Reduced Fitness of the Colorado Potato Beetle (Coleoptera: Chrysomelidae) on Potato Plants Grown in Manure-amended Soil

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Environ. Entomol. 34(4): 963–968 (2005)

ABSTRACT Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is the most important insect defoliator of potatoes worldwide. In this study, we conducted a series of no-choice assays comparing Colorado potato beetle reproduction and development on potato plants grown in manure-amended and synthetically fertilized soils. Manure-amended soil received annual applications of raw cow manure since 1991 and additional applications of cull potato compost and green manure between 1991 and 1998. Plants grown in manure-amended soil were inferior Colorado potato beetle hosts compared with plants grown in synthetically fertilized soil. The observed negative effects were broad in scope. Female fecundity was lower in field cages set up on manure-amended plots early in the season, although it later became comparable between the treatments. Fewer larvae survived past the first instar, and development of immature stages was slowed down on manure-amended plots. In the laboratory, first instars consumed less foliage from plants grown in manure-amended soils. These results show that organic soil management is associated with plant characteristics unfavorable for beetle reproduction and development, which should be taken into consideration when designing fully integrated crop management systems.

KEY WORDS Colorado potato beetle, manure, insect herbivory, mineral balance hypothesis, sustainable agriculture

COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is the most important insect defoliator of potatoes worldwide. Both adults and larvae feed on potato foliage, and the absence of control measures often results in complete destruction of potato crops. High fecundity combined with a diverse and flexible life history make the Colorado potato beetle well adapted to existence in agricultural habitats. The beetles overwinter as adults in woody vegetation along field borders. They colonize potato fields in spring by flight and by walking. In the absence of host plants, the beetles can easily fly for several kilometers. After encountering a host habitat, they begin to reproduce, with a single female laying up to 600 eggs (Weber and Ferro 1994).

Potato growers rely mostly on synthetic chemicals to control the Colorado potato beetle. However, overreliance on insecticides is a dangerous and unsustainable approach that often increases input costs, pollutes the environment, and eventually results in failure caused by resistance development. This is especially true for the Colorado potato beetle because of its remarkable ability to evolve resistance to a wide variety of toxins (Casagrande 1987, Weber and Ferro 1994).

Improving plant resistance to Colorado potato beetle damage by adjusting soil management techniques is an underused, yet potentially valuable, tool in beetle suppression. Plants grown on organically managed soils fertilized with manure and compost have been shown to be less favorable hosts for phytophagous insects than plants grown on conventionally managed soils fertilized with synthetic fertilizers (Eigenbrode and Pimentel 1988, Phelan et al. 1995, 1996). Phelan et al. (1996) and Phelan (1997) suggested a hypothesis that the organic matter and microbial activity associated with organically managed soils afford a buffering capability to maintain nutrient balance in plants. An optimal nutrient balance results in both good plant growth and resistance to herbivory, while crops growing in soils without these biologically based buffering capabilities are more likely to take up either excess or insufficient levels of certain nutrients. The resulting imbalance in the ratio of certain mineral nutrients may result in rapid plant growth. However, affected plants may have their primary and/or secondary metabolism impaired, thus compromising their ability to resist or tolerate insect damage.

Earlier field studies (Alyokhin et al. 2005) showed consistent reduction in the densities of Colorado po-

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tato beetle larvae and summer-generation adults on potatoes grown in manure-amended soils. The differences could not have been attributed to the reduction in plant vigor in the absence of chemical fertilizers because we did not detect any difference in plant size or canopy cover, while yields were actually higher in manure-amended plots. Because natural enemy pressure on Colorado potato beetle populations in northern Maine is extremely limited, Alyokhin et al. 2005 speculated that, in accordance with the mineral balance hypothesis (Phelan et al. 1996, Phelan 1997), the observed response was plant-mediated. However, before this study, no direct evidence was available to show that growing on manure-amended soils indeed makes potato plants less suitable Colorado potato beetle hosts.

