# MOTH EXPERIENCE AND NOT PLANT INJURY AFFECTED FEMALE CABBAGE LOOPER MOTH (LEPIDOPTERA: NOCTUIDAE) ORIENTATION TO POTATO PLANTS

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ABSTRACT

Naive mated female cabbage looper moths, *Trichoplusia ni* Hübner, responded in a flight tunnel to potted potato plants (*Solanum tuberosum*). Percentages of moths attracted to uninjured potato plants, mechanically-damaged potato plants, and potato plants treated with regurgitant from larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* Say, were similar, indicating no effect of plant treatment. Attraction of female cabbage looper moths to potato plants was increased following prior contact (experience) by the moth with a potato plant. This increase in responsiveness to potato plants with experienced moths occurred whether the plants were uninjured, mechanically damaged, or treated with Colorado potato beetle larval regurgitant. Moths preconditioned on potato plants treated with regurgitant exhibited similar rates of attraction to mechanically-damaged plants and to regurgitant-treated plants. However, moths preconditioned on mechanically-damaged plants were more responsive to mechanically damaged plants compared to regurgitant-treated plants.

Key Words: *Trichoplusia*, attraction, host-finding, learning, kairomone

RESUMEN

Polillas de repollo *Trichoplusia ni* Hübner, sin experiencia previa, respondieron en un túnel de vuela a plantas de papa en tiestos (*Solanum tuberosum*). Los porcentajes de polillas atraídas a plantas de papa sin daño, plantas de papa con daño mecánico, y plantas de papa tratadas con regurgitante de larvas del escarabajo de papa de Colorado, *Leptinotarsa decemlineata* Say, fueron similares, sindicando la falta de efecto al tratamiento de la planta. La atracción de hembras de polilla a plantas de papa fue incrementada siguiendo contacto previo (experiencia) de la polilla con la planta de papa. Este incremento en respuesta a plantas de papa con polillas con experiencia ocurrió aun si las plantas no tenían daño, tenían daño mecánico, o tratadas con regurgitante larval del escarabajo de papa de Colorado. Polillas preacondicionadas a plantas tratadas con regurgitante exhibieron tiempos similares de atracción a plantas mecánicamente dañadas y a plantas tratadas con regurgitante. Sin embargo, polillas preacondicionadas a plantas mecánicamente dañadas respondieron mas a plantas mecánicamente dañadas en comparación con plantas tratadas con regurgitante.

The cabbage looper, *Trichoplusia ni* (Hübner) is a polyphagous herbivore that can feed on a diversity of plant taxa (Sutherland & Greene 1984). The cabbage looper moth exhibits weak attraction responses to a wide range of host plants, a behavior that may bring it to a host habitat (Landolt 1989). This response is enhanced by conspecific larval feeding or mechanical damage to the plant (Landolt 1993). Attraction of cabbage looper moths to plants is also enhanced following contact with a host plant (experience), indicating learning of host plant odors (Landolt & Molina 1996). Cabbage looper moths previously exposed to celery (*Apium graveolens*) or cotton (*Gossypium hirsutum*) were more likely to orient to that same species of plant rather than to the other species of host plant (Landolt and Molina 1996). These previous studies did not consider possible differential roles of constitutive (stored and released) and induced (produced de novo) odor chemistry produced by plants in response to injury. That is, we do not know if cabbage looper moths are more strongly attracted to injured plants because of constitutive or induced plant odors, or how cabbage looper moth learning of host plant odor (Landolt & Molina 1996) might be affected by these changes in host plant chemistry.

The cabbage looper larvae are found on potato plants and complete development on potato foliage (Sutherland & Greene 1984; Landolt, unpublished data), qualifying potato as a host plant, although it is not considered to be a common pest of potato. Potato plants respond to mechanical injury, feeding by Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and applications of Colorado potato beetle regurgitant, in part by increasing the release of volatile chemicals (Bolter et al. 1997). Treatment of potato foliage with regurgitant from larvae of the Colorado potato beetle or from cabbage looper larvae makes potato plants more attractive to Colorado potato beetle females (Landolt et al. 1999). The Colorado potato beetle is a spe-

cialist on species of *Solanum* and might be expected to be adapted to the defensive chemicals, including volatiles, produced by induced potato plants. Karban and Baldwin (1997) suggest that specialist herbivores might respond positively and generalist herbivores might respond negatively to induced host plant kairomones. It would be of interest then to determine how a polyphagous herbivore such as the cabbage looper responds to plants following such treatments.

