Stimulatory and Suppressive Effects of Novaluron on the Colorado Potato Beetle Reproduction

ANDREI ALYOKHIN,[1] RYAN GUILLEMETTE, AND RAYMOND CHOBAN[2]

School of Biology and Ecology, University of Maine, 5722 Deering Hall, Orono, ME 04469

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ABSTRACT The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is one of the most damaging insect pests of potato, *Solanum tuberosum* L. Novaluron is a relatively new benzoylphenyl urea insect growth regulator with good activity against this pest. Earlier studies revealed that feeding on potato foliage treated with novaluron induces reversible egg hatch inhibition in adult Colorado potato beetles. We investigated whether novaluron effects depend on physiological state of the beetles at the time of exposure. The following four treatments were created: young beetles unmated at the beginning of the experiment and feeding on potato foliage treated with novaluron, young beetles unmated at the beginning of the experiment and feeding on untreated foliage, older beetles mated at the beginning of the experiment and feeding on foliage treated with novaluron, and older beetles mated at the beginning of the experiment and feeding on untreated foliage. The beetles were exposed to the respective treatments for 5 d. After that, both young and older beetles feeding on novaluron-treated leaves were switched onto untreated leaves and monitored for another 5 d to test their ability to recover. Young beetles unmated at the beginning of the experiment produced more eggs after feeding on the treated foliage, possibly indicating the presence of a pesticide-induced homeostatic modulation. No such effect was observed in the older beetles. Regardless of beetle physiological state at the beginning of the experiment, eggs produced on treated foliage did not hatch. The beetles eventually resumed laying viable eggs after being switched onto untreated foliage, with the recovery being delayed by ≈24 h in young beetles compared with older beetles. Our results corroborate that novaluron reduces fertility of treated adults.

KEY WORDS *Leptinotarsa decemlineata*, novaluron, inhibition of egg hatch, sublethal effect

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is one of the most damaging insect pests of potato, *Solanum tuberosum* L. Some beetle populations are also injurious to tomato, *Solanum lycopersicum* L., and eggplant, *Solanum melongena* L. High fecundity (≈600 eggs per female), a diverse and flexible life history, and an ability to develop resistance within a few generations to a variety of insecticides make Colorado potato beetle management a difficult task. Despite a considerable research effort, protection of affected crops remains a challenge (Weber and Ferro 1994, Alyokhin et al. 2008a).

The beetles overwinter in the soil as adults, often congregating in woody vegetation along field borders. After diapause termination in spring (mid- to late May in Maine), the overwintered beetles colonize potato fields by flight and by walking, and females start laying eggs soon after arriving to host habitats (Weber and Ferro 1994). A single generation is completed per year under climatic conditions typical for northern Maine (Drummond and Groden 1996), but two to three generations are typical for areas with warmer climates. Both adults and larvae feed on potato foliage, and the absence of control measures often result in complete defoliation of potato fields.

One of the major challenges in managing the Colorado potato beetle is its remarkable ability to develop insecticide resistance (for review, see Alyokhin et al. 2008a). Since the first case of DDT failure was observed in 1952 (Quinton 1955), the beetles have become resistant to numerous active ingredients in most major classes of insecticides. Although resistance problems could be attributed in part to traits inherent to this species, excessive and often uneducated use of chemicals greatly aggravates the situation (Casagrande 1987, Alyokhin et al. 2008a). With the era of abundant and cheap broad-spectrum insecticides coming to an end, development and registration of new compounds is an increasingly complicated and costly process. Therefore, good stewardship and maximum use of the existing materials is an important task for the grower and research communities alike.

Novaluron (1-[3-chloro-4-(1,1,2-trifluoro-2-trifluoromethoxy-ethoxy)phenyl]-3-(2,6-difluorobenzoyl)urea)

[1] Corresponding author, e-mail: alyokhin@potatobeetle.org.
[2] Chemtura Corporation, 1513 Briarwood Dr., Williamstown, NJ 08094.

