Comparative Feeding Preference and Food Intake and Utilization by the Cabbage Looper (Lepidoptera: Noctuidae) on Three Legume Species

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ABSTRACT Preference among, and relative consumption and use of several legumes by third instars of the cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), were studied under laboratory conditions. Leaf disks of the relatively insect-resistant 'PI 227687' and insect-susceptible 'Davis' soybean, *Glycine max* (L.) Merrill, and of snap bean, *Phaseolus vulgaris* L.; and 'Henderson's Bush' lima bean, *P. lunatus* L. were preferred to sucrose-treated elderberry-pith disks, thus, the phagoexcitant effects of primary and secondary substances from the leaves of all plants exceeded those of sucrose alone. Leaf disks of 'PI 227687' were significantly less preferred than those of 'Davis' soybean and lima bean. Consumption and utilization of 'Henderson's Bush' lima bean and 'Davis' soybean leaves were most efficient, and of 'PI 227687' soybean leaves were least efficient. A lower rate of food intake on snap bean was associated with a higher efficiency of conversion of ingested food into body matter. Efficiency of conversion of digested food (ECD) into body matter was significantly and positively associated with the growth rate (GR) of larvae on the most suitable host plant, lima bean, but was negatively associated in larvae on 'PI 227687', the least suitable host. The relatively high consumption index (CI) on 'PI 227687' indicated significant antibiotic effects from secondary substances in 'PI 227687'. Relative preference observed in leaf disk assays was not reflected in host-plant suitability based on consumption and utilization of foods. To understand better the insect-plant interrelationships, both insect preference for, and consumption and utilization as food should be studied.

KEY WORDS Insecta, plant preference, food utilization, legumes

THE CABBAGE LOOPER, *Trichoplusia ni* (Hübner), is a polyphagous herbivore (Henneberry & Kishaba 1966) that uses some Leguminosae as hosts. Some recent studies on plant resistance to *T. ni* have examined insect preference using leaf disk assays (Khan et al. 1986a,b; Chiang et al. 1986, 1987). However, such assays may not fully measure plant suitability for the growth and development of insects. Insect growth is influenced by both the quantity and quality of food consumed (Kogan 1972, Sharma & Agarwal 1982), and plant preference often is not correlated to food consumed (Kogan 1972). Studies on food consumption and utilization measure specifically the antibiotic effects of phytochemicals on growth and development. Thus, for a comprehensive understanding of insect-plant interactions, there is a need to link preference with overall plant suitability.

The current studies examined interrelationships between feeding preference, consumption, and utilization of soybean, snap bean, and lima bean as food by third instars of the cabbage looper.

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Materials and Methods

Plants. Plants of insect-resistant 'PI 227687' and insect-susceptible 'Davis' soybean, *Glycine max* (L.) Merrill; snap bean, *Phaseolus vulgaris* L.; and 'Henderson's Bush' lima bean, *Phaseolus lunatus* L., were raised in the greenhouse at the U.S. Dairy Forage Research Center, University of Wisconsin, Madison. Seeds were germinated in sterilized moistened vermiculite in plastic trays (27 by 27 by 7 cm) in a Percival (Percival Manufacturing, Boone, Iowa) growth chamber at 27 ± 1°C and a 16-h photophase. Seedlings at cotyledon openings were transplanted individually into earthen pots (20 cm diameter) containing a sterilized mixture of soil, sand, and vermiculite (2:1:1). Plants were watered on alternate days for the first 4 wk, and daily during the next 4 wk. The plants were fertilized every fortnight with 50 ml of Miracle-Gro (Stern's Nursery, Geneva, N.Y.) (1 tablespoonful per 2.78 liters).

Plants were grown under a 16-h photophase from Metalarc high-intensity (1,000-W) lighting which gave 28-36 moles of photon flux. Plants were sprayed once with 2.5% Safer (50.5% potassium salts of fatty acids, AgroChem., Jamul, Calif.) at 20 d after transplanting to suppress thrips. Leaves from 8-wk-old plants (i.e., V8-stage soybean, and

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preflowering snap bean and lima bean) were used to study insect preference for, and relative consumption and utilization of, the four legumes as food.

