

Consumption and utilization of celery, *Apium graveolens*, by the beet armyworm *Spodoptera exigua*

M. J. Griswold¹ & J. T. Trumble

Department of Entomology, University of California, Riverside, CA 92521 USA

¹ Present address: Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92717, USA

Keywords: Noctuidae, *Spodoptera exigua*, *Apium graveolens*, nutrition, nitrogen utilization, biomass conversion, digestion

Abstract

The biological impact of consumption and utilization of celery was examined for the generalist herbivore, *Spodoptera exigua* (Hübner). An analysis of leaves and petioles demonstrated that both plant parts contained high levels of water (>85%), but that leaves contained twice as much total organic nitrogen as petioles. Developmental and reproductive rates were significantly higher ($P < 0.01$, *t*-test) for larvae fed on leaves. Penultimate and final instars consumed significantly more ($P \leq 0.05$, *t*-test) dry weight of plant material when fed petioles as opposed to leaves. Although growth rates were similar regardless of food source for penultimate instars, conversion of food to body weight was lower for larvae limited to petioles. In the final instar, both growth and conversion rates were lower for larvae fed petioles than for those given leaves. Thus, since larvae exhibit preferences for the nutritionally less suitable petioles during later larval stages, environmental factors other than nutrition must influence movement and distribution of *S. exigua* in celery.

Introduction

Phytophagous insects may respond to within-plant variability of nutrients, allelochemicals and structural refuges by exploitation of particular plant parts (McNeill & Southwood, 1978; Mattson, 1980; Price *et al.*, 1980; Berenbaum, 1981; Thompson, 1983a). Therefore, because growth and development are of primary importance to all organisms, a behavioral response such as a shift in feeding sites may occur because of differences in nutrients (Mattson, 1980; Scriber & Slansky, 1981). Specifically, nitrogen availability seems to influence where many phytophagous insects feed (Feeny, 1970; McNeill & Southwood, 1978; Wint, 1981). Soo Hoo & Fraenkel (1966) observed that plants with higher protein levels were more acceptable to the southern armyworm, *Prodenia* (= *Spodoptera*) *eridania* (Cramer), and Thompson (1983b) reported larval feeding patterns of *Depressaria leptotaeniae* Clark following nitrogen levels in the Umbellifer *Lomatium*

dissectum (Nutt.). However, it is not only possible for insects to adjust to different nutrient levels or allelochemicals with pre-ingestive behavior but also post-ingestive adaptations such as modifications of absorption and utilization efficiencies (Scriber, 1979; Manuwoto & Scriber, 1982). Slansky & Feeny (1977) determined that *Pieris rapae* (L.) larvae stabilized nitrogen accumulation on plants of various nitrogen levels by modifications in both nitrogen utilization efficiency and nitrogen consumption rate.

Spodoptera exigua (Hübner), the beet armyworm, is a generalist feeder and an important pest of celery, *Apium graveolens* L. (Umbelliferae). Development of this insect on celery is characterized by a change in larval feeding sites from celery leaves in the first through third instars to the petioles in the fourth and fifth instars (Jones & Granett, 1982). This shift subsequently results in economic losses as the marketable portion of the celery crop is damaged. Factors affecting feeding site selection may

include: (1) an avoidance mechanism of parasites and predators (Price *et al.*, 1980), since mortality of *S. exigua* is greatest in the egg stage and exposed early instars (Eveleens *et al.*, 1973; Hogg & Gutierrez, 1980), (2) location and concentration of allelochemicals, such as linear furanocoumarins which have been reported in low concentrations in celery (Beier *et al.*, 1983), and which are toxic to other armyworms (Berenbaum, 1978), (3) a behavioral response of late instar larvae to illumination, such as that observed by Shields & Wyman (1984) for another noctuid species, or (4) a preference for a more suitable nutritional source within the plant (Feeny, 1970).

Because nutritional ecology as defined by Scriber & Slansky (1981) and Slansky (1982) is central to understanding an insect's response to the environment, our study considers a quantitative analysis of consumption and utilization, as well as development and fecundity, of *S. exigua* on different plant parts as an initial step in understanding the larval behavior of this insect.

Materials and methods

General. *S. exigua* larvae were collected from a culture established in August 1982 from insects collected from celery at the University of California's South Coast Field Station at Irvine, CA. The culture was maintained on a modified pinto bean diet (Shorey & Hale, 1965; Gelernter, 1984) with adults receiving 20% honey solution at 26.7 °C and a 16:8 h photo-scotophase. All experiments were conducted in a controlled environment at 16.7 °C and a 16:8 h photo-scotophase.

