SOYBEAN FOLIAGE CONSUMPTION BY *PSEUDOPLUSIA INCLUDENS* (WALKER) (LEPIDOPTERA: NOCTUIDAE) LARVAE INFECTED WITH NUCLEAR POLYHEDROSIS VIRUS[1,2]

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ABSTRACT

Consumption of greenhouse and field grown 'Bragg' soybean, *Glycine max* (L.) Merrill, foliage was determined for *Pseudoplusia includens* (Walker) larvae treated with varying dosages of *Pseudoplusia* nuclear polyhedrosis virus to produce different mortality levels. Uninfected *P. includens* larvae consumed an average of 158.3 and 78.7 cm^2 of greenhouse and field grown soybean foliage, respectively. More than 84% of the total leaf area consumed was by the final two larval instars. The amount of foliage consumed by larvae infected as first (greenhouse and field) or second (greenhouse) instars was significantly reduced with increasing NPV mortality level. Foliage consumption by larvae infected as second (field) and third (greenhouse and field) instars at all dosage levels was significantly reduced when compared to the untreated checks, but differences in foliage consumption at the two lower mortality levels were not significant. Frass produced by infected and uninfected larvae was significantly correlated with the amount of greenhouse or field grown foliage consumed.

Key Words: *Pseudoplusia includens*, nuclear polyhedrosis virus, soybean, foliage consumption, frass production.

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INTRODUCTION

Baculoviruses, nuclear polyhedrosis viruses (NPV) and granulosis viruses (GV), have been criticized as microbial insecticides because of the time-lag that occurs between the ingestion of virus and death of the infected larva. Glass (1958) found that damage by GV infected *Argyrontaenia velutinana* (Walker) larvae on apple occurred even when all larvae in the population died from the disease. Chamberlain and Dutky (1958) experienced a total crop loss on tobacco from *Heliothis virescens* (F.) following NPV treatment that resulted in 100% larval mortality. In both studies, it was noted that mortality did not occur until the larvae were almost fully developed. The length of time between ingestion of a baculovirus and death of the host insect is largely dependent on virus dosage and larval size at infection (Yearian and Young 1982). Host feeding rates decrease only in final stages of the disease (Harper 1973; Ramakrishnan and Chaudhari 1974; Tatchell 1981).

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Artificial diet consumption by *Trichoplusia ni* (Hubner) larvae lethally infected with NPV in the first through fourth instar was 10% or less in contrast to noninfected larvae during the entire larval stage (Harper 1973). However, the amount of food consumed was not significantly reduced if larvae were infected as fifth instars. Harper (1973) concluded that the larval stage in which lethal infection occurred was closely related to subsequent food consumption. Tatchell (1981) reported similar results with *Pieris rapae* (L.) larvae infected with a GV. Food intake, frass production and weight gain by *Spodoptera litura* (F.) larvae infected with NPV were significantly reduced 4 - 5 days after infection and were dosage dependent (Ramakrishnan and Chaudhari 1974). In studies on the effect of NPV infection on food consumption and molting of *S. litura,* larval instar at infection and NPV dosage affected the period of infection before mortality occurred and thusly the number of molts (Subramanyam and Ramakrishnan 1981). The occurence of one molt before the onset of symptoms was common. Both Harper (1973) with *T. ni* and Subramanyam and Ramakrishnan (1981) with *S. litura* found that when larvae were infected in the last developmental stage, larval life was prolonged by 2 - 3 days and the larvae consumed more food than healthy ones. Treatment of early *H. zea* (Boddie) larval instars with NPV was essential to significantly reduce food consumption (Flusche et al. 1986). Harper (1973) pointed out that food consumption by virus infected larvae may be important when an insect virus is considered as a control agent.

A nuclear polyhedrosis virus of the soybean looper, *Pseudoplusia includens* (Walker) (PINPV), described by Livingston and Yearian (1972) has shown promise in field tests for control of this pest on soybean, *Glycine max* (L.) Merrill (Cox et al. 1972; Kuo 1974; Young and Yearian 1979; Livingston et al. 1980; McLeod et al. 1982). Optimum use of PINPV is dependent upon a knowledge of the damage caused from the time of larval infection until death. With this information along with expected mortality levels resulting from field applications of the virus, maximum treatment levels for use of PINPV can be developed (Flusche et al. 1986). This study was undertaken to determine the effect of PINPV infection on soybean foliage consumption by *P. includens* larvae. Because previous work with NPVs has shown that infection of early instars is essential to significantly reduce food consumption, the study was limited to larvae infected as first, second, or third instars. Field application of NPV does not normally result in 100% larval mortality. Therefore, measurements were made of foliage consumption by cohorts of *P. includens* larvae infected to produce different mortality levels rather than of consumption by lethally infected larvae.

