Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): Comparative Effectiveness of Predator Developmental Stages and Effect of Temperature

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ABSTRACT Laboratory experiments were conducted to evaluate the voracity of adult and larval stages of the polyphagous predator *Coleomegilla maculata* DeGeer on the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), immature stages. After a period of 24 h at 25°C in 50-mm petri dishes, adult coccinellids attacked 11 eggs and killed 14 first instars and 4 second instars. Fourth-instar coccinellids attacked 9 eggs and killed 11 first instars and 3 second instars. Effect of temperature on predation effectiveness of *C. maculata* adults, third and fourth instars was studied on potato stems infested with *L. decemlineata* eggs, first or second instars. No predation activity occurred at 7.5°C. Predator effectiveness increased linearly with temperature in the subsequent 10–30°C temperature range studied. At each temperature, no significant difference in the number of prey killed was observed between *C. maculata* adults and fourth instars. The use of potato stems in assessing predation by *C. maculata* significantly reduced the number of prey killed by introducing the need for searching by the predator. Results suggest that inundative releases of third-instar *C. maculata* against eggs and first instars of Colorado potato beetles could be of interest in the case where releases of adult coccinellids would fail because of their tendency to rapidly fly out of the field.

KEY WORDS *Coleomegilla maculata, Leptinotarsa decemlineata,* predation

THE COLORADO POTATO beetle, *Leptinotarsa decemlineata* (Say), is the most important agricultural pest on potato in Canada and in many areas of the northeastern United States in terms of costs and quantities of insecticide used and its high ability to rapidly become resistant to insecticides (Harris & Svec 1981; Forgash 1981, 1985; Boiteau et al. 1987; Chagnon et al. 1990; Tisler & Zehnder 1990, Ioannidis et al. 1991, Boiteau & Le Blanc 1992). Resistance to biological insecticides such as M-One, *Bacillus thuringiensis* subsp. *san diego,* has also been observed recently (Whalon et al. 1993). Because management of this pest has been based almost entirely on repeated applications of synthetic insecticides, natural enemies have not been able to play a significant role (Ferro 1985, Duchesne & Boiteau 1987). However, parasites and predators may reach sufficient densities to maintain Colorado potato beetle populations below economically damaging levels if compatible integrated pest management (IPM) programs are used (Ferro 1985).

The twelvespotted ladybird beetle, *Coleomegilla maculata* DeGeer, is a polyphagous predator (Hodek 1973) commonly found in potato fields of Massachusetts (Hazzard et al. 1991), Delaware (Heimpel & Hough-Goldstein 1992), Rhode Island, and Michigan (Groden et al. 1990). *C. maculata* may feed on pollen (Hodek et al. 1978), aphids (Coderre et al. 1987), mites (Putman 1964), eggs of lepidopterans (Warren & Tadic 1967, Hudon 1986), or eggs and larvae of *L. decemlineata* (Groden et al. 1990). This predator can significantly contribute to reductions of Colorado potato beetle eggs and small larvae (Groden et al. 1990). In unsprayed plots within commercial potato fields in western Massachusetts, Hazzard et al. (1991) measured mortality of eggs of Colorado potato beetles from predation by *C. maculata* natural populations at 38–58%, depending on the year and pest generation.

Consumption of immature stages of Colorado potato beetles by *C. maculata* has only been evaluated for adults, using either petri dishes (Groden et al. 1990) or a single potato leaf placed in a plastic box (Hazzard & Ferro 1991). The functional response of adult *C. maculata* to densities of eggs of Colorado potato beetle obtained by Hazzard & Ferro (1991) was a convex curve with decreasing slope at high-prey densities, corresponding to Holling's type II (Holling 1959).

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In an eventual IPM program using releases of *C. maculata*, old larvae could be particularly interesting because they are much less mobile than adults and, therefore, less able to rapidly leave the potato field when released or when the prey density decreases. Although consumption studies done in petri dishes are necessary to evaluate the maximum daily food intake possible, similar experiments also need to be conducted on real plant structures to take predator searching effectiveness into account.

Consumption rates of Colorado potato beetle eggs by adult *C. maculata* in petri dishes studies were found to be linearly correlated with temperature over a range of 15–30°C (Groden et al. 1990). No studies have been published concerning the predation effectiveness of *C. maculata* immature stages on Colorado potato beetle eggs and larvae under different temperatures, or on adult predator activity at lower temperature.

