NUCLEAR POLYHEDROSIS VIRUS TRANSMISSION IN MULTIPLE GENERATIONS OF *ANTICARSIA GEMMATALIS* (LEPIDOPTERA: NOCTUIDAE) CAGED ON SOYBEAN[1,2]

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(Accepted for publication 5 August 1988)

ABSTRACT

Transmission of a nuclear polyhedrosis virus (AgNPV) of the velvetbean caterpillar, *Anticarsis gemmatalis* Hübner, in multiple generations on caged soybeans was examined. Introduction of primary infected larvae into larval populations on soybean resulted in low levels of mortality in the initially uninfected population in generation one. Larval mortality levels increased in succeeding generations and were higher in treatments with greater larval population density. The increase in epizootic development was much less, however, when the plants were not infested for one larval generation. AgNPV concentrations on foliage and in soil generally reflected the mortality levels from AgNPV in the respective treatments.

Key Words: *Anticarsia gemmatalis*, velvetbean caterpillar, Baculoviridae, Nuclear polyhedrosis virus, virus epizootic, virus persistence.

J. Entomol. Sci. 24(1): 133-141 (January 1989)

INTRODUCTION

The velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner), is a major pest of soybean in North and South America. A nuclear polyhedrosis virus (NPV) of *A. gemmatalis* (AgNPV) has been shown to be highly virulent and efficacious in small plot tests (Carner and Turnipseed 1977; Moscardi et al. 1981) and is promising as a viral insecticide (Beach et al. 1984; Richter and Fuxa 1984). The virus persists from one year to the next in soybean fields in areas of South America, and is a persistent mortality factor in *A. gemmatalis* populations with epizootics occurring periodically (Moscardi 1983). In the United States, AgNPV has persisted in test areas in Florida and Louisiana (Moscardi et al. 1981; Richter and Fuxa 1984). However, the virus was not recovered from test plots in South Carolina the year following application (Beach et al. 1984). Only a single generation of *A. gemmatalis* occurs annually in South Carolina. In Florida and Louisiana, where AgNPV persists from year to year, multiple generations of *A. gemmatalis* occur annually. Because these areas are more similar to areas of South America where AgNPV is native, Beach et al. (1984) suggested that AgNPV persistence and potential for epizootic development were much greater in areas with multiple *A. gemmatalis* generations.

We have previously reported on factors affecting AgNPV disease spread and epizootic development in a single generation of *A. gemmatalis* on soybean (Young et al. 1987). Disease spread was related to the population density of the initially infected larvae in the field and to the age of these larvae relative to that of the remainder of the population.

We report herein results of a test in which AgNPV epizootic development in multiple generations of *A. gemmatalis* populations on soybean was examined. Deposits of AgNPV on plants and in soil resulting from disease spread in each generation were also studied.

MATERIALS AND METHODS

Insect Culture and Virus Production.

Anticarsia gemmatalis larvae were obtained from a culture maintained in the laboratory on semisynthetic diet (Greene et al. 1976). The initial source of the culture was collected from soybean in Little River County, Arkansas.

The AgNPV was isolated from diseased *A. gemmatalis* larvae collected on soybean in Brazil (Carner and Turnipseed 1977). AgNPV was propagated in *A. gemmatalis* larvae, partially purified and quantified as described by Young and Yearian (1986).

Caged Soybeans

The test was conducted on "Centennial" soybean planted May 15, 1985, at the University of Arkansas, Agricultural Experiment Station, Fayetteville, AR. This area did not have a history of AgNPV or *A. gemmatalis* populations. The test was conducted using artificial infestations of *A. gemmatalis* larvae in saran screen (100-mesh) cages (1.8 × 3.7 m). The plants were caged 3 days prior to placing first-generation larvae on the plants, and the cages remained in place throughout the test. Each cage enclosed two rows of soybean 3.7 m in length, and cages were separated by a 2-m buffer. The caged plants were sprayed with 2% mevinphos (0.56 kg [AI]/ha, half life < 12h) 2 days prior to placing larvae on the plants in each of the three generations to reduce numbers of predators and parasitoids. First-generation *A. gemmatalis* were released when plants were in the V-10 growth stage (Fehr et al. 1971).

