

Intraspecific Competition by the Colorado Potato Beetle (Coleoptera: Chrysomelidae) on Potato Plants, *Solanum tuberosum*

ERIC LUCAS, DOMINGOS DE OLIVEIRA, AND MARIE-JOSEE HOULE

Université du Québec à Montréal, Département des sciences biologiques, C.P. 8888, Succursale Centre-ville, Montréal, PQ H3C 3P8 Canada

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ABSTRACT The aim of this study was to measure the effects of an increase in the density of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), on this insect. Two groups of 20 potato plants, *Solanum tuberosum* L., 'Superior', were subjected to defoliation by the Colorado potato beetle. The first group was infested by 15 larvae per plant and the second by 40 larvae per plant. Measurements of adult body weights were taken, as well as of the quantity of lipid reserves of adults collected upon emergence. Insects originating from plants infested by 15 larvae were significantly heavier and had accumulated significantly more lipid reserves than adults originating from plants infested by 40 larvae. The percentage of lipids over body weight was significantly lower at a density of 15 larvae per plant than at a density of 40 larvae per plant. The effects measured in the 40 larvae per plant group are the result of intraspecific competition phenomena.

KEY WORDS *Leptinotarsa decemlineata*, intraspecific competition, lipids

THE COLORADO POTATO beetle, *Leptinotarsa decemlineata* (Say), the most important potato pest in the world (Hare 1990), is the most injurious insect to agroecosystems in Quebec (Cloutier & Chagnon 1990). Recently, Tomlin & Sears (1992) have shown an interspecific competition phenomena between the Colorado potato beetle and the potato leafhopper, *Empoasca fabae* (Harris). This competition arises indirectly through reduced quality of food resources (Tomlin & Sears 1992).

During potato crop infestations, beetle densities can exceed 100 individuals per plant. Thus, it can be expected that Colorado potato beetle densities will give rise to an intraspecific competition phenomena by way of the reduction of leaf quality, in the same manner as in the study by Tomlin & Sears (1992).

Lipids are a good index of insect health and represent its principal energy source (Gillot 1980). They are particularly important during long-term processes, such as embryogenesis, metamorphosis, oogenesis, and survival in the absence of food, as well as during flight (Beenackers et al. 1981). Therefore, if there is competition, adult lipid reserves should be affected.

The aim of this work is to study the effect of an increase in the density of Colorado potato beetles on this pest. To evaluate the effects of a possible competition, we have chosen to measure larval survival, duration of larval development, total weight, and lipid mass of adults.

Materials and Methods

Field experiments were carried out in Sainte-Clotilde de Châteauguay (Québec) during the summer of 1989, and subsequent measurements were taken at l'Université du Québec à Montréal. Forty potato plants, *Solanum tuberosum* L., 'Superior', were isolated individually with muslin cages driven 25 cm into the ground to keep Colorado potato beetle adults from escaping after pupation and to prevent entrance by other adults. The 40 plants were divided into two experimental groups: 20 plants were artificially infested each with 15 first-instar Colorado potato beetle larvae (first treatment), and 20 plants were infested each with 40 first-instars (second treatment). Each potato plant represents a replication in the statistical analyses.

Adult descendents of first-generation larvae were collected at emergence and frozen at -18°C . It must be noted that in all cages the Colorado potato beetles had not entirely defoliated the plant. The leaves remaining on each plant after removal of adults were collected, dried at 70°C , after which dry weights were determined.

Because of important weight and size differences between male and female Colorado potato beetles (Balachowsky 1963), the sexes were separated, following Balachowsky's (1963) method.

To avoid weight fluctuations caused by ambient humidity, Colorado potato beetles were placed in

Table 1. Survival rate of *L. decemlineata* larvae on potato plants

Initial larval density	n (plants)	Survival rate	
		Mean	SD
15	19	0.814a	0.220
40	19	0.818a	0.221

Means followed by different letters indicate significant differences between groups ($\alpha = 0.05$).

a drying oven for 2 d at temperatures varying from 59 to 61°C. Beetles were then weighed by sex and by plant to 0.01 mg with an analytical balance. Weights were taken immediately after removal from the drying oven.