Insects. Insects were reared under laboratory conditions (27 ± 2°C and 60 ± 5% relative humidity) on a pinto bean-based artificial diet (Shorey & Hale 1965). Newly molted third instars were used in the bioassays. Larvae were kept in petri dishes (9 cm diameter) with a filter paper attached in the top and on the inside bottom. The one in the top was soaked with 2 ml of deionized water to keep the larvae water-satiated.

Plant Preference. Preference of third instars of the cabbage looper, *T. ni*, for leaf disks from 'PI 227687' or 'Davis' soybean, snap bean, or lima bean, or for elderberry-pith disks treated with sucrose, was studied in two- or multi-choice assays as described below.

Leaf Disks. Fully expanded, mature leaves were used for cutting assay disks to study insect preference. To keep the leaves fresh during the <15 min of transport time between the greenhouse and the laboratory, they were placed between folds of water-soaked filter paper in an ice chest. Disks were cut with a no. 7 cork borer, and were kept between folds of water-soaked filter paper until placed within minutes into an assay.

Elderberry-Pith Disks. Disks of elderberry, *Sambucus canadensis*, pith were prepared using a method of Norris & Baker (1967). Elderberry pith was purchased from Ward's General Biological Supply House, Chicago, Ill. The stalks were dried in an oven at 80 ± 2°C for 4–6 h before being cut into 400-μm thick disks with a sliding microtome. The cutting blade and pith stalk were kept wet with absolute ethanol during sectioning. Disks of uniform circumference were cut with a no. 7 cork borer, and were stored in absolute alcohol until used.

Pith disks were dried in air on a filter paper before they were used in an experiment. Dried pith disks were centered on insect pins, 1 cm above a 0.5-cm-thick layer of paraffin wax in a petri dish. Each pith disk was treated with 40 μl of 1% sucrose in water (i.e., 400 μg sucrose/disk) using a micropipette. Such sucrose is a proven phagostimulant to third instars of *T. ni*. Pith disks treated with sucrose were dried for 1 h at room temperature under a slow stream of air from a table fan. Such treated and dried disks were then used as a standard positive control in choice assays.

Two-Choice Assay. Two test disks were centered in an apposed arrangement, 5 mm apart, in a 9-cm diameter petri dish. Each petri dish had a 0.5-cm layer of paraffin wax covered with a 9-cm diameter filter paper. Disks were positioned on the filter paper using shortened no. 2 insect pins. A filter paper (9 cm diameter) soaked in 2 ml of deionized water was attached to the inner surface of a petri-dish cover. Disks of 'PI 227687' and 'Davis' soybean, snap bean, lima bean, and elderberry pith were tested in all combinations in a two-choice assay. A single third instar, starved for 4 h, was confined with the disks for 8 h. There were 10 replications of each comparison. After 8 h, the larva was removed from the petri dish, and each disk was passed through a leaf-area meter (LI 3100, LI-COR, Lincoln, Nebr.) to determine the unconsumed area. Treatment means were compared using the student paired *t* test.

Multi-Choice Assay. One leaf disk each of 'PI 227687' and 'Davis' soybean, snap bean, and lima bean was arranged in a standardized circle in a petri-dish arena prepared as described above. An elderberry-pith disk treated with sucrose was centered as a standardized control within the circle of leaf disks in each petri-dish arena. The order of leaf disks in the circle was randomized. There were 10 replications. Five third instars, starved for 4 h, were released in each petri dish. Larvae were confined with the disks for 8 h. At the end of an experiment, the larvae were removed from the Petri dish, and the insect-exposed disks were passed through the leaf-area meter to record the area of the unconsumed disk. Significance of differences between treatments was determined using analysis of variance, and the treatment means were compared using least significant difference (LSD).