MATERIALS AND METHODS

Pseudoplusia includens larvae used in this study were taken from a laboratory colony maintained at the Virology and Biocontrol Laboratory, University of Arkansas, Fayetteville, AR. The larvae were reared on a pinto bean artificial diet (Burton 1969). The rearing room in which the colony was held was maintained at $27 \pm 3°C$ without humidity control. The PINPV preparation was obtained from a previously prepared stock suspension (Livingston et al. 1980).

Soybean plants (cv. 'Bragg') were grown in both the field and greenhouse. They were initially planted in the greenhouse on Oct. 15, 1981, and Oct. 20, 1982. Additional plantings were made at 15-day intervals each year to provide a

continuous supply of uniformly aged foliage. The potting soil consisted of 3 parts clay loam topsoil, 3 parts washed sand and 1 part vermiculite, no fertilizer was added. The greenhouse was maintained on a 14 h light cycle; temperatures ranged from 25 - 35°C. Field plantings were made in late May of 1982 and 1983 with 2 additional plantings at 10-day intervals each year. The soil type for all plantings was clay loam. The plantings were hand weeded. No fungicides or fertilizers were used.

First, second and third instar *P. includens* larvae were infected with PINPV by individually exposing them to artificial diet in 32 ml plastic cups that had been surface treated with the virus (Ignoffo 1966). Virus dosages used were determined by preliminary bioassays to produce cumulative mortality levels of 25, 50, and 75% of each instar up to pupation. Specific NPV dosages (polyhedral inclusion bodies/ mm^2 diet surface) were 0.29, 1.05, 1.05 (25%); 1.13, 3.64, 4.45 (50%); and 4.48, 12.59, 18.79 (75%) for first, second and third instars, respectively. Each dosage rate was replicated three times with 10 larvae per replication for both foliage types. Larvae held on virus-free diet served as controls.

Larvae were transferred to soybean foliage after 24 h exposure to virus-treated diet. Foliage used in both greenhouse and field studies was the uppermost fully expanded, undamaged leaflets. Upon collection the leaflets were placed in a water-containing insulated chest to reduce leaf desiccation. Foliage then was gently washed to remove debris, blotted dry, and used within 2 h of excision. Leaflets were placed individually in a transparent plastic folder and measured (3×) with a LI-COR® Leaf Area Meter, Model LI 3100 (LAMBDA Instruments Corporation), and the mean leaf area recorded. After measurements were made, the petiole of individual leaflets was inserted through a Parafilm® plug sealing a 6 ml culture tube containing water. Each culture tube with leaflet along with a test larva was placed in a filter paper-lined plastic Petri dish (150 × 25 mm) and held in a temperature cabinet maintained at 28 ± 2°C, 75 ±10% RH and 14 h light cycle. Foliage was changed daily, and the remaining leaf area measured. At each larval molt the cumulative leaf area consumed was determined. Because of the small leaf area consumed by first instars, the area eaten was determined by tracing an outline of the damaged area on grid paper (6.45 cm^2 = 100 squares) and counting the outlined squares (Benjamin et al. 1968). The foliage consumed by second- through sixth-instar larvae was determined by measuring the remaining leaf area with the leaf area meter and subtracting the remaining area from the original values.

In order to examine the utility of using frass production as an indirect measure of food consumption, frass produced by each larva was collected when the foliage was changed. The frass was air dried in a 30 ± 2°C temperature cabinet (RH 75 ± 10%) for 15 days and then weighed on a Mettler H6T mechanical analytical balance. Because of the small quantity of frass produced by first instars, the frass recovered from the 10 larvae/replicate was pooled and weighed.

