Influence of Cotton Plant Structures on Heliothine Larval Development and the Production and Infectivity of Occlusion Bodies of Nucleopolyhedrovirus in Larvae[1]

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J. Entomol. Sci. 38(3): 368-376 (July 2003)

Abstract *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.), reared on different cotton structures, were studied for larval growth and development, susceptibility to *H. zea* nucleopolyhedrovirus (HzNPV), and production of occluded virus (OBs). Larval weight of both species after 10 d of rearing differed with larvae on artificial diet having the highest weight and those on square bracts the lowest weight. In both species, pupal weight and length of pupal developmental period were positively correlated with the larval weight, but length of the larval developmental period was negatively correlated with larval weight. Mortality from virus infection of *H. zea* and *H. virescens* larvae on squares, square bracts or flowers did not differ significantly among the structures. In both species, the number of viral OBs produced was greater in larvae fed flowers than those fed other structures and was positively correlated with the weight gained by a healthy larva on that plant structure. The mean LC_{50} for OBs produced in *H. zea* or *H. virescens* larvae on square, square bract or flower did not differ significantly. These results indicate that dietary difference in fruiting structures of cotton plants directly affects *H. zea* and *H. virescens* larval growth and development and indirectly affects the production of virus by HzNPV-infected larvae.

Key Words *Helicoverpa zea*, *Heliothis virescens*, fruiting structures, growth, nucleopolyhedrovirus, cotton

The *Helicoverpa zea* nucleopolyhedrovirus (HzNPV) has been developed as a viral pesticide against *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.) on certain agronomic crops including cotton (Federici 1999, Young et al. 2000). Mortality resulting from a baculovirus infection can differ with the host plant on which the larva feeds (Fuxa 1982, Richter et al. 1987, Keating and Yendol 1987, Santiago-Alvarez and Ortiz-Garcia 1992, Forschler et al. 1992, Diffey et al. 1995, Hoover et al. 1998, Ali et al. 1998, Farrar and Ridgway 2000), as well as within a host plant (Ali et al. 1998). Hoover et al. (2000) showed that the resistance to HzNPV of *H. zea* on cotton was midgut based, and negatively correlated with levels of foliar peroxidase.

Growth of *H. zea* and *H. virescens* fed various structures from the cotton plant has been shown to differ within the developmental stage (Hedin et al. 1991, Zummo et al. 1984). Numerous studies have shown that the cotton plant contains a range of vari-

[1]Received 14 May 2002; accepted for publication 24 September 2002.

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ous anti-nutritive chemicals (condensed tannin, flavonoids, terpene aldehydes, cyclopropenoid fatty acids) that affect the larval growth of *H. zea* and *H. virescens* (Chan et al. 1978, Jenkins et al. 1983, Hedin et al. 1991, 1992). These chemicals and their levels vary on and within different plant structures, i.e., in leaves, squares, flowers, anthers, etc. (Hedin et al. 1991, Zummo et al. 1984). In addition, the levels of nutritive elements, such as amino acids, also vary in different plant parts (Hedin et al. 1991).

Ali et al. (1998) showed that the susceptibility of *H. zea* and *H. virescens* larvae to HzNPV infection differed on vegetative and reproductive tissues of host plants. Furthermore, Ali et al. (2003) reported that HzNPV-treated *H. zea* and *H. virescens* larvae fed cotton leaves produced higher numbers of HzNPV occluded virus (OB) than larvae on squares. In this investigation, we compare the influence of fruiting structures and leaves from the cotton plant, and artificial diet on growth and development of *H. zea* and *H. virescens*, as well as their effect on larval susceptibility to HzNPV and production of virus.

Materials and Methods

Cotton, *Gossypium hirsutum* L. (cv. Stoneville 474), used in the tests was grown in 1999 on research plots at the Agricultural Experiment Station, University of Arkansas, Fayetteville using standard agronomic practices. *Helicoverpa zea* and *H. virescens* neonates were obtained from the insect rearing facility in the Entomology Department where they have been maintained for several years on artificial diet (Burton 1969).