Laboratory Rearing of Uninfected and Primary Infected Larvae.

Both infected and uninfected larvae were released in most treatments. Uninfected larvae for release in each generation were first placed as neonates (25/cup) on diet in 270-ml plastic-coated cups and held 2 d at 27° ± 1°C prior to release. This improved the success of larval establishment on the plants.

The NPV-infected larvae released served as the initial (primary) source of virus inoculum in the larval population, and these will be subsequently referred to as primary infected larvae (PIL). PIL were infected by a diet surface treatment method (Ignoffo 1966). Released PIL were an equal mixture of sizes with death from virus occurring when they were small (first and second instar - PIL 1,2), medium (PIL 3,4) or large (PIL 5,6). Dosages used were predetermined to result in 100% mortality at the desired size of development. PIL 1,2 were treated as neonates (1.3×10^5 polyhedral inclusion bodies (PIB)/mm2 diet surface), PIL 3,4 were treated as early third instars (1.0×10^6 PIB/mm^2 diet surface), and PIL 5,6 were treated as early fourth instars (1.1×10^7 PIB/mm^2 diet surface).

Establishment of Larval Populations in Cages.

Uninfected larvae (2 d old) were released in each of the treatments over the period of one week in order to create a mixed-age population within each

generation. One-third of these larvae were released on each of days 1, 4 and 7. Larvae were transferred to the plants using a soft camel's hair brush. Larvae were not released into the cages in generations 2 and 3 until one week after adult emergence had begun from the previous generation.

PIL were released in appropriate treatment cages at a density of 19.5 PIL/row-m/generation. PIL ages were divided equally between the age regimes (days 1, 4 and 7).

The test consisted of a total of 12 treatments with six larval release regimes at each of two larval release densities. The two larval release densities (PIL + uninfected larvae) were 59 and 176 larvae/row-meter (m). At each larval density level, the larval release regimes were: (1) control-uninfected larvae only in generations 1, 2, and 3; (2) uninfected larvae in generations 1 and 2, PIL in generation 1; (3) uninfected larvae in generations 1 and 3, PIL in generation 1; (4) uninfected larvae in generation 1, PIL in generation 1; (5 and 6) uninfected larvae in generations 1, 2 and 3, (5) PIL in generation 1 and (6) PIL in generations 1, 2, and 3 (See Tables 1-4).

Table 1. *Anticarsia gemmatalis* collected/row-m from caged soybean after release of combination of uninfected and nuclear polyhedrosis virus infected larvae.

Total larvae released/ row-m/gen.	Infected (I§) (19.5/row-m) and uninfected (U) larvae released/generation			Larvae collected/row-m‡		
				Generation		
	Gen 1 (Jul 8)†	Gen 2 (Aug 7)†	Gen 3 (Sep 5)†	1	2	3
59	U	U	U	4.3b	8.8 c	14.0 c
59	I,U	U	*—	9.8b	8.8 c	*—
59	I,U	*—	U	8.8b	*—	11.1 c
59	I,U	*—	*—	7.5b	*—	*—
59	I,U	U	U	8.1b	14.6 c	10.7 c
59	I,U	I,U	I,U	3.3b	12.4 c	13.3 c
Means of treatments with PIL				7.2B	12.0B	11.7B
176	U	U	U	37.4a	62.4a	53.3a
176	I,U	U	*—	36.7a	36.7 b	*—
176	I,U	*—	U	32.8a	*—	29.6 b
176	I,U	*—	*—	33.5a	*—	*—
176	I,U	U	U	37.1a	53.6ab	44.2a
176	I,U	I,U	I,U	30.2a	37.7 b	23.1 bc
Means of treatments with PIL				34.1A	37.7B	32.2A

* Larvae were not released in this treatment

† Date larvae were released

‡ The test was replicated three times. Means followed by the same lower case letter in a column or the same upper case letter in a column (means within a larval density) are not significantly different ($P > 0.5$); Duncan's (1955) Multiple Range Test.