Foliage consumption and frass production data were subjected to analysis of variance randomized complete design, with means separation by Duncan's (1955) multiple range test. Correlation coefficients were calculated for larval mortality:foliage consumption, larval mortality:frass production and foliage consumption:frass production. Significance of correlation coefficients were determined using the "t" test as described by Snedecor (1961).

The green weight per unit leaf area (mg/cm^2) and leaflet thickness (mm) were determined for greenhouse and field grown soybean plants. Fifty freshly excised leaflets were collected between nodes 7 - 12 from each locality. The area of each leaflet was measured with the leaf area meter, and the leaflets were weighed individually on an analytical balance. Leaflet thickness was determined for 8 - 10 randomly selected leaflets from each locality. Representative sub-samples were cut from the center, both sides and tip of each leaflet. Measurements were made as follows: Leaflet sub-samples were placed between two rectangular pieces of styrofoam; cross sections were made with a razorblade, sections were mounted in water on a microscope slide under cover glass and thickness was measured using an eyepiece micrometer in a phase contrast microscope. Areas containing veins were avoided when making measurements. Mean thickness was based on a total of 200 readings, for both greenhouse and field grown leaflets.

The null hypothesis that mean green leaflet weight (mg/cm^2) and mean leaflet thickness (mm) of field-grown foliage equals that of greenhouse-grown foliage was tested using the one-tailed "t" test for unpaired observations (Steel and Torrie 1960). Using foliage consumption and frass production for field-grown foliage as the expected values, Chi-square analysis (2 d.f.) was used to compare total foliage consumption (cm^2/larva and green weight (mg)/larvae) or frass production (mg/larva) of greenhouse- and field-grown soybean at the varying mortality levels and larval instars at infection.

RESULTS

Greenhouse Grown Foliage

Foliage Consumption — Consumption of greenhouse grown-foliage by non-infected *P. includens* larvae handled similarily to larvae infected as first, second or third instars averaged 158.3, 145.7, and 153.7 cm^2/larva, respectively. Sixth instar larvae were responsible for approximately 77% of the total leaf area consumed. The last two larval instars accounted for more than 90% of the total foliage consumed.

Pseudoplusia includens larval mortality levels from PINPV experienced in greenhouse studies were comparable to the expected mortality levels at the various PINPV dosages (Table 1). A significant reduction ($P \leq 0.05$) in total foliage consumption was experienced with each increasing NPV mortality level when larvae were infected in the first or second instars. Foliage consumption by larvae infected as third instars was significantly different from the control ($P \leq 0.05$), but mean consumption at the 26.6 and 50.0% mortality levels was not significantly different. Foliage consumption at the 70.0% mortality level was significantly less ($P \leq 0.05$) than at the 26.6 and 50.0% mortality levels. Larval mortality level and reduction in foliage consumption were significantly correlated ($P \leq 0.05$) regardless of the larval instar at infection; r = 0.98, 0.95, and 0.89 for larvae infected in the first, second and third instars, respectively. The percent reduction in foliage consumption was closely related to percent mortality when larvae were infected as first instars, i.e., the 75.0% expected mortality resulted in 77.8% reduction in foliage consumption. Reduction in foliage consumption was 65.9% and 38.4% for larvae infected as second and third instars, respectively, at the same mortality level.

Table 1. Mean consumption of greenhouse-grown 'Bragg' soybean foliage by *Pseudoplusia includens* larvae noninfected or infected with NPV at various mortality levels.

Mean % mortality*	Larval instar 1	2	3	4	5	6	Estimated mean total consumption (cm^2)	Reduction in foliage consumption (%)
					First†‡			
0	0.3a§	1.2a	2.8a	11.1a	24.2a	118.8a	158.3a	—
26.6	0.2b	1.1a	2.1b	9.0b	20.8b	89.5b	122.7b	22.5c
50.0	0.2b	1.2a	2.0b	7.6b	15.5b	59.2c	85.8c	45.8b
73.3	0.2b	1.1a	1.6c	5.2c	7.9c	19.1d	35.1d	77.8a
					Second†‡			
0	0.3¶	0.4a§	3.2a	8.5a	17.8a	115.5a	145.7a	—
24.1	0.3	0.4a	2.8a	7.6a	14.4b	80.0b	105.4b	27.6c
48.3	0.3	0.3a	2.4a	6.4b	12.3c	55.5c	77.2c	47.0b
72.4	0.3	0.4a	2.4a	5.9b	10.0d	30.8d	49.6d	65.9a
					Third†‡			
0	0.3¶	1.2¶	1.8a§	11.9a	18.8a	119.7a	153.7a	—
26.6	0.3	1.2	1.5b	8.5b	15.0b	100.2b	127.0b	17.3b
50.0	0.3	1.2	1.1c	8.0b	13.9b	96.5b	120.9b	21.3b
70.0	0.3	1.2	1.0c	7.5b	11.5c	73.2c	94.7c	38.4a

