Feeding and Life History of *Spodoptera exigua* (Lepidoptera: Noctuidae) on Different Host Plants

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ABSTRACT Consumption rates, development times, and life table parameters of the beet armyworm, *Spodoptera exigua* (Hübner), were determined on five host plants: cabbage, *Brassica oleracea capitata* L; cotton, *Gossypium hirsutum* L.; bell pepper, *Capsicum annuum* L.; pigweed, *Amaranthus retroflexus* L.; and sunflower, *Helianthus annuus* L. Mean total leaf weight consumed by larvae was highest in cabbage (2.7 g) and lowest in pigweed (1.6 g). The feeding index (pupal weight divided by total weight of leaf tissue consumed) was highest on pigweed, followed by cotton, pepper, sunflower, and cabbage. On all host plants, significant relationships were found between amount of leaf tissue consumed and resulting pupal weight. Likewise, significant relationships were found between pupal weight and subsequent adult fecundity on all host plants. The highest percentage of female progeny was recorded in *S. exigua* reared on pigweed (62.2%) and the lowest for larvae reared on cabbage (43.6%). Duration of the larval stage was shortest on pigweed (12.4 d) and longest on pepper (18.0 d). Larval survival was highest on pigweed (94.4%) and lowest on cabbage (67.1%). Three key statistics were used to assess performance of *S. exigua* on the different host plants: 1) feeding index, 2) intrinsic rate of increase, *r;* and 3) growth index (percentage immature survival divided by immature development time). Using these measures, *S. exigua* performance was best on pigweed, worst on cabbage, and intermediate on cotton, pepper, and sunflower. We discuss the implications of these findings for control of *S. exigua.*

KEY WORDS *Spodoptera exigua,* host plants, consumption rates, feeding and growth indices

THE BEET ARMYWORM, *Spodoptera exigua* (Hübner), is presumed to have been introduced into Oregon from Southeast Asia in 1876, and within a few years it became established across North America (Mitchell 1979). It is a cosmopolitan species that attacks >90 plant species in at least 18 families throughout North America, many of which are crop plants (Pearson 1982). Over the last 2 decades, it has become an increasingly destructive secondary pest of cotton in the United States. In 1998 alone, ≈5.1 million acres of cotton in the United States were infested with beet armyworm and total losses from this insect were ≈$19.2 million (Williams 1999). Although this pest historically has been perceived as an occasional late-season pest of cotton, population outbreaks experienced in the 1980s and early 1990s in Alabama, Georgia, Louisiana, and Mississippi (Douce and McPherson 1991, Burris et al. 1994a, Layton 1994, Smith 1994) and more recently in Texas (Huffman 1996, Summy et al. 1996) have demonstrated the potential damage it may cause. Chemical control programs against this pest have been complicated by its propensity to develop insecticide resistance (Cobb and Bass 1975, Brewer et al. 1990). Outbreaks of this insect in cotton are often associated with multiple early-season treatments with broad-spectrum insecticides, especially organophosphates, which are intended to reduce populations of key pests like the boll weevil, *Anthonomus grandis grandis* Boheman; pink bollworm, *Pectinophora gossypiella* (Saunders); or *Lygus* spp. bugs, but which severely reduce natural enemy numbers as well (Burris et al. 1994b, Ruberson et al. 1994, 1999, Mascarenhas et al. 1996).

Development of efficient strategies for controlling beet armyworm will require knowledge of its biological relationships with various host plants. Among these, an important component will be an understanding of host suitability. Quantitative analysis of consumption and utilization of host plants by insect herbivores is a commonly used tool in studies of plant-insect interactions (Scriber and Slansky 1981). Variables describing the consumption of food by an insect, how well this food is converted to insect biomass, and the rate at which the insect grows can lead to an understanding of how particular insect species respond to variation in host plant suitability. Study of the effect of food on the biology of insects is of particular importance in understanding host suitability of plant-infesting species and evaluating the magnitude of in-

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jury to the crops attacked by them. This may help, accordingly, in designing more economic control strategies. Various studies have evaluated host plant effects on beet armyworm growth potential (Strastova 1959, Afify et al. 1971, East et al. 1989, 1994) or investigated the impact of insect feeding on yield reduction (Shelton et al. 1982). Published information about other aspects of beet armyworm feeding biology, such as survival and reproductive potential, is incomplete. Our objectives were to determine (1) beet armyworm larval consumption rates on five common host plants, (2) effects of consumption rate on pupal weights and the latter on fecundity, and (3) effects of host plant on beet armyworm life table parameters.

Materials and Methods

Host Plants. The five plant species examined were cabbage, *Brassica oleracea capitata* L. (Earliana, W. Atlee Burpee, Warminster, PA); cotton, *Gossypium hirsutum* L. (DPL-50, UAP Southwest, Santa Rosa, TX); bell pepper, *Capsicum annuum* L. (Capistrano, Peto Seed, Saticoy, CA); pigweed, *Amaranthus retroflexus* L., and sunflower, *Helianthus annuus* L. Pigweed and sunflower seeds were collected from local wild plants the previous fall (Texas 1999). Selection of these plants was based on their importance as cultivated crops (cabbage, cotton, and pepper) and as widely distributed weeds (pigweed and wild sunflower) in the Lower Rio Grande Valley of Texas, as well as their known acceptability for beet armyworm oviposition. Seeds were planted in 30-cm pots in sunshine mixture #1 (SunGro Horticulture, Canada) ≈30 d before leaves were harvested for feeding trials. Plants were grown at 27–28°C, 65–75% RH, and a photoperiod of 12:12 (L:D) h.

Insects. Beet armyworm neonate larvae were obtained from an established colony maintained on a soybean-wheat germ diet (Shaver and Raulston 1971) at the Kika de la Garza Subtropical Agricultural Research Center in Weslaco, TX. Larvae were divided into five groups and reared for one generation on the same host plant species on which the following generation was evaluated. Neonate larvae from the next generation were used for tests.