The objectives of these studies were to determine if cabbage looper moths are attracted to potato plants, if they are attracted more strongly to potato plants that are mechanically injured (to release constitutive odorants), and if they are more weakly attracted to potato plants that are treated to produce and release induced odorants. Also, effects of previous exposure or experience with plants on cabbage looper moth attraction to uninjured and injured potato plants was examined, with the expectation that moth attraction responses might be enhanced following experience with undamaged and mechanically-damaged plants, but might not be enhanced following experience with induced plants.

## Materials And Methods

### General Methods

Russet-Burbank potato plants were used in all experiments. Plants were grown in a glass greenhouse from September through April in Yakima, Washington, but with supplemental lighting from sodium lamps and 400 watt metal halide lamps providing a 14:10 L:D photoperiod. Plants were started with potato eyes in soil in 15 cm diam pots. Soil was a mix of sand, peat moss and fertilizer. Plants were used in experiments when 4 to 6 weeks old (30-35 cm in height) and before blooming.

Three to five days before experiments, plants were placed in a controlled environment room at 25°C and 50% RH. Lighting was supplied with overhead 400 watt metal halide lamps on a light cycle coinciding with the light cycle for the cabbage looper moths.

Cabbage looper moths were obtained from a colony established in 1997 at the Yakima Agricultural Research Laboratory, with stock that originated from northern Florida in 1987. Pupae were sorted by sex and placed in cages with dishes of sugar water on cotton balls and with water dispensers on the cage tops. Pupae were moved daily to new cages to provide cohorts of moths of discrete ages. All pupae and adult moths (including mating cages, see below) were kept in an environmentally controlled room with reversed light cycle (lights off at 0900 h and lights on at 1700 h), 24°C, and 60% RH.

To obtain mated females, groups of 30 males (3-6 d old) and 25 females (2-3 d old) were placed together in screened cages ($45 \times 45 \times 45$ cm) at the beginning of the scotophase. Moths were provided sugar water and water as in the emergence cages. Females were removed from mating cages near the end of the subsequent photophase and were placed in another cage. Assays were conducted during the first 3 h of the following scotophase. For each set of assays, a subset of female moths were recaptured and were dissected to verify that they mated, evidenced by the presence of a spermatophore in the bursa copulatrix.

In all experiments, mated female moth responses to potted plants were evaluated in a flight tunnel that was similar to that described by Landolt and Molina (1996). Charcoal-impregnated fiberglass filters were used at both ends of the tunnel to minimize contamination of the tunnel and experimental room with plant and other odors. The experimental room was equipped with overhead red incandescent lamps to facilitate observation of moths. Flight tunnel room conditions were 22-24°C and 50-70% RH. Plants tested for attractiveness to moths were placed at the center of the upwind end of the flight tunnel. Moths were released from open 30 ml polystyrene vials near the center of the downwind end of the flight tunnel and were observed for two minutes. Released moths were scored for upwind oriented flight (zigzagging upwind flights within the probable boundaries of the odor plume) and for contact with the plant. A replicate consisted of a series of 5-10 moths tested per plant. No plant was used more than once either in a conditioning treatment or in an assay.

Four experiments were conducted to evaluate moth attraction to potato plants.

### Naive Moths to Uninjured Potato Plants

The first experiment tested the hypothesis that naive moths are attracted to uninjured potato plants. Naive mated female moths were assayed for attraction to an uninjured potato plant or to a pot of soil (as an experimental control). Ten replicates were conducted, with 80 moths tested to plants and 80 moths tested to pots of soil.

