.742	0.085	0.063	0.006	0.001	0.381
Shrubs and perennials	6	2 053	0.352	0.619	0.014	0.014	<0.001	<0.001	0.341
Cereals	6	1 444	0.367	0.602	0.017	0.013	0	<0.001	0.347
All vegetation (1988–2001)	11	18 756	0.256	0.578	0.087	0.035	0.029	0.011	0.499
Beach (1989–2001)	13	50 742	0.383	0.425	0.079	0.097	0.016	0	0.532

NOTE: Shannon–Weaver (H') index of community diversity where $H' = -\sum (p_i \log p_i)$ and p_i is the proportion of the ith species in the habitat. CT, *Coccinella transversoguttata*; C3, *Coccinella trifasciata*; H13, *Hippodamia tredecempunctata*; HC, *Hippodamia convergens*; and HP, *Hippodamia parenthesis*.

apart were collected, identified, and counted on 23 September 1993, 6 May 1998, and 18 September 1999. Two transects 10 m apart were similarly sampled on 8 May 1998.

One to three collections (25 in total) were made every year from 1989 to 2001. In the autumn (September, October), aggregations occurred every year except in 1997 and 1998, and in the spring (late April, May) in the years 1994–1998, 2000, and 2001. The sample size ranged from 118 to 7294 beetles and over 1000 beetles were present in 16 of 25 collections.

We had planned to use contingency analyses (Sokol and Rohlf 1981) to test for differences among replicate transects and among years in the relative abundance of species. However, preliminary analyses of the differences between samples collected in the same month of a year indicated that very small differences in the proportions were significant. Contingency analyses are sensitive to sample size and our large samples made it possible to detect statistical significance where no biological significance was apparent. Therefore, we did not analyse these data. Differences among years were greater than those within months.

Results

Species collected

In samples from alfalfa in 1983–1987 (Table 1) and in a collection from a beach in 1978 (Turnock and Turnock 1981), the most abundant coccinellid species were *Hippodamia tredecempunctata tibialis* (Say), *Hippodamia convergens* Guerin, *Coccinella transversoguttata richardsonii* Brown, and *Hippodamia parenthesis* (Say). *Coccinella trifasciata perplexa* Mulsant was less abundant. Additionally, *Coccinella hieroglyphica kirbyi* Crotch, *Hippodamia sinuata crotchi* Casey, *Anisostricta bitriangularis* (Say), *Anatis mali* (Say), *Psyllobora vigintimaculata* (Say), and *Coleomagilla maculata lengi* Timberlake occurred rarely.

In the annual samples from vegetation and the beach after 1988, 25 species in 14 genera were found, but only 6 species occurred in sufficient numbers to analyse

population trends. *Hippodamia tredecempunctata*, *H. convergens*, *Coccinella transversoguttata*, and C7 were consistently present in samples from the beach and vegetation, whereas *H. parenthesis* and *Coccinella trifasciata* were only found regularly in sweepnet samples. *Adalia bipunctata* (L.), *Anisostricta bitriangularis*, *Chilocoris stigma* (Say), *Coccinella hieroglyphica kirbyi*, and *Cycloneda polita* Casey were found occasionally in small numbers in beach and sweepnet samples. Periodically, one or two specimens of *Mulsantina picta* (Randall) and *Hippodamia quinquesignata* (Kirby) were found in samples from the beach, and similar numbers of *Anatis mali*, *Anatis labiculata* (Say), *Brachiacantha albifrons* (Say), *Brumoides septentrioniz septentrioniz* (Weise), *Hippodamia sinuata crotchei*, *Hippodamia moesta bowditchei* Johnson, *Hippodamia glacialis lecontei* Muls., *Hippodamia punctata* Lec., *Hyperaspis undulata* (Say), *P. vigintimaculata*, *Coleomagilla maculata lengi*, and *Calvia quatuordecimguttata* (L.) were in sweepnet samples. A new exotic species, *Harmonia axyridis* (Pallas), was found in September 2000 in Winnipeg and now appears to be established in southern Manitoba (Wise *et al.* 2002).

