Comparative Feeding and Development of *Pseudoplusia includens* (Lepidoptera: Noctuidae) on Kudzu and Soybean Foliage

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ABSTRACT   Kudzu, *Pueraria montana* (Lour.) Merr. variety *lobata* (Willd.) Maesen & Almeida, a close relative of soybean, *Glycine max* (L.) Merr., is an adventive and widely distributed weed in the southeastern United States. Conventional wisdom says that native arthropods do not feed heavily on kudzu, but recent evidence has indicated this is not the case. To better understand the interaction of kudzu and native insects, the biology of the soybean looper, *Pseudoplusia includens* (Walker), was compared on kudzu and soybean. Insects fed on kudzu had higher mortality, longer development times with supernumerary molts, and lower pupal weights than those fed on soybean. Rearing for up to three generations on either plant host had an effect on length of development time but did not affect other measured parameters. Foliage consumption did not differ between treatments, and nutritional quality of soybean and kudzu did not differ. The instar at which insects were transferred from artificial diet to either kudzu or soybean significantly influenced development time, number of instars, foliage consumption, and pupal weights, with instar 4 being the optimum stage for transfer. In an oviposition test, females readily oviposited on kudzu in a no choice test, but when both kudzu and soybean were provided, more eggs were deposited on soybean than on kudzu. Our studies show that although kudzu is an acceptable host, soybean is a preferred and better quality host.

KEY WORDS   *Pseudoplusia includens*, kudzu, soybean, host preference, preimaginal development, fecundity

Pueraria montana (Lour.) Merr. variety *lobata* (Willd.) Maesen & Almeida (kudzu), is a common adventive weed in the southeastern United States that belongs to the same tribe as soybean, *Glycine max* (L.) Merr. [family Fabaceae, subfamily Papilionatae (Lotoideae), tribe Phaseoleae] (Heywood 1971). Native to China, the vine is widely used in China and Japan for food and fiber (Shurtleff and Aoyagi 1977, Duke 1981). It was first introduced to the United States in 1876 at the Centennial Exposition in Philadelphia and promoted as an ornamental plant and for livestock feed. During the 1930s and 1940s, kudzu was recommended for erosion control, and in the 6 yr from 1935 to 1940, the U.S. Soil Conservation Service made available 73 million kudzu seedlings to landholders for erosion control (Tabor and Susott 1941).

Although quantitative data are lacking, anecdotal estimates suggest that over 7 million acres in the southeastern U.S. are infested (Everest et al. 1991), causing economic damage due to cost of control and lost production. Kudzu is widely acknowledged as a major weed pest of forests and rights of way in the southeast. Biological control of kudzu is being explored, because other options may not be feasible. An important component of a weed biological control program is the study of the target weed's biology and ecology as well as the population dynamics of its natural enemies in its area of origin. In addition, similar studies before the introduction of natural enemies from the area of origin are critical in the location where the plant has become a weed. Despite kudzu's pervasiveness, almost nothing is known of its ecology and interactions with native arthropods in the United States.

To begin these studies, we looked for a model herbivore that could be used in both field and laboratory experiments. Few insects have been reported feeding on kudzu in the United States. The velvetbean caterpillar, *Anticarsia gemmatalis* Hübner, uses the plant as an overwintering host in central and south Florida (Buschman et al. 1977). In 1995, larvae of *A. gemmatalis*, *Pseudoplusia includens* (Walker) (soybean looper), and *Estigmene acraea* (Drury) (saltmarsh caterpillar) were observed feeding on kudzu near Union, SC (L. Barber and D.O., unpublished data). We chose *P. includens* as a model herbivore in kudzu studies because it is attacked by a common, native egg-larval parasitoid, *Copidosoma truncatellum* (Dalman) (Burleigh 1971, Deitz et al. 1976, Daigle et al. 1990). This parasitoid allows hosts to complete larval development and spin cocoons then kills them just before pupation (Silvestri 1937). This would allow for the release of large numbers of insects into field plots without the concern of nontarget impacts.