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(Rimon, Chemtura Corporation, Middlebury, CT) is a relatively new benzoylphenyl urea insect growth regulator with good activity against the Colorado potato beetle (Cutler et al. 2005a,b, 2007) and low mammalian toxicity (Barazani 2001, Ishaaya and Horowitz 2002). Unfortunately, being a chitin synthesis inhibitor, novaluron is relatively slow to act on larvae and does not cause any adult mortality. Therefore, commercial growers are often reluctant to use it on their fields. Demonstrating additional negative effects on adult beetles is important for a wider acceptance of this insecticide.

Cutler et al. (2005a) observed that feeding on novaluron-treated potato plants by newly emerged adult Colorado potato beetles reduced both oviposition and hatch rates. Alyokhin et al. (2008b) recorded a similar reduction in the proportion of hatching eggs for overwintered beetles, but oviposition in their experiments was not significantly different between the treatments. To explain the observed difference, Alyokhin et al. (2008b) speculated that novaluron effects might depend in part on physiological state of the beetles at the time of the study. Testing this hypothesis was the main goal of the current study.

Materials and Methods

Colorado potato beetle egg masses were collected from untreated experimental plots on Aroostook Research Farm, Presque Isle, ME, and incubated in the environmental chamber under 25 ± 1°C and a photoperiod of 18:6 (L:D) h. First instars were placed on potted potato plants ('Katahdin') within 24 h from hatching and reared to adulthood in wooden frame screen cages in the greenhouse. Teneral adults were collected within 24 h after their emergence from the soil and used in the experiment.

Beetle sex was identified under the dissecting scope. Ten males and 10 females were placed in cages made of ventilated transparent plastic containers (32 by 20 by 12.5 cm) lined with moistened paper towels. Freshly excised terminal potato leaves ('Katahdin') were placed in each cage and replaced after approximately ≈75% of the leaf area was consumed by the beetles.

Half of the beetles were used immediately after collection (young unmated adults). Another half were incubated on untreated potato foliage in the environmental chamber (Percival Scientific, Inc., Perry, IA) under 25 ± 1°C and a photoperiod of 18:6 (L:D) h for 10 d (older mated adults). Earlier study has shown that under such conditions beetles become capable of mating ≈3 d after completing pupation and digging out of the soil (Alyokhin and Ferro 1999b).

Half of both young unmated and older mated adults were placed on freshly excised terminal potato leaves dipped in solution of novaluron (Rimon, 100 g liter^{-1} EC, Chemtura Corporation, Middlebury, CT) in distilled water with added surfactant (0.1% Tween, vol: vol). The solution was prepared at the concentration of 0.187 g (AI) liter^{-1} (equivalent to the high label rate of 87 g [AI] ha^{-1} assuming an application rate of 465 liters/ha). Another half of adults were placed on control leaves dipped in tap water with added surfactant. This created four treatments (young unmated beetles treated with novaluron, young unmated untreated beetles, older mated beetles treated with novaluron, and older mated untreated beetles). Obviously, young beetles became older and mated over the duration of the experiment, but for convenience we continue referring to them as young unmated adults.

The beetles were exposed to respective treatments for 5 d. After that, both young and older beetles feeding on novaluron-treated leaves were switched onto untreated leaves and monitored for another 5 d to test their ability to recover.

Cages were checked daily. To determine fecundity, eggs laid by the beetles were collected, counted under the dissecting scope, and placed in individual petri dishes (100 by 15 mm). Both the number of egg masses and the number of eggs in each mass were recorded. Dishes were incubated until hatching as described above. To determine fertility, the number of first instars hatching from each collected egg mass was recorded.

The experiment was replicated four times. Forty pairs of the young beetles per treatment were tested. Because some of the older beetles died during the 10-d incubation period before the beginning of the experiment, the number of tested beetles was reduced to five males and five females per cage, resulting in a total of 20 pairs per treatment.