Species abundance by vegetative habitat

The proportional abundance of the six most abundant species in 1989–2001 was recorded from five different habitats (Table 1). The perennial plant habitats were monocultures of Canada thistle [*Cirsium arvense* (L.) (Compositae)], perennial sow thistle [*Sonchus arvensis* L. (Compositae)], or forage grasses, or were habitats with a mixture of native and introduced plants. Alfalfa had the most diverse populations of coccinellines followed by canola and winter crucifers, whereas cereal crops and perennials had the least (Table 1). *Hippodamia tredecempunctata* was the dominant species, followed by C7 in all habitats. C7 was common in all habitats except winter annuals, where all collections were taken early in the season (April–June) before the plants senesced. *Hippodamia tredecempunctata* and C7 together made up over 75% of the lady beetles in all habitats, and were over 90% in canola and in perennial herbaceous plants and shrubs. *Coccinella transversoguttata* and *H. convergens* were mostly found on alfalfa, canola, or winter annuals, and were less common on cereal crops and perennials. *Hippodamia parenthesis* and *C. trifasciata* were rarely found on plants other than alfalfa.

Density and relative abundance in alfalfa fields in the Red River Valley

The mean density (mean no. of beetles per 200 sweeps) of C7 was low (<1) in 1987–1990, high (>7) in 1991–1992, and moderate (<7) and variable from 1993 to 2001 (Fig. 1*a*). The mean density for each of the five native species was significantly different between 1993–2001 and 1987–1990 (Table 2). Density changes among the native species were variable, but in four of the five native species, densities declined to low levels after the establishment of C7 (Figs. 1*c*–1*f*). Among these, the density of *H. parenthesis* was low (<1 per 200 sweeps) from 1990 to 1995 and this species has been very rarely collected since 1995 (Fig. 1*e*). The densities of *H. convergens* were similar to those of *H. parenthesis*, except in 1992, when there were 5.2 per 200 sweeps (Fig. 1*d*). *Coccinella transversogutta* densities varied from 1 to 5 per 200 sweeps from 1987 to 1992, were <0.5 from 1993 to 1996, and were 0 or very low in 1997–2001 (Fig. 1*c*). The density of *C. trifasciata* showed no evidence of an impact from C7 through 1995, but this species has not been collected since 1995 (Fig. 1*f*). The density of *H. tredecempunctata* declined from 1987 to 1992, peaked (>13 per 200 sweeps) from 1993 to 1995, and varied from 2 to 9 per 200 sweeps from 1996 to 2001 (Fig. 1*b*). In relation to the changes in density of C7, the density of *H. tredecempunctata* showed a