Feeding Tests. Larval feeding on the 5 different host plants was tested by placing one newly hatched larva on a leaf taken from the upper ⅔ of the plant canopy, which had reached its full dimensions. The leaf was placed inside a plastic petri dish (15 cm diameter) with a circular nylon screen window (5 cm diameter) on top for ventilation. Leaves were cut from undamaged plants at the midpoint of the petiole, weighed, and the ends of the petioles wrapped in moistened cotton to prevent desiccation. After 24 h, excreta were removed from the leaves, which were then weighed. Petri dishes were cleaned, and new weighed leaves were supplied. This process was continued each day for each larva until feeding ceased in the prepupal stage. Petri dishes were held in an environmental chamber at 26 ± 1°C and a photoperiod of 12:12 (L:D) h. To determine weight loss caused by evaporation, leaves of known weight were exposed to the same conditions for a similar period without larvae and weighed thereafter. Daily food consumption per larva was estimated by subtracting weight of remaining leaf tissue from weight of leaf provided and correcting for evaporation. Thirty replications (larvae) were used for each host plant. All pupae were weighed and their sex determined. A feeding index was calculated by dividing mean pupal weight by mean weight of leaf tissue consumed for each host plant.

To study fecundity, test leaves were excised and each leaf petiole was placed in a floral aquapic with hydroponic solution (Aqua-Ponic International, Los Angeles, CA). These leaves could be used for 14 d under laboratory conditions. Two leaves of each host plant were placed in a cylindrical plastic cage (25 cm diameter, 30 cm high) with a nylon top. Newly emerged females and males were confined as pairs in cages until female death. Adults were supplied with a cotton ball soaked with 10% sucrose for feeding. Cages were examined daily to record female mortality, preoviposition period, and number of eggs laid (10 replicates per set). The stage-specific and overall survival of beet armyworm on different host plants were calculated as number of eggs (or larvae, or pupae) hatched (or developed to the next stage) divided by the initial number. The number of insects tested in different sets depended on survival from the previous stage and ranged from 67 to 121. Time for development from egg to adult was recorded for each individual. The number of insects tested for each host plant ranged from 20 to 70.

Life Table Statistics. An estimation of *S. exigua* growth rates on the different host plants was obtained by calculating life table statistics (Southwood 1966). For each host plant, the jackknife program of Hulting et al. (1990) was used to calculate the net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), the finite capacity of increase (λ, defined as the number of times a population multiplies itself per unit of time), the mean generation time (T), the doubling time (DT) of the population, and the total progeny produced per female. The growth index (GI) was calculated by dividing the percentage survival of immatures by developmental time (Sétamou et al. 1999).

Statistical Analysis. The effects of host plant on larval consumption rate and the life history parameters of *S. exigua* were evaluated using one-way analysis of variance (ANOVA). The sex ratio of beet armyworm offspring of parents reared on each individual type of host plant was compared with a 1:1 ratio by chi-square tests. Means associated with host plant for each variable were separated using the Tukey honestly significant difference (HSD) test when significant F values were obtained. For each type of host plant, simple linear regression analysis was used to examine the relationship between the amount of diet consumed and pupal weight, as well as the relationship between female pupal weight and progeny fecundity. For each type of relationship, parallel line analysis was applied to compare the regressions of the five host plants studied using the PROC MIXED procedure of

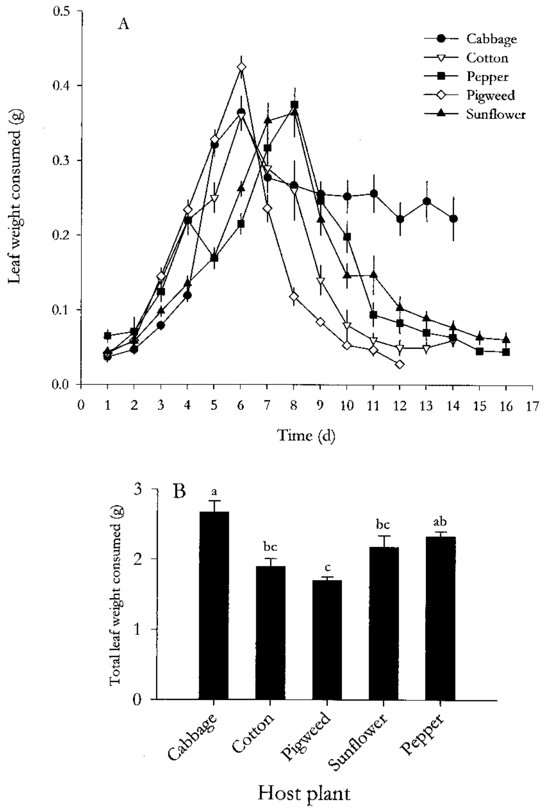

Fig. 1. Consumption of five different host plants by larvae of *S.exigua* (bars indicate SE). (A) Mean weight of leaf tissue consumed per larva measured at 24-h intervals. (B) Total weight of leaf tissue consumed per larva for each host plant ($F = 8.3$; df = 4, 52; $P < 0.01$). Means with the same letter are not significantly different (Tukey HSD, $P < 0.05$).

SAS (Littell et al. 1997, Sétamou et al. 2000). The homogeneity of the regression coefficients between the different host plants was tested first, and whenever the slopes were homogenous, least square (LS) means were compared using multiple *t*-tests (Zar 1996, Littell et al. 1997).

Results

Larval Consumption Rates. *Spodoptera exigua* larvae consumed a maximum of 0.364–0.425 g of leaf tissue per 24-h feeding period on all host plants tested (Fig. 1A). Peak consumption occurred at 6 d in pigweed, cotton, and cabbage, and at 8 d in pepper and sunflower. Consumption rates declined thereafter until pupation, except in cabbage where rates remained high and relatively constant. Total consumption per *S. exigua* larva was highest in cabbage (2.7 g) and lowest in pigweed (1.7 g) (Fig. 1B) ($F = 8.3$; df = 4, 52; $P < 0.01$).