Consumption and Utilization of Food. Consumption and utilization of food were studied using fully expanded mature leaves as described earlier. Freshly detached leaves were weighed on a Mettler balance, and each was placed in a plastic cup with a diameter of 9 cm and depth of 5 cm. The cups were covered with a lid that had a water-soaked filter paper (9 cm diameter) attached to its inner surface. Water-satiated, preweighed third instars, starved for 4 h, were confined individually with a leaf for 2 d. Five leaves of each plant were kept in a similar manner, but without larvae, as a control to determine the natural loss in leaf mass. The cups were kept in a plastic tray (27 by 27 by 7 cm), which was covered with a similar inverted tray. The trays were kept at 27 ± 1°C under laboratory conditions. Two days after confinement, the larvae, uneaten food, and control leaves were weighed and then placed in an oven at 80 ± 2°C for 24 h to dry. The larvae were killed with benzene before drying. Dry masses of leaves, larvae, and feces were recorded. Dry masses of 10 larvae also were determined individually at the beginning of the experiment to compute a mean dry mass of larva before feeding. Natural loss of leaf mass was calculated as described by Sharma & Agarwal (1982), and the actual masses were corrected for the natural loss of leaf mass.

Indices of consumption and utilization of food were computed on fresh- and dry-mass bases as defined by Waldbauer (1968). Significance of differences between treatments were determined by analysis of variance, and the treatment means were compared using least significant difference (LSD). A correlation matrix between various indices of

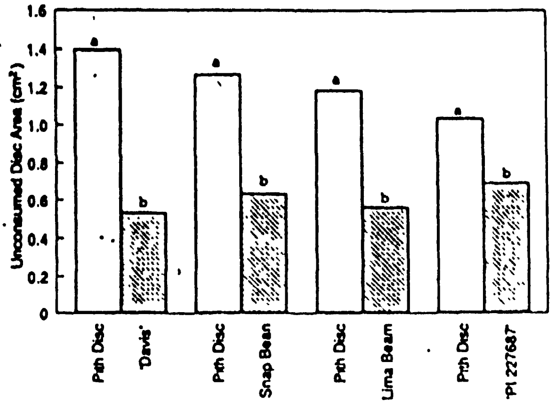

Fig. 1. Relative preference of third instars of cabbage looper for sucrose-treated elderberry-pith disk versus a leaf disk from 'PI 227687' or 'Davis' soybean, snap bean, or lima bean in a two-choice assay (elderberry-pith disks were treated with 400 μg of sucrose). Bars followed by the same letter in a pair are not significantly different at $P < 0.05$.

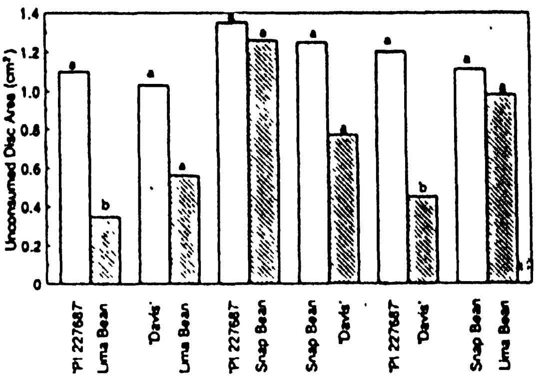

Fig. 2. Relative preference of third instars of cabbage looper for 'PI 227687' or 'Davis' soybean, snap bean, or lima bean in different combinations in a two-choice assay. Bars followed by the same letter within a pair are not significantly different at $P < 0.05$.

consumption and utilization of food was computed for each plant species and cultivar.