Fecundity was compared between the treatments using the number of egg masses and eggs per living female in the cage on the day of egg collection. Fertility was compared using proportion of fertile eggs, calculated separately for each egg mass as the ratio of hatching larvae to the number of eggs in that mass. Fecundity data were transformed using rank transformations (Conover and Iman 1981), whereas fertility data were transferred using arc$\sqrt{x}$ transformations (Zar 1999). All the data were analyzed using two-way repeated measures analysis of variance (ANOVA) (PROC MIXED, SAS Institute 1999). Beetle physiological state at the beginning of the experiment (young unmated or older mated) and exposure to novaluron were regarded as the main effects. Because of significant interactions (see below), novaluron effects were further analyzed separately for the young unmated and older mated beetles using one-way repeated measures ANOVA (PROC MIXED, SAS Institute 1999), followed by separate *t*-tests on each day of the experiment conducted as described above (PROC TTEST, SAS Institute 1999). Presented means and standard errors were calculated from the untransformed data.

Results

Each female produced 0.78 ± 0.05 (mean ± SE) egg masses per day of experiment. Neither physiological state (ANOVA: $F = 1.81$; df = 1, 12; $P = 0.2033$) nor novaluron (ANOVA: $F = 0.01$; df = 1, 12; $P = 0.9814$) affected that parameter. However, the interaction be-

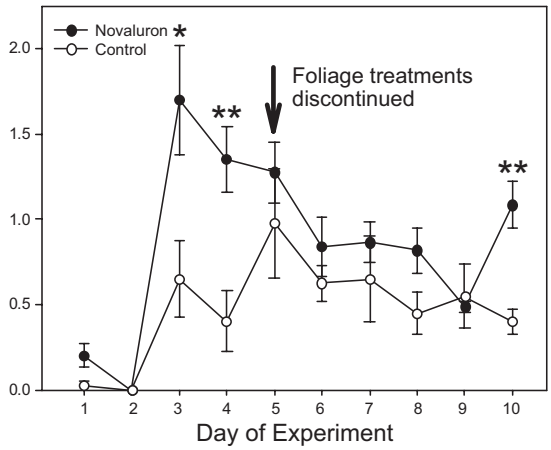

Fig. 1. Egg mass production by young Colorado potato beetles treated with novaluron. Error bars indicate standard errors. Asterisks indicate significant difference based on *t*-tests (*$P < 0.05$, **$P < 0.01$).

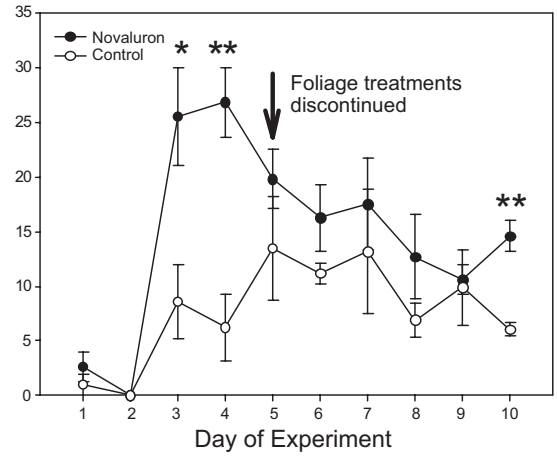

Fig. 2. Fecundity of young Colorado potato beetles treated with novaluron. Error bars indicate standard errors. Asterisks indicate significant difference based on *t*-tests (*$P < 0.05$, **$P < 0.01$).

tween those two factors was highly significant (ANOVA: $F = 10.21$; df = 1, 12; $P = 0.0077$). Young adults unmated at the beginning of the experiment produced significantly more egg masses after exposure to novaluron (ANOVA: $F = 9.18$; df = 1, 6; $P = 0.0231$) (Fig. 1), whereas egg mass production by older mated adults was not affected (ANOVA: $F = 3.50$; df = 1, 6; $P = 0.1104$). Interaction between novaluron and the day of the experiment was highly significant for the young unmated beetles (ANOVA: $F = 2.95$; df = 9, 54; $P = 0.0064$) but not for the older mated beetles (ANOVA: $F = 0.56$; df = 9, 54; $P = 0.8239$).