Effects of Consumption on Pupal Weights and Fecundity. Regression analyses showed significant relationships between amount of leaf tissue consumed and resulting pupal weight for each host plant (Fig. 2 A-E). The parallel line regression analyses also revealed significant relationships between total weight of diet consumed and pupal weight (Table 1) with the amount of variance explained ranging from 63% on pepper to 92% on sunflower. Mean pupal weight was highest on pigweed, followed by cabbage, cotton, and pepper, and lowest on sunflower ($F = 3.5$; df = 4, 55; $P < 0.05$; Fig. 2F). Parallel line analysis revealed heterogeneity of regression slopes between host plants as shown by the significant interaction between the dependent and the independent variables in the covariance analysis ($F = 3.77$; df 4, 37; $P = 0.014$). The highest pupal weight gain per unit of diet consumed (46.01 mg/g) was obtained on pigweed ($F = 3.77$; df = 4, 37; $P = 0.011$) (Fig. 2C), whereas each unit of cabbage consumed by larvae produced only 20.89 mg of pupal weight gain (Fig. 2A). However, the least square means comparison showed that cabbage and sunflower ($t = 1.55$; df = 50; $P = 0.13$), and sunflower and pepper ($t = 1.35$; df = 50; $P = 0.18$) had comparable respective effects on *S. exigua* pupal weight. The feeding index was highest in pigweed, followed by cotton. Indices for pepper and sunflower were not significantly different. Cabbage had the lowest index (Fig. 3) ($F = 101.4$; df = 4, 55; $P < 0.01$).

Regression analyses also indicated significant relationships between pupal weight and adult fecundity (Fig. 4 A–E), but fecundity was similar for each host plant ($F = 1.6$; df = 4, 84; $P = 0.2$; Fig. 4F). Female pupal weight strongly influenced fecundity and explained 84–97% of the variance in fecundity. Parallel line analysis indicated the slopes of the regression lines differed among host plants for pupal weight-fecundity relationships (Table 1). *S. exigua* females laid significantly more eggs per mg of pupal weight (18.9 eggs) when larvae fed on cotton compared with other host plants ($F = 17.31$; df = 4, 79; $P < 0.0001$) (Fig. 4B). The lowest pupal weight-to-fecundity ratio was recorded on pigweed (Fig. 4C), whereas *S. exigua* reared on cabbage, sunflower, and pepper laid intermediate and comparable numbers of eggs per unit weight of females.

Effects of Host Plant on Sex Ratio, Development, and Survival. Host plant significantly affected percentage female progeny (Table 2) ($F = 7.8$; df = 4, 13; $P < 0.01$). The highest percentage of female progeny was recorded from *S. exigua* reared on pigweed (62.2%) and the lowest from moths reared on cabbage (43.6%). Except for pigweed ($\chi^2 = 4.87$, $P < 0.05$), the sex ratios did not differ significantly from a 1:1 ratio. Duration of the larval stage (Table 2) averaged more than 5 d less on pigweed than on pepper ($F = 28.7$; df = 4, 219; $P < 0.01$). Total development time also was shortest on pigweed (20.2 d), and was highest on cabbage, sunflower, and pepper (25.2–26.6 d) (Table 2) ($F = 34.8$; df = 4, 219; $P < 0.01$). Larval and total development times on cotton were intermediate. Host plant did not significantly affect percentages of egg hatch ($F = 2.2$; df = 4, 13; $P = 0.13$) or pupal survival ($F = 0.4$; df = 4, 13; $P = 0.8$) (Table 3). However, larval survival differed among host plants ($F = 25.9$; df = 4,

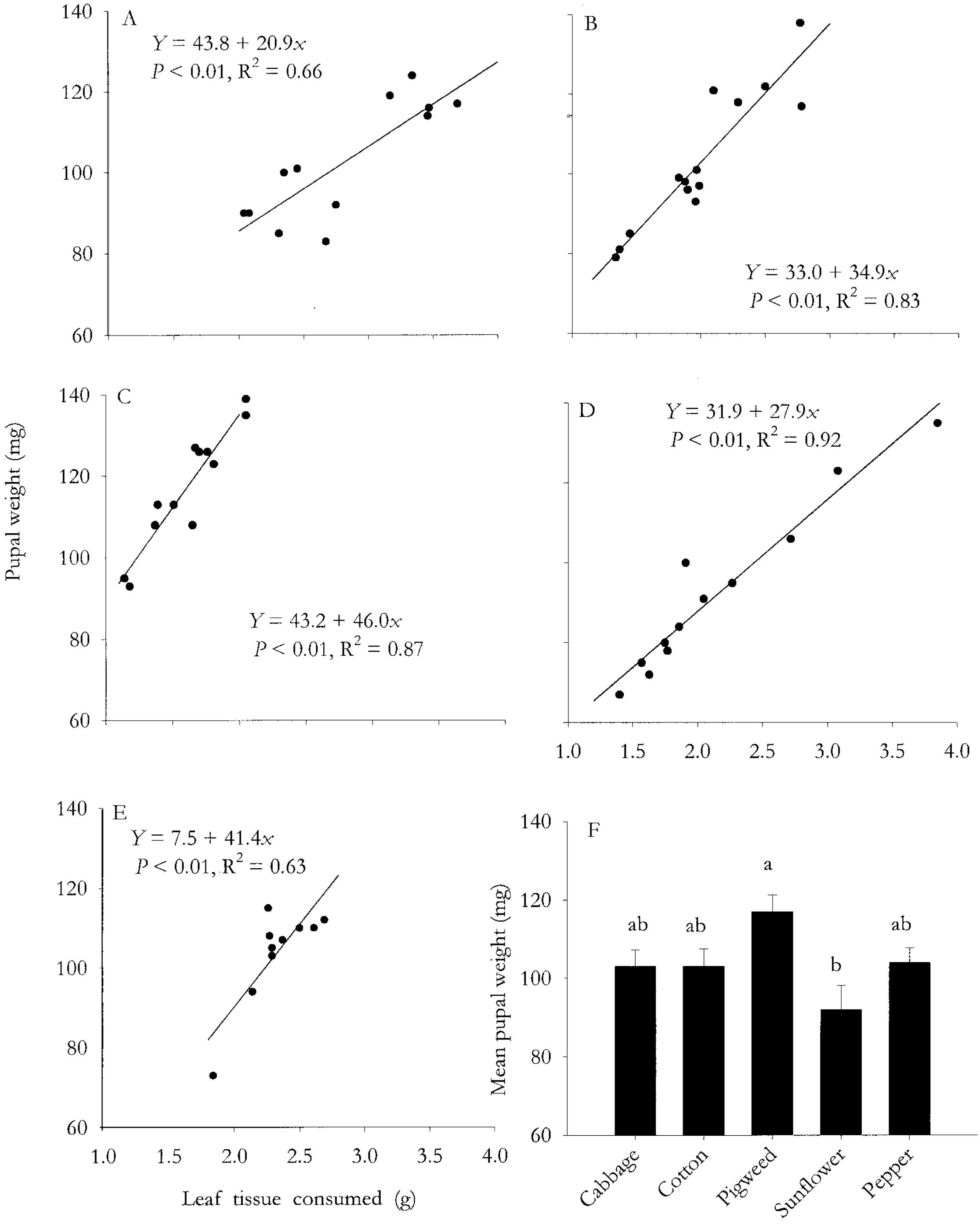

Fig. 2. Relationships between pupal weight and leaf tissue of 5 host plants (A-E) consumed by *Spodoptera exigua* larvae, and mean pupal weights for each host plant treatment (F). (A) Cabbage. (B) Cotton. (C) Pigweed. (D) Sunflower. (E) Pepper. (F) Error bars indicate SE; different letters indicate significant differences (Tukey HSD; $P < 0.05$).