Celery used in all experiments was 'Utah Tall 5270-R', grown in the glasshouse using standard U.C. mix (Matkin & Chandler, 1957) supplemented with a slow release fertilizer (Osmocote®) and a micronutrient solution applied twice monthly. Plant material used in the tests was analyzed for water content and percent total organic nitrogen, using a micro-Kjeldahl technique (McKenzie & Wallace, 1954).

Development and fecundity. Developmental tests were conducted by confining neonate larvae individually in plastic petri dishes with excised celery as the food source. The larvae were randomly divided

into two groups of 80, and development was monitored every eight hours; the food source was replaced every 24 h. From the beginning of the fourth instar until pupation, the food source of one group was changed from celery leaves to celery petioles while the other group remained confined with leaves. Resulting pupae were weighed and sexed 24 h after pupation and then held for adult emergence. Adult males and females within each group were paired and individual pairs were placed in clear plastic containers, and supplied with a 20% honey solution. These mating cages were replaced daily, eggs were counted and the number of subsequently eclosing larvae was recorded.

Consumption and utilization tests were conducted with penultimate (fourth) and final (fifth) instar larvae of *S. exigua*. Since rates of growth and nitrogen accumulation are usually different among instars (Waldbauer, 1964), fourth and fifth instars were tested separately.

Freshly molted fourth instar larvae were randomly divided into two groups, weighed and placed individually in plastic petri dishes lined with moistened filter paper. Either pre-weighed leaves or petioles were supplied to the larvae. The food was changed every 24 h; feces and uneaten food were collected, frozen and dried at 80 °C to constant weight. After the initial weighing, experimental larvae were weighed every 24 h. A final weight was taken when the larvae entered the pre-molt stage, after which larvae were frozen and dried at 80 °C.

Newly molted fifth instar larvae were tested as previously described for the fourth instars. These larvae also were confined on leaves or petioles from the beginning of the fourth instar. A final weight was taken at the onset of the prepupal stage, after which larvae completed development and subsequent pupae were weighed, frozen and dried at 80 °C.

Food consumption was estimated by standard gravimetric technique (Waldbauer, 1968). All calculations were based on dry weight determinations. The initial dry weights of experimental larvae and the daily dry weights throughout the feeding period were calculated based on means of groups of 5 to 10 larvae reared concurrently and under identical conditions to the experimental larvae in each test. Mean dry weights were calculated by the weighted average method described by Waldbauer (1964).

Total organic nitrogen content of larvae, pupae and plants was determined using a micro-Kjeldahl technique (McKenzie & Wallace, 1954).

The following parameters of larval growth and feeding efficiency were calculated using previously reported formulae (Waldbauer, 1968; Scriber, 1978), and are defined as follows: relative consumption rate (RCR) = mg of biomass ingested per mg of larval biomass per day; relative growth rate (RGR) = mg of biomass gained per mg of larval biomass per day; assimilation efficiency (AD) = (food ingested - feces) / (food ingested) × 100; efficiency of conversion of digested food or net efficiency (ECD) = biomass gained / (food ingested - feces) × 100; efficiency of conversion of ingested food or gross efficiency (ECI) = (biomass gained) / (food ingested) × 100; relative nitrogen consumption rate (RNCR) = mg of N ingested per g of larval biomass per day; relative nitrogen accumulation rate (RNAR) = mg of N gained per g of larval biomass per day; nitrogen utilization efficiency (NUE) = (mg N gained / mg N ingested) × 100.

Results and discussion

The growth, development, and reproduction of *S. exigua* was significantly greater when larvae were raised on celery leaves compared to petioles (Table 1, Fig. 1). Since such biological parameters depend on food quality, especially nitrogen (Rodriguez, 1960; Scriber, 1984), the results of this study are not surprising in view of the differences in nutrient levels between celery plant parts (Table 2). Both nitrogen and water have been shown to influence metabolism efficiencies and growth rates of insects (Reese & Beck, 1978; Scriber, 1984); therefore, these two dietary components were analyzed and evaluated in the present study.

Table 1. Mean pupal weight, adult longevity and fecundity of *Spodoptera exigua* on celery.

