Responses of *Spodoptera exigua* (Lepidoptera: Noctuidae) Larvae to Light

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ABSTRACT Influence of light on larvae movement and distribution was investigated for the beet armyworm (BAW), *Spodoptera exigua* (Hübner), in the laboratory and the field. Laboratory tests with five light intensities ranging from 0–3,400 lx indicated that first instars were photopositive, second instars were weakly photonegative, neither third nor fourth instars responded behaviorally to light, and fifth instars demonstrated a strong photonegative reaction. Distribution within celery plants for fourth instars was unaffected by light in the laboratory. Fifth instar larvae responded to light in both the laboratory and the field: most larvae were found on leaves during dark phase, while during light phase a significant majority was observed in sheltered areas in celery hearts or on the ground. Implications for sampling BAW based on these results are discussed.

Spodoptera exigua (Hübner), the beet armyworm (BAW), is a noctuid with a wide host range and broad distribution (Steiner 1936, Mitchell 1979). Greenhouse studies (Jones and Granett 1982) and field observations indicate that development of BAW larvae on celery is characterized by a change in feeding site with larvae development: first through third instars feed on leaves, while fourth and fifth instars prefer the lower petioles and celery heart area. This shift results in economic losses as the marketable portion of the celery crop is damaged by the late instars. Previous research has demonstrated that nutritional variation is not responsible for changes in feeding site (Griswold and Trumble 1985).

Several studies on other noctuid larvae show differences in larvae response to light between early and late instars. Larvae of the European cutworm, *Trypnaena pronuba* (L.) (Madge 1964); the spotted cutworm, *Amathes c-nigrum* (L.) (Olson and Rings 1969); and the variegated cutworm, *Peridroma saucia* (Hübner) (Shields and Wyman 1984), all show a positive response to light in the early larval instars with a photonegative response developing in the later instars. Feeding behavior of the variegated cutworm in the field changes from diurnal to nocturnal feeding in the later instars, corresponding to changes in light responses by this insect in the laboratory by Shields and Wyman (1984). The black cutworm, *Agrotis ipsilon* (Hufnagel), feeds on foliage of corn plants in all larval stages but during the later instars this insect develops a subterranean feeding behavior during the day, emerging at night to cut corn foliage. In laboratory tests black cutworms show significant photonegative responses in later larval stages (Archer and Musick 1976). Therefore, one purpose of the research reported here was to document the general light responses of all larval instars of BAW to determine if behavior patterns were similar to those observed in other noctuid genera. A second objective was to determine the impact of light on the behavior and distribution of late-instar BAW on celery.

Materials and Methods

General. *S. exigua* larvae used in these trials were originally colonized in August 1982 from insects collected on celery at the University of California's South Coast Field Station (SCFS) in Irvine, Calif. The culture was maintained on a modified pinto bean diet (Shorey and Hale 1965, Gelernter 1984) at 26.7 ± 1.0°C and a 16:8 (L:D) photoperiod. Only larvae that had molted 12–24 h before each test were used.

Celery 'Tall Utah 5720-R' was used in all tests. Field plots were transplanted on 10 August 1983 at SCFS and grown according to commercial practices. Celery used for laboratory tests was grown in the greenhouse in University of California soil mix (Matkin and Chandler 1957) supplemented with a slow-release fertilizer (Osmocote) and a micronutrient solution supplied twice a month.

Larvae Movement and Distribution. Larvae movement of BAW in celery was observed in field tests using fifth instars that were initially placed individually on plants on midlevel leaves. Larvae were released at 1.5-m intervals along the row and release plants were marked with stakes. The insects were placed in the field at midday, and their positions were monitored at intervals of 4–5 h for 24 h. The location of each larva was recorded as on a leaf, a petiole, or on the ground. Immediately before each test, larvae were dusted with fluorescent orange pigment (Heleon, Radium Corp.; Devilbiss pigment applicator) and a portable black light was used to locate and identify test larvae.