The soybean looper is a plusiine noctuid that feeds on numerous plants, but soybeans, cotton, and sweetpotatoes are its primary hosts (Hensley et al. 1964, Canerday and Arant 1967, Mitchell 1967, Herzog

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1980). *Pseudoplusia includens* has been reported to feed on plants in 28 different families, including eight species of legumes (Herzog 1980). Martin et al. (1976) tested a number of crops including bush beans, field peas, peanuts, and soybeans; and, based on the abundance of larvae on plants, reported that soybeans were the preferred host followed by peanuts. Additional host plants included collards, bell peppers, and tomatoes, but *P. includens* did not oviposit or feed on bush beans and field peas. An annual legume, *Desmodium toruosum* (Swartz) de Candolle (beggarweed), is also an acceptable host plant for *P. includens*, and laboratory studies demonstrated that it provides sufficient nutrition for the insect's development (Beach and Todd 1988).

Pseudoplusia includens can be laboratory-reared successfully using an artificial diet (Shorey and Hale 1965, Burton 1969, Greene et al. 1976, Shour and Sparks 1981), an important factor for selecting it as a model insect for study. The development of the insect under various conditions has been described (Canerday and Arant 1967, Mitchell 1967, Reid and Greene 1973, King 1981, Shour and Sparks 1981, Trichilo and Mack 1989, Strand 1990). The purpose of our study was to compare the preimaginal development, foliage consumption, and reproduction of *P. includens* reared on kudzu compared with soybean in a laboratory study and to determine the optimum stadium to use for field studies.

Materials and Methods

Insect Colonies. Soybean looper larvae used in this study were originally collected from Open Grounds Farm, Carteret County, NC, in October 1997 and maintained in a laboratory colony on an artificial diet (Burton 1969). Several additional subcolonies of *P. includens* were developed with the following rearing histories: (1) loopers from the laboratory colony, (2) loopers reared for one generation on soybean leaves (S-1), (3) loopers reared for one generation on kudzu leaves (K-1), (4) loopers reared for two generations on soybean leaves (S-2), and (5) loopers reared for two generations on kudzu leaves (K-2). For the S-1 and K-1 colonies, a new cohort was started each week with ≈100 neonate larvae from the laboratory colony to provide a constant supply of insects. From 1 May to 3 July 1998, foliage was collected from greenhouse grown soybean (variety Brim) and kudzu plants. After 3 July, foliage was collected from plants grown in small plots on the NCSU campus. All leaves were rinsed with a dilute (0.035%) sodium hypochlorite solution then tap water to remove any entomopathogens before feeding (Beach et al. 1985) and placed in test tubes fitted with a single hole rubber stopper. Test tubes containing foliage were placed in 12-liter square, polyethylene boxes (Rubbermaid, Twinsburg, OH) and held upright with wire supports. Foliage was added as needed, and pupae were removed and their numbers recorded as they developed. All pupae from a cohort were placed in a separate polyethylene box with sugar water for adult feeding and a leaf in a test tube as described above for oviposition. Initially, leaves of the same species on which the insects had developed were provided, but the quantity of eggs being laid on kudzu leaves was not satisfactory, so soybean leaves were provided in all oviposition boxes. Eggs were rinsed from the foliage with a dilute sodium hypochlorite solution (≈0.015%) and served as the foundation of the S-2 and K-2 subcolonies. All of these subcolonies were maintained in a growth chamber (model 35VL, Percival, Boone, IA) at 25°C, 80% RH, and a photoperiod of 14:10 (L:D) h (Beach and Todd 1988).

Feeding, Development, and Fecundity. To test the influence of plant species and rearing history on feeding, development, and fecundity, *P. includens* reared 0, 1, or 2 generations on either kudzu or soybean were compared in a laboratory experiment. The experiment was a 2 × 5 factorial design. Treatments were kudzu or soybean, and the factors were the five rearing histories described above (K-1, K-2, S-1, S-2, or diet). The experiment was conducted twice with 25 replications in trial 1 (18 July–11 August 1998) and 15 in trial 2 (27 August–19 September 1998).