Influence of cotton plant structures on larval growth. Neonates of *H. zea* and *H. virescens* were confined individually in 30-mL plastic cups (Solo Cup Company, Urbana, IL) containing either (1) terminal leaves, (2) young squares with bract (approximately 8 to 12 mm dia), (3) square bracts, (4) newly-bloomed flower, or (5) artificial diet, and reared at 28°C until pupation (25 larvae/treatment, each treatment replicated four times). A thin layer of 4% agar-water covered the bottom of cups to minimize desiccation of tissues. Tissues in the cups were changed on alternate days. Neonates fed squares with bracts tended to feed on the bracts first and as they grew older bored into the square. The neonates fed flowers tended to feed on flower-petals initially, and later moved to flower anthers. Larval survival was recorded daily and larval weight of survivors was recorded after 10 d. Data on the percent of larvae that survived to pupation, length of larval developmental period, length of pupal developmental period and pupal weight were recorded.

Influence of cotton fruiting structures on larval susceptibility to HzNPV. Young squares, square bracts, or white flowers collected from the field were placed in 500-mL plastic containers (Fabri-Kal Co., Kalamazoo, MI). Moistened filter paper (Whatman No. 1) was placed in the bottom of the container to minimize drying of the tissues. Neonates were reared 20 per container at 28°C to the second stadium.

The bioassay arena was made by embedding plastic grids in a Petri dish with a layer of 4% agar-water to create 25 individual cells (14 × 14 mm). Larvae were treated with virus on a 4-mm diam disk of plant tissue. Disks for virus treatment of larvae on squares and square bracts were both cut from square bracts, and those for larvae fed blooms from flower petals. The disks were treated with virus by placing 300 OB in 0.1 µl of aqueous suspension of HzNPV (Elcar®, "Novartis" formally Sandoz Crop Protection, Des Plaines, IL) on the disk using a 1-µl Hamilton micro syringe. A virus-treated disk of plant material was placed on a layer of agar gel in each cell. A

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second-instar *H. zea* or *H. virescens* reared either on square, square bract, or flower was confined for 24 h in a cell (25 larvae/replicate) containing a virus-treated disk. Similar arenas without virus served as controls. After 24 h, 20 of the larvae that consumed the entire disk of tissue for each replicate were transferred individually to 30-mL clear plastic cups containing 4% agar-water and reared on the respective tissue for 10 d. Tissue in the cup was replaced with fresh tissue on alternate days. Larval survival was recorded daily. Cadavers from HzNPV-infected larvae were collected and preserved at –4.0°C in 1.5-mL plastic Eppendorf microcentrifuge tubes. Each of the three treatments was replicated four times.

Counting viral OBs from cadavers. Ten virus-killed cadavers were randomly selected in each treatment for counting OBs. Each cadaver was prepared for counting by placing it in a 1.5-mL microcentrifuge tube, and macerating and homogenizing it with a plastic pestle. Distilled water was added to make a 1.0-mL aliquot. Counts of viral OBs were made by diluting the viral suspension, and counting with an improved Neubauer hemacytometer under a phase contrast microscope.

Bioassay of viral OBs from cadavers. A 0.5-mL aliquot of the stock preparation of each virus-killed larva for which OBs had been counted was diluted to prepare a series of concentrations (0.1, 0.5, 1.4, and 4.6 OBs/mm^2 of diet surface) of the virus in distilled water that provided a wide range in larval mortality. A 100-µL Eppendorf pipette was used to apply 0.1-mL of each solution on artificial diet in a 30-mL clear plastic cup. For the control, 0.1-mL of distilled water was applied instead of the viral suspension. The suspensions were spread uniformly over the diet surface by gently blowing air over the surface and allowing it to dry for 30 min. An individual neonate of *H. zea* or *H. virescens* was confined in each cup and reared at 29.5 ± 1.0°C until pupation or a maximum period of 14 d. A total of 25 larvae was tested for each concentration, and each concentration was replicated four times. Larval survival was recorded on alternate days.

Data analyses. HzNPV-related larval mortality data were subjected to arc-sine transformation. Larval mortality, larval weight, length of larval developmental period, pupal weight, length of pupal period and OB production per infected larvae were analyzed following analysis of variance (ANOVA) and means separated by LSD (SAS Institute 1998). Larval survivorship, length of larval developmental period, pupal weight, length of pupal developmental period, and number of OBs produced by an infected larva were also plotted against the larval weight to calculate their logarithmic regression relationships with the larval weight (JMP/SAS Institute 1998). Bioassay results of OB infectivity were used to determine LC_{50}s using the Probit Procedure (SAS Institute 1998).