§ (I), Primary infected larvae released into the uninfected (U) larval population.

Larval Collections

A larval collection was made from all treatments in each generation when the oldest larvae, those released on day 1, were sixth instar. Twenty collected larvae

Table 2. Percentage mortality from nuclear polyhedrosis virus of untreated *Anticarsia gemmatalis* larvae collected from caged soybean after release of infected and uninfected larvae.

Total larvae released/ row-m/gen.	Infected (I§) (19.5/row-m) and uninfected (U) larvae released/generation			% Mortality from NPV‡		
	Gen 1 (Jul 8)†	Gen 2 (Aug 7)†	Gen 3 (Sep 5)†	Generation 1	2	3
59	U	U	U	3.0 c	8.0 c	5.0 e
59	I,U	U	*—	10.5 bc	20.7 bc	*—
59	I,U	*—	U	11.0 bc	*—	17.3 de
59	I,U	*—	*—	17.2 bc	*—	*—
59	I,U	U	U	18.7 b	29.1 bc	49.7 bc
59	I,U	I,U	I,U	4.5 bc	31.7 b	58.7 ab
Means of treatments with PIL				12.4 A	27.2 B	41.9 B
176	U	U	U	5.8 bc	16.7 bc	29.3 cd
176	I,U	U	*—	17.6 bc	60.6 a	*—
176	I,U	*—	U	18.6 b	*—	35.0 bcd
176	I,U	*—	*—	10.9 bc	*—	*—
176	I,U	U	U	38.5 a	68.5 a	58.7 ab
176	I,U	I,U	I,U	16.3 bc	67.6 a	83.0 a
Means of treatments with PIL				20.4 A	65.6 A	58.9 A

* Larvae were not released in this treatment
† Date larvae were released
‡ The test was replicated three times. Means followed by the same lower case letter in a column or the same upper case letter in a column (means within a larval density) are not significantly different (P > 0.5); Duncan's (1955) Multiple Range Test.
§ (I), Primary infected larvae released into the uninfected (U) larval population.

Table 3. Nuclear polyhedrosis virus concentrations on foliage after epizootics in *Anticarsia gemmatalis* populations on soybean.

Total larvae released/ row-m/gen.	Infected (I§) (19.5/row-m) and uninfected (U) larvae released/generation			PIB/g × 10^2‡		
	Gen 1 (Jul 8)†	Gen 2 (Aug 7)†	Gen 3 (Sep 5)†	Generation 1	2	3
59	U	U	U	< 0.1 c	1.0 d	< 0.1 d
59	I,U	U	*—	5.4 ab	13.7 bc	* 3.3 cd
59	I,U	*—	U	3.1 ab	2.3 cd	2.7 cd
59	I,U	*—	*—	0.2 bc	2.0 cd	* 2.5 cd
59	I,U	U	U	3.8 ab	191.1 a	248.4 ab
59	I,U	I,U	I,U	2.1 ab	140.1 ab	62.3 abc
Means of treatments with PIL				2.9 A	69.9 B	63.8 B
176	U	U	U	0.2 bc	158.2 a	611.5 a
176	I,U	U	*—	5.3 ab	291.9 a	*156.4 ab
176	I,U	*—	U	1.3 ab	* 14.0 bc	74.0 ab
176	I,U	*—	*—	31.3 a	* 15.4 bc	15.7 bc
176	I,U	U	U	4.2 ab	122.8 ab	467.0 a
176	I,U	I,U	I,U	23.7 a	1067.3 a	650.6 a
Means of treatments with PIL				13.2 A	302.3 A	272.7 A

* Larvae were not released in this treatment
† Date larvae were released
‡ The test was replicated three times. Means followed by the same lower case letter in a column or the same upper case letter in a column (means within a larval density) are not significantly different (P > 0.5); Duncan's (1955) Multiple Range Test.
§ (I), Primary infected larvae released into the uninfected (U) larval population.