### Naive Moths to Injured Potato Plants

The second experiment evaluated the effects of plant injury on attraction of naive moths to potato plants. Two non-competitive tests were conducted using naive female moths. These two tests were 1) a comparison of moth responses to uninjured potato plants and to potato plants that were damaged mechanically and 2) a comparison of moth responses to uninjured potato plants and potato plants treated with regurgitant from larvae of the Colorado potato beetle. To incur mechanical damage to the potato plants, three leaves on a potato plant were cut with scissors, lengthwise about 3 cm

along the main leaf axis. This was done one hour before assays were started. Treatment of plants with beetle regurgitant were made to three leaves of each plant. Leaves were first scraped with a razor blade (about one $cm^2$). A fourth or fifth instar beetle larva was gently squeezed until it produced a droplet of regurgitant at the mouthparts which was then applied to the scraped area of leaf. This was done 24 h before assays were started.

Nine bioassay replicates were conducted, with 90 moths tested per treatment and 90 per control. In both studies, the sequence of plants tested (treatment and control) was reversed daily for the 9 days.

### Experienced Moths to Uninjured and Injured Potato Plants

The third experiment evaluated the effects of prior contact (experience) with potato plants on moth attraction to potato plants. Three tests were conducted to compare the responses of naive versus experienced mated female moths to potato plants that were either uninjured, were mechanically-damaged, or were treated with Colorado potato beetle regurgitant. For each assay, mated females were divided into 2 equal groups when separated from males in the mating cages. One group was placed in a larger screened cage ($45 \times 45 \times 45$ cm) with a potted potato plant, at the onset of the scotophase (experienced moth group). The other group was placed in a similar cage with no plant (naive moth group). Both cages were kept in the controlled environment room used to hold plants for bioassays, on a 14:10 L:D light cycle, 50% RH and 25°C for 24 h. Female moths were then removed from these cages and held in $30 \times 30 \times 30$ cm screened cages in the controlled environment room holding moths and no plants, with water and sugar water, until used in bioassays in the following scotophase. A comparison was first made of naive versus experienced moths to an undamaged plant. Naive moths were tested for attraction to and contact with an uninjured potato plant, followed by the testing of experienced moths tested to the same plant. The following day, using a new plant, a set of experienced moths were tested for responses to an uninjured plant, followed by the testing of naive moths. This was continued for 12 assay sets, with 80 naive and 80 experienced moths tested to uninjured potato plants. This protocol was then followed to compare naive versus experienced moth responses to a mechanically damaged plant, with a total of 80 naive and 80 experienced moths tested to mechanically damaged plants in 16 bioassay sets. A comparison was then made of naive versus experienced moth responses to regurgitant treated potato plants, with 60 naive and 60 experienced moths tested to regurgitant treated potato plants in 10 bioassay sets.

### Discrimination of Uninjured vs Injured Potato by Experienced Moths

The fourth experiment evaluated the ability of experienced moths to discriminate between mechanically-damaged plants and plants that had been treated with Colorado potato beetle regurgitant. The objective of this experiment was to determine if moths preconditioned on one type of injured potato plant (mechanically-damaged or regurgitant-treated) would respond better to the type of plant they were preconditioned with, compared to the other type of plant. There were 4 treatment regimes: 1) moths that were placed with mechanically-damaged plants in one scotophase and were then tested for responses to mechanically-damaged plants in the following scotophase, 2) moths that were placed with mechanically-damaged plants in one scotophase and were then tested for responses to regurgitant-treated plants in the following scotophase, 3) moths that were placed with regurgitant-treated plants in one scotophase and were then tested for responses to mechanically-damaged plants in the following scotophase, and 4) moths that were placed with regurgitant-treated plants in one scotophase and were then tested for responses to regurgitant-treated plants in the following scotophase.

Mated females were subdivided into 2 equal groups when initially separated from males in the mating cages, near the end of a photophase. These female moths were placed either in a cage with a mechanically-damaged plant (cut with scissors as before) or in a cage with a regurgitant-treated plant (Colorado potato beetle larval regurgitant applied to scrapes on 3 leaves 24 h before). After 24 h, during the last 2 h of the photophase, these moths were then removed from the cages containing plants and were placed in 2 clean cages and held another 2-4 h until they were used in bioassays. For the bioassay, a mechanically-damaged plant was placed in the flight tunnel and 5 moths that had been preconditioned with a mechanically-damaged plant and 5 moths that had been preconditioned with a regurgitant-treated plant were then tested alternately for responses to the same plant. A regurgitant-treated plant was then placed in the flight tunnel and 5 moths that had been preconditioned with a mechanically-damaged plant and 5 moths that had been preconditioned with a regurgitant-treated plant were tested alternately for responses to this plant. This protocol was followed on 10 different days, providing a total of 50 moths tested for each treatment category.