* Mean mortality (%) of three replications of ten larvae each at each dosage rate and larval stage at infection. At NPV dosages used, expected mortality were 0, 25, 50, and 75%.

† Larval instar infected.

‡ Means within columns for each larval instar at infection followed by the same letter are not significantly different ($P \leq 0.05$), Duncan's (1955) multiple range test.

§ Numbers in column do not include food consumption during the 24 hr virus treatment period.

¶ Numbers in column are assumed consumption based on consumption by the 0.0% mortality group.

Frass Production — Mean weight of air dried frass produced by non-infected *P. includens* larvae handled similarly to larvae infected as first, second or third instars was 199.0, 186.3, and 186.4 mg/larva, respectively (Table 2). Greater than 76% of the total frass produced by the control larvae was by the sixth instars with the fifth and sixth instars accounting for more than 90% of the total frass production. Mean frass production was significantly reduced ($P \leq 0.05$) with each increasing NPV mortality level when larvae were infected as first or second instars (Table 2). Mean frass production by larvae infected as third instars at 26.6 or 50.0% mortality levels was significantly lower from the control group, but differences between the two mortality levels were not significant. Frass production at the 70.0% mortality level was significantly less than that at 26.6 and 50.0% mortality levels. Mortality level and reduction in frass production were significantly correlated ($P \leq 0.05$) for larvae infected as first instars ($r = 0.88$) or second instars ($r = 0.92$). The correlation between mortality level and frass production for larvae infected as third instars ($r = 0.66$) was not significant. Consumption of greenhouse foliage and frass production were significantly correlated ($P \leq 0.05$) with r values > 0.99 for all larval instars at infection and virus mortality levels.

Field-Grown Foliage

Foliage Consumption — Consumption of field-grown foliage by non-infected *P. includens* larvae handled similarly to larvae infected as first, second or third instars averaged 78.7, 93.5, and 92.0 cm^2/larva, respectively (Table 3). More than 69% of the total leaf area consumed was by sixth instars with more than 86% of the total leaf area consumed by fifth and sixth instars.

Larval mortality levels from PINPV observed in field-leaf consumption studies was substantially lower in most cases than the expected mortality levels at the various PINPV dosages (Table 3). Foliage consumption was significantly reduced ($P \leq 0.05$) with each increasing mortality level when larve were infected as first instars (Table 3). Mean foliage consumption by larvae infected as second instars at each mortality level was significantly less than that by the control group ($P \leq 0.05$). Mean foliage consumption by these larvae at the two higher mortality levels, 40.7 and 55.6%, was not significantly less but foliage consumption at these levels was significantly different ($P \leq 0.05$) than that of larvae at the 22.2% mortality level. Foliage consumption by larvae infected as third instars was significantly less than that by the control group at all mortality levels. At the highest mortality level, 63%, foliage consumption was significantly ($P \leq 0.05$) less than the 31.0 or 37.9% mortality levels.

As with studies utilizing greenhouse-grown foliage, mortality level from virus and reduction in consumption of field-grown foliage were significantly correlated ($P \leq 0.05$) regardless of larval instar at infection; $r = 0.83$, 0.93, and 0.94 for first, second, and third instars, respectively. Although mortality levels were substantially less than expected, percent reduction in foliage consumption was very closely related to mortality levels from virus (Table 3).

Frass Production — Mean weight of air dried frass produced by non-infected *P. includens* larvae handled similarly to larvae infected as first, second, or third instars was 157.6, 171.9, and 191.9 mg/larva, respectively (Table 4). Greater than 79% of the total frass production was by the sixth instar larvae with fifth and sixth instars accounting for more than 90% of the total frass produced. Frass produced by larvae infected as first instars at each of the three virus mortality levels was

Table 2. Mean frass production by *Pseudoplusia includens* larvae noninfected and infected with NPV at various mortality levels reared on greenhouse grown 'Bragg' soybean foliage.

