Analysis of Injury Timing and Compensatory Reaction of Soybean to Feeding of the Southern Green Stink Bug and the Bean Bug

Nobuhiko SUZUKI,^{1,3} Nobuhiko HOKYO² and Keizi KIRITANI^{2,4}

¹Department of Biology, Faculty of Science, Kyushu University, 33, Fukuoka 812, Japan

²Division of Entomology, National Institute of Agro-Environmental Sciences,
Kannondai, Tsukuba, Ibaraki 305, Japan

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Injury occurrence and compensatory reactions of soybean to feeding of *Nezara viridula* and *Riptortus clavatus* were experimentally analyzed in relation to the density, duration of release and period of release of bugs. Severe feeding interference among individuals occurred on large pods, especially in *N. viridula*. The density effect considerably affected feeding frequency and consequently the total feeding time. On infested plants, seed biomass decreased remarkably, while the biomass of leaves, stems and roots increased with bug density. The total biomass of injured plants was nearly equal to that on control (non-injured) plants. During the early pod growing stage, a compensatory reaction of plants to the feeding of bugs manifested as an increase in pods. Injury levels decreased when bugs were released later in the plant life cycle. The timing of feeding had a sensitive influence on soybean yield.

Key words: injury occurrence, soybean, bugs, *Nezara viridula*, *Riptortus clavatus*

INTRODUCTION

Various species of insect pests with different modes of feeding have been reported on soybean (MIKOSHIBA, 1975; KOBAYASHI, 1983). Among them, several species of heteropterous stink bugs are especially important because of their direct sucking of pods. Two types of injury are caused by these stink bugs. One is quantitative injury at the early pod growing stage which reduces pod survival before seed growth. The other is qualitative injury at the seed growing stage which decreases commercial or nutritional values of beans. The effects of these injuries on bean yield have been studied by many authors (e.g., DAUGHERTY et al., 1964; SMITH and BASS, 1972; CHERRY, 1973; TODD and TURNIPSEED, 1974; THOMAS et al., 1974a, b, 1976; YEARGAN, 1977). The process of injury, however, has not been dealt with in relation to plant compensatory growth.

The high compensatory growth of soybean under the influence of herbivory was recently demonstrated by artificial defoliation experiments (e.g., SAITO et al., 1983) and a dynamic soybean growth model that simulates the effects of artificial defoliation on yield (KAWAMOTO et al., 1986; KAWAMOTO, 1987). The influence of herbivory by

³ Present address: Nagasaki Prefectural University, Sasebo, Nagasaki 858, Japan

⁴ Present address: Food & Fertilizer Technology Center, Taipei, Taiwan, ROC

sucking type insects has remained unexplored, although preliminary modelling of pod feeding behavior of stink bugs was done by KAWAMOTO et al. (1987).

In this paper, the process of injury occurrence (infestation) and compensatory reaction of soybean to feeding of the southern green stink bug, *Nezara viridula* L. and the bean bug, *Riptortus clavatus* THUNB. were studied experimentally in relation to the density, duration of release, and period of release of bugs.

MATERIALS AND METHODS

Soybeans (variety Tamahomare) were grown individually on 1/5000 a pots in a greenhouse under controlled mean temperature about 25°C and 45% RH. Photo-period was controlled at 14L-10D. Each soybean plant was enclosed in a vinyl cylinder with nylon gauze at the top (30 cm diameter and 67 cm ht.), when they entered the early pod growing stage.

Sexually matured adults of 5 to 7-days post-emergence which had been reared in the laboratory were used for experiments following the design shown in Table 1. The effects of the duration of release and density of bugs on injury level of soybean were analyzed in Experiments I-III. The effects of the period of release of bugs at the density of 4 per seedling on plant injury level were analyzed in Experiments I, IV and V for release durations of 10 days and in Experiments II and VI for release durations of 20 days. Adults were marked individually with paint markers. Ten plants were used as a control (no infestation). During the course of the experiment, the few adults that died were replaced with new ones. All the eggs laid in the cages were removed.

Six hr continuous observations of the behavior of adults were conducted on 2 arbitrarily selected cages in each treatment group at 5-day intervals after the release. Feeding activities were individually recorded in terms of time spent in each feeding trial at a particular feeding site of a plant.

The number of pods of 3 size classes (large: more than 30 mm, medium: 11-29 mm, small: less than 10 mm pod length) was recorded for all the plants at 5-day intervals after the release of bugs. At the end of the experiment, all the plants were sampled. Numbers of pods and seeds on individual plants were counted, and dry weights of individual seeds in the each pod and other organs of each plant were measured.