Lipids were dissolved according to the methods by Huey (1966) and Zitzman & May (1989). Beetles were grouped by plant and by sex. They were immersed in a mixture of methanol and chloroform (1:2) for 3 d. During this period the solvents dissolved the fats diffusing from the insects. The beetles were then dried for 24 h to allow evaporation of the solvents, after which they were placed in a drying oven for 48 h as previously described. The insects were weighed again upon removal from the drying oven. The weight of lipid reserves was obtained by subtracting the total dry weight after lipid extraction from the initial dry weight before extraction.

Larval survival rate was determined by dividing the total number of adults collected per plant by the number of larvae introduced, and then analyzed through a one-way analysis of variance (ANOVA) that compared the mean survival rate per plant for each treatment. The duration of larval development corresponds to the time between the introduction of first instars and the collection of adults upon emergence. Mean durations of the two larval density groups were compared through a one-way ANOVA (Scherrer 1984).

For each subgroup corresponding to a given plant and sex, mean individual body weight and lipid weight were calculated. From these results, mean body weight and lipid weight were calculated for the two 20-plant groups, and then compared through a two-way ANOVA (sex and treatment) (Scherrer 1984). The lipid reserve ratio was calculated by dividing lipid weight by total dry weight. A one-way ANOVA (Scherrer 1984) was then carried out to compare lipid ratios between the two larval density groups.

Statistical analyses were carried out with the SUPERANOVA software (Abacus Concepts 1989).

Results

The dry weight of the subsisting foliage after removal of adults did not differ significantly between the group with 15 introduced larvae and that with 40 introduced larvae. Larval survival rate was not significantly different between the two

Table 2. Mean duration of development of *L. decemlineata* from larval hatching until emergence of adults, on potato plants

Initial larval density	Duration of development, d		
	n	Mean duration	SD
15	235	31.166a	3.152
40	611	30.056b	2.765

Means followed by different letters indicate significant differences between groups ($\alpha = 0.05$).

treatments: 81.4% for the 15 larvae per plant group and 81.8% for the 40 larvae per plant group (Table 1).

The mean duration of larval development and pupation of 845 individuals was significantly longer for the 15 larvae per plant group (31.17 d) than for the 40 larvae per plant group (30.06 d) (ANOVA, $F = 25.268$, $df = 1$, $P = 0.0001$) (Table 2).

For adult dry weight, females were significantly heavier than males (ANOVA, $F = 7.411$, $df = 1$, $P = 0.0081$). There was no significant interaction between sex and treatment. The mean difference obtained between the two larval density groups was 16.3% for females and 14.6% for males. The differences according to treatment (ANOVA, $F = 14.286$, $df = 1$, $P = 0.0003$) show that adults of the 40 larvae per plant group were significantly lighter than those of the 15 larvae per plant group (Fig. 1).

The lipid reserve values differed significantly according to treatment (ANOVA, $F = 17.101$, $df = 1$, $P = 0.0001$) and showed, as previously, that the insects from the 40 larvae per plant group accumulated significantly less reserves than the 15 larvae per plant group (Fig. 2). The lipid reserve difference recorded for the group with 40 larvae per plant was, on average, 44.6% for females and 33.0% for males. There was no sex by treatment interaction and the values did not differ significantly according to sex.

The lipid mass ratio was significantly higher for males (13.9%) than for females (11.8%) (ANOVA, $F = 5.149$, $df = 1$, $P = 0.0263$) (Fig. 3). The group

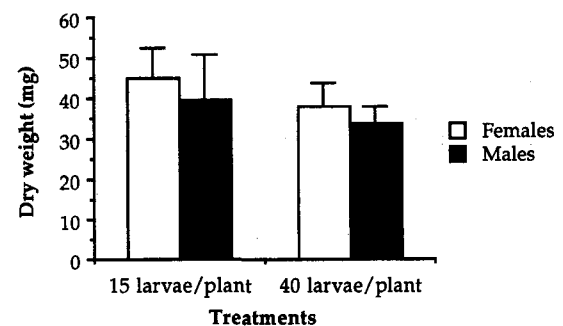


Fig. 1. Mean Colorado potato beetle dry weights on emergence, with standard deviations (treatment, $P = 0.0003$; sex, $P = 0.0081$).