Materials and Methods

Field Plot Layout and Maintenance. The study was conducted during the 2004 growing season at the Maine Agricultural and Forest Research Station's Aroostook Research Farm in Presque Isle, ME. Eight plots used in this study were part of the Potato Ecosystem Project, described in detail elsewhere (Porter 1996, Gallandt et al. 1998, Alyokhin et al. 2005). Each plot was 41.0 m long and 14.6 m wide. Potatoes in all plots were planted in late May using a pick-type planter at the depth of 5–10 cm. Blended fertilizer was applied in a band 5 cm below and 5 cm to the side of the seed pieces at planting. Seed tubers were hand cut into ≈50-g pieces before planting. The distance between the rows was 90 cm, and tuber spacing within the rows was 23 cm. Potatoes were hilled ≈4 wk after planting (near the time of tuber initiation). During the preceding 2003 growing season, the plots were planted to barley, a rotation sequence common for commercial potato growers in the area. Fungal diseases were controlled by foliar applications of chlorothalonil (Bravo) and strobilurin (Quadris), and excessive Colorado potato beetle defoliation was prevented by foliar applications of *Bacillus thuringiensis* (Novodor) and *Beauveria bassiana* (BotaniGard). Spraying was done simultaneously on amended and nonamended plots using a tractor-mounted sprayer with raindrop nozzle. Insecticides were applied on 22 July, 30 July, and 20 August.

The eight plots were arranged in four blocks following randomized complete block design, so that one plot in each block received only synthetic fertilizer, whereas the other plot was amended with manure. Position of a plot within the block was selected at random. Nutrient needs of the synthetic system were met with chemical fertilizer applied at recommended rates (1344 kg/ha of 10-10-10 applied at planting and 56 kg/ha of urea ammonium nitrate solution side dressed at tuber initiation). Additional potash fertilizer was also broadcast in the spring based on soil test recommendations. Nutrients in the manure-amended system were provided by raw cow manure (rates adjusted to provide an average of 107 kg/ha of N available to plants based on laboratory analysis), residual soil fertility, and an at-planting application of ammonium sulfate fertilizer (78 kg/ha of actual N) to make up the balance of N fertilizer needs.

This fertilization regimen had been maintained since 1999. Potato plots in the manure-amended system had also been receiving annual applications of waste potato compost (22 t/ha) and cattle manure (44 t/ha) before primary tillage each spring from 1991 to 1998 (Alyokhin et al. 2005). The rotation crop used from 1991 to 1998 in the manure-amended system during that period was a green manure crop consisting of peas, oats, and hairy vetch. As a result, fertility, organic matter levels, and physical properties of the soils in synthetically fertilized and manure-amended plots were already different at the beginning of this study (Porter and McBurnie 1996, Gallandt et al. 1998).

Adult Mortality and Reproduction. Three plants were selected within each of the four manure-amended plots, and another three plants were selected within each of the four synthetically fertilized plots. The plants were selected at random, but none of them was located closer than 1.5 m to the plot edge. A wire frame screen cage (38 cm in diameter by 47 cm high) was fitted over each selected plant. All naturally occurring insects (including Colorado potato beetles) were removed from caged plants before the beginning of the experiment. Four female and three male field-collected adult overwintered beetles were introduced into each cage. All beetles were collected from an untreated potato plot located ~2 mi from the Potato Ecosystem Project plots. Cages were checked every other day, and the number of dead beetles and the number of eggs were recorded. The experiment took place from 15 July to 26 July 2004.

Because large cages interfered with tractor-mounted equipment, adults were transferred from the wire frame screen cages described above into the ventilated transparent cylindrical plastic cages (11.4 cm in diameter by 4 cm high). Three plants were selected within each of the plots as described above. A single cage was fitted at each selected plant over a randomly chosen undamaged potato leaf covering two to three of its leaflets. In total, four pairs of adults were transferred into each plot (a pair of adults was introduced into two of the three cages and two pairs were introduced into the remaining cage). Cages were checked every other day, and the number of dead beetles and the number of eggs were recorded. When plots were sprayed with insecticides or fungicides, the cages were completely covered with plastic bags. The bags were removed 15 min after the spraying. The experiment took place from 27 July to 25 August 2004.