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Field tests were carried out during three 24-h periods in 1983: 20–21 October, 12.5–27.0°C, 60–90% RH in plant canopy; 25–26 October, 12.0–33.0°C, 40–90% RH; and 15–16 November, 10 to 24°C, 65–90% RH. Forty larvae were included in each of the October tests and 10 larvae were monitored in the November test.

Field data for larvae within-plant distribution were analyzed using linear regression $r \times 2$ tables with time periods organized in logical progression (Steel and Torrie 1980). Regression data were necessarily pooled, which also minimized the effect of changing sample size as larvae were lost during the course of each trial.

In the laboratory, fourth and fifth instars were observed in an arena (90 by 90 cm) containing six celery plants ca. 20 cm apart and 20 cm from the sides. Test plants transplanted in the arena from the greenhouse were selected to correspond to the average size (height and number of petioles) of the plants used in the field tests. One larva was placed on each of the six plants on midlevel leaves at midday; subsequent locations of these larvae were monitored every 4–5 h for 24 h. Tests were replicated four times for fourth instars (24 larvae) and five times for fifth instars (30 larvae). Locations of larvae were again noted as on a leaf, a petiole, or on the ground during each sample. The arena was lined with plastic (7.7 cm above the soil level, coated on the exterior surface with Tac Trap) so that any larvae attempting to leave the arena were trapped. Larvae captured by the coated surface were not included in subsequent analysis. The arena was located in a windowless room that was maintained at 26.7 ± 1.0°C and 60–75% RH. Fluorescent lamps and a 150-W a.c. incandescent lamp were used as the light source for a 14:10 (L:D) photoperiod. The lamps were ca. 91 cm above the plants. During light phase, the light intensity in leaves at the top of the plants was 3,400 lx and at the base of the plants in petioles and at ground level was 500 lx. To monitor the larvae during the dark phase, a 40-W red lamp or a flashlight equipped with a red filter, or both, were used.

Numbers of larvae in high-light conditions (leaves) versus numbers in low-light conditions (petioles and ground) were compared for each time period for both fourth and fifth instars, using Student's t test ($P < 0.01$). Comparisons of counts made during all light-phase periods versus counts during dark phase periods throughout each 24-h test were made separately for numbers of larvae on leaves and numbers of larvae on petioles and ground, using analysis of variance with time period as main effect. Duncan's (1955) multiple range test was used to determine differences in time period means for each location category.

Light Response. Experiments to determine larval response to light were conducted in a windowless, temperature-controlled room with a 150-W a.c. incandescent lamp. The test arena consisted of a heavy cardboard cylinder (28 cm diam by 32 cm high) that was coated on the interior with flat-black paint. The cylinder was open at the top to allow light to enter directly from above. Petri dishes, which were coated halfway with flat black paint to allow larvae to choose between light and dark (Madge 1964), were placed inside the cylinder arena. A 14.5-cm glass petri dish was used for fourth and fifth instars, a 9.5-cm glass petri dish for second and third instars, and a 9.5-cm plastic petri dish for first instars. Five light intensities were evaluated: 3,400, 1,100, 500, and 100 lx, and dark. Light levels were measured at the surface of the petri dish with a photospectrometer (Li-Cor). Selected levels of illumination were achieved by adjusting the distance and aperture of the light source above the test arena. The temperature at the surface of both sides of the petri dish was 27.0 ± 0.1°C for all light levels. Larvae were distributed equally on the dark and light sides of the choice chamber before exposure to each light intensity; exposure time was 15 min. Each test used 10 larvae in the choice chamber and was replicated five times per larval instar at each light intensity. The order of exposure of larvae to each intensity was random. Exposure was conducted midway through each larval stadium and during the light phase of the 16:8 (L:D) photoperiod of the laboratory colony. a.c. was used since, unlike compound eyes of adults (Shields 1982), stemmata of larvae have not been shown to detect the flicker associated with a.c.

The data are represented as a reaction index value (RI) as described by Madge (1964): RI = 100 (L minus D)/N, where L is the number of larvae in the light side, D is the number of larvae in the dark side, and N is the total number evaluated. The choice for the light side is shown as a positive value, for the dark, as a negative one. When a larva was on the light–dark boundary, the location of the head determined the reading.