Table 1. Outline of the experimental design

Experiment no.	Period of release (days)	Duration of release (days)	Density		
			2 (♀1♂1)	4 (♀2♂2)	8 (♀4♂4)
I	1st-10th	10	5	5	5
II	1st-20th	20	5	5	5
III	1st-30th	30	5	5	5
IV	11th-20th	10	—	5	—
V	21st-30th	10	—	5	—
VI	11th-30th	20	—	5	—

Numerals in the table represent the number of replications in each treatment of both *N. viridula* and *R. clavatus*. Ten plants were reserved as control (no infestation).

Table 2. Feeding activities of *N. viridula* and *R. clavatus* in Experiment III ($\bar{X} \pm \text{S.E.}$)

Species		Density		
		2	4	8
<i>N. viridula</i>	Feeding time/day/ plant (min)	1056 $\pm$ 114 a	1138 $\pm$ 118 b	1506 $\pm$ 198 b
	Feeding time/day/ individual (min)	528 $\pm$ 57 a	284 $\pm$ 30 b	188 $\pm$ 25 b
	Feeding frequency/ day/plant	29.2 $\pm$ 2.6 a	39.8 $\pm$ 4.2 ab	57.5 $\pm$ 5.7 b
	Feeding frequency/ day/individual	14.6 $\pm$ 1.3 a	10.0 $\pm$ 1.1 ab	7.2 $\pm$ 0.7 b
	Feeding time/ feeding trial (min)	36.3 $\pm$ 3.9 a	27.6 $\pm$ 2.8 ab	23.5 $\pm$ 1.9 b
	% feeding time from pods	78.48	50.36	37.19
	% feeding time from leaves	9.03	20.63	22.32
	% feeding time from stems	12.49	29.01	40.48
<i>R. clavatus</i>	Feeding time/day/ plant (min)	500 $\pm$ 58 a	1051 $\pm$ 91 b	1258 $\pm$ 159 b
	Feeding time/day/ individual (min)	250 $\pm$ 29 ab	263 $\pm$ 23 a	157 $\pm$ 20 b
	Feeding frequency/ day/plant	26.2 $\pm$ 2.9 a	58.0 $\pm$ 5.2 b	91.2 $\pm$ 8.3 c
	Feeding frequency/ day/individual	13.1 $\pm$ 1.5 a	14.5 $\pm$ 1.3 a	11.4 $\pm$ 1.0 a
	Feeding time/ feeding trial (min)	18.5 $\pm$ 2.1 a	17.8 $\pm$ 1.2 a	13.7 $\pm$ 0.9 a
	% feeding time from pods	61.02	69.22	52.98
	% feeding time from leaves	26.78	26.73	36.46
	% feeding time from stems	7.79	4.05	10.57

Means in same row followed by different letters are significantly different ($p < 0.05$, STUDENT's *t*-test).

RESULTS

Feeding activity

Feeding activities of *N. viridula* and *R. clavatus* in Experiment III are shown in Table 2. The feeding time per day per plant did not change in proportion to adult densities of either species. The density effect (density was defined as number of adults per plant) began to occur at the density 4 in *N. viridula* and density 8 in *R. clavatus*, respectively.

Density dependent decrease of the feeding frequency per day per individual was more sensitive than that of the feeding time per feeding trial, especially in *N. viridula*. This indicates that the proportion of individuals that restrained their feeding increased with a rise in bug density. As a result, a significant difference greater than 100% in the length of feeding time per day per individual was found between the 2 species at density 2. The difference was less at the densities 4 and 8.

In regard to the sucking from pods, most individuals selected large pods more than

30 mm in length, i.e., 90.2% and 82.5% in *N. viridula* and *R. clavatus*, respectively. The proportion of time spent sucking pods decreased with a rise in *N. viridula* bug density. This density dependent decrease was weak in *R. clavatus*.

At density 8, the proportion of time spent on sucking stems was higher than from pods and leaves in *N. viridula*, while the reverse was found in *R. clavatus*. *R. clavatus* persisted more intensely in pod feeding than *N. viridula*.

Effects of density and duration of release on injury response

Changes in the numbers of large, medium and small pods produced on plants infested by *N. viridula* are shown in Fig. 1. Although there was no difference in the number of large pods between infested and control plants, the numbers of medium and small pods began to increase 10 days after the release of the bugs, especially at densities 4 and 8. Although the increase in number of medium pods in response to feeding by *R. clavatus* was less conspicuous, a similar tendency was observed.