The objectives of this study were to evaluate and compare the voracity of each developmental stage of *C. maculata* on the eggs and larvae of the Colorado potato beetle, and to study the effect of temperature on predation effectiveness of adults and larvae of *C. maculata*.

Materials and Methods

Insects. Adult *C. maculata* were collected in early May 1993, from hibernation sites close to corn fields in Saint-Hyacinthe (72° 56′ W, 45° 39′ N), PQ, Canada. They were kept in an incubator on a diet of liver, aphids, and wild flower pollen at 25°C, 70% RH, and a photoperiod of 16:8 (L:D) h. Eggs were collected daily and put in petri dishes for hatching. Larvae were fed on pollen. Before each experiment, the coccinellids were placed individually in 50-mm petri dishes and starved for 24 h.

Eggs and larvae of the Colorado potato beetle were obtained from a stock of individuals collected at L'Assomption (73° 25′ W, 45° 50′ N), PQ, Canada, in May 1993 and reared on 'Kennebec' potato plants. All eggs used in the tests were <24 h old. First instars were used the day following hatching. Older larvae were categorized using the Boiteau & Le Blanc (1992) key based on width of cephalic capsule.

Voracity Studies in Petri Dishes. For all stages, a minimum of 15 predators were individually given either eggs, first-, second-, third-, or fourth-instar Colorado potato beetles. Number of prey offered, between 2 and 20, was greater than the maximum daily attack rate observed in preliminary tests. Experiments were held at 25°C in 50-mm petri dishes under a photoperiod of 16:8 (L:D) h. Killed prey (as determined by broken chorion for eggs and by death for larvae) were counted after 24 h. Mortality data were corrected by subtracting the mean mortality observed in the controls (same system without the predator). For each prey, rates of attack by the different predators were compared using an analysis of variance (ANOVA) followed by a Fisher's protected least significance difference (LSD) test if necessary.

Temperature Effect on Predation Effectiveness. The effect of temperature on predation effectiveness of *C. maculata* adults and larvae was studied using four-leaf potato stem sections placed in a hole made in 2-liter plastic containers. These were placed in a second container with 200 ml of water to prevent the potato leaflets from drying during the experiment. The system was closed with muslin held by a rubber band around the top container.

Adult, third-, and fourth-instar *C. maculata* were individually placed on a potato leaflet previously infested with either one Colorado potato beetle egg mass or with first or second instars randomly placed on the plant. The number of prey offered to each predator was the same as that used in the petri dish experiments. The test was repeated 20 times for every predator–prey combination. Because of the relatively low attack rate observed in the petri dish experiment, the *C. maculata* third-instar/Colorado potato beetle second-instar combination was not tested. Experiments were conducted under a photoperiod of 16:8 (L:D) h, at 7.5, 10, 15, 20, 25, and 30°C. Killed prey were counted after 24 h. Mortality data were corrected by subtracting the mean mortality observed in the controls (same system without the predator). Linear regressions were done for each predator–prey combination using the number of prey killed as a function of temperature. Two factor ANOVA and Fisher's protected LSD tests were carried out to compare effectiveness of different predator stages over all temperatures.

Plant Structure Effect in Predation Assessments. For each predator–prey combination, predation data obtained at 25°C in the potato stem experiments were compared (ANOVA and Fisher's protected LSD tests) with the data obtained in the petri dish studies (done at 25°C) to look at the effect of using a plant structure in the measurement of predator effectiveness. Both experiments were conducted in the same incubator, under the same conditions of light and humidity. For all experiments, statistical tests were done with the software SuperAnova (Abacus Concepts 1989).