Food source	Pupal weight (mg)	Adult longevity (days)	Eggs per female	% hatch
Leaf	101.0 ± 1.6 (N = 60)	12.3 ± 0.52 (N = 60)	1195.9 ± 45.6 ^a (N = 29)	66.3 ± 5.2
Petiole	101.9 ± 1.8 (N = 49)	11.6 ± 0.49 (N = 49)	784.2 ± 48.8 (N = 19)	59.8 ± 7.7

^a Significant at P < 0.01 level, *t*-test; values represent means ± standard error.

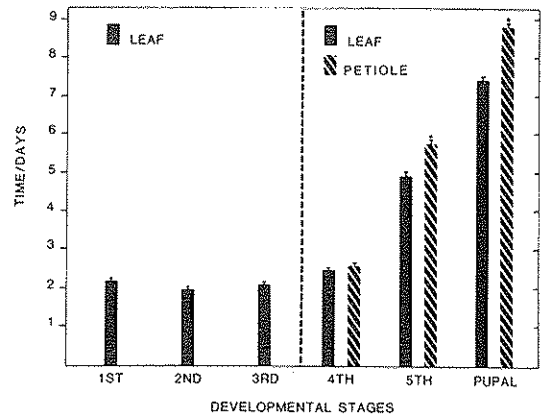


Fig. 1. Developmental rates of *S. exigua* on celery. Solid bar: a group fed leaves throughout test; striped bar: a group fed leaves for the first three instars and petioles during the last two instars. N = 160 for first through third instars, 80 for both groups in the fourth instar, 79 for leaf and 76 for petioles in the fifth instar, and 60 for leaf and 49 for petioles in pupal stage. Brackets: ± s.e. - * significance at P < 0.01 level, *t*-test.

Table 2. Water content and total organic nitrogen of celery leaves and petioles fed to *Spodoptera exigua*.

	Plant part	Water (%)	Nitrogen (%)
Development/fecundity test ^a	Leaf	90.2 ± 0.31	4.5 ± 0.07*
	Petiole	96.5 ± 0.26*	1.8 ± 0.08
Consumption/utilization test ^b	Penultimate instar	Leaf 86.5 ± 0.26	4.2 ± 0.09*
	Petiole	94.5 ± 0.12*	2.0 ± 0.08
Final instar	Leaf	86.5 ± 0.54	4.1 ± 0.10*
	Petiole	93.6 ± 0.31*	1.8 ± 0.10

^a N = 15 plants; * = significant at P < 0.01 level, *t*-test; values represent means ± standard error.

^b N = 12 plants per test.

Petioles had significantly lower nitrogen content ($P < 0.01$, t -test) with levels ca. half that of leaves (Table 2). Water content was also statistically different ($P < 0.01$, t -test) between the two plant parts with petioles containing 5 to 8% more water. Although most experiments on insect growth and nutrient utilization have shown a positive covariance of nitrogen and water within plants (Mattson, 1980), in our study low nitrogen content was paired with high water content. However, since water content in both leaves and petioles was over 85%, any limiting effects of water would be less obvious (Scriber, 1979) than differences in nitrogen on post-ingestive utilization of celery plant parts.

Development and fecundity. Developmental time of *S. exigua* was prolonged significantly in the fifth larval instar and pupal stage when larvae were reared on petioles as compared with leaves (Fig. 1). There was no difference in developmental time between the two groups for the fourth instar; however, this result could be due to a 'transition effect' (Gordon, 1972) in the petiole feeder caused by switching food sources. Since the larvae apparently change diets under natural circumstances (Jones & Granett, 1982), any such effect would still occur outside of the experimental procedure and cannot be attributable to experimental artifact.

Pupal weight (wet weight) and adult life span were not significantly different for insects reared on either food source (Table 1), indicating a minimum weight for pupation as has been suggested for other lepidopterans (Slansky, 1982). However, the fecundity of the petiole feeders was significantly ($P <$

0.01, t -test) lower than the leaf feeders. This reduction may have resulted from the difference in nitrogen levels, since protein is essential for yolk deposition in eggs. Similarly, McClure (1980) has shown that foliar nitrogen levels positively influenced the fecundity of *Fiornia externa* Ferris. Although fecundity differed between the two groups, percent egg hatch was not statistically different, indicating that quantity and not quality of the eggs was reduced by the lower nitrogen level in the petioles.

Consumption and utilization. Growth and consumption rates and utilization efficiencies of penultimate and final instars are presented in Tables 3 and 4. As a food source, petioles and leaves were exploited differently by the larvae, and the indices calculated from the experiments were used to evaluate the contrast in nutritional quality of these two diets.