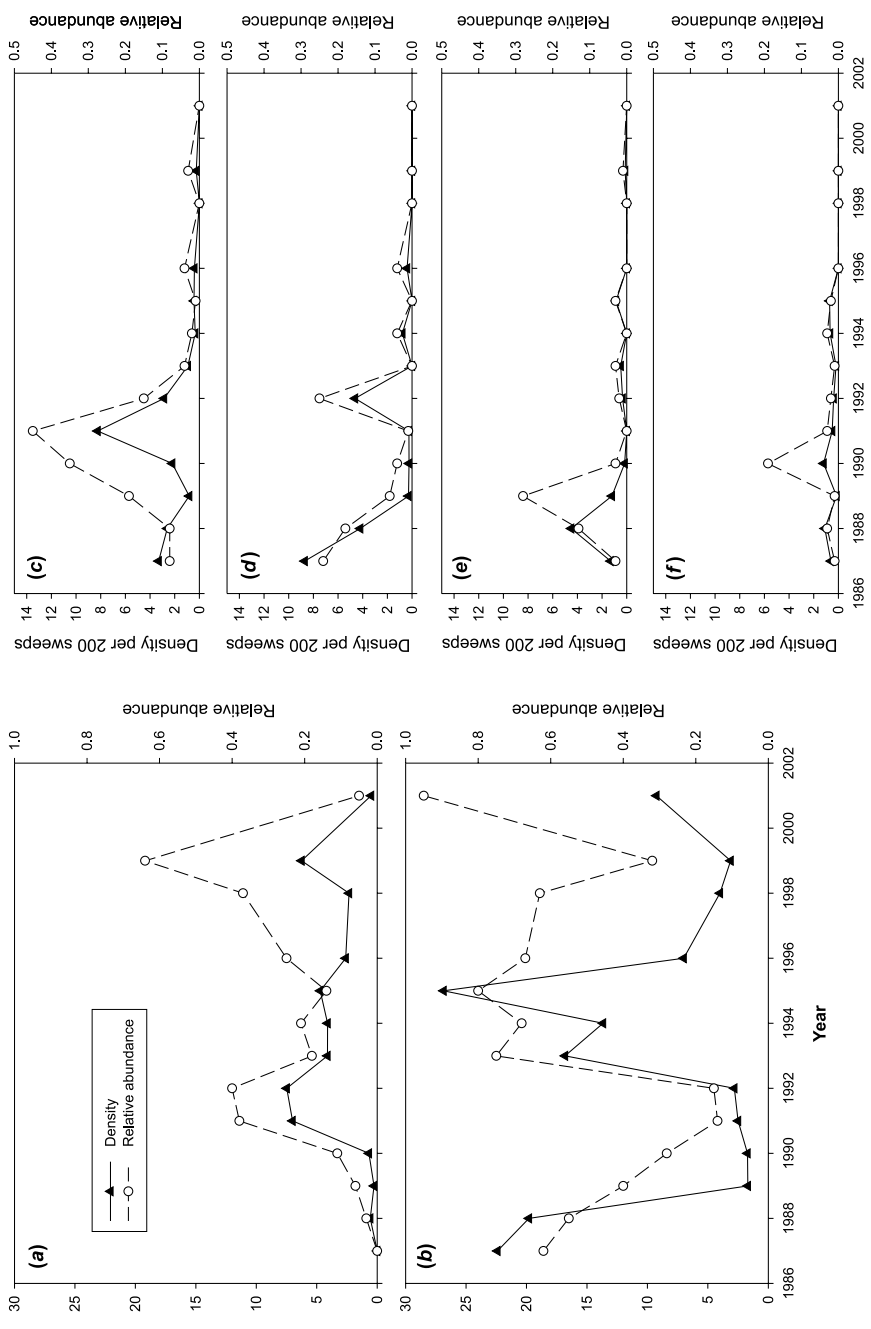

FIGURE 1. **Mean density per 200 sweeps and relative abundance of *Coccinella septempunctata* (*a*), *Hippodamia tredecempunctata* (*b*), *Coccinella transversoguttata* (*c*), *Hippodamia convergens* (*d*), *Hippodamia parenthesis* (*e*), and *Coccinella trifasciata* (*f*) in alfalfa fields in southern Manitoba from 1987 to 2001.**

TABLE 2. Weighted number of *Coccinella septempunctata* and five native coccinellid species per 200 sweeps in alfalfa fields before (1987–1990), during (1991–1992), and after (1993–2001) the peak density of *Coccinella septempunctata*.

Period	No. of fields	Species					
		C7	H13	CT	HC	HP	C3
1987–1990	117	0.43±0.13*c*	3.41±0.64*b*	1.47±0.21*b*	0.90±0.17*b*	1.03±0.15*a*	0.51±0.09*a*
1991–1992	25	7.40±0.90*a*	2.76±0.98*b*	3.72±0.56*a*	3.92±0.59*a*	0.28±0.14*b*	0.40±0.14*ab*
1993–2001	63	4.02±0.42*b*	13.87±1.38*a*	0.56±0.14*c*	0.14±0.07*c*	0.38±0.10*b*	0.25±0.07*b*

NOTE: Values are means ± SE. Means followed by the same letter in each column are not different (negative binomial model, $P > 0.05$). See Table 1 for species names.

TABLE 3. Mean and range (in parentheses) of estimated proportions of coccinellid species collected in transects from the waters edge to beach ridge at the Delta Field Station on Lake Manitoba.

	23 Sept. 1993	6 May 1998	8 May 1998	18 Sept. 1999
No. of transects	3	3	2	3
No. of beetles	2965	492	1998	2075
Species*				
C7	0.335 (0.237–0.366)	0.325 (0.0–0.463)	0.269 (0.254–0.314)	0.960 (0.951–0.971)
H13	0.624 (0.579–0.733)	0.606 (0.481–1.00)	0.727 (0.683–0.742)	0.035 (0.027–0.046)
CT	0.003 (0.002–0.006)	0 (0)	0.002 (0.0–0.003)	0.001 (0.000–0.004)
HC	0.034 (0.018–0.050)	0.010 (0.0–0.011)	0.001 (0.0–0.002)	0.003 (0.001–0.006)
HP	0.003 (0.001–0.006)	0.059 (0.0–0.067)	0.002 (0.002–0.002)	0 (0)

* See Table 1 for species names.

different pattern to that of the densities of the other four native species, which have been lower since the establishment of C7. The changes in relative abundance of these species are closely related to the C7 density (Fig. 1*a*–1*f*), and the conclusions regarding the effect of C7 on the native species are the same for both methods of analysis.