Table 4. Nuclear polyhedrosis virus in soil after epizootic in *Anticarsia gemmatalis* populations on soybean.

Total larvae released/ row-m/gen.	Infected (I§) (19.5/row-m) and uninfected (U) larvae released/generation Gen 1 (Jul 8)†	Gen 2 (Aug 7)†	Gen 3 (Sep 5)†	PIB/g × 10²‡ Generation 1	2	3	One month after pupation
59	U	U	U	0.6 a	0.7 c	3.3 c	1.6 f
59	I,U	U	*—	2.1 a	6.0 bc	* 10.5 bc	5.7 def
59	I,U	*—	U	2.9 a	*11.9 ab	2.5 c	7.8 de
59	I,U	*—	*—	7.4 a	*16.9 ab	* 2.0 c	2.4 ef
59	I,U	U	U	1.0 a	2.7 bc	3.9 c	38.7 bc
59	I,U	I,U	I,U	0.8 a	16.5 ab	15.2 bc	13.8 cd
Means of treatments with PIL				2.4 A	10.8 B	6.8 B	13.7 B
176	U	U	U	0.8 a	11.8 ab	10.6 bc	119.8 ab
176	I,U	U	*—	9.3 a	47.0 a	* 21.4 abc	36.0 bc
176	I,U	*—	U	8.4 a	*30.2 ab	15.0 bc	19.2 ab
176	I,U	*—	*—	1.3 a	*21.3 ab	55.1 ab	44.2 bc
176	I,U	U	U	3.6 a	70.0 ab	230.3 a	74.2 ab
176	I,U	I,U	I,U	8.0 a	20.1 ab	117.0 ab	286.0 a
Means of treatments with PIL				6.1 A	37.7 A	87.8 A	91.9 A

* Larvae were not released in this treatment
† Date larvae were released
‡ The test was replicated three times. Means followed by the same lower case letter in a column or the same upper case letter in a column (means within a larval density) are not significantly different (P > 0.5); Duncan's (1955) Multiple Range Test.
§ (I), Primary infected larvae released into the uninfected (U) larval population.

were transferred to diet in 28-ml cups and reared individually in the laboratory until death or pupation. The collections were made by the ground cloth method (Boyer and Dumas 1963). Larvae were collected from a section of row 1 m in length, or 2 m in length if less than 20 larvae were collected from 1 m of row. Numbers of larvae/row-m were recorded. Each collection was made from plants in a different area of the cage. All larvae that died with definitive signs and symptoms of virus infection were recorded as virus dead. Tissue smears were prepared from the remaining dead larvae and examined using phase-contrast optics for the presence of polyhedra.

Collection and Assay of Foliage and Soil for Presence of AgNPV

Foliage and soil samples were collected before larvae were released in generation one and immediately after all larvae had died or pupated in each generation from unsampled areas of caged plots. Additional samples were collected one month after the last generation.

Aliquots in excess of 50 g each of foliage and soil were collected in each cage, from an area in which larvae had not been collected. Foliage samples were taken by removing leaves at random from the plants. Soil samples were dug with a hand trowel to a depth of 5.0 cm at three locations within each cage. Samples were stored in plastic bags at -20°C until AgNPV was extracted. AgNPV was extracted as described by Young and Yearian (1986). Extracts were bioassayed for AgNPV with a diet surface bioassay (Ignoffo 1966) as described by Young and Yearian (1979). Bioassay mortality data was interpolated to PIB/ha (soil) and PIB/g (foliage), utilizing AgNPV dosage mortality curves previously developed with neonatal *A. gemmatalis* larvae (Young and Yearian 1986). The test was replicated three times with a separate cage for each replication. Data were analyzed by

analysis of variance (ANOVA) and means separated by Duncan's (1955) multiple range test.