Mean % mortality* (%)	Larval instar 1	2	3	4	5	6	Estimated mean total frass production (mg)	Reduction in frass production (%)
				First†‡				
0	0.5a§	1.6a	3.2a	15.5a	30.2a	148.0a	199.0a	—
26.6	0.4b	1.4b	2.5b	12.7b	25.2b	113.8b	155.9b	21.6b
50.0	0.4b	1.3b	2.3b	10.4c	18.8c	78.5c	111.6c	43.9b
73.3	0.2c	1.0c	1.6c	5.4d	9.3d	22.7d	40.2d	79.8c
				Second†‡				
0	0.5¶	0.8a§	3.4a	11.3a	22.5a	147.8a	186.3a	—
24.1	0.5	0.7b	3.1b	10.8b	19.8b	108.2b	143.0b	23.2a
48.3	0.5	0.6c	2.8c	9.9c	17.3c	67.7c	98.7c	47.0b
72.4	0.5	0.5d	2.3d	8.9d	14.9d	45.7d	72.7d	61.0c
				Third†‡				
0	0.5¶	1.6¶	2.0a§	16.7a	23.1a	142.5a	186.4a	—
26.6	0.5	1.6	1.6b	11.6b	19.6b	112.1b	147.0b	21.1b
50.0	0.5	1.6	1.1c	10.3b	18.0b	112.2b	143.7b	22.9b
70.0	0.5	1.6	0.9c	9.4b	14.9c	88.8c	114.0c	38.8a

* Mean mortality (%) of tree replications of ten larvae each at each dosage rate and larval stage at infection. At NPV dosages used, expected mortalities were 0, 25, 50, and 75%.

† Larval instar at infection.

‡ Means within columns for each larval instar at infection followed by the same letter are not significantly different ($P \leq 0.05$); Duncan's (1955) multiple range test.

§ Numbers in column do not include frass production during the 24 hr virus treatment period.

¶ Numbers in column are assumed frass production based on frass production by the 0.0% mortality group.

Table 3. Mean consumption of field-grown 'Bragg' soybean foliage by *Pseudoplusia includens* larvae noninfected and infected with NPV at various mortality levels.

Mean % mortality* (%)	Larval instar						Estimated mean total consumption (cm^2)	Reduction in consumption (%)
	1	2	3	4	5	6		
				First†‡				
0	0.1a§	0.7a	1.7a	9.8a	10.8a	55.7a	78.7a	—
22.2	0.1a	0.7a	1.4a	7.7b	8.6b	41.4b	60.0b	23.9c
40.7	0.2a	0.7a	1.3bc	6.4c	6.7c	34.9b	51.2c	35.0b
48.1	0.1a	0.6a	1.0c	4.4d	5.0d	27.3c	38.3d	51.3a
				Second†‡				
0	0.1¶	0.3a§	2.1a	9.9a	17.8a	63.3a	93.6a	—
22.2	0.1	0.3a	1.5b	7.6b	13.1b	49.6b	72.2b	22.9b
40.7	0.1	0.3a	1.5b	6.9b	9.7c	35.2c	53.7c	42.6a
55.6	0.1	0.3a	1.3b	6.5b	8.5c	25.9c	42.5c	54.6a
				Third†‡				
0	0.1¶	0.7¶	1.3a§	9.3a	15.8a	65.6a	92.8a	—
31.0	0.1	0.7	1.2a	7.3a	11.2b	44.5b	64.8b	30.2b
37.9	0.1	0.7	0.9a	7.1a	11.2b	34.0bc	53.9c	41.9b
63.0	0.1	0.7	0.9a	6.2a	6.2c	22.8cd	36.9c	60.3a

* Mean mortality (%) of three replications of ten larvae each at each dosage rate and larval stage at infection. At NPV dosages used, expected mortalities were 0, 25, 50, and 75%.

† Larval instar at infection.

‡ Means within columns for each larval instar at infection followed by the same letter are not significantly different ($P \leq 0.05$); Duncan's (1955) multiple range test.

§ Numbers in column do not include food consumption during the 243 hr virus treatment period.