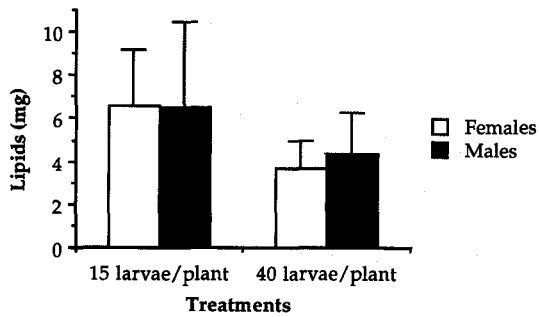


Fig. 2. Mean Colorado potato beetle lipid reserve weights upon emergence after desiccation, with standard deviations (treatment, $P = 0.0001$; sex, $P = 0.6102$).

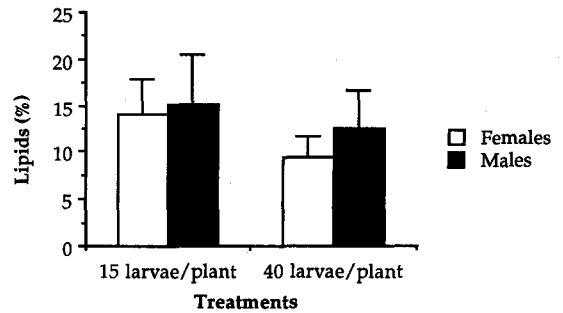


Fig. 3. Mean lipid reserve percentages of Colorado potato beetle dry weight upon emergence after desiccation, with standard deviations (treatment, $P = 0.0002$; sex, $P = 0.0263$).

with a density of 15 larvae per plant possessed a lipid mass ratio of 14.6%, which was significantly higher than the 11.0% ratio of the 40 larvae density group (ANOVA, $F = 15.845$, $df = 1$, $P = 0.0002$). There was no sex by treatment interaction (Fig. 3).

Discussion

The development of Colorado potato beetles collected from the high larval density group of plants, when compared with that of the low larval density group, was impeded. The dry weight of leaves remaining after removal of adults does not differ significantly between larval densities. Foliage was still present on every plant, thereby indicating that the insects did not lack food. Two possibilities can be considered: either the larvae from the 40 larvae per plant group on average consumed less than those from the 15 larvae per plant group (competition), or the potato plants compensated for the damages they sustained according to their extent (compensation). Had there been compensation by the plant, the Colorado potato beetles of both groups would roughly have had the same weight and the same quantity of lipid reserves, which is not the case. There must, therefore, have been greater intraspecific competition between the larvae of the 40 larvae per plant group.

The Colorado potato beetle is characterized by exploitation competition, one larva affecting the others through its consumption. Intraspecific competition causes either a decrease in the quantity of resources available for other individuals of the same species, or a decrease in the quality of the resource (Begon et al. 1990). The foliage was still present in each experimental unit at the end of the experiment, which means that the beetles did not defoliate the plants and were not deprived of food during the experiment. If differences in lipid reserves were not caused by starvation of the higher density group, the quality of the foliage should then have decreased.

Many hypotheses can explain this reduced quality. First, individuals of the high density group, because of their higher numbers, consume food of a

lower quality than individuals of the low density group that have access to resources of a higher quality. Young Colorado potato beetles explore the plant and select leaves according to their olfactory and gustatory qualities (Balachowsky 1963). Because of an increase in tannin and alkaloid ratios, leaf nutritive value decreases with age (Scriber & Slansky 1981). It was shown by de Wilde et al. (1969) that Colorado potato beetles were capable to distinguish between old and new leaves. Colorado potato beetles show a preference for young leaves (de Wilde et al. 1969, Houle 1991). Furthermore, Tomlin & Sears (1992) have shown that Colorado potato beetle larvae can distinguish leaves damaged by the potato leafhopper from healthy leaves, and that they prefer the latter.