The biomass of pods (not including seeds), seeds and other organs of the plant at 30 days after the release of bugs is shown in Fig. 2. The total biomass on injured plants was nearly equal to that on control plants. The biomass of leaves, stems and roots was the lowest on control plants, increasing with higher densities of bugs on injured plants. The biomass of pods on injured plants was the largest at density 2 and decreased with higher densities of bugs. The biomass of seeds on injured plants was much smaller than that on control plants and decreased with higher bug densities. Seeds were scarcely produced when the bug density was 8. This tendency was consistent with elongation of release duration.

About 90% of seeds on control plants weighed between 100 mg and 300 mg (dry weight). The proportion of small seeds on injured plants increased with higher bug densities and elongation of release duration. There was no seed weighing more than

Fig. 1. Changes in the numbers of large (L), medium (M) and small (S) pods produced on the plants infested by *N. viridula* for 10, 20 and 30 days (Experiments I–III). ○: control (non-injured plants), ●: density of 2 bugs/plant, △: density of 4 bugs/plant, ▲: density of 8 bugs/plant.

Fig. 2. Average biomass (SE shown by bars) of each organ of the plants at 30 days after the release of *N. viridula* (○) and *R. clavatus* (●) (Experiments I–III). Upper, middle and lower figures represent the biomass on the plants infested for 10, 20 and 30 days, respectively. Density 0 indicates control (non-injured plants).

50 mg on the plants fed upon for more than 20 days at density 8.

On both injured and control plants, seeds were not produced in the pods with lengths of less than 10 mm. Of pods longer than 11 mm, 3.5 ± 0.6 and 1.8 ± 0.6 ($\bar{X} \pm \text{S.E.}$) pods had no seeds when subjected to density 8, from the plants fed upon by *N. viridula* and *R. clavatus*, respectively. The number of pods without seeds was only 0.2 ± 0.1 on control plants. About 97% of pods were more than 6 mm thick on control plants. On the other hand, the proportion of thin pods increased with higher bug densities and elongation of release duration on infested plants. The ratio of pods less than 2 mm thick to the pods longer than 11 mm reached about 40–50% at density 8.

Effects of timing of release on injury response

Changes in the numbers of large, medium and small pods produced by the plants injured for 10 days (Experiments I, IV and V) are shown in Fig. 3. Only on the plants injured for 10 “early” days (Experiment I) did the number of small pods increase conspicuously throughout the reproductive stage. A similar tendency was found on the plants injured for 20 “early” days (Experiment II). On the plants injured for 10 days (Experiments I, IV and V), the biomass of pods, seeds and other plant organs at 30 days after bug release is shown in Fig. 4. The total biomass on injured plants was nearly equal to that on control plants. The effect of timing of release of bugs on the total biomass of plants was also not found on the plants infested by either species.

The biomass of leaves, stems, roots and pods was the largest on the plants infested for 10 “early” days and decreased as the bugs were released later in the plants’ growth. On the other hand, the biomass of seeds showed an opposite trend. Response of plants

Fig. 3. Changes in the numbers of large (L), medium (M) and small (S) pods produced on the plants injured for 10 days by *N. viridula* and *R. clavatus* (Experiments I, IV and V). ○: control (non-injured plants), ●: early 10-day release period, △: middle 10-day release period, ▲: late 10-day release period.

Fig. 4. The biomass of each organ of the plants injured by *N. viridula* (upper) and *R. clavatus* (lower) for 10 days at 30 days after the release of bugs (Experiments I, IV and V). C, E, M and L represent control and injured plants for early, middle and late 10-day periods, respectively.

infested for 20 days was similar between groups subjected to the 2 species (Experiments II and VI). An exception occurred in the case of pods infested by *N. viridula* with a late 20-day period of release (Experiment VI). Pod biomass was larger than in Experiment II (early release); 2.2 ± 0.2 g vs. 3.2 ± 0.2 g ($\bar{X} \pm \text{S.E.}$). Pod biomass did not differ between early and late release groups of plants infested by *R. clavatus* (2.4 ± 0.4 g and 2.4 ± 0.3 g ($\bar{X} \pm \text{S.E.}$), respectively).

Seeds on the plants infested for 10 and 20 days by each species were larger on

plants with late release of bugs than with early ones. Overall, the pattern in the frequency distribution of seed weight from late 10-day release period groups was similar to that from control plants.