The number of eggs followed the same pattern as the number of egg masses. A young female unmated at the beginning of the experiment produced, on average, 17.14 ± 1.38 eggs per day, whereas an older mated female produced 11.12 ± 1.02 eggs per day. The difference was marginally significant (ANOVA: $F = 4.61$; df = 1, 12; $P = 0.0529$). Novaluron did not have a statistically significant effect on female fecundity (ANOVA: $F = 4.41$; df = 1, 12; $P = 0.0574$). The interaction between physiological state at the beginning of the experiment and novaluron was highly significant (ANOVA: $F = 9.76$; df = 1, 12; $P = 0.0088$). For the young unmated beetles, exposure to novaluron significantly increased the number of eggs laid (ANOVA: $F = 8.37$; df = 1, 6; $P = 0.0276$) (Fig. 2). The interaction between egg production and the day of experiment was also significant (ANOVA: $F = 2.76$; df = 9, 54; $P = 0.0098$). Novaluron application resulted in a spike of egg laying on days 3 and 4 of the experiment. The difference disappeared afterward, although it again became significant on the very last day of the experiment (Fig. 2). For the older mated beetles, neither effect of novaluron (ANOVA: $F = 3.82$; df = 1, 6; $P = 0.0983$) nor its interaction with the day of the experiment (ANOVA: $F = 0.71$; df = 9, 54; $P = 0.6995$) were statistically significant.

Although the young beetles unmated at the beginning of the experiment laid more eggs, their fertility was actually reduced compared with the older mated beetles. Only 35.83 ± 1.78% eggs laid by the young beetles hatched, compared with 53.77 ± 2.24% laid by the older beetles (ANOVA: $F = 8.38$; df = 1, 12; $P = 0.0135$). There was also a significant interaction between physiological state and the day of the experiment (ANOVA: $F = 4.51$; df = 8, 88; $P = 0.0001$), with fertility of the older mated beetles being higher in the beginning of the experiment (Fig. 3). Novaluron significantly reduced egg hatch (ANOVA: $F = 284.79$; df = 1, 12; $P < 0.0001$) (Fig. 3). There was a significant interaction between novaluron and the day of the experiment (ANOVA: $F = 8.88$; df = 9, 88; $P < 0.0001$). However, temporal dynamics of novaluron effects were similar for regardless of the physiological state, as evidenced by a lack of significant interaction (ANOVA: $F = 0.62$; df = 1, 12; $P = 0.4447$).

Separate analyses confirmed that novaluron significantly suppressed egg hatch in both young beetles unmated at the beginning of the experiment (ANOVA: $F = 164.14$; df = 1, 6; $P < 0.0001$) and older mated (ANOVA: $F = 116.70$; df = 1, 6; $P < 0.0001$) beetles. Interactions between novaluron and the day of the experiment were also significant (ANOVA: $F = 15.02$; df = 8, 43; $P < 0.0001$ and $F = 2.32$; df = 9, 45; $P = 0.0303$, respectively). All the beetles stopped reproducing while feeding on the novaluron-treated foliage and then recovered afterward (Fig. 3). However, older mated beetles continued laying viable eggs, although at a reduced rate, for 24 h after being placed on the treated foliage. This was not the case with the young beetles unmated at the beginning of the experiment. Also, older beetles seemed to recover more quickly after being switched on the untreated foliage.

Discussion

Results of the current study generally confirm earlier findings by Cutler et al. (2005a) and Alyokhin et al.