Larval Mortality and Development. Five plants were selected within each plot following the same protocol as in the previous experiment. A single transparent plastic cage (see description above) was fitted over a randomly chosen undamaged potato leaf at each selected plant. Colorado potato beetle larvae were collected within 24 h after their hatching from field-gathered eggs. Collected larvae were transferred into the cage using a soft camel hair brush. Four larvae were introduced into each cage. Larvae hatching from the eggs collected at manure-amended plots were introduced into manure-amended plots, and larvae hatching from the eggs collected at synthetically fertilized plots were introduced into synthetically fertilized plots. All naturally occurring insects (including Colorado potato beetles) were removed from caged leaves before the beginning of the experiment.

Cages were checked every day. The number of larvae dying and the number of larvae molting to the next instar were recorded. The larvae were transferred to new leaves as original leaves deteriorated. After larvae reached the end of the fourth instar, a layer of field-collected soil was added to each cage to provide them with pupation substrate. The number of adult beetles that eclosed from pupae were recorded daily. When plots were sprayed with insecticides or fungicides, the cages were completely covered with plastic bags. The bags were removed 15 min after the spraying. The experiment took place from 16 July to 22 August 2004.

Foliage Consumption. Experiments were conducted in petri dishes (9.5 cm in diameter) in the laboratory. Feeding on potato foliage grown in manure-amended and synthetically fertilized soils was measured for first-instar larvae, fourth-instar larvae, and summer adults using a slightly modified technique originally described by Ferro et al. (1985). We chose the first-instar larvae because they were most affected by the soil management history in the previous experiments and fourth-instar larvae and adults because they consume more foliage compared with other stages (Ferro et al. 1985).

Larvae were reared from the egg masses collected in the field and incubated in an environmental chamber (Percival Scientific, Perry, IA) maintained at a 18 L:6 D photoperiod and 18°C. First-instar larvae were collected within 24 h after hatching from eggs. Fourth-instar larvae were collected within 24 h after molting to that stage. Adults were reared from field-collected late fourth-instar larvae that were brought to the laboratory and placed in ventilated plastic containers filled with field-collected soil. Emerging adults were collected within 24 h of eclosion from pupae and used in the experiment.

Potato leaflets used in the experiments were selected at random from manure-amended and -nonamended plots, excised, brought to the laboratory, and kept in vials with tap water. At the beginning of the experiments, their surface areas were measured using a LI-3000A portable leaf area meter (LiCor, Lincoln, NE). Then leaf petioles were wrapped in moist pieces of cotton, and the leaflets were placed into individual petri dishes.

Insects that were reared from eggs collected from manure-amended plots were positioned on potato leaves collected from manure-amended plots, whereas insects that were reared from eggs collected from nonamended plots were positioned on potato leaves collected from nonamended plots. Fifty first-instar larvae (five larvae per dish), 10 fourth-instar larvae (one larva per dish), and 10 beetle pairs (one male + one female per dish) were tested for each of the two soil treatments. In each experiment, an equal number of leaflets did not receive any larvae or adults and were used to correct consumption rates for natural leaflet growth. Insect and leaf condition was monitored daily.

The experiment with the first-instar larvae continued until all of them molted to the second instar, the experiment with the fourth-instar larvae continued for 2 d, and the experiment with adults continued for 10 d. Leaflets were changed daily. The areas of experimental and control leaves were measured immediately after removal from petri dishes. Leaf consumption was calculated as the difference between the leaf area at the beginning and at the end of 24 h, plus the mean difference in the area of control leaves at the beginning and at the end of the same period.

Statistical Analyses. Data normality was tested before the analyses at $\alpha = 0.01$ using Kolmogorov-Smirnov tests (PROC UNIVARIATE; SAS Institute 1999). When necessary, the data were transformed using rank transformations (Conover and Iman 1981). Means and SEs were calculated from the untransformed data. The effect of soil amendment on duration of larval development and adult fecundity was tested by analysis of variance (ANOVA; PROC GLM; SAS Institute 1999). Fecundity was calculated by dividing the number of eggs counted in a cage by the number of females that remained alive in that cage on the day of sampling. Mortality was compared between treatments using χ^2 tests (PROC FREQ; SAS Institute 1999). Consumption of foliage collected from manure-amended and synthetically fertilized plots was analyzed using *t*-tests (PROC TTEST; SAS Institute 1999).