13; $P < 0.01$), being highest in pigweed (94.4%) and lowest in cabbage (67.1%).

Life Table Statistics. Life table statistics calculated for *S. exigua* varied significantly with the host plant (Table 4). Growth rates and total progeny production by females of *S. exigua* were highest on pigweed, and the generation and doubling times were also shortest on this host plant. This suggests that pigweed is a

Table 1. Standard errors of regression parameters

Host plant	Leaf tissue consumed vs. pupal wt		Pupal wt vs. fecundity	
	Slope	Intercept	Slope	Intercept
Cabbage	4.4	12.6	1.1	114.6
Cotton	4.3	8.8	1.8	165.1
Pepper	10.3	24.0	0.6	55.1
Pigweed	5.3	8.6	0.6	76.2
Sunflower	2.4	5.4	0.5	61.3

better food source for larval growth and development than the other host plants tested. Of the five host plants studied, cabbage was least suitable for *S. exigua*, as shown by the lowest growth rates and progeny production, and the longest generation and doubling times (Table 4).

Discussion

Beet armyworm larval feeding efficiency was evaluated on excised leaves of five common host plants in southern Texas. Many plants contain secondary substances that deter feeding and oviposition in phytophagous insects (Gupta and Thorsteinson 1960; Yamamoto and Fraenkel 1960; Hsiao and Fraenkel 1968), and there is evidence of substances in pigweed that can deter beet armyworm feeding (Mitchell and Heath 1985). It is possible that mobilized plant defenses induced by feeding damage could affect larval feeding parameters and development time differently on whole plants than on excised leaves. However, hierarchical relationships between feeding efficiency found in this study and those of oviposition preference on whole plants which we have observed in a parallel study are essentially the same (S.M.G. and T.W.S., unpublished data), suggesting that the results of this study reflect genuine differences in host plant suitability. The purpose of using excised leaves was to limit uncontrolled variation among whole plants within species so that the insect parameters of interest, in this case consumption and development rates, could be fairly assessed across host plant species. The use of excised leaves is a standard method for providing uniform plant material in laboratory feeding studies of this kind (Afify et al. 1971, Griswold and Trumble 1985, East et al. 1989, Meade and Hare 1991, Yoshida and Parrella 1992, Caulfield and Bunce 1994, Loughrin et al. 1995, Stapel et al. 1998).

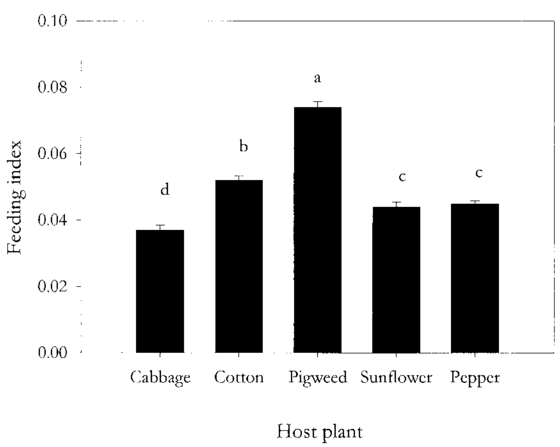

Fig. 3. Mean feeding indices (pupal weight/tissue consumed) of *S. exigua* on different host plants; bars indicate SE; means with the same letter are not significantly different (Tukey HSD, $P < 0.05$).

East et al. (1989) examined larval consumption rates among larvae of *S. exigua* on cabbage. Mean larval consumption was 0.039 g of cabbage daily, or 1.53 g per larva for the entire larval feeding period at 25 ± 1°C and a photoperiod of 12:12 (L:D) h. We found higher consumption levels of 2.7 ± 0.16 g (mean ± SE) of cabbage per larva. Reasons for the differences are unclear, but are likely caused by such factors as experimental conditions and variations in strains of cabbage and larvae.

In this study, *S. exigua* larvae feeding on cotton, sunflower, pepper, and pigweed all exhibited similar patterns of consumption. Consumption rates (measured as grams plant material consumed per 48-h period) increased to a peak less than halfway through the larval stage, then declined before pupation. However, larvae feeding on cabbage sustained high consumption rates until pupation, resulting in higher total consumption per larva. Total larval consumption of pigweed was lowest among all treatments studied because peak consumption was reached early and ceased by 12 d, compared with 14–16 d in the other treatments.

Within each feeding treatment, weight of leaf tissue consumed was positively related to pupal weight. Although total larval consumption was lowest on pigweed, pupal weight was highest in this treatment. Larvae feeding on pigweed produced pupae that averaged 117 mg, compared with 103 mg for cotton, cabbage, and pepper, and 92 mg for sunflower. Similar results were reported by Ali and Gaylor (1992), who studied the effects of temperature and three diets on the development of *S. exigua.* Among eight constant temperatures ranging from 15 to 38°C, pupae averaged 80–100 mg when reared on cotton, compared with 100–120 mg when reared on pigweed. The highest pupal weights (110–130 mg) were obtained on artificial diet. The low consumption rates observed on pigweed are, therefore, not likely to be the result of an aversion to pigweed as a host plant. A more plausible explanation is that pigweed is of higher nutritional quality for *S. exigua* than the other host plants tested. In the case of other host plants, pupal weight was found to vary with cultivar (Meade and Hare 1991, Yoshida and Parrella 1992).