In the penultimate instar no significant difference was observed between the relative growth rates (RGR) of the two groups (Table 3). However, the petiole feeders consumed almost three times as much dry matter (RCR) as the leaf feeders, apparently in compensation for low nitrogen content. The phenomenon of increased consumption with decreased nutrient value of food has been recognized throughout the animal kingdom (Dethier, 1970), and specifically with regard to phytophagous insects (Schoonhoven, 1972; McNeill & Southwood, 1978; Reese, 1981). McGinnis & Kastings (1967) determined that the grasshopper *Melanoplus bivittatus* (Say) increased consumption in order to compensate for low nutrient levels.

Table 3. Growth rates and utilization efficiencies of penultimate and final larval instars of *Spodoptera exigua* on celery leaves and petioles^a.

Larval instar	Food source	RCR (mg/mg/day)	RGR (mg/mg/day)	AD (%)	ECD (%)	ECI (%)
Penultimate ^b (Fourth)	Leaf	1.64 ± 0.09	0.337 ± 0.03	52.5 ± 2.31	42.1 ± 4.36*	20.9 ± 1.78*
	Petiole	4.59 ± 0.29*	0.318 ± 0.03	81.9 ± 1.58*	8.2 ± 1.08	6.6 ± 0.68
Final ^c (Fifth)	Leaf	1.19 ± 0.15	0.317 ± 0.01*	57.9 ± 2.46	44.4 ± 2.37*	22.7 ± 1.13*
	Petiole	2.14 ± 0.09*	0.212 ± 0.02	76.8 ± 1.94*	14.5 ± 0.50	10.2 ± 0.25

^a RCR = relative consumption rate; RGR = relative growth rate; AD = approximate digestibility; ECD = efficiency of conversion of digested matter; ECI = efficiency of conversion of ingested matter. * = significant at $P < 0.01$ level, t -test; values represent means ± s.e.

^b N = 19 per treatment.

^c N = 9 per treatment.

In the final instar, the differences in consumption rates between the two groups was smaller than was observed in the penultimate instar but was still significant. However, in contrast to the penultimate instar, growth rates in the final instar were significantly different between groups ($P < 0.01$, t -test). Larvae which fed on petioles consumed about one and a half times the amount of dry material as those which fed on leaves; this consumption level did not compensate for the difference in food quality between the food sources as demonstrated by the slower growth rate on petioles (Table 3).

Although many studies suggest increased food consumption is correlated with a decrease in the efficiency of digestion (AD) (Soo Hoo & Fraenkel, 1966; Slansky & Feeney, 1977; McNeill & Southwood, 1978), the proportion of food assimilated increased with higher consumption for *S. exigua* when comparing petiole and leaf feeders both in the penultimate and final instars (Table 3). These results may have been caused by the high water content (93.5 to 94.5%) and possible low cellulose content of the petioles. Dadd (1960) found higher AD's for *Locusta migratoria* L. and *Schistocerca gregaria* (Forsk.) on diets with low cellulose than on diets with a higher cellulose content. This might be the case if celery leaves contain more cellulose than the petioles.

The efficiency with which larvae converted digested food to biomass (ECD) was significantly lower for petiole feeders, which may reflect higher metabolic costs resulting from the greater intake of food by these larvae (Calow, 1977). These differences in efficiency were observed in both the penultimate

and final instars (Table 3). Thus, *S. exigua* assimilated celery petioles more efficiently than leaves, but actually converted only a small amount of petiole to body weight, whereas a high proportion of assimilated leaf material was converted to larval biomass. Fox & Macauley (1977) found a similar relationship between high AD and low ECD with *Paropsis atomaria* Ol. on low nitrogen *Eucalyptus* leaves. Gross efficiency of conversion (ECI), the product of AD and ECD, generated similar trends to the ECD values in our study; overall, leaves were more efficiently converted to larval biomass than petioles.