Comparisons of collections from the beach

The proportion of living beetles in the samples from the beach was generally high, with a mean of 0.805. In samples with <80% living beetles, C7 had the lowest proportion living in the spring collections, but there were no consistent differences among species in the autumn collections.

In general, the later collections in the spring and the earlier ones in the autumn had higher proportions of C7 and *C. transversoguttata* and lower proportions of the other species than those taken earlier in the spring or later in the autumn. These two species may be less active at cooler temperatures than the other three species. *Hippodamia tredecempunctata* was the most active species at lower temperatures, always being the first species to fly as beach temperatures rose in the morning. The ranking of the species was the same among transects within sampling dates (Table 3), and usually was consistent among collections within the spring and autumn collections of each year. The exceptionally high relative abundance (96%) of C7 in the collection of 18 September 1999 (Table 3, Fig. 2*a*) is partially related to the early collection date, but C7 was also higher in density in alfalfa fields (Fig. 1*a*) and in relative abundance in vegetative collections (Fig. 2*a*) than in 1998 or 2000. High proportions of *H. tredecempunctata* in late collections occurred on 20 October 1994 (96%) and on 13 October 1996 (92%) (Fig. 2*b*), and *H. convergens* comprised 96% of a collection on 2 November 1979

(Turnock and Turnock 1981). A very high proportion of C7 (92%) was also found in a collection (in August 1994) from a stand of common reed grass [*Phragmites communis* Trin. (Festuceae)], growing in the Delta Marsh, that was severely infested by aphids.

Relative abundance

Fluctuations in the relative abundance of the most common species found in the collections from the beach and those from vegetation since the appearance of C7 were remarkably similar (Fig. 2). This similarity from two very different sampling techniques plus the coincidence of annual estimates of density and relative abundance (Fig. 1) increases our confidence in the validity of using changes in relative abundance in determining the impact of C7 on coccinellines in southern Manitoba. In general, the estimates from beach samples are more variable than those from vegetation, perhaps because each sample of the former reflects the species composition of lady beetles that were active during a very short period, whereas those from vegetation are based on many small collections over more time and space. The trends in relative abundance of the six most abundant species were as follows.

Coccinella septempunctata

The incidence of this species after its appearance in Manitoba in 1988 showed a rapid increase in the first few years followed by a decrease in relative abundance and fluctuations around a lower relative abundance (Fig. 2*a*). The proportion of C7 in the September beach samples rose steadily from 0.143 in 1989 to 0.594 in 1992, and after a drop in 1993 to 0.665 in 1994 (Fig. 2*a*). Subsequently, the proportion varied around 0.400, except in September collections of 1999 (0.967) and 2001 (0.977). The high proportions of C7 in these collections reflect the earlier flight of this species in the autumn. In general, C7 tended to be more abundant on beaches in September and less abundant in October (Fig. 2*a*). Samples from vegetation showed a similar trend: C7 relative abundance peaked in 1992 and has subsequently varied from 0.1 to 0.5 (Fig. 2*a*). If we consider 1995–2001 to represent the stabilized position of C7 in the coccinellid population of Manitoba, its incidence was 0.241 ± 0.156 (mean ± SE, n = 7490) of the annual samples from vegetation and 0.251 ± 0.056 (n = 23 650) for the beach samples (excluding the two samples in which C7 was at 0.96).

Hippodamia tredecempunctata

This species had the highest relative abundance in samples from vegetation in southern Manitoba before the appearance of C7, with an annual incidence of 0.592 ± 0.127 (n = 1047) of the coccinellid population. Its relative abundance declined from 1988 to 1992 (Fig. 2*b*), then increased in 1993 to again become the most abundant species in all annual collections from vegetation and most beach samples. We observed that this species is active at lower temperatures than other common species, especially C7, and that the warmer summers of 1989–1991 (Fig. 3) may have reduced its relative competitive ability. This species appears to migrate later in the autumn than C7, as its proportion in beach samples is lower in early-autumn than in late-autumn collections (Fig. 2*b*), which may explain some of the fluctuations in relative abundance among the beach samples.