¶ Numbers in column are assumed consumption based on consumption by the 0.0% mortality group.

Table 4. Mean frass production by *Pseudoplusia includens* larvae noninfected and infected with NPV at various mortality levels reared on field grown 'Bragg' soybean foliage.

Mortality* (%)	Larval instar						Estimated mean total frass production (mg)
	1	2	3	4	5	6	
				First†‡			
0	0.2a§	1.2a	3.5a	11.7a	13.4a	128.3a	157.6a
22.2	0.2a	1.1a	2.8a	8.4b	9.2b	99.7b	121.3b
40.7	0.2a	1.1a	2.5a	7.2c	7.4c	85.9b	107.7b
48.1	0.2a	0.9a	1.8a	4.7d	5.9d	65.6c	78.7c
				Second†‡			
0	0.2¶	0.4a§	3.1a	13.4a	19.4a	135.4a	171.9a
22.2	0.2	0.3a	2.6a	9.7b	16.3a	105.7b	134.8b
40.7	0.2	0.3a	2.7a	9.6b	12.2b	81.5bc	106.5bc
55.6	0.2	0.3a	2.3a	9.4b	11.3b	60.1c	83.7c
				Third†‡			
0	0.2¶	1.2¶	1.9a§	13.2a	22.7a	152.7a	191.9a
31.0	0.2	1.2	2.0a	9.7a	16.5b	114.8a	141.6b
37.9	0.2	1.2	1.7a	10.0a	14.2bc	88.5b	115.7bc
63.0	0.2	1.2	1.7a	10.0a	10.1c	58.5b	81.7c

* Mean mortality (%) of three replications of ten larvae each at each dosage rate and larval stage at infection. At NPV dosages used, expected mortalities were 0, 25, 50, and 75%.

† Larval instar at infection.

‡ Means within columns for each larval instar at infection followed by the same letter are not significantly different ($P \leq 0.05$); Duncan's (1955) multiple range test.

§ Numbers in column do not include frass production during the 24 hr virus treatment period.

¶ Numbers in column are assumed frass production based on frass production by the 0.0% mortality group.

significantly ($P \leq 0.05$) less than that produced by the control group. No significant differences in frass production by larvae infected as first instars were detected between the 22.2% and 40.7% mortality levels. Estimated total frass production at the 48.1% mortality level was significantly ($P \leq 0.05$) less than at the 22.2% and 40.7% mortality levels. Larvae infected as second instars produced significantly less frass at the 22.2% mortality level than at the 55.6% mortality level. Frass produced at the 40.7% and 55.6% mortality levels was not significantly different. Comparable results were obtained for larvae infected as third instars.

Mortality level from virus and reduction in frass production were significantly correlated ($P \leq 0.05$) for larvae infected in the first, second or third instars; r = 0.80, 0.96 or 0.98, respectively. Consumption of field-grown foliage and frass production were significantly ($P \leq 0.05$) correlated with "r" values greater than 0.99 for all larval instars and virus mortality levels.

Comparison of Greenhouse- and Field-Grown Foliage Consumption

Mean green weight of field-grown soybean foliage (nodes 7 - 12) was 17.9 mg/cm^2 and was significantly ($P \leq 0.05$) greater than greenhouse-grown foliage, 12.2 mg/cm^2. Similarly, the leaflet thickness of field-grown soybean, 0.21 ± 0.03 mm, was significantly ($P \leq 0.05$) greater than that of greenhouse grown soybean, 0.16 ± 0.02 mm.

At all mortality levels and larval instars at infection, significantly more ($P \leq 0.05$) greenhouse foliage area and green weight was consumed than field grown foliage according to Chi-square analyses. Larvae infected as first or third instars that were fed on greenhouse foliage produced significantly greater ($P \leq 0.05$) quantities of frass than those similarly treated and fed on field grown foliage. However, the quantity of frass produced by larvae fed on greenhouse foliage was not significantly different from that produced by larvae fed on field grown foliage when both groups were infected as second instars.