For experiments 1, 2 and 3, percentage response data for treatment pairs were analyzed by a paired t test to determine if responses differed between treatments or between treatment and control, with a significance level of $P \leq 0.05$. Per-

centage response data for the treatment regimes of experiment 4 were compared using Tukey's Test following an ANOVA.

## RESULTS

### Naive Moths to Uninjured Potato Plants

The percentages of naive moths that flew upwind towards uninjured Russet Burbank potato plants were significantly greater than the percentages of moths responding to a pot of soil (Table 1). A significant percentage of moths tested also landed on uninjured potato plants and none landed on pots of soil (Table 1).

### Moths to Injured Potato Plants

Percentages of naive moths attracted to mechanically-damaged and uninjured plants were not significantly different (Table 1). Percentages of naive moths attracted to uninjured plants were not significantly different from those attracted to regurgitant-treated plants. There were also no significant differences between percentages of moths landing on plants, for either of the treatment comparisons (Table 1).

### Experienced Moths to Uninjured and Injured Potato Plants

Moths preconditioned (experienced) on potato plants were attracted significantly more often to potato plants, than were naive moths (Table 2). Increased attraction of preconditioned moths to potato plants was observed when those plants were uninjured, mechanically-damaged, or treated with Colorado potato beetle regurgitant (Table 2). Additionally, increased landing was observed in moths that were preconditioned either on uninjured plants or on plants with mechanical damage (Table 2). Percentages of preconditioned moths landing on regurgitant-treated plants were numerically but not statistically greater than percentages of naive moths landing on those same plants.

### Discrimination of Uninjured vs Injured Potato by Experienced Moths

Greatest attraction response rates were seen for moths preconditioned on mechanically-damaged plants and were assayed to other mechanically-damaged plants (Fig. 1). The attraction of moths that were preconditioned on regurgitant-treated plants to either mechanically-damaged or regurgitant-treated plants was similar. These responses, both attraction and landing on plants, were also similar to those of moths preconditioned on mechanically-damaged plants and assayed to regurgitant-treated plants (Fig. 1).

## DISCUSSION

Results indicate significant but weak attraction of naive cabbage looper moths to Russet Burbank potato plants. This finding is similar to the weak attraction responses of naive cabbage looper moths to cabbage (*Brassica oleracea*), celery, tomato (*Lycopersicon esculentum*), and soybean (*Glycine max*) plants (Landolt 1989). This low level attraction to a wide variety of plants (Landolt 1989) may be a host-habitat finding strategy rather than a host-finding behavior, as was suggested previously (Landolt 1993).

There was no significant enhancement of attraction of cabbage looper moths to potato plants cut with scissors to produce mechanical damage. Because mechanical damage causes short term increased emission of volatile chemicals from potato (Bolter et al. 1997), a heightened response by cabbage looper moths was expected. Similar mechanical damage to foliage of cotton plants (*Gossypium hirsutum*) increased their attractiveness to cabbage looper moths (Landolt 1993) and similar damage to cabbage plants increased their attractiveness to *Mamestra brassicae* (L.) moths (Rojas 1999). However, this effect was not observed

TABLE 1. MEAN (±SE) PERCENTAGES OF CABBAGE LOOPER FEMALES THAT WERE ATTRACTED TO AND CONTACTED POTATO PLANTS IN A NO-CHOICE TEST CONDUCTED IN A FLIGHT TUNNEL.