Within each host plant treatment, increased pupal weight resulted in increased fecundity. Mean ± SD lifetime fecundity of *S. exigua* ranged from 1,019.8 ± 68.0 eggs in pepper to 1,310.3 ± 99.2 eggs in pigweed, but the differences were not statistically significant. Tisdale and Sappington (2001) showed that both potential and realized lifetime fecundity were signifi-

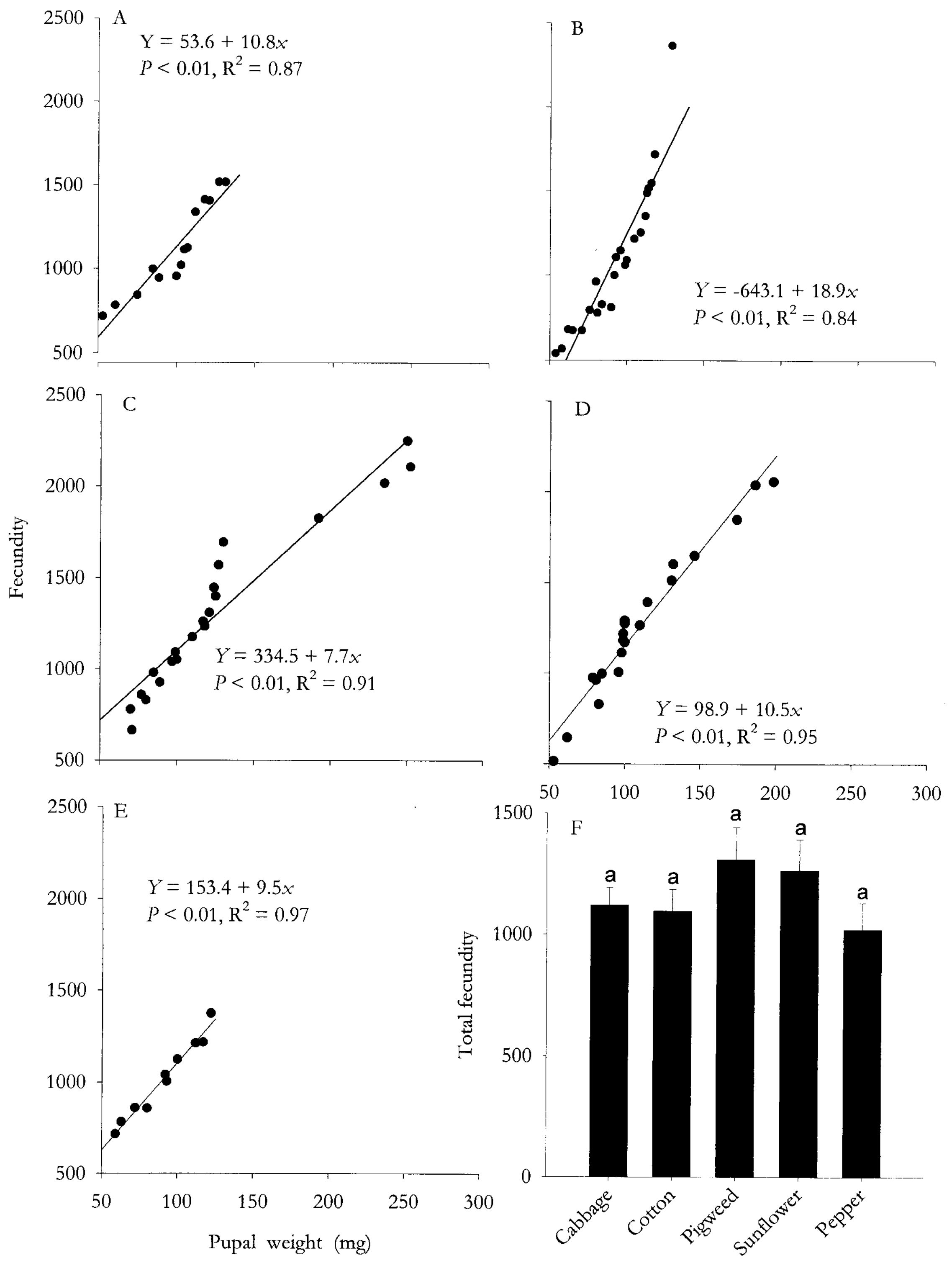

Fig. 4. Relationships between pupal weight of *S. exigua* and total adult fecundity for each host plant treatment (A–E), and mean adult fecundity for each host plant treatment (F). (A) Cabbage. (B) Cotton. (C) Pigweed. (D) Sunflower. (E) Pepper. (F) Error bars indicate SE; different letters indicate significant differences (Tukey HSD; $P < 0.05$).

Table 2. Effects of different host plants on sex ratio and development times of *S. exigua*

Host plant	% female progeny (n)	χ^2 (1:1)	Development time, d (n)	
			Larval	Total
Cabbage	43.6 ± 1.3c (39)	0.643	16.9 ± 0.3a (47)	26.4 ± 0.4a (47)
Cotton	58.3 ± 3.0ab (107)	2.712	14.3 ± 0.2b (35)	22.5 ± 0.2b (35)
Pepper	49.5 ± 5.5bc (33)	0.03	18.0 ± 0.8a (20)	26.6 ± 0.8a (20)
Pigweed	62.2 ± 1.3a (75)	4.87[a]	12.4 ± 0.3c (52)	20.2 ± 0.4c (52)
Sunflower	48.8 ± 1.2bc (70)	0.06	16.3 ± 0.4a (70)	25.2 ± 0.5a (70)

[1] Means (±SD) within a column followed by the same letter are not significantly different (Tukey HSD, $P < 0.05$).
[a] Sex ratio of offspring of parents reared on a given host plant differs significantly from a 1:1 ratio ($P < 0.05$).

cantly related to pupal weight for *S. exigua* reared on artificial diet, but that fecundity was also affected by adult diet. They reported lifetime realized fecundity (±SE) of 1,382 ± 48 eggs for moths reared on a soybean-wheat germ diet and 10% sucrose as adults.

We were unable to locate previous studies on progeny sex ratios in *S. exigua.* In this study, we found that larvae reared on pigweed produced the highest percentage of female progeny (62.2%), whreas those reared on cabbage produced the lowest (43.6%). No significant correlations were found between percentage female progeny and mean parent pupal weight (Pearson correlation coefficient $r = 0.46$) or mean parent fecundity ($r = 0.4$) ($P > 0.05$). It is difficult to imagine that a female lepidopteran can actively influence the sex ratio of her progeny. However, it seems unlikely that the relationship reported here arose by chance, because the hierarchical pattern of percentage female progeny across host plants (Table 2) is very similar to that for other parameters measured in this study (e.g., Tables 3 and 4). Thus, it seems evident that larval nutrition can affect the sex ratio of the next generation, but the mechanism is unknown.