The data were evaluated by χ^2 analysis, based on an expected L:D distribution of larvae as 50:50. The response categories of photopositive, neutral, and photonegative were established by calculating a 95% CL ca. an RI of 0, with those responses above and below this limit designated positive (+) or negative (−), respectively.

Results and Discussion

Larvae Movement and Distribution. The proportion of the fifth-instar BAW foraging on the leaves decreased linearly with increasing exposure to light (linear regression, $r \times 2$ table; $\chi^2 = 17.56$; $P < 0.001$). In controlled laboratory studies, similar trends were observed. Significantly more fifth instars ($P < 0.01$; t test) were observed in petioles and on the ground near the base of the plants than in the leaves during light periods 7:00–8:00 a.m. and 1:00–2:00 p.m. (Fig. 1B). In contrast, during dark periods significantly more larvae ($P < 0.01$; t test) were found on leaves than on petioles and

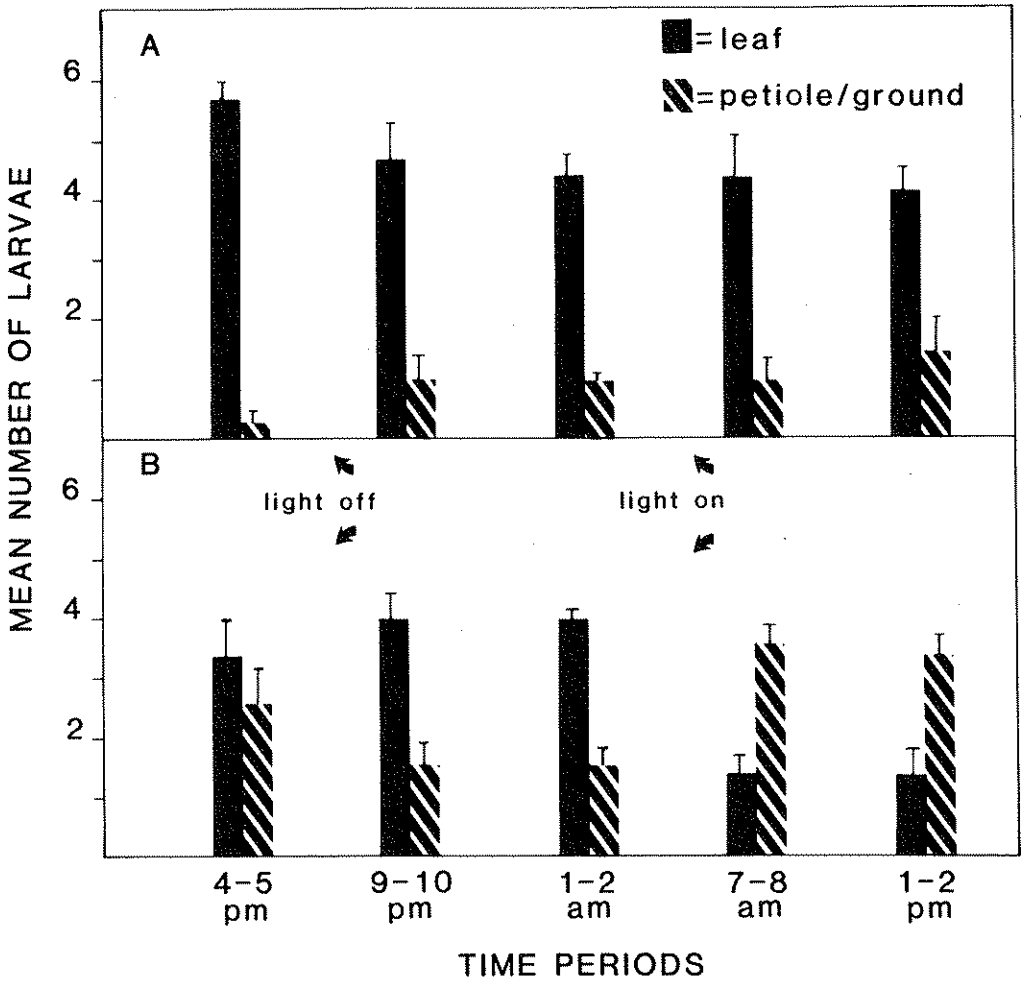

Fig. 1. BAW spatial distribution on celery in laboratory tests. (A) Fourth instars: first time period, 24; second time, 23; third through fifth time period, 22. (B) Fifth instars: first time period, 30; second time period, 25; third through fifth time period, 25. Brackets on data points indicate standard error.

ground areas. These results suggest that fifth-instar movement and consequent choice of feeding sites in celery were influenced by light phase. In laboratory trials, fourth instars exhibited no such marked movement between areas of the celery plants; significantly more larvae were found in the leaves ($P < 0.01$; t test) during all time periods (Fig. 1A). Results of the laboratory tests with fourth instars were not entirely in agreement with observations of Jones and Granett (1982), who suggested that fourth instars have a slight preference for celery petioles and plant hearts.

Light Response. BAW larvae response to light changed between different larval instars as shown in Table 1. First instars exhibited a strong photopositive response at 3,400 lx, but showed variable, but generally positive, responses at lower light intensities. Second instars showed a weak negative response at 3,400 and 1,100 lx, but lower light elicited a neutral response. Generally, third and fourth instars demonstrated neutral reactions to light at nearly all intensities. The neutral response to light in fourth instars parallels the observations in our movement/distribution tests, which indicated that fourth instars did not move in celery plants in relation to light/dark periods.