Results

Influence of cotton plant structures on growth and development of larvae. *Helicoverpa zea* larval weight at 10 d of age differed with diet (Table 1). The weight of larvae fed artificial diet was over two-fold greater than those fed any plant structure ($F = 1143.83$; df = 4, 19; $P < 0.0001$). Among the plant structures, larvae fed flowers had the highest weight and those fed square bracts the lowest weight. The length of larval developmental period differed among diets ($F = 2265.17$; df = 4,19; $P < 0.0001$) and was negatively correlated with larval weights ($R^2 = 0.82$, df = 3,y = 4.94 – 0.39 log(Larval wt.), $P < 0.05$). *Helicoverpa zea* larvae fed artificial diet had the shortest and those fed square bracts had the longest larval developmental period. Larval

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Table 1. Influence of cotton plant structures on the growth of *H. zea* and *H. virescens* larvae*

Diet	Larval weight (mg)**	Larval period (days)	Larval survival (%)		Pupal weight (mg)	Pupal period (days)
			10 days	Pupation		
Helicoverpa zea						
Leaves	110.5 (±4.5) c	19.4 (±0.2) c	96.7 (±0.1)†	96.3 (±2.4) a	261.3 (±5.9) bc	10.1 (±0.1) b
Squares	104.2 (±5.1) c	20.0 (±0.2) b	98.7 (±0.1)	75.0 (±6.4) b	±252.5 (±6.3) cd	10.1 (±0.1) b
Square bracts	76.7 (±3.3) b	32.7 (±0.4) a	96.7 (±0.1)	61.3 (±1.3) c	224.1 (±8.9) d	9.9 (±0.1) b
Flowers	246.2 (±9.4) b	16.7 (±0.2) d	96.7 (±0.1)	77.5 (±1.4) b	297.6 (±5.9) b	10.1 (±0.1) b
Artificial diet	610.1 (±9.2) a	12.0 (±0.1) e	96.7 (±0.1)	96.3 (±2.4) a	447.5 (±6.7) a	10.5 (±0.2) a
Heliothis virescens						
Leaves	94.5 (±5.2) b	18.7 (±0.2) c	96.7 (±0.1)†	92.5 (±2.5) a	187.3 (±3.2) b	10.4 (±0.1) ab
Squares	64.0 (±3.9) c	20.4 (±0.3) b	91.7 (±0.1)	65.0 (±5.4) c	145.1 (±3.7) c	10.2 (±0.1) bc
Square bracts	29.5 (±3.0) d	28.7 (±0.3) a	95.0 (±0.1)	62.5 (±1.4) c	146.8 (±2.5) c	10.0 (±0.1) c
Flowers	99.8 (±2.8) b	17.8 (±0.2) c	95.0 (±0.1)	75.0 (±2.9) b	190.2 (±2.5) b	10.3 (±0.1) bc
Artificial diet	413.0 (±8.2) a	11.5 (±0.1) d	96.7 (±0.1)	96.3 (±2.4) a	328.4 (±2.5) a	10.5 (±0.1) a

* Means (±SEM) in column (within the species) followed by the same letter(s) are not signficantly different ($P < 0.05$).
** After 10 days of rearing.
† Treatment means in columns without letters were not significantly different.

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survival at 10 d of age was greater than 95% in all treatments and did not differ significantly among treatments ($F = 0.13$; df = 4,19; $P = 0.9701$). Survival to pupation differed with treatment ($F = 19.89$; df = 4,19; $P < 0.0001$), but was not correlated with the larval weight after 10 d ($R^2 = 0.37$, df = 3,y = 3.70 + 0.14 log(Larval wt.), $P < 0.27$). Larvae fed artificial diet or leaves had the greatest survival to pupation among the diets. *Helicoverpa zea* pupal weights differed among the diets ($F = 51.81$; df = 4,19; $P < 0.0001$) and were positively correlated ($P < 0.05$) with larval weights ($R^2 = 0.96$, df = 3, y = 4.07 0.33 log(Larval wt.), $P < 0.05$). The length of pupal developmental period was greater for larvae on artificial diet ($F = 10.22$, df = 4,19; $P = 0.0003$) and was positively correlated ($R^2 = 0.83$, df = 3, y = 2.20 + 0.02 log(Larval wt.), $P < 0.04$) with the larval weight.