Larval development time was longest on pepper, sunflower, and cabbage (17 d), followed by cotton (14.3 d), and was shortest on pigweed (12.4 d). East et al. (1989) reported longer development times (first instar to prepupae) of 39.3 d on cabbage at 25°C. Al-Zubaidi and Capinera (1984) found larval development times of 18.4, 22.0, and 22.8 d on sugar beet, pigweed, and lambsquarter, respectively, at 24.8°C. Larval development times on chrysanthemum ranged from 14.9 to 25.6 d at 27°C, depending on cultivar and age of the plants (Yoshida and Parrella 1992). On celery, larval development time ranged from 13.7 to 18.5 d (average of 14.9 d) at 26°C, depending on cultivar (Meade and Hare 1991). Itoyama et al. (1999) found that the duration of the final larval stadium of *Spodoptera litura* (F.) became significantly longer as diet quality decreased. Total development time of *S. exigua* followed the same pattern as larval development: longest times were recorded on sunflower, pepper, and cabbage (≈26.0 d), followed by cotton (22.5 d), and pigweed (20.2 d). In comparison, Yoshida and Parrella (1992) reported total development times (egg hatch to adult emergence) ranging from 22.0 to 28.4 d on different cultivars of chrysanthemum at 27°C. We found that duration of the pupal stage was relatively constant at 8.0 d. Similar durations of the pupal stage were recorded for sugar beet, pigweed, and lambsquarter (7.9, 9.0, and 9.7 d, respectively; Al-Zubaidi and Capinera 1984), and cultivars of chrysanthemum (7.1–8.2 d; Yoshida and Parrella, 1992).

Table 3. Stage-specific and overall survival (%) of *S. exigua* on different host plants

Host plant	n	Eggs	Larvae	Pupae	Overall
Cabbage	73	91.6 ± 2.6a	67.1 ± 3.4d	87.4 ± 6.3a	53.5 ± 2.8d
Cotton	121	91.5 ± 1.4a	88.7 ± 1.8ab	92.8 ± 2.6a	75.2 ± 1.2b
Pepper	67	91.3 ± 1.9a	81.8 ± 2.0bc	90.1 ± 1.5a	67.2 ± 1.5bc
Pigweed	97	94.7 ± 0.8a	94.4 ± 0.9a	95.5 ± 1.7a	85.4 ± 1.7a
Sunflower	98	88.7 ± 1.1a	75.9 ± 2.6cd	92.5 ± 3.7a	62.4 ± 3.7cd

Means (±SD) within a column followed by the same letter are not significantly different (Tukey HSD, $P < 0.05$).

Host plant affected survival of *S. exigua* only in the larval stage. Egg survival (percentage hatch) averaged 91.6%, and survival to adulthood from the pupal stage 91.7%, regardless of host plant. However, larval survival was dramatically affected, ranging from 94.4% on pigweed to 61.7% on cabbage. The differential survival rates of larvae affected overall survival, resulting in a similar pattern: pigweed > cotton > pepper > sunflower > cabbage. In celery, overall survival to pupation was only 55%, ranging from 27.5 to 82.5%, depending on cultivar (Meade and Hare 1991). Survival to pupation ranged from 40 to 100% depending on age and cultivar of chrysanthemum at 27°C (Yoshida and Parrella 1992). Ali and Gaylor (1992) found that survival was highest on artificial diet (close to 100% except at temperature extremes), whereas 60–80% survived on pigweed, and 50–80% survived on cotton depending on rearing temperature.

For an overall assessment of the effects of the different host plants on *S. exigua*, we focused on three key statistics: the feeding index (Fig. 3), the intrinsic rate of increase, and the growth index (Table 4). The feeding index reflects the convertibility of plant biomass into insect body weight. A ranking of the feeding index in order of decreasing convertibility is: pigweed > cotton > sunflower = pepper > cabbage. Therefore, greater amounts of cabbage must be consumed to produce a given pupal weight. The intrinsic rate of increase, r (as well as the net reproductive rate), indicates the potential of a population to increase under the conditions tested. Ranking the host plants based on statistically significant decreasing values of r yields: pigweed > cotton > sunflower >

Table 4. Means of life table statistics (±SE) and growth index of *S. exigua* as affected by different host plants

Host plant	R_o	r_m	λ	T	DT	Total progeny	GI[a]
Cabbage	139.3 ± 9.3d	0.156 ± 0.002e	1.17	31.6	4.44	319.4 ± 21.3e	2.03
Cotton	359.3 ± 29.8b	0.221 ± 0.003b	1.25	26.7	3.14	616.4 ± 51.2c	3.34
Pepper	228.0 ± 15.2c	0.174 ± 0.003d	1.19	31.3	4.00	460.5 ± 30.7d	2.53
Pigweed	596.0 ± 45.0a	0.264 ± 0.004a	1.30	24.2	2.62	958.3 ± 72.4a	4.23
Sunflower	342.2 ± 24.3b	0.192 ± 0.002c	1.21	30.3	3.6	701.3 ± 49.9b	2.48

Means (±SE) followed by the same letter in the same column are not significantly different ($P > 0.05$) using the Student-Newmann-Keuls sequential test.

R_o, net reproductive rate; r_m, intrinsic rate of increase; λ, finite rate of increase; T, generation time (d); DT, doubling time of the population (d); total progeny production calculated using the jackknife program of Hulting et al. (1990).

[a] Growth index (GI), computed as the ratio between the percentage of adults emerged and the duration of the immature period (larval and pupal stages only) (Sétamou et al. 1999).

pepper > cabbage. The growth index (GI) emphasizes the importance of both survival and developmental time in measuring food quality (Sétamou et al. 1999). Higher survival rates and shorter development times yield higher values of GI, thus indicating better food quality. We were unable to perform a statistical analysis on this index because only one value was obtained for each treatment. Host plants listed in order of decreasing GI values are pigweed > cotton > pepper > sunflower > cabbage. All three indices indicate that *S. exigua* performed best on pigweed and worst on cabbage. Measures on sunflower, cotton, and pepper were mixed, although always intermediate between pigweed and cabbage. Therefore, we conclude that pigweed provides the best food quality for *S. exigua*, cabbage the worst, and the other host plants of intermediate quality. Levels of nitrogen content reported for these plant species in the literature show the same hierarchy (Telek and Graham 1984, USDA 1984, Caulfield and Bunce 1994, Wiedenfeld et al. 1995, Scheiner and Lavado 1999, Makus and Smart 2000) as beet armyworm performance reported here, but it is not known if the two hierarchies are causally linked.