Results

Plant Preference. Leaf disks of 'PI 227687' or 'Davis' soybean, snap bean, or lima bean were significantly preferred ($P < 0.05$) by the cabbage looper larva over the standardized sucrose-treated elderberry-pith disk in a two-choice assay (Fig. 1). Greatest feeding was recorded on 'Davis' soybean and lima bean disks compared with the elderberry-pith disks. The amount of feeding on elderberry-pith disks treated with sucrose was greatest when offered in combination with 'PI 227687' soybean. 'PI 227687' soybean leaf disks were significantly ($P < 0.05$) less preferred to those from 'Davis' soybean, and lima bean (Fig. 2). Differences in feeding between 'PI 227687' soybean versus snap bean were not significant at $P < 0.05$. Differences in feeding between 'Davis' soybean, snap bean, and lima bean also were not significant ($P < 0.05$). However, leaf disks from 'Davis' soybean were less preferred than those of lima bean, but more preferred than those of snap bean. Leaf disks from snap bean and lima bean were preferred similarly.

In multi-choice assays, 'PI 227687' leaf disks were significantly ($P < 0.05$) less preferred than those of sucrose-treated elderberry-pith disk, snap bean, 'Davis' soybean, and lima bean (Fig. 3). Sucrose-treated elderberry-pith disks and those of snap bean elicited similar preference. 'Davis' soybean and lima bean disks were most preferred.

Consumption and Utilization of Food. There were significant ($P < 0.05$) differences in consumption and utilization of leaves from different plants on a dry-mass basis (Table 1). Consumption index (CI) was greater on 'Davis' soybean followed by 'PI 227687' soybean, lima bean, and snap bean. Larvae grew faster when reared on lima bean and 'Davis' soybean, and slower on 'PI 227687' soybean and snap bean. Efficiency of conversion of ingested food into body matter (ECI) was least on 'PI 227687' soybean. Approximate digestibility (AD) was greater in larvae that fed on snap bean. Differences in AD between 'PI 227687' and 'Davis' soybean and lima bean were not significant ($P < 0.05$). Rate of conversion of digested food into body matter (ECD) was least in larvae that fed on 'PI 227687' soybean and snap bean, and greatest in those that fed on lima bean.

On a wet-mass basis, larvae consumed significantly ($P < 0.05$) more food from lima bean and 'Davis' soybean than from 'PI 227687' soybean and snap bean (Table 2). The greatest larval growth was recorded on lima bean and 'Davis' soybean. Differences in efficiency of conversion of ingested

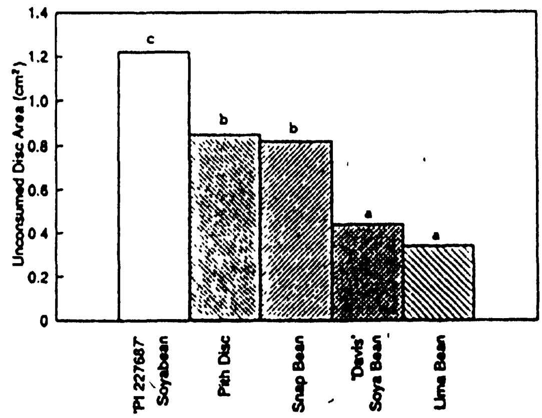

Fig. 3. Relative preference of third instars of cabbage looper for 'PI 227687' or 'Davis' soybean, snap bean, or lima bean leaf disks versus a sucrose-treated (400 μg/disk) elderberry-pith disk in a multi-choice assay. Bars followed by the same letter are not significantly different at $P < 0.05$.

Table 1. Consumption and utilization of food by third instars of the cabbage lopper, *T. ni* (indices calculated on dry-mass basis)

Plant	Initial mass of larvae, mg	Mass of larvae after feeding, mg	Mass of leaves ingested, mg	Mass of feces produced, mg	Consumption index	Growth rate	Efficiency of conversion of ingested food	Efficiency of conversion of digested food	Approximate digestibility
Soybean									
'PI 227687'	3.3a	5.8a	26.9ab	15.1b	2.9b	0 356b	9 0c	25.0a	39.5a
'Davis'	3.9a	9.9b	49 6c	28 5c	3 7c	0.429c	12 5ab	37.5ab	40.9a
Snap bean	3.7a	6 3a	16 5a	5 2a	1.6a	0 235a	17.5b	26.7a	66.3b
Lima bean	3.8a	9 9b	36 5b	19 2b	2 7b	0.434c	16.8b	38.3b	48.3a
SE	0.95	0 76	3 75	1 85	0 25	0.026	2.12	4.62	3.82

Means followed by the same letter in a column are not significantly different at $P < 0.05$

food into body matter were not significant ($P < 0.05$).