| | | % Attracted | | | % Contact | | |
|---|---|---|---|---|---|---|---|
| Treatment comparisons | n* | $\bar{x}$ + SE | t | p | $\bar{x}$ + SE | t | p |
| Pot of Soil | 10 | 0.0 ± 0.0 | 2.58 | 0.01 | 0.0 ± 0.0 | 2.14 | 0.03 |
| Untreated plant | 10 | 20.0 ± 7.7 | | | 14.0 ± 6.5 | | |
| Untreated plant | 9 | 25.7 ± 3.7 | 1.25 | 0.24 | 5.8 ± 2.7 | 0.90 | 0.39 |
| Mechanically-damaged plant | 9 | 32.1 ± 5.9 | | | 8.1 ± 2.7 | | |
| Untreated plant | 9 | 20.0 ± 6.7 | 0.96 | 0.37 | 6.7 ± 1.7 | 1.04 | 0.33 |
| Regurgitant-treated plant | 9 | 14.4 ± 3.8 | | | 10.2 ± 4.1 | | |

*n = number of replicates with 5 moths tested per replicate.

TABLE 2. MEAN (±SE) PERCENTAGES OF NAIVE AND EXPERIENCED CABBAGE LOOPER FEMALES ATTRACTED TO AND CONTACTING POTATO PLANTS IN A NO-CHOICE FLIGHT TUNNEL ASSAY.

| | | % Attracted | | | % Contact | | |
|---|---|---|---|---|---|---|---|
| Moth treatment | n* | $\bar{x}$ + SE | t | p | $\bar{x}$ + SE | t | p |
| Undamaged plants | | | | | | | |
| Naive | 12 | 25.9 ± 6.6 | 3.12 | <0.01 | 9.2 ± 5.4 | 2.30 | 0.02 |
| Experienced | 12 | 44.3 ± 5.7 | | | 21.9 ± 6.6 | | |
| Mechanically-damaged plants | | | | | | | |
| Naive | 16 | 27.5 ± 4.9 | 7.25 | <0.01 | 8.8 ± 4.1 | 4.48 | <0.01 |
| Experienced | 16 | 55.4 ± 4.2 | | | 24.8 ± 4.2 | | |
| Regurgitant-treated plants | | | | | | | |
| Naive | 15 | 42.5 ± 6.0 | 2.19 | 0.03 | 25.1 ± 5.1 | 1.58 | 0.07 |
| Experienced | 15 | 62.1 ± 4.1 | | | 40.0 ± 7.4 | | |

*n = number of assay replicates with 5 moths tested per assay replicate.

with cabbage looper attraction to mechanically-damaged cabbage plants (Landolt 1993). It is not yet evident why orientation to mechanically-damaged plants may be enhanced in some cases and not in others.

There was also no enhancement of moth attraction to potato plants treated with regurgitant of larvae of the Colorado potato beetle. This treatment is known to stimulate the production and prolonged release of odorants from potato (Bolter et al. 1997) and makes potato plants more attractive to female Colorado potato beetle (Landolt et al. 1999). In previous studies, conspecific larval damage made cotton plants more attractive to cabbage looper moths (Landolt 1993) and made cabbage plants more attractive to *M. brassica*e moths (Rojas 1999). However, such damage to cabbage plants made them less attractive to cabbage looper moths (Landolt 1993) and such damage to chrysanthemum plants made them less attractive to *M. brassicae* moths (Rojas 1999). As with the varying responses of moths to mechanically-damaged plants, the varying responses of moths to insect damaged and regurgitant-treated plants calls for an explanation.

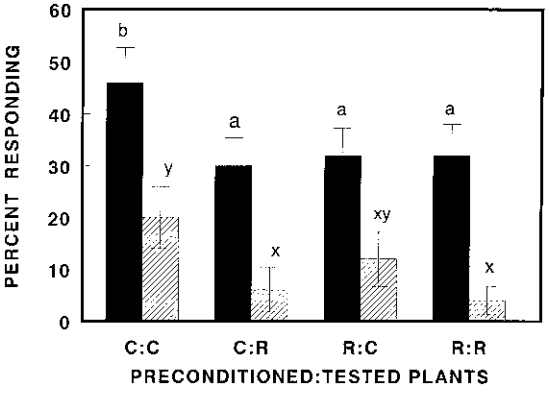


Fig. 1. Mean (±SE) percentages of mated female cabbage loopers attracted to (solid bars) and contacting (open bars) Russet Burbank potato plants in a flight tunnel, after preconditioning contact with other potato plants during the previous scotophase. The first treatment letter indicates the type of plant the moths were preconditioned with and the second letter indicates the type of plant the moths were presented with in the flight tunnel assays. Plants for preconditioning and for flight tunnel assays were either mechanically-damaged (C) or were regurgitant-treated (R). Bars with the same letter are not significantly different by Tukey's Test ($P \leq 0.05$).