A distinct photonegative response was demonstrated by fifth instars at all light levels. This negative response also parallels the results of the larvae movement/distribution tests in the laboratory, which showed fifth-stage larvae moving down celery plants during the day from the leaves to the petioles and ground areas at the base of the plant. The results of these experiments indicate that light influences fifth-instar behavior and distribution in celery, causing larvae to move from areas of higher light intensity to shaded and dark sections within and near celery plants. These behavioral responses of BAW to light phase and various light levels are similar to those reported by Shields and Wyman

Table 1. RI values for BAW instars to different light levels

Instar	Light levels (lx)				
	3,400	1,100	500	100	Dark
I	+(72)	0(24)	+(44)	+(52)	0 (4)
II	−(40)	−(40)	0(16)	0(12)	0(12)
III	0(16)	0(12)	0 (8)	0 (4)	0(12)
IV	0(16)	0(16)	−(36)	0 (8)	0(12)
V	−(72)	−(80)	−(84)	−(72)	0 (4)

Symbols indicate positive (+), neutral (0), or negative (−) responses. Numbers in parentheses represent reaction index values (RI); RI values outside the confidence interval ($-27 < 0 < 27$) are significantly different from no response ($P < 0.05$).

(1984) and Archer and Musick (1976) for noctuid cutworms; thus, negative response to light in late larval instars may have some adaptive significance in the Noctuidae. Potential advantages from such an adaptation include water conservation and avoidance of natural enemies (Price et al. 1980).

A photonegative response also may provide a specific advantage to BAW in celery. Celery has been found to contain low concentrations of phototoactive linear furanocoumarins (Beier et al. 1983); these chemicals have been shown to cause mortality to other armyworms when ingested under UV light (Berenbaum 1978). Late-instar BAW larvae, feeding without protection of the web that is characteristic of the early instars (Wilson 1932; Griswold, unpublished data), may move during daylight hours to protected or shaded areas within and around the celery plant, thereby avoiding the possible toxic effect of the linear furanocoumarins. Additional bioassays are necessary to evaluate the influence of celery secondary metabolites on the behavior of BAW.

This study also has some potentially important implications for integrated pest management programs for BAW in celery. Jones and Granett (1982) discussed the importance of age distribution of celery pests in formulating sampling plans; our study indicates that, to assess fifth-instar BAW populations during daylight hours, the ground, as well as the petioles and plant heart, should be sampled.

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