Nitrogen budgets generally paralleled the results of the larval biomass budgets. Larvae which fed on leaves with high nitrogen content utilized and accumulated nitrogen more effectively than those larvae confined to petioles with low nitrogen content (Table 4). In the fourth instar the high consumption rates for larvae fed petioles resulted in significantly greater ingestion of nitrogen, but less than ca. 26% of this element was converted to biomass as reflected in the lower accumulation rate (RNAR). Thus, larvae were more efficient in utilizing nitrogen on a food source with higher levels of nitrogen. This result does not agree with the report of Slansky & Feeney (1977) which indicated that nitrogen utilization efficiency (NUE) was inversely related to nitrogen levels. However, our results again agree with findings on *P. atomaria* on *Eucalyptus* reported by Fox and Macauley (1977), who suggested that the apparent differences in the relationship of NUE to nitrogen content were the result of low nitrogen levels (<1.85%); they maintain that there must be a

Table 4. Nitrogen consumption and utilization by penultimate and final larval instars of *Spodoptera exigua* on celery leaves and petioles^a.

Larval instar	Food source	RNCR (mg N/g/day)	RNAR (mg N/g/day)	NUE (%)
Penultimate ^b (Fourth)	Leaf	72.9 ± 3.59	37.4 ± 7.10**	51.5 ± 4.29**
	Petiole	92.0 ± 6.63*	22.3 ± 5.20	26.3 ± 3.34
Final ^c (Fifth)	Leaf	53.9 ± 8.56**	25.7 ± 1.50**	49.5 ± 2.01**
	Petiole	37.5 ± 5.26	10.9 ± 1.00	29.8 ± 2.59

^a RNCR = relative nitrogen consumption rate; RNAR = relative nitrogen accumulation rate; NUE = nitrogen utilization efficiency; * = significant at $P < 0.05$ level; ** = $P < 0.01$ level, t -test; values represent means ± s.e.

^{b, c} See Table 3.

major change in insect metabolism with low nitrogen levels. In the present study, the relationship of low NUE and low nitrogen content, as well as the inverse relationship of AD and ECD discussed previously, may be due not only to the low nitrogen levels in the petioles (1.8 to 2.0%) but also to the accompanying high water content (93.5 to 94.5%) which has not been found in most low nitrogen material used for nutritional studies.

Conclusions

Although many insects feed on different plant tissue in relation to maximal nitrogen availability (McNeill & Southwood 1978), *S. exigua* larvae move from leaf tissue which contains 4.2 to 4.1% nitrogen to petiole tissue which contains 1.8 to 2.0%. This study has demonstrated that in terms of growth, development and reproduction, petioles are a suboptimal food source relative to celery leaves. Therefore, larval movement of *S. exigua* is probably related to other environmental influences which affect insect nutritional or behavioral ecology.

Acknowledgements

The authors thank Drs. T. C. Baker, G. P. Walker and J. D. Hare for criticism, and D. A. Reiersen, Dr. T. W. Embleton and M. Matsumura for use of laboratory facilities at the University of California at Riverside.

Résumé

Consommation et utilisation d'Apium graveolens par Spodoptera exigua

L'impact biologique de la consommation et de l'utilisation du céleri a été examiné sur un herbivore généraliste *Spodoptera exigua* Hübner. Une analyse de feuilles et de pétioles montre que ces deux parties de la plante ont une haute teneur en eau (>85%), mais que les feuilles contiennent deux fois plus d'azote organique total que les pétioles. Les taux de développement et de reproduction ont été significativement plus élevés (<0,01 test *t*) pour les

chenilles nourries sur feuilles. Les 2 derniers stades ont consommé significativement plus ($P < 0,05$ test *t*) de poids sec de matière végétale en s'alimentant sur pétioles qu'en s'alimentant sur feuilles. Bien que les taux de croissance aient été voisins quel que soit l'aliment pour les avant-derniers stades, la conversion d'aliment en poids de corps était inférieure pour les chenilles ne consommant que des pétioles. Au dernier stade, tant les taux de croissance que de conversion des chenilles élevées sur pétioles étaient inférieurs à ceux des chenilles élevées sur feuilles. Ainsi, puisque les chenilles présentent une préférence pour les pétioles moins nutritifs au dernier stade larvaire, des paramètres écologiques autres que l'alimentation doivent influencer les mouvements et la distribution de *S. exigua* sur céleri.