Growth and development of *H. virescens* on diet were similar in most respects to that of *H. zea* (Table 1). The larval weight at 10 d of age differed ($F = 433.66$; df = 4, 19; $P < 0.0001$) among the diets and was greatest on artificial diet. The weight on plant structures was highest for larvae fed leaves and flowers, while larvae fed square bracts weighed the least. The length of larval developmental period differed over two-fold among the diets ($F = 387.00$; df = 4, 19; $P < 0.0001$) and was negatively correlated with the larval weights ($R^2 = 0.99$, df = 3, y = 4.47 – 0.34 log(Larval wt.), $P < 0.01$). Larval development on square bracts took approximately 1 wk longer than those on any other tissue. Larval survival after 10 d was >90% in all treatments and did not differ significantly between treatments ($F = 0.83$; df = 4, 19; $P = 0.5339$). Survival to pupation differed by 34% among the diets ($F = 23.30$; df = 4, 19; $P < 0.0001$), but was not correlated with larval weights ($R^2 = 0.70$, df = 3, y = 3.56 + 0.17 log(Larval wt.), $P < 0.07$). Survival on leaves was significantly better than on any of the fruiting structures. Pupal weights also differed among the diets ($F = 215.07$; df = 4, 19; $P < 0.0001$) and was positively correlated with larval weights ($R^2 = 0.91$, df = 3, y = 3.75 + 0.33 log(Larval wt.), $P < 0.01$). Pupae from larvae fed artificial diet weighed approximately 150 mg more than those from larvae on cotton. Length of the pupal developmental period differed among the diets ($F = 4.62$; df = 4, 19; $P = 0.0124$) and was positively correlated with larval weight ($R^2 = 0.86$, df = 3,y = 2.25 + 0.02 log(Larval wt.), $P < 0.03$).

Influence of cotton plant structures on HzNPV-treated larvae. The percentage of mortality from virus of HzNPV-treated larvae fed squares, square bracts and flowers did not differ significantly with diet in either species (for *H. zea*: $F = 0.32$; df = 2,11; $P = 0.7344$; *H. virescens*: $F = 0.61$; df = 2,11; $P = 0.5620$). In all treatments of both species, the number of OBs produced by a larva was greater than 1×10^7. Also, the number of OBs produced in both species was three to nine fold greater in larvae fed flowers than in larvae fed squares or square bracts (for *H. zea*: $F = 3.22$; df = 2,26; $P = 0.0579$; *H. virescens*: $F = 5.33$; df = 2,29; $P = 0.0097$) and was positively correlated ($P < 0.05$) with the weight of larvae reared on these reproductive structures in (Table 2). LC_{50}s for OBs produced in HzNPV-treated larvae of both species reared on these plant structures did not differ based on overlapping LC_{50}s (Table 3).

Discussion

The role that a host plant can play in susceptibility of an insect host to a baculovirus has been recognized for some time (Fuxa 1982). Ali et al. (1998) also reported that HzNPV activity can differ with vegetative and reproductive tissues of cotton, soybean and clover. In this study on cotton, we tested for activity of HzNPV against *H. zea* and

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Table 2. Influence of cotton plant fruiting structures on the larval mortality and number of viral occlusion bodies (OB) produced in HzNPV-killed heliothine larvae treated as second instars (3×10^2 OBs/larva)*

Diet	Mortality (%)	OB produced (No $\times 10^6$)
Helicoverpa zea		
Squares	64.8 (±3.9) a	19.9 (±4.4) b
Square bracts	65.1 (±2.7) a	22.1 (±5.2) b
Flowers	67.9 (±2.7) a	66.0 (±24.0) a
Heliothis virescens		
Squares	60.1 (±11.8) a	21.7 (±6.6) b
Square bracts	50.5 (±10.1) a	10.7 (±1.8) b
Flowers	60.1 (±1.4) a	96.1 (±31.9) a

* Means (±SEM) in column (within an insect species) followed by same letter(s) are not significantly different ($P < 0.05$) (ANOVA, LSD). There was no mortality in the control group.