Results of experiments 3 and 4 indicate a positive effect of cabbage looper moth experience with potato plants prior to testing moths in flight tunnel assays. This enhancement of attraction responses occurred regardless of whether the plant was uninjured, mechanically-damaged or regurgitant-treated. Similarly, greater numbers of moths contacted the plants if they had prior experience with the same type of plants, compared to moths with no such experience, with the exception of regurgitant treated plants. Such an effect of preconditioning is considered a form of learning, as described by Papaj and Prokopy (1989). Landolt and Molina (1996) reported strong enhancement of host attraction responses by mated female cabbage looper moths following prior experience with host plants, using cotton, celery, and soybean plants. In those studies it was shown that brief contact with the plant was all that was required to strongly increase the subsequent response of the moth to that plant species. Evidence of learning of host plant odor chemistry also exists for the moths *Helicoverpa armigera* (Hübner) (Cunningham et al. 1998), *Heliothis virescens* (Hartlieb 1996) and *Spodoptera littoralis* (Boisdu-

val) (Fan et al. 1997) and for the phytophagous beetles *L. decemlineata* (Say) (Visser & Thiery 1986) and *Diaprepes abbreviatus* (L.) (Harari & Landolt 1999). In contrast, Rojas and Wyatt (1999) noted decreased responsiveness to host plants by *Mamestra brassicae* L. following earlier contact with host plants.

In previous studies (Landolt and Molina 1996), it was shown that cabbage looper moth learning of host plant odor was specific to the plant species used in preconditioning. When moths had prior contact with cotton plants, they were more strongly attracted to other cotton plants and not to celery plants. Similarly, when moths had prior contact with celery plants, they were more strongly attracted to other celery plants and not to cotton plants. In the studies described herein, this discrimination between plants did not occur when moths had prior contact with mechanically-damaged potato plants or regurgitant-treated potato plants and were tested for attraction to both types of potato plants. There was some enhancement of response to those plants following moth preconditioning on mechanically-damaged plants, but moths responded similarly to the two types of injury. Apparently, cotton and celery plants have strongly divergent odor chemistries with little, if any, qualitative overlap, making it more likely that an insect could learn and discriminate separate odors. However, the odor chemistries of mechanically-damaged (to release constitutive odors) and regurgitant-treated (to release induced odors) potato plants overlap extensively (Bolter et al. 1997) and moths that are preconditioned on potato plants with one type of injury may be unable to discriminate between plants with either type of injury.

It was hypothesized that the cabbage looper moth, as a generalist herbivore, might show enhanced attraction to mechanically-damaged plants because of increased emission of volatiles and might show decreased attraction to Colorado potato beetle regurgitant-treated plants because of the induction of defensive chemistry associated with that treatment to potato (Bolter et al 1997) and similar treatments with lepidopterous larvae to other plants (Tumlinson et al. 1992; Turlings et al. 1995). In the case of cabbage looper orientation to potato odor, those expectations appear incorrect because observed response rates were similar to uninjured and injured potato, both by naive and by experienced moths.

Host-finding by the cabbage looper moth appears to involve several behavioral strategies, host-habitat location, responses to some plant injury volatiles, and learning of host plant odor. Evidence indicates a weak response to a variety of plant species that may bring them into the vicinity of possible hosts (Landolt 1989). Injury to plants may (cotton) or may not (cabbage, potato) increase a plant's attractiveness to cabbage looper (Landolt 1993). Additional work is needed to determine the chemical bases for the response differences observed among plants. Prior contact with a plant increases the subsequent responsiveness of the moth to the same type of plant, indicating associative learning of host plant odor when contact is made with plant foliage. The inability of the moth to selectively respond to potato plants with different types of injury still leaves open the question of the relative significance of constitutive versus induced odorants to cabbage looper host finding with other species of plants.

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