RESULTS AND DISCUSSION

Larval Density on Recovery Dates

The density of larvae recovered in generation one collections did not differ significantly within either larval release density level (59 or 176 larvae/row-m) among treatments. The mean larval recovery density in treatments with PIL was 7.2/row-m at the lower larval density level and 34.1/row-m at the higher larval density level, representing larval recovery rates of 13.0% and 19.4%, respectively (Table 1).

At the lower larval release density level, the larval recovery density in treatments with PIL also did not differ significantly from the control in generations two and three (Table 1). These results indicate that mortality from AgNPV of untreated larvae in the cages was very low prior to the collection dates. Therefore, mortality of collected larvae would represent essentially all of the mortality from AgNPV in these treatments. However, at the higher larval release density level, the mean larval recovery density was generally lower in treatments with PIL than in the controls in generations 2 and 3 ($P < 0.05$). In these treatments significant larval mortality from AgNPV appeared to occur prior to the collection dates, indicating that virus spread in larval populations was more rapid at the higher than at the lower larval release density level.

Mortality from AgNPV in Larval Collections

Mortality from AgNPV occurred in collections of untreated larvae from all treatments in each generation (Table 2). Although they had received only uninfected larvae, a low level of mortality from virus also occurred in the controls. Mortality in controls remained low during all generations at the lower larval density level, averaging 5.3%. At the higher larval release density level, however, mortality in the controls increased each generation from 5.8% in generations 1 to 29.3% in generation 3. Mortality in the controls in generations 2 and 3 remained generally less than in treatments with PIL.

Across all treatments with PIL in a density level, the mean percentage larval mortality did not differ significantly between larval density levels in generation 1, but was significantly greater at the higher larval release density level in generations 2 and 3 ($P < 0.05$). At the lower larval release density levels, mean mortality in treatments with PIL increased significantly with each succeeding generation from 12.4% in generation 1 to 41.9% in generation 3 ($P < 0.05$). However, at the higher density level, mean mortality in these treatments increased significantly from 20.4% in generation 1 to 65.6% in generation two ($P < 0.05$), but remained unchanged in generation 3 (58.9%).

Mortality in the treatment that received PIL in all generations was not significantly different from the corresponding treatment that received PIL only in generation one at each larval density level in any generation, except at the higher density level ($P < 0.05$) (Table 2). At the higher density level in generation 1 mortality was significantly higher in the treatment that received PIL in all generations. Also, in generation three, mortality in treatments with only generations 1 and 3 established was significantly lower than treatments with all generations established ($P < 0.05$).

A separate analysis of only the treatments that received larvae in all generations revealed that there were group effects. Mortality increased significantly with each

generation with 14.5%, 36.9%, and 47.4% mortality in generations 1, 2 and 3, respectively ($P < 0.05$). Across all generations mean mortality increased significantly with larval density from 23.1% at the low density to 43.0% at the high density ($P < 0.05$). Within each density, however, mortality did not differ significantly, between the treatment that received PIL in generation 1 only and the treatment that received PIL in all generations.

These results show that disease outbreaks in *A. gemmatalis* populations on soybean are potentially greater when multiple generations of larvae occur in a field than when only a single generation occurs. These results support the conclusions of Beach et al. (1984) that spread of AgNPV in a population is much better when more than one generation of the larvae occur on soybean in a season. The results also suggest that in areas with multiple generations of *A. gemmatalis* in a field, it is necessary to have the primary source of AgNPV in the host population for only one early generation for disease spread to continue during the season. This was especially evident at the higher larval density rate when the low level of mortality in the control resulted in increased disease spread in the following generations. Inoculum from even small numbers of disease-killed cadavers in an early generation appears to be sufficient to spread the disease in succeeding generations during that season if the larval population is high. If there is a lengthy time interval between *A. gemmatalis* broods in a field during the season, the spread of disease from the initially infected generation will still occur but be less than that when successive generations are present on the plants.