Table 3. LC_{50}s of occluded virus (OB) produced by HzNPV-killed heliothine larvae fed on reproductive structures of cotton plants

Diet	LC_{50} OBs/mm	95% Fiducial limit		Slope (±)	Intercept
		Lower	Upper		
Helicoverpa zea					
Squares	0.4	0.1	1.6	1.5 (0.23)	0.5
Square bracts	0.6	0.5	0.7	1.1 (0.06)	0.3
Flowers	0.3	0.3	0.4	1.2 (0.08)	0.5
Heliothis virescens					
Squares	2.1	0.1	145.7	0.6 (0.12)	−0.2
Square bracts	0.8	0.1	3.6	0.6 (0.08)	0.1
Flowers	2.6	1.5	4.8	0.4 (0.05)	−0.2

H. virescens on fruiting structures of the cotton plant and found no significant differences in larval mortality among larvae on squares, square bracts or flowers for either insect host. Richter et al. (1987) had suggested that NPV were more active against insects on plants that were better hosts. This was not the case when we compared NPV activity among reproductive structures on cotton plants, as flowers were a much superior host to squares, and square bracts were the poorest host for growth and development. While blooms were a satisfactory diet for growth and development of larvae, leaves were as good or better for *H. virescens* than any of the fruiting structures used. The artificial diet (Burton 1969) on which this culture had been reared for many generations was the superior diet for growth and development. The relationship

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of cotton plant chemistry (Lukefahr and Martin 1966, Shaver et al. 1977, Chan et al. 1978, Zummo et al. 1983, 1984) to growth and development of *H. zea* and *H. virescens* has been studied. Hedin et al. (1988, 1991) reported for *H. virescens* that allelochemicals such as some terpenoid aldehydes can slow development, while growth was best where amino acid content was highest, which was in the anthers of blooms.

Although larval mortality did not differ with fruiting structures on which they were reared for either *H. zea* or *H. virescens*, OB production was much greater in flowers than in larvae on squares or square bracts. In both insect species, the greater OB production in larvae on flowers may be related to flowers being a superior diet. The larval weight was greater on flowers than on squares or square bracts, and larval development was more rapid. Production of OBs in both insect hosts was also positively correlated with larval weight. It was previously shown that OB production in NPV-infected *H. armigera* (Hübner) or *Mamestra brassicae* (L.) larvae is directly correlated with the larval weight and age at death (Evans 1981, Teakle et al. 1995, Teakle and Byrne 1989). However, quality of diet for growth and development of insect host may not be the only factor included in OB production. Squares were superior to square bracts for larval development in our test, but OB production did not differ significantly between them. Other factors, such as non-nutritional constituents of plants may also have a role in OB production. Some of the same plant factors that alter viral activity in insect, such as tanins and other allelochemicals (Felton et al. 1987, Young et al. 1995) and organic acids (Schultz and Keating 1996) may have a role in OB production.

While there was not a significant difference in the LC_{50} of OBs produced in larvae on different fruiting structures of the cotton plant in either insect species, there was a difference in the slope of the lines among OBs from larvae of both species fed different fruiting structures. These results indicate that a difference did exist in the activity of OBs produced on different plant structures. Ali et al. (2003) found differences in the quantity of OBs produced in *H. zea* and *H. virescens* on leaves and reproductive structures of cotton and soybean. In most instances, they found total activity was greater in OBs from larvae on the vegetative than the reproductive structure. These results indicate that there are less differences in regard to OB production among the reproductive plant structures used in this study than between leaves and reproductive structures in the previous study. However, this study has shown that OB production can differ in larvae reared on different fruiting structures of the same host plant. Therefore, the stage of host plant development, and thus the feeding sites of same insect hosts, could make a difference in the quantity of NPV inoculum produced by NPV-infected larvae. This should be considered when examining the spread of a disease in an insect population and its role in management of insect pest species.

Acknowledgment

This manuscript is based upon work supported in part by USDA Grant (95-34103-1542), and published with the approval of the Director, Arkansas Agricultural Experiment Station.

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