The feeding arena used in this study was an inverted 150 by 15-mm plastic petri dish, with moistened filter paper lining the lid. Neonate larvae from each subcolony were randomly assigned to individual dishes within a treatment group and provided with an individual leaflet from the first fully expanded leaf from soybean plants and fully expanded young leaves from kudzu vines. Foliage was collected and treated as described for insect colonies.

All dishes were held at 25°C, 80% RH, and a photoperiod of 14:10 (L:D) h in an environmental chamber (model 35VL, Percival, Boone, IA) (Boldt et al. 1975, Richter and Fuxa 1984, Beach and Todd 1988). To control error due to variability of temperature, light or humidity within the chamber, dishes were arranged in a randomized complete block design, consisting of five or three blocks (trials 1 and 2, respectively) with five dishes of each treatment combination per block. Leaflets were changed every 48 h or as needed.

Larval development was recorded as the length of time spent in each stadium and total development time. Throughout the study, dishes were examined twice daily at 1 h after lights on and 2 h before lights out, and the day of molt to a new instar was recorded. Shour and Sparks (1981) found no differences in weights of *P. includens* larvae reared on artificial media until the fourth larval instar, regardless of the number of instars required to complete development. Therefore, beginning in the fourth instar, larvae were weighed in the premolt stage to the nearest 0.1 mg.

When the larvae reached the fourth or fifth instar, foliage consumption was estimated by measuring individual leaflets with an area meter (model LI-3100 Li-Cor, Lincoln, NE). During the first trial we found that feeding by fourth instars on kudzu was not measurable with the area meter, therefore measurements were initiated with the fifth instars in the second trial. To compensate for different leaflet thickness, feeding rate was estimated as the consumption of dry matter.

At three points during each trial, 10 leaflets of each plant species were measured in the area meter and then weighed to the nearest 0.1 mg with an analytical balance (model M220D, Denver Instrument, Arvada, CO). Leaves were dried in an oven at 45°C for at least 72 h, then weighed, and the percentage of dry matter was converted to the weight (mg) of dry matter per leaf area (cm^2) (Beach and Todd 1986, 1988). The amount of leaf area consumed in the experiment was converted to milligrams of dry matter consumed using the average dry matter value.

Ten leaflets of each species were used to determine the amount of shrinkage due to water loss during the feeding period. Measured leaves were placed in individual petri dishes identical to the feeding dishes, randomly placed in the incubator, and held under the same conditions. Leaflets were set up every 1.5–3 d throughout the test period when leaf area was measured. Approximately 4 liters of fresh foliage was collected from the NCSU campus plots and submitted to the Forage Testing Laboratory of the North Carolina Department of Agriculture and Consumer Services for standard forage analysis.

Day of pupation was recorded, and pupae were weighed within 24 h. Sex of the pupae was determined, and up to 10 females (depending on how many females completed development) from each treatment group were randomly selected for the fecundity study. To measure fecundity, individual females from each treatment and two males from the laboratory colony were placed in paper cartons (0.5 liter) (Sweet Paper, Raleigh, NC) lined with waxed paper 6 d after pupation. Cartons were placed back in the incubator where rearing dishes were held, maintaining the same randomization. As a control, 10 randomly selected females from the laboratory colony that eclosed approximately midway between the soybean-fed and kudzu-fed insects were placed in cartons as above. Control females were placed in the incubator in the position previously occupied by the dishes holding leaves measured for shrinkage. All cartons were supplied with a 16% sucrose solution in 30-ml plastic cups (Polar Plastics, Mooresville, NC) for the moths and an excised soybean leaflet in an Aquapic (Syndicate Sales, Kokomo, IN). Tops of the cartons were covered with cheesecloth (50 grade, American Fiber and Finishing, Burlington, MA) held in place by the rim of the lid. Three days after the leaflets were introduced, and every 3 d until the female died, the leaflet, sugar water cup, waxed paper, and cheesecloth were changed. All materials from an oviposition carton were bagged and frozen at −17°C until the eggs were counted.