Understanding the differences in food quality among the five host plants could have practical implications for the management of *S. exigua.* It is intuitive that greater consumption of plant material sprayed with an insecticide will increase the dose of that insecticide ingested. Our study suggests that the relatively low food quality of cabbage for *S. exigua* requires prolonged feeding relative to other crops such as cotton and pepper, and consequently leads to higher levels of leaf consumption and crop damage. The longer feeding and development times of *S. exigua* on cabbage may allow longer windows of opportunity for the use of biological control agents. Although the beet armyworm infests a wide variety of plants (Mitchell 1979, Pearson 1982, Ruberson et al. 1994), it is clear that some hosts, especially pigweed, *Amaranthus* spp., (Howard 1907, Wene and Sheets 1965, Tingle et al. 1978), are preferred over others. The hierarchies of oviposition preferences have not been elucidated, but we are investigating this question for the same 5 host plants examined here. An oviposition preference for pigweed would make evolutionary sense considering the substantial developmental advantages accrued by larvae feeding on this host plant compared with others, as revealed by this study.

Pigweed and sunflower are abundant weeds throughout the Lower Rio Grande Valley of Texas, as well as in many other areas of the Cotton Belt, and may serve as reservoir hosts for infestation of cultivated crops. The intrinsic rate of increase is high for beet armyworm, especially on pigweed, and if weed host availability becomes limiting, oviposition in crops such as cotton, pepper, and cabbage may occur at levels leading to outbreaks, even if these are not the most preferred or most nutritious hosts. Similarly, populations may build in one cultivated host followed by a shift to another, because crop phenologies change differentially through the season. Understanding such patterns of host utilization will contribute to development of tactics involving manipulation of wild and cultivated hosts for incorporation into areawide management strategies.

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References Cited

Afify, A. M., M. N. El-Kady, and F. N. Zaki. 1971. Difference in effectiveness of three kinds of foliage on larval growth and adult fecundity of the sugarbeet armyworm, *Spodoptera exigua* Hbn. (Lepidoptera: Noctuidae). Acta Entomol. Bohem. 68: 77–82.

Al-Zubaidi, F. S., and J. L. Capinera. 1984. Utilization of food and nitrogen by the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), in relation to food type and dietary nitrogen levels. Environ. Entomol. 13: 1604–1608.

Ali, A., and M. J. Gaylor. 1992. Effects of temperature and larval diet on development of the beet armyworm (Lepidoptera: Noctuidae). Environ. Entomol. 21: 780–786.

Brewer, M. J., J. T. Trumble, B. Alvarado-Rodriques, and W. E. Chaney. 1990. Beet armyworm (Lepidoptera: Noctuidae) adult and larval susceptibility to three insecticides in managed habitats and relationship to laboratory selection for resistance. J. Econ. Entomol. 83: 2136–2146.

Burris, E., S. Micinski, B. R. Leonard, J. B. Graves, and R. D. Bagwell. 1994a. Dimilin, evaluated for control of beet armyworms, p. 63–64. *In* G. Smith and B. Hatchison [eds.], The performance of cotton insecticides in Louisiana, 1994. Louisiana State University, Baton Rouge, LA.

Burris, E., J. B. Graves, B. R. Leonard, and C. A. White. 1994b. Beet armyworms (Lepidoptera: Noctuidae) in northeast Louisiana: observations on an uncommon insect pest. Fla. Entomol. 77: 454–459.

Caulfield, F., and J. A. Bunce. 1994. Elevated atmospheric carbon dioxide concentration affects interactions between *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae and two host plant species outdoors. Environ. Entomol. 23: 999–1005.

Cobb, P. P., and M. H. Bass. 1975. Beet armyworm: dosage-mortality studies on California and Florida strains. J. Econ. Entomol. 68: 813–814.

Douce, G. K., and R. M. McPherson. 1991. Summary of losses from insect damage and cost of control in Georgia, 1989. Ga. Agric. Exp. Stn. Spec. Publ. 70.

East, D. A., J. V. Edelson, and B. Cartwright. 1989. Relative cabbage consumption by the cabbage looper (Lepidoptera: Noctuidae), beet armyworm (Lepidoptera: Noctuidae), and diamondback moth (Lepidoptera: Plutellidae). J. Econ. Entomol. 82: 1367–1369.

East, D. A., J. V. Edelson, B. Cartwright, and M. K. Harris. 1994. Beet armyworm (Lepidoptera: Noctuidae) feeding impact on cabbage development and marketability. J. Econ. Entomol. 87: 1641–1646.

Griswold, M. J., and J. T. Trumble. 1985. Consumption and utilization of celery, *Apium graveolens*, by the beet armyworm, *Spodoptera exigua*. Entomol. Exp. Appl. 38: 73–79.

Gupta, P. D., and A. J. Thorsteinson. 1960. Food plant relationships of the diamondback moth [*Plutella maculipennis* (Curt.)]. II. Sensory regulation of oviposition of the adult female. Entomol. Exp. Appl. 3: 305–314.

Howard, C. W. 1907. The pigweed caterpillar (*Caradrina exigua*). Transvaal Agric. J. 5: 173–176.

Hsiao, T. H., and G. Fraenkel. 1968. Selection and specificity of the colorado potato beetle for solanaceous and nonsolanaceous plants. Ann. Entomol. Soc. Am. 61: 493–503.

Huffman, R. 1996. The beet armyworm in Texas and Oklahoma 1995, pp. 113–116. *In* D. A. Richter and J. Armour [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Hulting, F. L., B. Orr, and J. J. Obrycki. 1990. A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life table parameters. Fla. Entomol. 73: 601–612.

Itoyama, K., Y. Kawahira, M. Murata, and S. Tojo. 1999. Fluctuation of some characteristics in the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae) reared under different diets. Appl. Entomol. Zool. 34: 315–321.