In the pods longer than 11 mm, absence of seeds and cases of thin pod walls decreased with the delay of bug release.

DISCUSSION

Density had considerable effect on the feeding frequency of individual bugs and consequently on the total feeding time per individual (Table 2). This resulted from interference among individuals on the large pods which were suitable food resources. The density effect in *R. clavatus* was less pronounced than in *N. viridula*. This may be due to the former's lower food resource demand (SUZUKI, unpublished).

Although both species preferred to feed on pods, *N. viridula* fed more frequently on leaves and stems than *R. clavatus* in accordance to the decrease of food resource in pods. These results indicate the different feeding properties of the 2 species. In *N. viridula* (which has larger demand of food resource than *R. clavatus*), severe interference among individuals occurs on large pods, causing bugs to feed on the leaves and stems which are generally inferior in nutritive value (SOUTHWOOD, 1973; HODKINSON and HUGHES, 1982). In *R. clavatus*, individuals persist more intensely in pod feeding. Furthermore, the feeding time per feeding trial in *R. clavatus* is shorter than in *N. viridula*. The bugs move frequently, searching for suitable pods. Such an intense preference for pods in *R. clavatus* may be related to the high mobility of this species.

The difference in density, duration of release and period of release resulted in various patterns of soybean response. At high density, the number of small pods increased considerably, compared with that on control plants (Fig. 1). This may result from the following process. The assimilated substances which should be translocated to pods for pod growth and seed production begin to be partly translocated for the production of new pods replacing the pods fed on by bugs. Consequently, this compensatory reaction results in increase in number of pods.

However, the number of small pods scarcely increased when the bugs fed on the plants at the middle and late 10-day and late 20-day release periods. This shows that the compensatory reaction occurs only at the early pod-growing stage. A similar tendency was reported in artificial depodding (KAWAMOTO, 1987).

Generally, the development of vegetative organs of the soybean ceases at the pod-growing stage (MIKOSHIBA, 1975). In this study, the increase in number of leaves and expansion in leaf area were not found after the pod-growing stage, even on injured plants. On injured plants, the biomass of seeds decreased remarkably with higher bug densities, while biomass of the leaves, stems and roots showed an opposite trend. These results show that much of the assimilate substance is not translocated to pods and continues moving to the vegetative organs due to pod feeding of the bugs.

Naturally, elongation and subsequent thickening of pods occur and the assimilates are temporarily stored in pods prior to seed production (MIKOSHIBA, 1975). Such a phenomenon might occur on pest-free plants. The biomass of pods at density 2 was more abundant than that of the control. It is possible that the assimilates reached pods rather than seeds, due to the bugs' seed feeding. On the other hand, smaller pod biomass at higher densities may be the result of assimilates in the vegetative organs

Fig. 5. The relationship between the yield of soybean (the biomass of seeds weighing more than 100 mg) and the total intensity of injury (density of bugs $\times$ duration of injury). +: control, ○: early, 10-day release of bugs, ●: middle 10 days, ▲: late 10 days, △: early 20 days, ■: late 20 days, □: 30 days.

not even reaching pods due to the severe pod feeding of the bugs.

Soybean injury became less severe with the delay of bug release (Fig. 4). A similar tendency was also reported by YEARGAN (1977). In order to evaluate the compound effects of density, duration of release and period of release on the soybean, the relationship between the yield and total intensity of injury (defined as density $\times$ duration of release of bugs) is examined in Fig. 5. Only the biomass of seeds weighing more than 100 mg was regarded as yield, because about 90% of seeds weighed more than 100 mg (dry weight) in control plants.

When the bugs commenced to feed on plants from the early pod-growing stage, the difference in the yield was low between high-density, short release duration treatment and low-density, long release duration plants. The yield decreased gradually with higher levels of infestation. A 50% decrease in the yield was found at the total injury intensity level of about 30.

Soybean yield was high when bugs were released later in the plants' growth, even at the same total intensity of injury. This was particularly evident in the late 10-day release period (yield decrease of about only 20%). These results suggest that the timing of feeding (period of bug release) correlates strongly to soybean yield.

Considering that assimilates still remained in abundance in the vegetative organs (i.e., leaves, stems and roots) of injured plants 30 days after the release of bugs, there may be a possibility that small pods produced by compensatory reaction can thereafter grow fully, if not restricted by abiotic factors.

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