Virus Concentrations on Foliage

Results of the bioassay indicated a low level of AgNPV on foliage prior to release of virus-infected larvae. The concentration did not differ between treatments and the mean concentration for all treatments was 6.1 PIB/g. The death of virus-infected larvae in each generation resulted in virus deposits on the plants (Table 3). The AgNPV concentration on foliage in controls was low after generation 1 and at the lower larval release density level the deposits in the control remained low after generations 2 and 3. The low level of virus deposits on foliage in the control at the lower larvae density level reflected the low mortality levels of larvae collected from the control throughout the test. At the higher larval release density level, however, the virus concentration on foliage in the control increased rapidly during generations 2 and 3, as did the larval mortality.

A separate analysis of only the treatments with PIL revealed that the mean virus concentration on foliage in treatments with PIL was significantly greater at the higher larval density level than at the lower larval density level after generations 2 and 3 ($P < 0.05$). At the lower larval density level, virus concentration on foliage in treatments with PIL tended to be higher than in the control after each generation, and was always significantly higher in the PIL treatments with all three generations established ($P < 0.05$). However, at the higher larval density level, the virus concentration on foliage in the control was usually comparable to the PIL treatments.

A separate analysis of only the PIL treatments that received larvae in all generations revealed that at both larval release density levels, the mean virus concentrations on foliage in all treatments containing PIL increased significantly after generation 2, but appeared to decrease slightly after generation 3. The highest virus concentrations on foliage were generally in those treatments in which all three generations were established (Table 3). At the higher release density

level, this pattern was also reflected in the control. Although the mortality in the control was generally less than in the treatments with PIL at the higher density level, the virus concentration on foliage in the low-density control was not. This may have been related to size of the larvae that died from the disease. It was observed that most of the larvae that died in the control cages were last instar at death whereas, most in the PIL treatments were smaller at death. Large larvae produce a much greater quantity of virus than larvae that are smaller at death (Young et al. 1987).

Virus Concentration in Soil

Results of the bioassay suggested a very low level of AgNPV in the soil prior to release of infected larvae. The AgNPV concentration did not differ significantly between treatments and the mean of all treatments was 0.3 PIB/g $\times$ 10^2. After generation 1 the mean concentration in the controls was 0.7 $\times$ 10^2 PIB/g, and did not differ significantly among treatments (Table 4). In all subsequent collections, across all treatments within a density level the mean virus levels in soil were greater at the higher larval density level than at the lower density level. A separate analysis of only the PIL treatments that received larvae in all generations revealed that the mean virus concentration of PIL treatments increased significantly in the soil between generations 1 and 2 at each larval density level but not thereafter ($P < 0.05$). Virus concentration in the soil one month after pupation of generation 3 tended to increase only in some of the plots that received larvae in each generation. These results indicated that most virus activity deposited in the soil after generation 2 did so within a month and was present there at the time generation 3 soil samples were taken.

In summary, results of this study showed that greater epizootic development of AgNPV in *A. gemmatalis* populations on soybean occurred in multiple continuous generations of the insect at high population density. After the first generation, the viral inoculum from larval remains from the previous generation was sufficient to bring about higher levels of mortality in the following generation. The increase in epizootic development was much less, however, when a larval generation was missing. The epizootic developed more rapidly and reached higher levels at higher larval density than at lower density. AgNPV concentrations on foliage and in soil generally reflected the mortality levels in larvae on the plants.

ACKNOWLEDGMENTS

We thank Gabriele Boys and John Guerber for their technical assistance. This material is based upon work supported in part by the U.S. Department of Agriculture: Grant No. 83-CRCR-1-1212.

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ERRATA

Scale bars were inadvertently cropped out of figures 2a, 2b, and 3a on pages 336, 337, and 339 of the October 1988 (volume 23:4) issue of the Journal of Entomological Science. These scale bars are as follows:

page 336 figure 2a: ———
page 337 figure 2b: ———
page 339 figure 3a: ——