The correlation coefficients between consumption index and growth rate were not statistically significant ($P < 0.05$) (Tables 3 and 4). Higher rates of leaf intake were associated with decreased efficiency of conversion of ingested (ECI) and digested (ECD) food into body matter. However, the correlation coefficients were not significant in some cases. Consumption index was significantly associated with approximate digestibility only for 'PI 227687' soybean. Growth rate was positively associated with ECI. However, the correlation coefficients were significant only for 'PI 227687' and lima bean. Growth rate was positively correlated with AD in 'PI 227687' soybean, but negatively in lima bean. It was correlated with ECD in an opposite manner for 'PI 227687' soybean and lima bean. ECI and ECD showed a significant ($P < 0.05$) positive correlation except for 'PI 227687'. Approximate digestibility and ECI were associated negatively for 'Davis' soybean and lima bean. Approximate digestibility and ECD were correlated negatively (except in snap bean).

Discussion

Sucrose-treated elderberry-pith (control) disks were preferred less than leaf disks from any of the four plants in a two-choice assay. These results emphasize the point that the net phagoexcitant effects of a mixture of primary or secondary substances (or both) from even nonpreferred plants such as 'PI 227687' may significantly exceed those effects of sucrose on elderberry pith. The relative succulency of leaf disks as compared with pith disks may also have played a significant role in observed insect preferences. Nonpreference for 'PI 227687' soybean as compared with 'Davis' soybean or lima bean in both two- and multi-choice assays confirms its resistance to the cabbage looper (Leudders & Dickerson 1977; Khan et al. 1986 a,b). Larval preferences between snap bean and the sucrose-treated elderberry-pith disk, and 'Davis' soybean versus lima bean were not significant ($P < 0.05$) in the multi-choice assay. However, differences between these pairs were significant in the two-choice assay. Such differences in measured host-plant preference may result from the choice offered to the larvae, and the presence of more than one larva in the Petri-dish arena in the multi-choice assay.

Insect growth rate, a major consideration in determining the relative suitability of a plant for an insect, was lower with 'PI 227687' soybean (0.356) and snap bean (0.235) than with 'Davis' soybean (0.429) and lima bean (0.434). Lower ECI, ECD, and AD in larvae fed on 'PI 227687' soybean than in those fed on snap bean indicate the poor suitability of 'PI 227687' for the *T. ni* larvae. Poor efficiency of food utilization on 'PI 227687' may involve antibiotic effects of secondary plant substances (Norris et al. 1988).

Lower rates of food intake as observed in snap bean have been associated with a higher efficiency of conversion and utilization of food (Gordon 1972, Sharma & Agarwal 1982). Larvae of *Manduca sex-*

Table 2. Consumption and utilization of food by third instars of cabbage looper, *T. ni* (indices calculated on wet-mass basis)

Plant	Initial mass of larva, mg	Mass of larva after feeding, mg	Mass of leaves ingested, mg	Consumption index	Growth rate	Efficiency of conversion of ingested food
Soybean						
'PI 2278687'	36.6ab	64 1a	130.9b	1.3a	0.266a	20.8a
'Davis'	39.5b	107.9b	249.0c	1.7ab	0.460b	28.4a
Snap bean	34.6a	56.1a	107.2a	1.3a	0.227a	23.3a
Lima bean	35.6a	92.3b	259.6c	2.1b	0.434b	23.3a
SE	1.68	6.77	20.95	0.17	0.030	4.28

Figures followed by the same letter in a row are not significantly different at $P = 0.05$.