Coccinella transversoguttata

This species had the second highest relative abundance in samples from vegetation before C7, with an incidence of 0.253 ± 0.162, but has not exceeded 0.005 in samples taken from 1992 to 2001 (Fig. 2*c*). Until 1991, this species was less abundant in

years with warm summers, but from 1993 to 2001, its incidence has remained low regardless of fluctuations in summer temperatures (Figs. 2*c*, 3).

Hippodamia convergens

The relative abundance of this species before the appearance of C7 was 0.082 ± 0.113 in vegetation samples in southern Manitoba (Table 1). Its incidence in 1993–2001 on vegetation has only been 0.016 ± 0.032, suggesting an 80% decline. The relative abundance in beach samples was occasionally high after it became low in vegetative habitats (Fig. 2*d*). This may indicate that the beach aggregations include *H. convergens* from some nonagricultural habitats that were not sampled in our study. Other than in the samples from September 1996 to October 2000 (Fig. 2*d*), its incidence in collections from beaches in 1995–2001 did not exceed 0.01.

Hippodamia parenthesis

The relative abundance of this species was low (0.051 ± 0.059) before 1988, and it has not exceeded 0.01 in any annual collection since 1990 (Fig. 2*e*). Only two specimens were collected from vegetation from 1995 to 2001 (n = 6115), and its incidence in collections from beaches in 1989–2001 were 0.003 ± 0.004 (n = 10 222).

Coccinella trifasciata

The relative abundance of this species never exceeded 0.03 in sweepnet samples before the arrival of C7 but did reach a high of 0.062 in 1990 when C7 was becoming established (Fig. 2*f*). This species was nearly completely absent in collections from beaches and was almost exclusively found on alfalfa (Table 1). Its preference for alfalfa inflated its relative abundance on vegetation before C7 became established because all samples before 1989 and most samples from 1989 to 1990 were from alfalfa. Only one specimen of *C. trifasciata* was found on alfalfa from late 1995 to 2001 (n = 6115) and none from other vegetation, suggesting that it has been displaced by C7.

Temperatures during the main reproductive period of these coccinellines in southern Manitoba (degree-days >5°C, 1 April–31 July) were high in 1987–1989 and 1991, just before the appearance and during the buildup of C7. Low temperatures occurred in 1992 and 1993, and moderate temperatures in the other years (Fig. 3).

Discussion

The coccinellid fauna of Manitoba, composed of 68 species in 28 genera (Wise *et al.* 2002), is slightly less rich than the coccinellid fauna in areas in Europe with similar southern boundaries, *e.g.*, Poland with 78 species in 37 genera; eastern Germany with 71 species in 28 genera; and eastern Ukraine with 67 species in 33 genera (Hodek and Honěk 1996).

Prior to the arrival of C7 in Manitoba, the most abundant species in order of average proportion were *H. tredecempunctata*, *C. transversoguttata*, *H. convergens*, *H. parenthesis*, and *C. trifasciata*. The populations of C7 increased rapidly in the years following its appearance in Manitoba, peaked, and then decreased. This pattern is consistent with the hypothesis that populations of a successful invading species first increase to high numbers but decline to lower numbers as the species becomes a permanent part of the fauna. During the post-invasion increase of C7, the relative abundance of *H. convergens* decreased, whereas the other species appeared to be unaffected. Subsequently, with populations of C7 apparently stabilizing at between 20 and 40% of the collections, *H. tredecempunctata* has again become the most abundant species, followed by C7, *C. transversoguttata*, *H. convergens*, and *H. parenthesis*. The last three