Diet Switching Study. The purpose of this study was to determine the optimum stadium for use in field studies. The experiment was designed as a 2 × 5 factorial, with treatments being kudzu or soybean and the factors being developmental stage (instars 1–5) at which larvae were moved from artificial diet to leaves. Each treatment by factor group consisted of 24 replications; 24 larvae served as controls, and the larvae remained on diet throughout their development. Neonate larvae from the laboratory colony were ran-

domly assigned to a treatment by factor group and fed artificial diet until reaching the assigned stage to be placed on foliage. Artificial diet prepared in 30-ml cups was sliced into disks ≈5 mm thick and pressed gently onto the inner surface of the bottom half of a 150 by 15-mm plastic petri dish. When larvae were fed leaflets, petri dish lids were lined with moistened filter paper, but when diet was provided, no filter paper was used. Leaflets were field collected from plots on the NCSU campus and treated as in the feeding study. Soybeans were mistakenly fertilized with an unknown quantity of controlled-release fertilizer (Osmocote 14-14-14, Scotts, Columbus, OH) after planting in 1999, but none was applied to kudzu plantings. Dishes were arranged in a completely randomized design in a rearing room at 24.5°C (±1.5°C), 70% RH, and a photoperiod of 14:10 (L:D) h. Larvae were examined once a day, and the day of molting to a new instar was recorded. The number of instars required to complete development and day of pupation was recorded. Within 24 h of pupation, sex was determined, and pupae were weighed to the nearest 0.1 mg. When larvae reached the fifth instar, foliar feeding was measured as dry matter (milligrams) consumed as in the feeding study. Leaf shrinkage or expansion was also considered as in the feeding study.

Oviposition Choice Test. To test the influence of host plant on oviposition in a laboratory experiment, *P. includens* reared on artificial media were offered three foliage treatments: (1) one soybean leaf, (2) one kudzu leaf, or (3) one kudzu and one soybean leaf. Testing arenas were cylindrical cages (30.5 cm in diameter and 30.5 cm high) constructed of aluminum window screen (7 mesh/cm) with a cardboard bottom and screen top. Sugar water (16%) was supplied for the moths.

Female pupae were weighed within 24 h of pupation and held individually in 30-ml cups until eclosion. Upon eclosion, females of the same age were placed individually into arenas with two males that eclosed on the same or next day. Arenas were arranged in a randomized complete block design with selective placement of treatments on a metal shelving unit with three shelves. Each shelf was divided into two blocks (front and back halves) to control error due to variability in lighting or air circulation. The experiment was conducted in a rearing room maintained at 24.5°C (±1.5°C), 70% RH, and a photoperiod of 14:10 (L:D) h, with two small nightlights to simulate moonlight.

Three days after female eclosion, foliage for oviposition was introduced. The first fully expanded leaves from the terminals of either kudzu vines or soybean plants were collected and treated as in the feeding study. Leaf area was measured with the area meter and only those leaves with an area of ≈240–280 cm^2 were used. Leaves were placed individually in water-filled test tubes fitted with rubber stoppers held upright in the arenas and monitored every 24 h until oviposition started. When oviposition began, leaves were discarded, and replaced with fresh leaves. After 24 h, these leaves were removed, frozen at −17°C and replaced with a second set of leaves that was also re-

Table 1. Development, dry weight of foliage consumed and total number of eggs laid by *P. includens* with various feeding histories on kudzu and soybean foliage in the laboratory (mean ± SD)