A second hypothesis holds that the observed differences arise from the need of the Colorado potato beetles to move around more in the high density group to find places where food is suitable. These displacements give rise to energy expenditures and should, therefore, be reflected in lipid reserves that are, above all, energy reserves. Upon eclosion, Colorado potato beetle larvae are aggregated. According to Martel et al. (1986), during development larvae migrate and aggregations are reduced. Aggregations seemed greatest when population densities were very low (Martel et al. 1986). The 40 larvae per plant group could have spent more energy by attempting to disperse, thereby reducing their lipid reserves.

A third hypothesis states that the observed results arise from the production of secondary compounds by the plant that affect feeding behavior, development, and digestion of pests. The stress brought on the plant by 40 defoliating larvae would then have induced or increased the secretion of defense compounds. Green & Ryan (1971) have shown that damages suffered by potato plants following defoliation by Colorado potato beetles (larvae or adults) induce a rapid accumulation of secondary plant substances (proteinase inhibitors) in the exposed parts of the plant. These substances have proven efficient by affecting, among other things, the duration of larval development (Hare

1987), mortality on hatching, and defoliation rate (Sinden et al. 1986). The commercial potato plant, *S. tuberosum*, is characterized by the presence of two glycoalkaloids, solanin and chaconin, that could be responsible for the observed phenomena (Sinden et al. 1991). Solanin and chaconin were found to discourage intake of food (Stürckow & Löw 1961) yet solanin (Hsiao & Fraenkel 1968), at its natural concentration in leaves, has little or no effect on larval growth, and chaconin has no deterrent effect on Colorado potato beetles (Schreiber 1958).

Results concerning larval survival rate show that intraspecific competition had no lethal effect on the defoliators. The duration of larval development and pupation indicates that the group with a larval density of 15, with a 1-d delay, developed more slowly than the group with a larval density of 40. It has been shown by de Wilde et al. (1969) that older leaves, of a lesser quality, can induce premature diapause and a regression of the corpora allata in the Colorado potato beetle. The corpora allata are responsible for the secretion of juvenile hormone, which keeps the insects in the larval stage (Borror et al. 1989). It is, thereby, possible to formulate the following hypothesis: if foliage quality is reduced in the group with a larval density of 40, there could be reduction of the corpora allata and, therefore, a reduction in the secretion of juvenile hormone leading to an early metamorphosis.

The results pertaining to weight and lipid reserves clearly show that individuals from the density 40 larvae are weakened relative to those of density 15. The weight differences between the two treatments are greater for females than for males. The differences can then be explained by the fact that female larvae must consume more food than male larvae to reach a superior size and should, therefore, be more sensitive to a decrease in the quality of this food.

A decrease in lipid reserves could have an impact on pest population, particularly in the next generation. Lipids are the predominant energy source during embryonic development of insects (Beenackers et al. 1981). They represent an important part of mature insect eggs (Engelmann 1970) and they are found in considerable quantities in the yolk (Gillot 1980). This reduction in lipid reserves could, therefore, be reflected in female egg production, although there do not exist precise data to allow measurement of the direct impact of this reduction. Females, which at a larval density of 15 have a quantity of lipids similar to that of males, have much less lipids than males at a larval density of 40. This is probably the result, as with weight, of greater nutritional needs for females than males.

Lipid rates are lower in both groups for females than for males. Colorado potato beetles, however, double their lipid reserve weight during their adult life (Cherghel 1985), and female adults consume

more food than male adults (Balachowsky 1963). The proportion of the body weight represented by lipids is much higher in beetles from plants with a larval density of 15, which clearly shows that intraspecific competition acts more particularly at the level of fat accumulation by the organism. The energy required during diapause may be largely derived from the oxidation of fatty acids (Beenackers et al. 1981) and, hence, adults of the 40 larvae group, with a lower proportion of lipid reserves, should have a lower survival rate during diapause or a reduced fitness after diapause.

This study shows that a species such as the Colorado potato beetle, which can reach very high densities in agroecosystems, is affected by intraspecific competition. Further studies should be carried out to determine if secondary plant substances are produced, measure the impact of reductions of lipid reserves on Colorado potato beetle development and egg production, and measure the effects of competition at lower densities.

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