Results

Voracity Studies in Petri Dishes. Every predator stage attacked every prey stage, except the youngest coccinellids (first instars) upon the oldest potato beetles (fourth instars) (Table 1). Some small larval predators fed by sucking the body fluids of larger prey. However, most of these large prey survived. The highest voracity was obtained by the adult predators who attacked an average of 11.1 eggs, and killed an average of 14.0 first instars and 4.3 second instars in 24 h. On both eggs and

Table 1. Comparative voracity of adults and larval instars of *C. maculata* toward Colorado potato beetle immature stages (mean number of prey killed ± SEM)

Predator	Prey				
	Eggs	First instars	Second instars	Third instars	Fourth instars
Adults	11.1 ± 0.7a (20)[a]	14.0 ± 0.8a (20)	4.3 ± 0.5a (10)	1.1 ± 0.2a (6)	0.4 ± 0.2ab (2)
Fourth instars	9.0 ± 0.3b (15)	11.2 ± 0.5b (15)	3.4 ± 0.2b (7)	0.9 ± 0.1ab (4)	0.7 ± 0.2a (2)
Third instars	6.1 ± 0.3c (10)	6.3 ± 0.2c (10)	2.0 ± 0.2c (5)	0.8 ± 0.1ab (3)	0.5 ± 0.1ab (2)
Second instars	2.9 ± 0.2d (8)	2.4 ± 0.1d (8)	0.8 ± 0.2d (4)	0.6 ± 0.2bc (2)	0.2 ± 0.1bc (2)
First instars	1.0 ± 0.2e (5)	0.7 ± 0.1e (5)	0.6 ± 0.1d (2)	0.2 ± 0.1c (2)	0.0 ± 0.0c (2)

Means followed by different letters within the same column are significantly different (Fisher's protected LSD test; $P < 0.05$).
[a] Numbers in parenthesis indicate density of prey offered.

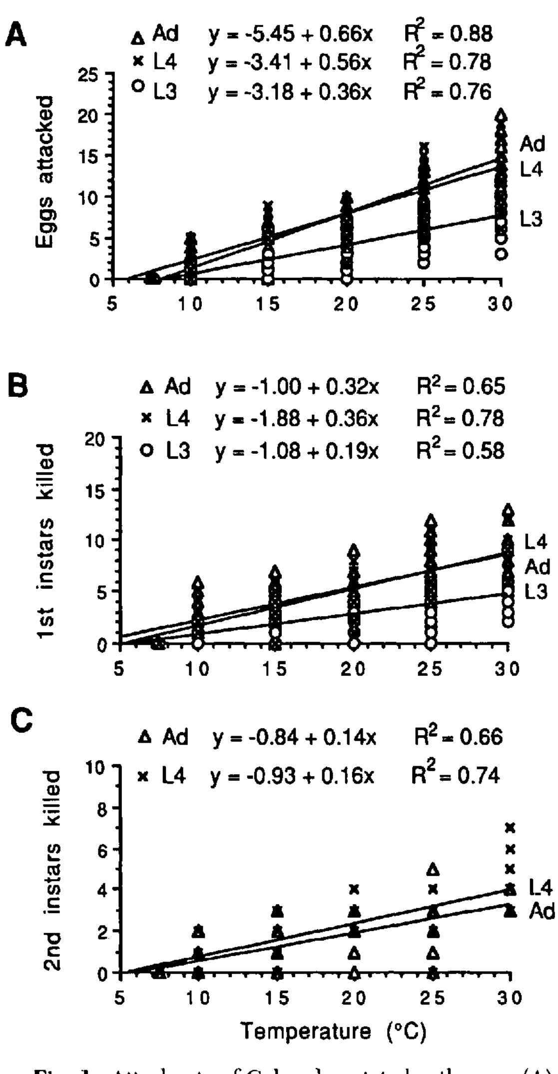

Fig. 1. Attack rate of Colorado potato beetle eggs, (A) first instars, (B) and second instars, (C) by *C. maculata* adults, fourth, and third instars over a 24-h period as a function of temperature.

first instars of Colorado potato beetles, predation by third- and fourth-instar *C. maculata* was ≈50 and 80% of the adults voracity (Table 1). Except for the two youngest predator stages, the number of first-instar prey killed by the predator was greater than the number of eggs attacked.

Temperature Effect on Predation Effectiveness. Regression analysis performed on the data showed a significant effect of temperature on all the predator–prey combinations tested (P = 0.0001). No predation was observed at 7.5°C. From 10 to 30°C, the number of prey killed by the three life stages of the predator increased as a strictly linear fit with temperature for eggs, first instars, and second instars (Fig. 1). At each temperature, predation effectiveness by *C. maculata* fourth instars toward Colorado potato beetle immature stages did not differ significantly from that of the adult coccinellids, except on second instars at 20°C (Tables 2, 3, and 4). Predation of *C. maculata* third instars on eggs and first-instar prey was ≈50% of that observed with adult and fourth-instar predators (Tables 2 and 3).