Plant[a]	History[b]	n	% survival	No. days to pupation	No. instars	4th instar wt (mg)[c]	Pupal wt (mg)	Consumption (mg dry wt)	n (♀)	Eggs/female
Kudzu	Diet	20	50.0 ± 33.8b	18.9 ± 1.3cd	6.8 ± 0.6b	6.8 ± 1.9b	169.4 ± 2.8b	287.0 ± 147.3a	6	924.7 ± 567.4a
	K-1	25	62.5 ± 22.5b	18.7 ± 1.4c	6.7 ± 0.5b	6.1 ± 2.0b	165.7 ± 3.6b	306.6 ± 112.3a	9	766.8 ± 413.8a
	K-2	30	75.0 ± 20.7b	19.4 ± 2.3de	6.8 ± 0.7b	6.7 ± 2.0b	178.4 ± 3.8b	341.0 ± 130.2a	14	808.1 ± 540.1a
	S-1	23	57.5 ± 19.8b	19.6 ± 1.7e	6.9 ± 0.5b	6.9 ± 1.7b	176.4 ± 3.3b	303.0 ± 133.9a	7	871.3 ± 474.3a
	S-2	25	62.5 ± 32.8b	19.2 ± 1.8cde	6.9 ± 0.6b	6.8 ± 2.4b	175.4 ± 4.3b	310.4 ± 134.6a	11	894.3 ± 701.3a
	Total n/Mean	123	61.5 ± 26.6	19.2 ± 1.8	6.8 ± 0.6	6.7 ± 2.0	173.4 ± 3.6	311.4 ± 131.8	47	844.7 ± 535.4
Soybean	Diet	38	95.0 ± 9.3a	12.7 ± 0.8a	5.2 ± 0.4a	14.6 ± 4.5a	231.7 ± 3.5a	274.5 ± 73.5a	17	878.2 ± 680.0a
	K-1	38	95.0 ± 9.3a	12.9 ± 0.8a	5.2 ± 0.4a	12.8 ± 3.2a	230.4 ± 2.3a	297.3 ± 87.4a	18	1,109.7 ± 620.7a
	K-2	38	95.0 ± 9.3a	13.6 ± 1.5b	5.3 ± 0.4a	14.6 ± 3.8a	232.3 ± 3.2a	304.5 ± 88.0a	15	943.6 ± 613.2a
	S-1	38	95.0 ± 9.3a	13.3 ± 0.7ab	5.2 ± 0.4a	13.7 ± 3.7a	228.8 ± 2.8a	270.0 ± 70.8a	17	1,106.4 ± 423.1a
	S-2	37	92.5 ± 10.4a	13.6 ± 1.1b	5.4 ± 0.5a	12.7 ± 4.9a	234.0 ± 2.2a	300.9 ± 84.5a	16	1,447.4 ± 595.1a
	Total n/Mean	189	94.5 ± 9.1	13.2 ± 1.1	5.3 ± 0.5	13.7 ± 4.1	231.6 ± 2.9	284.2 ± 81.2	83	1,096.7 ± 610.1
Colony									17	1,147.3 ± 807.0a

Values within a column followed by the same letter are not significantly different ($P > 0.05$, LSD).
[a] Plant: species being fed upon in the test, kudzu or soybean.
[b] History: food previous generation(s) reared on diet = insects from laboratory colony; K-1, S-1 = one generation reared on kudzu or soybean foliage; K-2, S-2 = two generations reared on kudzu or soybean foliage.
[c] Purged larvae were weighed within 12 h of molting to the fourth instar.

moved and frozen after 24 h. Eggs on these leaves were later counted, and numbers for both days were summed for each female.

Data Analysis. To achieve homogeneity of variance, pupal weight, fecundity, and oviposition data were square-root transformed, survival data were arcsine transformed, and data for the fourth and fifth instar larval weights were log transformed. Only data for individuals that survived to pupation were analyzed. All data were analyzed using the general linear model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD, SAS Institute 1996).

Results

Feeding, Development, and Fecundity. Survival to pupation of *P. includens* larvae feeding on kudzu was significantly lower than that of larvae feeding on soybeans (61.5 versus 94.5%) ($F = 34.3$; df = 1, 9; $P \leq 0.001$); rearing history of larvae had no significant effect on survival on either of the plants ($F = 0.8$; df = 4, 9; $P \geq 0.05$) (Table 1). Feeding on kudzu resulted in significantly increased development times (19.2 versus 13.2 d) ($F = 759.4$; df = 1, 60; $P \leq 0.001$) and number of instars (6.8 versus 5.3) ($F = 348.1$; df = 1, 9; $P \leq 0.001$). Rearing history had a significant effect on development time ($F = 3.0$; df = 4, 60; $P \leq 0.001$). Insects reared on either kind of foliage for two generations before the study tended to have longer development times than other larvae feeding on the same plant, but differences were not always statistically significant.