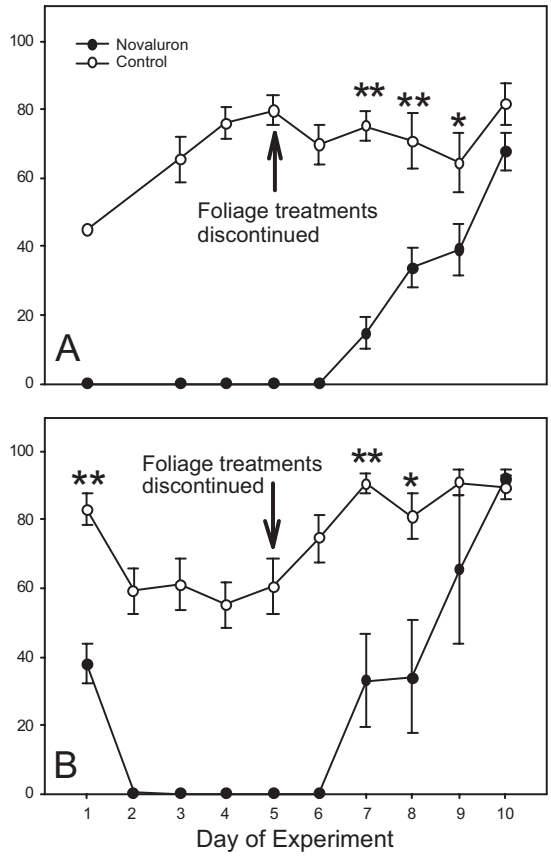

Fig. 3. Fertility of Colorado potato beetles treated with novaluron. (A) Young beetles. (B) Older beetles. Error bars indicate standard errors. Asterisks indicate significant difference based on *t*-tests (*$P < 0.05$, **$P < 0.01$). No separate *t*-tests were conducted when treated beetles produced no larvae.

(2008b) that feeding on novaluron-treated foliage induces reversible inhibition of egg hatch in adult Colorado potato beetles. Temporal patterns in the observed inhibition were very similar between older mated summer-generation beetles tested in this study and postdiapause beetle studied by Alyokhin et al. (2008b): production of viable eggs continued for 24 h after initiation of feeding on treated foliage, then seized completely and then resumed after the beetles were switched onto the untreated foliage. Young beetles did not lay any viable eggs when feeding on treated foliage in the beginning of the experiment, probably because they have not yet accumulated a minimum of 34 degree-days required to become reproductive (Alyokhin and Ferro 1999b) before being affected by novaluron. It also took them ≈24 h longer to reach full reproductive capacity after switching onto the untreated foliage. Similarly, in the study by Alyokhin and Ferro (1999a) ingestion of *Bacillus thuringiensis* delta-endotoxin was more deleterious to recently eclosed adults compared with older beetles that had completed reproductive development while feeding on untreated foliage.

Interestingly, we also observed an increase in fecundity of young beetles exposed to novaluron. Similarly, El Tahtaoui (1962) and Bajan and Kmitova (1972) observed increased fecundity in the Colorado potato beetles surviving infection by entomopathogenic fungus *Beauveria bassiana* (Bals.) Vuillemin. Also, Cutler et al. (2005a) reported that larvae hatching from the novaluron-treated eggs and surviving to the second instars weighed more compared with the larvae hatching from the control eggs.

Because sublethal effects historically received less attention compared to with the acute toxicity (Calabrese 2009), interpretation of our results represents a certain challenge. A phenomenon where exposure to low (sublethal or subtoxic) doses of chemical and other stressors has stimulatory effects on the exposed organism is known as hormesis. The stimulatory effects are believed to be the result of compensatory biochemical processes after a destabilization of normal homeostasis (Calabrese and Baldwin 2001, 2003; Cohen 2006; Calabrese 2009). Although hormetic response may involve a number of life history parameters, enhanced oviposition is probably the most common one in insects (Cohen 2006). The documented examples were extensively reviewed by Cohen (2006) and include stored-product weevil *Sitophilus granarius* (L.) (Kuenen 1958) exposed to DDT; *Spodoptera littoralis* Boisduval exposed to chlorpyrifos and phosfolan (Mansour 1978); wooly apple aphid, *Eriosoma lanigerum* (Hausmann), exposed to pyrethroids (Croft and Hoyt 1978, Penman and Chapman 1980); *Choristoneura fumifurana* Clemens exposed to fenitrothion and fenvalerate (Smirnoff 1983); *Nilaparvata lugens* Stål exposed to deltamethrin (Heinrichs and Mochida 1984); green peach aphid, *Myzus persicae* (Sulzer), exposed to azinphosmethyl (Lowery and Sear 1986); the stored-product weevil *Callosobruchus maculatus* (F.) exposed to several essential oils extracted from citronella, clove, and lemon (Lale 1991); citrus thrips, *Scirtothrips citri* (Moulton), exposed to malathion (Morse and Zareh 1991); and diamond back moth, *Plutella xylostella* (L.), exposed to fenvalerate and methomyl (Sota et al. 1988, Fujiwara et al. 2002).