DISCUSSION

Consumption of greenhouse-grown 'Bragg' soybean foliage by non-infected control *P. includens* larvae averaged 158.3 cm^2 and was somewhat greater than that reported by Boldt et al. (1975) for greenhouse-grown 'Clark' soybean, 114.0 cm^2. Although the amount of foliage consumed was different, the relative consumption by larvae was comparable. Boldt et al. (1975) found, as did this study, that the last two larval instars (fifth and sixth) accounted for approximately 90% of the total foliage consumed. In this study consumption of field grown 'Bragg' foliage by control larvae averaged 88.4 cm^2. This is somewhat in agreement with the observation of Reid and Greene (1973) who reported that 82.0 cm^2 of field grown 'Bragg' soybean foliage was consumed by *P. includens* larvae. More than 86% of the total leaf area was consumed by the last two larval instars in our study as compared to 87% reported by Reid and Greene (1973).

Significant reduction (both greenhouse- and field-grown foliage studies) in total foliage consumption (cm^2) and frass production (mg) was generally experienced with each increasing mortality level when larvae were infected as first, second or third instar. These results are comparable to those reported for other lepidopterous species infected with baculoviruses. Food intake, frass production, and weight gain of *S. litura* larvae infected with NPV were significantly reduced and were dosage

dependent (Ramakrishnan and Chaudhari 1974). Harper (1973) noted a reduction in feeding by NPV infected *T. ni* larvae 2 days after infection, and as virus dosage was increased, food consumption and length of feeding period significantly decreased. Tatchell (1981) reported that food consumption of *P. rapae* was reduced as GV dosage increased.

Reduction in foliage consumption and frass production in both greenhouse- and field-grown foliage studies were significantly correlated with the mortality levels in all developmental stages at treatment. These results suggest that if frass collection traps as described by Graham (1963) for forest insect defoliators could be adapted for use in agricultural crops, measurements of frass production in soybean, could be used to indirectly estimate leaf area consumption in the field.

Green weight per unit leaf area was significantly greater ($P \leq 0.05$) for field grown foliage (17.9 mg/cm^2) than for greenhouse grown foliage (12.2 mg/cm^2). Boldt et al. (1975) also found that the weight per unit area for young leaves of 'Clark' soybean was greater in the field (14.7 ± 0.2 mg/cm^2) than the greenhouse (11.2 ± 0.5 mg/cm^2). In our study, thickness of field-grown leaves (0.21 mm) was also significantly greater ($P \leq 0.05$) than that of greenhouse leaves (0.16 mm). These results are at variance to those of Reid and Greene (1973). They reported a mean leaf thickness of only 0.06 ± 0.01 mm for greenhouse-grown 'Bragg' soybean. They did not indicate the procedures that were used to measure leaf thickness in their study; thus suggested reasons for the marked discrepancy cannot be offered.

Leaf area consumption of greenhouse foliage was significantly greater than consumption of foliage from the field. This could be caused by the difference in thickness of between greenhouse- and field-grown leaves or the difference between the green weight per unit area of greenhouse- and field-grown leaves. In addition, *P. includens* larvae consumed approximately 30% more green weight of greenhouse-grown soybean foliage than field-grown foliage. This may indicate that the nutrient value of greenhouse foliage was less than that of field-grown foliage but such determinations were beyond the scope of this study. Boldt et al. (1975) also reported significantly greater consumption of greenhouse foliage than of field-grown foliage by healthy *P. includens* larvae.

Pseudoplusia includens larvae infected as first or third instars and fed on greenhouse foliage produced significantly more frass than those that fed on field-grown foliage. This was probably caused by a delay in mortality until the larvae were fifth or sixth instars: 86.4% and 100.0% for those infected as first and third instars, respectively. Greater than 50% of the mortality for the three groups of infected larvae fed on field foliage occurred before the larvae were fifth instars. Prolonged infection and delayed mortality could cause prolonged larval life, increased consumption of foliage and increased production of frass before death. Harper (1973) and Subrahmanyam and Ramakrishnan (1981) found that larvae infected in the late developmental stages exhibited a prolonged larval life and consumed more food.

Although the amount of foliage consumed and quantity of frass produced differed between greenhouse- and field-grown foliage, relative reductions in foliage consumption and frass production were similar at the various larval mortality levels. Higher dosages resulted in greater larval mortality, and this, in turn, resulted in reduced feeding damage. Results of this study, indicate that the stage at which larvae are infected is critical to appreciably reduce food consumption.

Treatment in an early instar developmental stage is essential in order to obtain a maximum reduction in food consumption.

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