Larvae that had fed on soybean were twice as large as those fed on kudzu by the fourth instar ($F = 269.3$; df = 1, 9; $P \leq 0.001$). Significant differences due to host plant ($F = 276.9$; df = 1, 0; $P \leq 0.001$) and sex ($F = 8.9$; df = 1, 233; $P \leq 0.001$) were also found in the weights of premolt fifth instar larvae (data not shown). Pupae from the kudzu treatments were significantly smaller

(average weight 173.4 mg) than soybean-reared *P. includens* (231.6 mg) ($F = 126.6$; df = 1, 9; $P \leq 0.001$). Male pupae were significantly larger than females (216.9 ± 40.9 mg versus 201.0 ± 42.8 mg) ($F = 23.7$; df = 1, 233; $P \leq 0.001$).

No significant differences in the fecundity of females due to plant ($F = 1.7$; df = 1, 10; $P \geq 0.05$) or rearing history ($F = 1.3$; df = 4, 10; $P \geq 0.05$) were found. A relationship between pupal weight and the number of eggs was found ($F = 6.1$; df = 1, 102; $P \leq 0.001$). However, pupal weight was affected by plant, and it cannot be considered a true covariate with fecundity.

No significant differences in the total amount of foliage consumed were found regardless of plant type ($F = 0.7$; df = 1, 9; $P \geq 0.05$) or feeding history ($F = 0.4$; df = 4, 9; $P \geq 0.05$). Forage analysis showed that the two plants have similar crude protein content (23.7 and 24.7% for kudzu and soybean, respectively), and dry matter content was slightly higher for soybean (25%) compared with kudzu (22.5%).

Diet Switching. Larvae fed kudzu had significantly longer development times ($F = 47.2$; df = 1, 228; $P \leq 0.001$; $F = 31.1$) and lower pupal weights ($F = 236.9$; df = 1, 228; $P \leq 0.001$) than larvae fed soybeans or artificial diet (Table 2). Those switched in the first through fourth instars required more molts to complete development than other larvae ($F = 31.1$; df = 1, 228; $P \leq 0.001$). The stadium at which larvae were switched also had an effect, although a pattern is clearer for the larvae fed on kudzu ($F = 11.2$; df = 4, 228; $P \leq 0.001$). The earlier in their development that larvae were switched to kudzu, the longer their development time and the greater the number of molts. Larvae switched to kudzu for the fourth instar developed in a significantly shorter time (LSD; $P \leq 0.001$), but consumed a similar amount of food to those switched in earlier instars (LSD; $P \geq 0.05$). This trend was not seen for larvae switched to soybean at this stage. *Pseudoplusia includens* switched from artificial

Table 2. Development of *P. includens* switched from artificial diet to kudzu and soybean foliage at different stages in the laboratory (mean ± SD)