Table 3. Correlation matrix between indices of consumption and utilization of different plants for food by third instars of the cabbage looper, *T. ni* (based on dry-mass basis)

Indices	Soybean		Snap bean	Lima bean
	'PI 227687'	'Davis'		
CI GR	0 62	0 34	0 51	−0 38
CI ECI	−0 14	−0 79**	−0 51	−0 84**
CI AD	0 84**	0 59	0 29	0 39
CI ECD	−0 96**	−0 69*	−0 54	−0 56
GR ECI	0 68*	0 30	0 32	0 82**
GR AD	0 91**	−0 24	0 08	−0 85**
GR ECD	−0 65*	0 28	0 31	0 85**
ECI AD	0 35	−0 73**	0 02	−0 74
ECI ECD	0 08	0 87**	0 96*	0 86**
AD ECD	−0 89**	−0 83**	−0 23	−0 94**

CI, Consumption index, GR, growth rate, ECI, efficiency of conversion of ingested food into body matter, ECD, efficiency of conversion of digested food into body matter, AD, approximate digestibility
*, **, Significant at $P = 0.05$ and $P = 0.01$, respectively

ta L digest preferred host plants less efficiently, but convert the digested food into body matter more efficiently (Waldbauer 1968) Similar trends were observed in *T ni* larvae fed on 'Davis' soybean Because there is no obvious advantage in less efficient food digestion, the lower efficiency may result passively from a higher rate of food intake Observed variation in indices of food utilization also may be attributable to transition effects (Soo Hoo & Fraenkel 1966, Gordon 1972), host-plant suitability to the larvae, and the intrinsic capacity of the species to utilize different host plants ECI, ECD, AD, and GR are all quite high with lima bean and 'Davis' soybean Thus, the overall suitability of these legumes for the *T ni* larvae seems to be well explained by our findings

Snap bean leaf disks were not significantly ($P < 0.05$) preferred to those of lima bean in two-choice tests, and were moderately preferred by the larvae under multi-choice conditions Higher rates of ECI and AD observed in larvae that fed on snap bean leaves may be associated with lower rates of food intake (Kogan 1972).

'PI 227687' soybean, which was less preferred by the larvae in leaf-disk assays, had a relatively higher rate of feeding per unit of body mass (CI) under no-choice conditions However, the indices of food utilization (ECI, AD, and ECD) were lowest on this genotype. Thus, preference tests involving leaf-disk assays at least partially reflected 'PI 227687' unsuitability for the growth and development of larvae. However, higher CI values indicated that the nonpreference observed in choice tests was overridden under no-choice conditions, and that the antibiosis components of resistance appear to be dominant in the latter situations.

'Davis' soybean and lima bean leaf disks were preferred by the cabbage looper larvae. However, a higher CI was observed only with 'Davis' soybean. Indices of food utilization indicated that these

Table 4. Correlation matrix between the various indices of utilization of different host plants for food by third instars of the cabbage looper, *T. ni* (based on wet-mass basis)

	Soybean		Snap bean	Lima bean
	PI 227687	'Davis'		
CI GR	0 51	0 44	−0 05	−0 49
CI ECI	−0 31	−0 75*	−0 68*	0 98**
GR ECI	0 65*	0 24	0 60	0 62

*, ** Significant at $P = 0.05$ and $P = 0.01$, respectively
CI, Consumption index, GR, Growth rate, ECI, Efficiency of conversion of ingested food

plants are suitable for the growth and development of larvae However, the ECI and AD were relatively lower on 'Davis' soybean, and this legume has been associated with higher rates of food intake (Kogan 1972) Preference for 'Davis' soybean and lima bean, as observed in leaf-disk assays, was compatible with their suitabilities for the growth and development of larvae

Relative preference for 'PI 227687' soybean, snap bean, and lima bean, as observed in leaf-disk assays,' was not confirmed in terms of CI under no-choice conditions However, relative preference or nonpreference for leaf disks of 'PI 227687' and 'Davis' soybean and lima bean was compatible with their suitabilities for the growth and development of larvae Therefore, studies to improve the understanding of host-plant resistance should include both investigations of insect preference, and food utilization for growth and development

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