Layton, M. B. 1994. The 1993 beet armyworm outbreak in Mississippi and future management guidelines, pp. 854–856. *In* D. J. Herber and D. A. Richter [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Littell, R. C., G. A. Milliken, W. W. Stoup, and R. D. Wolfinger. 1997. SAS system for mixed models. SAS Institute, Cary, NC.

Loughrin, J. H., A. Manukian, R. R. Heath, and J. H. Tumlinson. 1995. Volatiles emitted by different cotton varieties damaged by feeding beet armyworm larvae. J. Chem. Ecol. 21: 1217–1227.

Makus, D. J., and J. R. Smart. 2000. Tillage practice affects edaphic conditions in producer fields, pp. 1431–1433. *In* P. Dugger and D. Richter [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Mascarenhas, V. J., B. R. Leonard, E. Burris, and J. B. Graves. 1996. Beet armyworm (Lepidoptera: Noctuidae) control on cotton in Louisiana. Fla. Entomol. 79: 336–343.

Meade, T., and J. D. Hare. 1991. Differential performance of beet armyworm and cabbage looper (Lepidoptera: Noctuidae) larvae on selected *Apium graveolens* cultivars. Environ. Entomol. 20:1636–1644.

Mitchell, E. R. 1979. Migration by *Spodoptera exigua* and *S. frugiperda*, North American style, pp. 386–393. *In* R. L. Rabb and G. E. Kennedy [eds.], Movement of highly mobile insects: concepts and methodology in research. North Carolina State University, Raleigh, NC.

Mitchell, E. R., and R. R. Heath. 1985. Influence of *Amaranthus hybridus* L. allelochemics on oviposition behavior of *Spodoptera exigua* and *S. eridania* (Lepidoptera: Noctuidae). J. Chem. Ecol. 11: 609–618.

Pearson, A. C. 1982. Biology, population dynamics, and pest status of the beet armyworm (*Spodoptera exigua*) in the Imperial Valley of California. Ph.D. dissertation, University of California, Riverside.

Ruberson, J. R., G. A. Herzog, W. R. Lambert, and W. J. Lewis. 1994. Management of the beet armyworm in cotton: role of natural enemies. Fla. Entomol. 77: 440–453.

Ruberson, J. R., J. R. Nechols, and M. J. Tauber. 1999. Biological control of arthropod pests, pp. 417–448. *In* J. R. Ruberson [ed.], Handbook of pest management. Dekker, New York.

Scheiner, J. D., and R. Lavado. 1999. Soil water content, absorption of nutrient elements, and responses to fertilization of sunflower: a case study. J. Plant Nutr. 22: 369–377.

Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of insects. Annu. Rev. Entomol. 26: 183–211.

Sétamou, M., F. Schulthess, N. A. Bosque-Perez, H.-M. Poehling, and C. Borgemeister. 1999. Bionomics of *Mussidia nigrivenella* (Lepidoptera: Pyralidae) on three host plants. Bull. Entomol. Res. 89: 465–471.

Sétamou, M., F. Schulthess, H.-M. Poehling, and C. Borgemeister. 2000. Spatial distribution of and sampling plans for *Mussidia nigrivenella* (Lepidoptera: Pyralidae) on cultivated and wild host plants in Benin. Environ. Entomol. 29: 1216–1225.

Shaver, T. N., and J. R. Raulston. 1971. A soybean-wheat germ diet for rearing the tobacco budworm. Ann. Entomol. Soc. Am. 64: 1077–1079.

Shelton, A. M., J. T. Andaloro, and J. Barnard. 1982. Effects of cabbage looper, imported cabbageworm, and diamondback moth on fresh market and processing cabbage. J. Econ. Entomol. 75: 742–745.

Smith, R. H. 1994. Changes in secondary pests during and after boll weevil eradication, pp. 796–797. *In* D. J. Herber and D. A. Richter [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Southwood, T.R.E. 1966. Ecological methods: with particular reference to the study of insect populations. Kluwer, Dordrecht, The Netherlands.

Stapel, J. O., D. J. Waters, J. R. Ruberson, and W. J. Lewis. 1998. Development and behavior of *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae in choice tests with food substrates containing toxins of *Bacillus thuringiensis.* Biol. Control 11: 29–37.

Strastova, B. K. 1959. Growth potential of *Laphygma exigua* Hbn. in relation to winter food plants. Madras Agric. J. 46: 255–259.

Summy, K. R., J. R. Raulston, D. Spurgeon, and J. Vargas. 1996. An analysis of the beet armyworm outbreak on cotton in the Lower Rio Grande Valley of Texas during 1995 production season, pp. 837–843. *In* P. Dugger and D. Richter [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Telek, L., and H. D. Graham. 1984. Leaf protein concentration. AVI, Westport, CT.

Tingle, F. C., T. R. Ashley, and E. R. Mitchell. 1978. Parasites of *Spodoptera exigua, S. eridania* (Lep.: Noctuidae) and *Herpetogramma bipunctalis* (Lep.: Pyralidae) collected from *Amaranthus hybridus* in field corn. Entomophaga 23: 343- 347.

Tisdale, R. A., and T. W. Sappington. 2001. Realized and potential fecundity, eggs fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. Ann. Entomol. Soc. Am. 94: 415–441.

[USDA] United States Department of Agriculture. 1984. Composition of foods, vegetables and vegetable products. USDA Agric. Handb. 8–11.

Wene, G. P., and L. W. Sheets. 1965. Migration of beet armyworm larvae. J. Econ. Entomol. 58: 168–169.

Wiedenfeld, B., L. Brandenberger, and D. Makus. 1995. Pepper fertilization practices in the Lower Rio Grande Valley of Texas. Subtrop. Plant Sci. 47: 59–64.

Williams, M. R. 1999. Cotton insect losses 1998, pp. 785–806. *In* P. Dugger and D. Richter [eds.], Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Yamamoto, R. T., and G. Fraenkel. 1960. The physiological basis for the selection of plants for egg-laying in the tobacco hornworm, *Protoparce sexta* (Johan.). 11 Int. Congr. Entomol. 3: 127–133.

Yoshida, H. A., and M. P. Parrella. 1992. Development and use of selected chrysanthemum cultivars by *Spodoptera exigua* (Lepidoptera: Noctuidae). Environ. Entomol. 85: 2377–2382.

Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

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