Plant[a]	Stage[b]	n	Days to pupation	Wt of pupae, mg	No. instars	Consumption (mg dry wt)
Kudzu	1	21	20.2 ± 1.9a	200.8 ± 30.8e	7.0 ± 0.6a	493.3 ± 112.4a
	2	22	20.4 ± 1.4a	203.1 ± 22.4e	7.3 ± 0.5a	481.7 ± 81.2a
	3	22	19.9 ± 2.1a	186.4 ± 38.8e	6.7 ± 0.5b	468.1 ± 107.2a
	4	22	18.5 ± 1.3b	193.9 ± 28.1e	6.3 ± 0.5b	471.8 ± 107.3a
	5	22	16.2 ± 1.9c	152.3 ± 50.6f	5.6 ± 0.8de	254.0 ± 133.9c
Soybean	1	24	13.0 ± 1.1f	248.9 ± 32.9bcd	5.1 ± 0.3f	276.8 ± 57.3bc
	2	23	14.4 ± 1.2d	269.1 ± 27.0a	5.8 ± 0.5d	313.8 ± 47.0b
	3	24	13.5 ± 1.4ef	253.3 ± 20.4abc	5.6 ± 0.5ef	289.1 ± 44.1bc
	4	23	13.9 ± 0.6de	262.2 ± 27.2ab	5.5 ± 0.5e	307.9 ± 64.3bc
	5	23	14.4 ± 1.3d	232.8 ± 51.1d	5.4 ± 0.5ef	256.8 ± 68.1c
Diet	—	20	14.2 ± 1.3de	240.2 ± 35.4cd	5.4 ± 0.5ef	—

Values within a column followed by the same letter are not significantly different ($P > 0.05$, LSD).
[a] Plant: species being fed upon in the test, kudzu or soybean, or artificial diet.
[b] Stage: instar at which larvae were switched from artificial diet to foliage.

diet to kudzu for the fifth instar had a significantly shorter development time and fewer instars than other kudzu feeders (LSD; $P \leq 0.001$), but lower pupal weights than all other treatments (LSD; $P \leq 0.001$). In contrast to the feeding study presented above, significant differences in food consumption were found based on plant ($F = 111.6$; df = 1, 206; $P \leq 0.001$), stadium at which larvae were switched ($F = 18.9$; df = 4, 206; $P \leq 0.001$), the interaction of plant and stadium ($F = 8.6$; df = 4, 206; $P \leq 0.001$), and sex ($F = 8.8$; df = 1, 206; $P \leq 0.001$). Larvae switched to kudzu in the first through fourth instars consumed similar amounts of dry matter (LSD, $P \geq 0.05$). Larvae switched to kudzu in the fifth instar consumed similar amounts of dry matter as those switched to soybean at all stadia but the second.

Oviposition Choice. When presented soybean and kudzu in choice and no-choice tests, *P. includens* laid significantly more eggs on soybean leaves in either treatment than on kudzu in either treatment ($F = 91.64$; df = 1, 68; $P \leq 0.001$) (Table 3). The fewest eggs were laid on kudzu in the choice treatment; significantly more eggs were laid on kudzu in the no-choice treatment. Mean leaf areas ranged from 255.0 to 267.3 cm^2. Despite this narrow range, kudzu leaves were significantly larger than soybean leaves ($F = 7.74$; df = 3,80; $P \leq 0.001$; $F = 9.8$; df = 1, 72; $P \leq 0.001$). Weights of pupae were not significantly different by treatment ($F = 1.4$; df = 2, 79; $P \geq 0.05$).

Table 3. Number of *P. includens* eggs laid on kudzu and soybean in oviposition choice and no choice tests in the laboratory (mean ± SD)

Oviposition substrate	n	Wt of pupae (mg)	Leaf area (cm^2)	Eggs/Female
No choice				
Kudzu	28	215.4 ± 28.9a	264.8 ± 10.4ab	325.7 ± 202.9b
Soybean	26	221.5 ± 34.7a	259.6 ± 11.3bc	570.9 ± 228.7a
Choice				
Kudzu	28	224.6 ± 29.9a	267.3 ± 10.9a	44.0 ± 72.8c
Soybean	28	224.8 ± 29.9a	255.0 ± 9.1c	468.5 ± 224.3a

Values followed by the same letter are not significantly different ($P > 0.05$, LSD).