Plant Structure Effect in Predation Assessments. Comparing egg predation obtained in petri dishes and on potato stems, no significant differences can be observed between the two systems (Table 5). Conversely, predation on first and second instars decreased significantly by 38 to 56% in the potato stem system compared with the petri dish tests (Table 5).

Discussion

Voracity of adult *C. maculata* observed in petri dishes was similar to results obtained by Groden et al. (1990), although their mean daily consumptions, 8 eggs, 11 first instars, 3 second instars, 0.6 third instar, and 0.1 fourth instar, were slightly lower. This may be caused by the lower temperature (22–23°C) and larger petri dishes (90 mm) under which their experiments were conducted.

Table 2. One-factor ANOVA values and mean number of Colorado potato beetle eggs attacked by adults and larval instars of *C. maculata* on potato stems at different temperatures

Predator	Temp, °C					
	7.5	10	15	20	25	30
Adults	0.00a	1.65a	3.85a	7.30a	10.20a	15.85a
Fourth instars	0.00a	2.20a	4.65a	7.50a	10.05a	13.75a
Third instars	0.00a	0.45b	2.15b	3.39b	5.90b	8.21b
df	2	2	2	2	2	2
F value	—	7.82	12.253	29.11	19.40	18.62
P value	—	0.001	0.0001	0.0001	0.0001	0.0001

Means followed by different letters within the same column are significantly different (Fisher's protected LSD test; $P < 0.05$).

Predation rates on eggs observed in the potato stems experiments were also comparable with those observed in petri dishes by Groden et al. (1990). Over a 15–30°C range, the mean daily consumption rates of *C. maculata* adults on eggs of the Colorado potato beetle were linearly correlated with temperature, going from about 4 eggs consumed at 15°C to 14 eggs consumed at 30°C. Mack & Smilowitz (1982) obtained similar responses to temperature with *C. maculata* adults and third instars feeding on green peach aphids, *Myzus persicae* (Sulzer), placed on three-leaf potato stems, with both handling rates increasing linearly with temperature between 15.6 and 32.2°C.

It is of great importance that the predator can be active under the low temperatures encountered during early season, particularly in Quebec. Although its predation is reduced, *C. maculata* adults and older larvae are active when temperature is as low as 10°C. The lower predation activity is counterbalanced by the fact that feeding and development of the prey is also seriously affected by low temperatures (Logan et al. 1985, Ferro et al. 1985). Effect of temperature on other natural enemies of the Colorado potato beetle has also been reported. Obrycki et al. (1985, 1987) showed that the egg parasitoid *Edovum puttleri* Grissell (Hymenoptera: Eulophidae) did not survive under a temperature of 12.8°C. Also, no probing or parasitism was observed below 17°C (Lashomb et al. 1987). Although predation of Colorado potato beetles immature stages by *Podisus maculiventris* (Say) and *Perillus bioculatus* (F.) (Hemiptera: Pentatomidae) is well known, the effect of temperature on their predation does not seem to be documented. Nevertheless their lower developmental thresholds have been estimated respectively to be 10.7–11.7°C (De Clercq & Degheele 1992) and 14.6–16.5°C (Shagov 1968). Developmental thresholds of *C. maculata* preimaginal stages range between 9.4 and 12.7°C (Obrycki & Tauber 1978). Compared with *P. maculiventris* and *C. maculata*, *P. bioculatus* seems to be more disadvantaged under low temperatures because the egg and larval developmental thresholds of the Colorado potato beetles were estimated to be 10°C (Logan & Casagrande 1980).