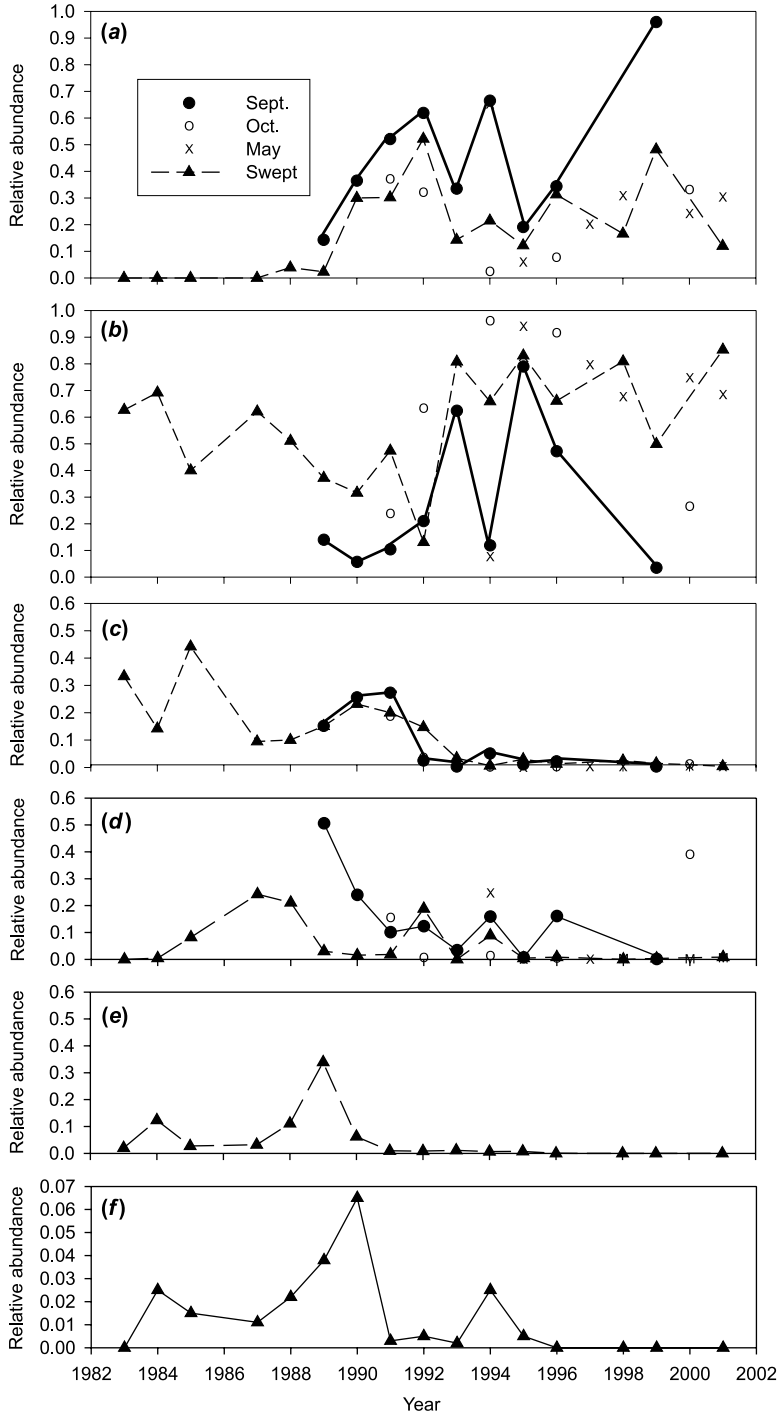

FIGURE 2. Relative abundance of *Coccinella septempunctata* (*a*), *Hippodamia tredecempunctata* (*b*), *Coccinella transversoguttata* (*c*), and *Hippodamia convergens* (*d*) in annual samples from a Lake Manitoba beach (1989–2001) and from vegetation (1983–2001); relative abundance of *Hippodamia parenthesis* (*e*) and *Coccinella trifasciata* (*f*) from vegetation in southern Manitoba.

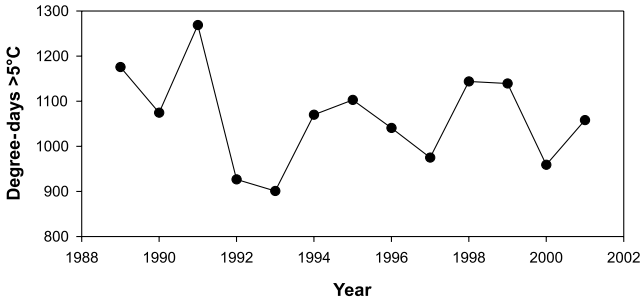

FIGURE 3. Total number of degree-days over 5°C from 1 April to 31 July at Glenlea, Manitoba, from 1983 to 2001.

species have been consistently lower in relative abundance than before the establishment of C7, and *C. trifasciata* has become too rare to find with our sampling methods.