Discussion

Results of this study show that kudzu is an acceptable host plant for *P. includens* development and reproduction. However, larvae fed kudzu showed increased mortality, longer development times, supernumerary molts, and lower pupal weights compared with larvae fed soybean. The effect of feeding on kudzu is comparable to that seen when *P. includens* develops on a mildly resistant soybean genotype or a less preferred host (Beach et al. 1985; Beach and Todd 1986, 1988). Beach and Todd (1988) demonstrated that mortality of *P. includens* on a susceptible soybean variety was 4% compared with 16% for larvae fed on Florida beggarweed (*Desmodium toruosum*) and a resistant soybean line (GatIR 81–296). *Pseudoplusia includens* fed on resistant soybeans required ≈2 d longer to pupate and had lower pupal weights than *P. includens* feeding on a susceptible variety (Beach et al. 1985, Beach and Todd 1986). Development time also increased for *P. includens* fed cotton compared with larvae fed soybeans (Wier and Boethel 1995a). Additional studies of *P. includens* development have shown that its growth rate is affected by a number of factors including leaf position, plant age, and wounding on a resistant line of soybeans (Reynolds and Smith 1985). Larval development time and mortality were inversely affected by the level of nitrogen fertilizer (Wier and Boethel 1995b).

Size differences were observed at the fourth instar; larvae fed kudzu were smaller than those fed soybean. The number of instars required for pupation is associated with a minimum weight at the end of the penultimate instar (Strand 1990). Larvae feeding on kudzu did not attain the body size to complete development after five instars; therefore they required more molts. The range of mean pupal weights in our feeding study regardless of treatment (165.7–234.0 mg) was within the range of pupal weights reported in other studies (Mitchell 1967, Reid and Greene 1973 Jensen et al. 1974, Felland and Pitre 1991, Wier and Boethel 1995b). Higher values have also been reported (Canerday and Arant 1967, Kogan and Cope 1974).

The mean soybean dry matter consumed in the feeding and diet switching studies falls within the range of soybean consumption found in previous studies (Reid and Greene 1973, Kogan and Cope 1974, Beach and Todd 1988). In our development study, the amount of kudzu consumed was not significantly different from the amount of soybean consumed. In contrast, larvae switched from diet to kudzu foliage in the first through fourth instars consumed significantly more dry matter than those feeding on soybeans. One possible explanation for these observations may be the lack of fertilization for kudzu plots compared with soybean. No fertilizer was applied to kudzu plots, but fertilizer was applied to soybean plots. Nitrogen fertilization affects the nutritional makeup of plants, and the ability to convert plant N affects an insect's ability to grow and reproduce (Scriber 1984). Beach and Todd (1988) found the greatest amount of feeding occurred on a susceptible soybean variety and less on a weed and resistant soybeans. Wier and Boethel (1995a) reported *P. includens* consumed significantly less cotton foliage than soybean foliage, an indication that cotton is less suitable as a host plant than soybeans.

Egg production in our study ranged from 766.8 to 1441.4 eggs per female and was high compared with other studies (Mitchell 1967, Jensen et al. 1974, Beach et al. 1985). Mitchell (1967) reported an average number of 240.2 eggs deposited per female, and Jensen et al. (1974) reported egg numbers between 425.9 and 671.3 eggs/female from a series of experiments on adult nutrition. In a comparison of susceptible and resistant lines of soybean, *P. includens* that developed on a susceptible line (Ransom) deposited an average of 340 eggs/female, and significantly fewer eggs were laid on resistant varieties (Beach et al. 1985).

In the laboratory, kudzu is an acceptable, but less suitable and preferred host plant compared with soybean for *P. includens.* Interestingly, Thornton (2001) demonstrated that foliage feeding in the field by native and naturalized insects resulted in seasonal levels of defoliation in kudzu identical to that in soybean.

Both soybean and kudzu originated in Asia and appear to harbor the same communities of many generalist herbivores (Thornton 2001). Before any biological control agents are introduced to the United States from China, we feel it is important to develop at least a basic understanding of the ecology of kudzu and its associated arthropods in both countries. This approach has been recommended by McClay (1995) as one way to improve the overall success of classical biological control programs against weeds. The information collected in this study will enable us to use *P. includens* as a model foliar-feeding insect for comparisons between kudzu populations from the United States and China and provide baseline information to study the interaction of native predators and parasitoids with foliage-feeding insects on kudzu in the field.

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