Laboratory experiments in a small arena such as petri dishes furnish estimates of the maximum potential of predator consumption under near-optimum conditions (Tamaki & Olsen 1979, Tamaki et al. 1981). The use of a plant structure provides data relating more to the field conditions by adding components such as searching of predator and the possibility of refuges for prey (Tamaki & Olsen 1979). The similarity of egg predation level observed in both experimental systems can be explained by the fact that a single egg mass was put on the plant, as it was done in the petri dish tests. Once the predator had found the egg mass, it did not need to search much to find other prey. However, because the larval prey were placed randomly and able to move on the leaflets, the predator had to spend more time searching for food. Carter et al. (1984) showed that plant structure is an important factor affecting predator efficiency. Morphological characteristics of the plant species influence prey distribution, predator encounter rate with

Table 3. One-factor ANOVA values and mean number of Colorado potato beetle first instars killed by adults and larval instars of *C. maculata* on potato stems at different temperatures

Predator	Temp, °C					
	7.5	10	15	20	25	30
Adults	0.00a	3.40a	3.95a	5.62a	6.95a	8.07a
Fourth instars	0.00a	2.60a	3.40a	5.05a	7.40a	8.56a
Third instars	0.00a	1.20b	2.10b	2.80b	3.65b	4.57b
df	2	2	2	2	2	2
F value	—	14.91	5.32	20.88	17.55	18.12
P value	—	0.0001	0.0076	0.0001	0.0001	0.0001

Means followed by different letters within the same column are significantly different (Fisher's protected LSD test; $P < 0.05$).

Table 4. One-factor ANOVA values and mean number of Colorado potato beetle second instars killed by adults and larval instars of *C. maculata* on potato stems at different temperatures

Predator	Temp, °C					
	7.5	10	15	20	25	30
Adults	0.00a	0.85a	1.30a	1.70a	2.40a	3.46a
Fourth instars	0.00a	1.00a	1.60a	2.35b	2.90a	4.00a
Third instars	—[a]	—	—	—	2.60a	—
df	1	1	1	1	2	1
F value	—	0.42	1.18	7.74	1.18	2.17
P value	—	0.5228	0.2843	0.0084	0.3159	0.1514

Means followed by different letters within the same column are significantly different (Fisher's protected LSD test; $P < 0.05$).
[a] Experiment with third instars conducted only at 25°C.

prey, and consequently the energy spent searching (Belcher & Thurston 1982, Carter et al. 1984). The comparison of the results obtained in the two experimental systems clearly illustrates the importance of using the target plant species when evaluating predator activity. Although the four-leaf potato stem sections were quite simple and corresponded in a certain way to the young potato plant in the early season, the complexity of the environment is obviously much greater in the field. Consequently, we should expect the actual predation effectiveness to be much less.

The objectives of this study were not to estimate the predation of *C. maculata* in a field situation, but to study the effectiveness of larvae and adults, under a certain range of temperatures. The results presented here showed that in a simple system where flight is not needed or permitted, predation on Colorado potato beetle eggs and young instars by fourth-instar *C. maculata* is comparable with predation by adults, and predation by third instars is approximately half of that. Younger than third instars, *C. maculata* seem not to be of interest for eventual inundative releases. These results also indicate that the target developmental stages of the prey would be essentially the eggs, first instars, and second instars.

It would be now needed to determine how adults would behave after being mass released in a potato field in early season during the peak of the egg-laying period of Colorado potato beetles. In the case where most coccinellids would fly away and leave the field, releases of third instars should be assessed to use entirely the duration of the fourth larval stage. Because the predation activity of third and fourth instars would only last about a week, depending on temperature and food availability, it would also be important to know if the time spent eating in potato fields, since their release, could lessen their tendency to fly away once the beetles become adults.

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Table 5. Effect of using a plant structure in the measurement of predation effectiveness on eggs, first, and second instars of Colorado potato beetles by adults, fourth-, and third-instar *C. maculata*

Predator	Prey								
	Eggs			First instars			Second instars		
	Dish[a]	Stem[b]	Δ	Dish	Stem	Δ	Dish	Stem	Δ
Adults	11.1	10.2	−8%	14.0	6.9*	−51%	4.3	2.4*	−44%
Fourth instars	9.0	10.1	+12%	11.2	7.4*	−38%	3.4	2.2*	−35%
Third instars	6.1	5.9	−3%	6.3	3.7*	−41%		—	

Mean number of prey killed at 25°C over 24 h (petri dish tests/potato stems tests). * Indicates means are significantly different between the two experimental systems (Fisher's protected LSD test, $P < 0.001$). Δ Indicates the difference in percentage.
[a] Mean number of prey killed in the petri dish experiments.
[b] Mean number of prey killed in the potato stem experiments.

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