The invasion and buildup of C7 may have been enhanced by higher temperatures during 3 of its first 4 years in southern Manitoba. This effect may have been direct, by increasing its survival and reproduction, or indirect, by reducing populations of *H. tredecempunctata*, which is active at lower temperatures. The greater abundance of *H. tredecempunctata* since 1992 may be related to the return to moderate temperatures but also to the lower populations of the other native species. The annual densities (no. of beetles per 200 sweeps) trends of these six species in alfalfa fields in the Red River Valley are the same as the trends in relative abundance based on several sampling techniques in a variety of habitats across southern Manitoba. The impact of the establishment of C7 on the native coccinellines thus seems to have been a reduction in the abundance of four of the five most abundant species in agricultural habitats, and possibly because of this, an increase in the abundance of *H. tredecempunctata*.

In Alberta, C7 is believed to have reduced the abundance of the common native species *C. transversoguttata* and *Coccinella novemnotata* Herbst (Ryan and Acorn 1999). In South Dakota, C7 reduced the relative abundance of *C. transversoguttata* and *A. bipunctata* in the 7 years following its appearance in 1987, whereas *H. convergens*, *H. tredecempunctata*, and *H. parenthesis* were not affected (Elliott *et al.* 1996). Our results are similar for *C. transversoguttata* but differ for other species in that the relative abundance of *H. tredecempunctata* increased, whereas those of *H. convergens* and *H. parenthesis* decreased. In Manitoba, the latter two species are approaching their northern limits of distribution. *Hippodamia convergens* extends to the northern limits of the parkland–forest zone in the Manitoba lowlands (approximately 53°N), whereas *H. parenthesis* reaches its northern limit at approximately 51°N in Manitoba (Gordon 1985). Thus, in Manitoba these two more southerly species may be more susceptible to competition from a new species than in South Dakota.

The different response of *C. transversoguttata* and *H. tredecempunctata* to the establishment of C7 was not directly related to their distributions in central North America. Both have holarctic distributions and they have the most northerly distribution of the common native coccinellines in Manitoba, extending past the northern limit of the boreal forest zone in Manitoba (60°N). C7 appears to occur throughout the boreal forest in Manitoba and Saskatchewan, having reached Ile-a-la-Crosse, Saskatchewan (57°27′N), in 1989 (Turnock *et al.* 1990). In Eurasia, C7 shares ranges with *H. tredecempunctata* and *C. transversoguttata*, and its distribution extends north to the forest tundra of eastern Siberia (Kuznetsov 1997). Some evidence of resource partitioning appears in eastern Siberia (Kutznetzov 1997). All three species occur in agricultural areas, but their occurrence in seven natural plant formations differed. *Hippodamia*

tredecempunctata occurred in meadows and mires; *C. transversoguttata* in broadleafed forests, spruce forests, and tundra; whereas C7 occurred in all of the natural formations. Thus, C7 may be more opportunistic and less restrictive in its hosts and habitats than the other species, but its relationships with the two Holarctic species may be different in Manitoba.

The size of these species, using adult length as recorded by Gordon (1985) as the criterion, is not related to the impact of C7. The species, in decreasing order of size, are C7, *C. transversoguttata*, *H. convergens*, *H. tredecempunctata*, and *H. parenthesis*. Perhaps the smaller size of *H. tredecempunctata* increases its ability to coexist with C7, whereas the larger size of *C. transversoguttata* causes it to be more directly affected. Given that the limits of abundance of coccinellids are regulated not only by prey abundance but also by a complex of other requisites, explanations for these differences among species are difficult.

During its first 12 years in Manitoba, C7 quickly became widespread and soon increased to become the most abundant species in our collections. After an initial period of dominance, C7 has become an integral part of the coccinelline fauna of southern Manitoba, generally being the second most abundant species after *H. tredecempunctata*. With the appearance of a second exotic species, *Harmonia axyridis*, in Manitoba (Wise *et al.* 2002), the species balance will probably change again. These two introduced species are similar in size and both are opportunistic in their feeding habits. *Harmonia axyridis* may be less cold-resistant than C7, as it does not occur in the "mountain alpine and forest tundra" habitat of Asia (Kutznetzov 1997). In Manitoba, this could make it a less effective competitor with *H. tredecempunctata* than C7. During the next decade, a new pattern of invasion and possible competitive displacement may be observed.

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