Although hormesis is somewhat similar to our observations, the results do not fully fit the hormetic model and the definition of "hormesis." The hormesis is described by a biphasic dose–response curve with a stressor/chemical that is normally toxic to the organism at higher doses being stimulatory for some biological parameters at very low doses (Calabrese and Baldwin 2001, 2003; Cohen 2006; Calabrese 2009). Although inhibition of egg hatch could be qualified as a kind of stress, novaluron is not an adulticide. Therefore, in terms of the dose–response concept for hormesis, terms like "mild dose," "low dose," "sublethal dose," and "lethal dose" are essentially meaningless when considering Colorado potato beetle adults and novaluron. Furthermore, hormesis typically results in 0.3- to 0.6-fold increase in the measured parameter compared with a control group (Calabrese and Baldwin 2003), which is significantly smaller than a three-fold

increase in egg production observed in the current study.

Cohen (2006) suggested a broader term of pesticide-induced homeostatic modulation to include both hormesis and stimulatory effects of pesticides on nontarget organisms to which they are not lethal at label rates. For example, the fungicide mancozeb, the herbicide glyphosate, and the insecticide methyl parathion stimulated oviposition in the spider mite *Tetranichus urticae* (Boykin and Campbell 1982, , Maggi and Leigh 1983). Similarly, the herbicides acifluorfen and bentazon enhanced oviposition in the seed bugs *Geocoris punctipes* (Farlow and Pitre 1983) and *Geocoris pallens* (Yokoyama and Pritchard 1984). Increase in the fecundity of the Colorado potato beetles that were young and unmated at the beginning of the experiment seems to fit within the concept of the pesticide-induced homeostatic modulation. However, increase in the production of non-viable eggs does not really qualify as a stimulatory response because such eggs have no impact on net reproductive rate and intrinsic rate of population growth that would have been indicative of a true homeostatic modulation (Guedes et al. 2009). Although dumping eggs without leaving viable offspring may occasionally increase the overall efficiency of egg maturation and oviposition and result in a higher lifetime reproductive success in insects (Wang and Horng 2004), the opposite may also be true (Messina et al. 2007).). Therefore, we cannot be sure if we observed a true stimulatory effect.

Our original hypothesis that young beetles respond to novaluron by producing fewer eggs seems to be false. Thus, the difference between the findings of the current and earlier studies (Alyokhin et al. 2008b) and those of Cutler et al. (2005a) remains to be explained. El Tahtaoui (1962) and Bajan and Kmitova (1972) also observed increased oviposition by the Colorado potato beetles surviving infection by *B. bassiana*, whereas Fargues et al. (1991) saw decreased oviposition at 22°C and no change at 25°C. It is possible that different geographic populations respond differently to the same stress factor and/or that the response is modulated by microenvironmental conditions. Also, beetles used in the current experiments were from a field-collected population, whereas those used by Cutler et al. (2005a) were from a strain maintained in the laboratory for >50 generations. It is possible that insecticide detoxification mechanisms are very different between a highly susceptible laboratory population and a natural population.

Although increased fecundity of a pest insect is not exactly a desirable consequence of an insecticide application, none of the eggs produced by young beetles in the current study hatched. So, the reported increase in the number of produced eggs will not result in the higher populations of damaging larvae in the field. On the opposite, the affected beetles will be forced to waste energy reserves on producing nonviable eggs, which might affect their reproductive success and possibly other vital functions in the future (Messina and Fry 2003, Messina et al. 2007)). Overall, our results corroborate that novaluron reduces fertility of treated adults. Therefore, benefits of its application go beyond simply killing the larvae. One area of future investigation should be to study the embryonic development of eggs from novaluron-treated adults. Because novaluron is a chitin inhibitor, it is likely that the inability of eggs to hatch when oviposited by novaluron-treated adults is due to the lack of an adequate exoskeleton (Cutler et al. 2005a)). Electron microscopic observations revealed abnormal cuticular structure in embryos developing from the eggs laid by the Colorado potato beetle females that had ingested another chitin synthesis inhibitor diflubenzuron (Grosscurt 1978). This does not rule out other physiological effects but clearly needs clarification if a complete understanding of this phenomenon is to be achieved.

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