Results

Adult Mortality and Reproduction. Mortality was not significantly different between the treatments. Very few beetles died during the first 2 wk of the study when beetles were kept in large field cages: 7.7% on manure-amended plots and 3.0% on synthetically fertilized plots ($\chi^2 = 1.41$; df = 1; $P = 0.2355$). Not surprisingly, mortality rate increased as beetles grew older. In the end of the second part of the study, it reached 37.5% on manure-amended plots and 28.1% on synthetically fertilized plots ($\chi^2 = 0.64$; df = 1; $P = 0.4245$).

Overall, the effect of soil amendment on female fecundity was not statistically significant ($F = 3.08$; df = 1,16; $P = 0.0985$) during the first part of the study when the beetles were kept in large cages. However, there was a significant interaction between soil amendment and sampling date ($F = 2.89$; df = 5, 80; $P = 0.0189$). Females laid noticeably fewer eggs on the manure plots on the first four sampling dates, but egg production became comparable between the treatments on the last two sampling dates (Fig. 1A). The latter trend continued during the second part of the study when the beetles were kept in small cages, with neither soil amendment ($F = 0.01$; df = 1,16; $P = 0.9310$) nor its interaction with sampling date ($F =$

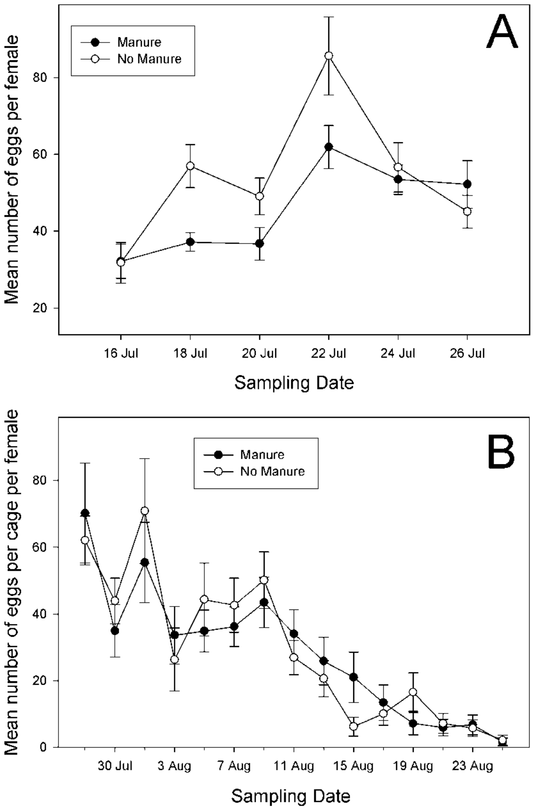

Fig. 1. Fecundity of Colorado potato beetle females on plants growing on manure-amended and synthetically fertilized soils. (A) Beetles kept in large metal screen cages. (B) Beetles kept in small plastic cages.

1.17; df = 14,224; P = 0.3033) being significant (Fig. 1B).

Larval Mortality and Development. Mortality of first instars was four times higher on manure-amended plots ($\chi^2 = 3.89$; df = 1; $P = 0.0485$), but we detected no effect on fourth instars ($\chi^2 = 0.19$; df = 1; $P = 0.6597$) or pupae ($\chi^2 = 0.16$; df = 1; $P = 0.6929$; Fig. 2). Mortality of second and third instars was too low for statistical comparison (Fig. 2). Total mortality (first instar to adult) was 53.8% on manure-amended plots and 46.9% on the synthetically fertilized plots ($\chi^2 = 0.4815$; df = 1; $P = 0.4877$).

On plants grown on manure-amended soil, development was significantly slower for the first ($F = 10.43$; df = 1,54; $P = 0.0021$) and fourth ($F = 11.98$; df = 1, 61; $P = 0.0011$) instars (Fig. 3). No such effect was observed for the second ($F = 1.19$; df = 1,54; $P = 0.2811$) or third instars ($F = 0.31$; df = 1,54; $P = 0.5776$; Fig. 3). Overall, larvae required 13.38 ± 0.32 (SE) d to complete development from the first instar to pupa on manure-amended plots, but only 12.85 ± 0.14 d on synthetically fertilized plots ($F = 26.63$; df = 1,54; $P < 0.0001$). The period spent as pupae was also longer on manure-amended plots ($F = 9.43$; df = 1,42; $P = 0.0037$) (Fig. 3). In total, it took 32.25 ± 0.39 d for the beetles to develop from first instars to adults on manure-amended plots compared with 30.15 ± 0.76 d on the synthetically fertilized plots ($F = 5.93$; df = 1,42; $P = 0.0192$).

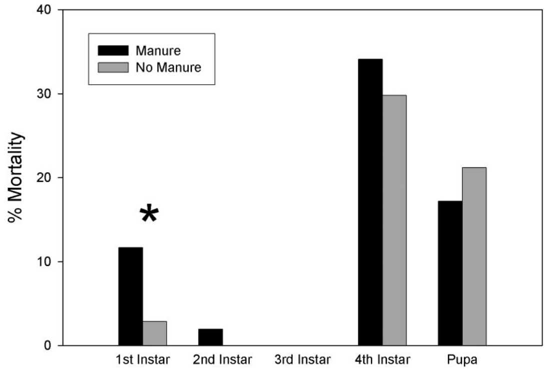

Fig. 2. Mortality of Colorado potato larvae on plants growing on manure-amended and synthetically fertilized soils. *Treatments that were significantly different from each other ($P < 0.05$).

Foliage Consumption. First instars feeding on foliage collected from manure-amended plots consumed, on average, 0.37 ± 0.02 cm^2 of foliage per larva before molting to the second instar. First-instar larvae feeding on the foliage collected from synthetically fertilized plots consumed 0.47 ± 0.03 cm^2 of foliage. This 27% difference was statistically significant ($t = 2.31$; df = 18; $P = 0.0328$). Fourth-instar larvae consumed 5.11 ± 0.62 cm^2/larva per day of foliage from manure-amended plots and 5.76 ± 0.53 cm^2/larva per day of foliage from synthetically fertilized plots (12% reduction on the manure-amended plots; $t = 0.80$; df = 18; $P = 0.4353$). Similarly, adults consumed 2.41 ± 0.12 cm^2/beetle per day of foliage from manure-amended plots and 2.69 ± 0.15 cm^2/beetle per day of foliage from synthetically fertilized plots (11% reduction caused by manure amendment; $t = 1.44$; df = 18; $P = 0.1678$).

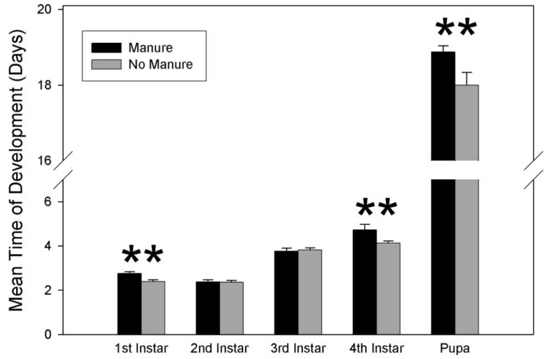

Fig. 3. Time of development to adulthood of Colorado potato larvae on plants growing on manure-amended and synthetically fertilized soils. **Treatments that were significantly different from each other ($P < 0.01$).

Discussion

Our findings indicate that potato plants grown in manure-amended soil were inferior hosts to the Colorado potato beetle compared with plants grown in synthetically fertilized soil. The observed multiple effects were broad in scope, including lower fecundity, higher mortality, slower development, and lower foliage consumption on manure-amended plots. First-instar larvae appeared to be most vulnerable, with statistically significant differences detected in each experiment involving them. Results for other life stages were less consistent. However, even in the absence of statistically significant differences, the general trend usually remained toward lower beetle performance on plants from manure-amended plots. This was true for the mortality of overwintered adults and fourth-instar larvae, as well as for the foliage consumption by the fourth-instar larvae and summer adults.

Results of these experiments are consistent with the results of a 5-yr field study by Alyokhin et al. (2005), who reported lower Colorado potato beetle densities on plants grown in manure-amended soil. Moreover, a similar situation was observed in at least two other crop/pest systems. Eigenbrode and Pimentel (1988) recorded significantly lower peak densities of two flea beetle species, *Phyllotreta cruciferа* (Goeze) and *P. striolata* (F.), on collards grown in manure-amended soil compared with the collards receiving a comparable amount of macronutrients from synthetic fertilizers. Also, when given a choice between corn plants grown in manure-amended and synthetically fertilized soils, European corn borer [*Ostrinia nubilalis* (Hübner)] females strongly preferred to oviposit on the latter (Phelan et al. 1995, 1996). By directly measuring Colorado potato beetle performance on plants under different fertilization regimens, we obtained further evidence of plant-mediated effects of soil amendments on herbivore populations.

Although manure amendment was the main treatment variable in this study, the observed differences should not be automatically attributed to the short-term effects of manure application during the 2004 growing season. Manure-amended plots were receiving organic amendments for 13 yr before the beginning of this study. In addition to raw cow manure, this included potato compost and green manure applied between 1991 and 1998 (Porter and McBurnie 1996, Gallandt et al. 1998). In the study by Phelan et al. (1995), multiyear organic management was required for soils to acquire their buffering capacity. Therefore, it is likely that the reported effect was caused by the soil management history on manure-amended plots and not to the immediate effects of manure application.

The exact mechanisms of the observed phenomenon still remain to be determined. Earlier studies have shown that performance of phytophagous insects is determined in large part by concentrations of various mineral elements in host plants and by their ratios to one another (Clancy et al. 1988, Clancy 1992, Clancy and King 1993, Busch and Phelan 1999, Beanland et al. 2003). Phelan et al. (1996) and Phelan (1997) suggested that plants grown on organically amended soils have a more optimal mineral balance than plants grown on synthetically fertilized soils. Evolving on soils amended with natural equivalents of manure and compost, plants developed ability to use available nutrients to achieve the most favorable equilibrium between growth, reproduction, and defense against insect herbivores. Using synthetic fertilizers may shift this balance toward growth and reproduction, while compromising defense capabilities of affected plants.

In direct accordance with the mineral balance hypothesis (Phelan et al. 1996, Phelan 1997), Alyokhin et al. (2005) found significant differences in mineral composition of potato leaves collected from manure-amended and synthetic fertilizer–treated plots. Colorado potato beetle infestations were consistently heavier on synthetically fertilized plots. Furthermore, mineral content of potato leaves explained 40–57% of the variation in beetle populations observed among the experimental plots in that study. Therefore, we believe that the observed reduction in beetle fitness could be explained by less favorable biochemical composition of potato foliage on manure-amended plots. However, additional studies are required to determine more specific mechanisms responsible for the described phenomenon.

The Colorado potato beetle is a very prolific and voracious pest. Therefore, the decrease in female fecundity and larval survivorship observed in this study is unlikely to be sufficient for keeping beetle densities below economically damaging levels. Nevertheless, they might complement other mortality sources, thus decreasing the amount of chemicals necessary to suppress beetle populations. In addition, development slowdown may allow plants more opportunity to compensate for damage, especially in combination with lower leaf consumption by the beetles. Also, it may extend a window of opportunity for using *Bacillus thuringiensis*–based insecticides, which are most efficient against early instars. Furthermore, a slower rate of development may allow more predation and parasitism in areas with significant natural enemies. Without question, manure cannot by itself be considered as an alternative to insecticides in commercial potato production. However, it does create a less favorable environment for beetle reproduction and development. Therefore, it should be considered when designing fully integrated, ecologically sound crop management systems.

Acknowledgments

We thank E. Ganga and G. Sewell for technical assistance. This work was supported in part by the Scientific and Technical Research Council of Turkey (the NATO Science Fellowship to Remzi Atlihan), USDA-CSREES-IFAFS 2001-52101-11308, the University of Maine/CSREES Hatch Project ME08912-02, and the Maine Potato Board. This is Publication 2799 of the Maine Agricultural and Forest Experiment Station.

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Received for publication 10 February 2005; accepted 14 May 2005.