References

- Beier, R. C., G. W. Ivie, E. H. Oertli & D. L. Holt, 1983. HPLC analysis of linear furanocoumarins (psoralens) in healthy celery (*Apium graveolens*). *Fd. Chem. Toxic.* 21: 163-165.
- Berenbaum, M., 1978. Toxicity of a furanocoumarin to armyworms: A case of biosynthetic escape from insect herbivores. *Science* 201: 532-534.
- Berenbaum, M., 1981. Patterns of furanocoumarin production and insect herbivory in a population of wild parsnip (*Pastinaca sativa*). *Oecologia* 49: 236-244.
- Calow, P., 1977. Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52: 385-409.
- Dadd, R. H., 1960. The nutritional requirements of locusts. *J. Ins. Physiol.* 4: 319-347.
- Dethier, V. G., 1970. Chemical interactions between plants and insects, pp. 83-102. In E. Sondheimer & J. B. Simeone (eds.), *Chemical Ecology*. London, Academic press, 336 pp.
- Eveleens, K. G., R. Van Den Bosch & E. L. Ehler, 1973. Secondary outbreak induction of beet armyworm by experimental insecticide applications in cotton in California. *Environ. Entomol.* 2: 497-503.
- Feeny, P. P., 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.
- Fox, L. R. & B. J. Macauley, 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. *Oecologia* 29: 145-162.
- Gelernter, W. D., 1984. Characterization, genetic variation and control potential of a nucleic polyhedrosis virus from *Spodoptera exigua* (Hübner). Ph.D. thesis, Univ. Calif., Riverside.
- Gordon, H. T., 1972. Interpretations of insect quantitative nutrition, pp. 73-105. In J. G. Rodriguez (ed.), *Insect and Mite Nutrition*. Amsterdam, North-Holland Publishing Co., 702 pp.
- Hogg, D. B. & A. P. Gutierrez, 1980. A model of the flight phenology of the beet armyworm (Lepidoptera: Noctuidae) in central California. *Hilgardia* 48: 1-35.

- Jones, D. & J. Granett, 1982. Feeding site preferences of seven lepidopteran pests of celery. *J. Econ. Entomol.* 75: 449-453.
- Manuwoto, S. & J. M. Scriber, 1982. Consumption and utilization of three maize genotypes by the southern armyworm. *J. Econ. Entomol.* 74: 165-167.
- Matkin, O. A. & P. A. Chandler, 1957. The U.C.-type soil mixes, pp. 68-85. In K. F. Baker (ed.), *The U.C. system for producing healthy container grown plants*. Calif. Agric. Exp. Stn. Man. 23, 332 pp.
- Mattson, W. J., Jr., 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* 11: 119-161.
- McClure, M. S., 1980. Foliar nitrogen: A basis for host suitability for elongate hemlock scale, *Fiorninia externa* (Homoptera: Diaspididae). *Ecology* 61: 72-79.
- McGinnis, A. J. & R. Kastings, 1967. Dietary cellulose: Effect on food consumption and growth of a grasshopper. *Can. J. Zool.* 45: 365-367.
- McKenzie, H. A. & H. S. Wallace, 1954. The Kjeldahl determination of nitrogen: a critical study of digestion conditions - temperature, catalyst, and oxidizing agent. *Aust. J. Chem.* 7: 55-70.
- McNeill, S. & T. R. E. Southwood, 1978. The role of nitrogen in the development of insect/plant relationships, pp. 77-98. In J. B. Harborne (ed.), *Biochemical Aspects of Plant and Animal Coevolution*, London, Academic Press, 435 pp.
- Price, P. W., C. E. Bauton, P. Gross, B. A. McPherson, J. N. Thompson & A. E. Weis, 1980. Interactions among three trophic levels: Influence of plants on the interactions between insect herbivores and natural enemies. *A. Rev. Ecol. Syst.* 11: 41-65.
- Reese, J. C., 1981. Insect dietetics: Complexities of plant-insect interactions, pp. 317-335. In G. Bhaskaran, *et al.* (eds.), *Current Topics in Insect Endocrinology and Nutrition*, New York, Plenum Press, 362 pp.
- Reese, J. C. & S. D. Beck, 1978. Interrelationships of nutritional indices and dietary moisture in the black cutworm (*Agrotis ipsilon*) digestive efficiency. *J. Ins. Physiol.* 24: 473-479.
- Rodriguez, J. G., 1960. Nutrition of host plant and reaction to pests, pp. 149-168. In L. P. Reitz (ed.), *Biological and Chemical Control of Plants and Animal Pests*. Am. Ass. Adv. Sci. Publ. #61, Washington, D.C., 273 pp.
- Schoonhoven, L. M., 1972. Some aspects of host selection and feeding in phytophagous insects, pp. 556-566. In J. G. Rodriguez (ed.), *Insect and Mite Nutrition*, Amsterdam, North Holland Publishing Co., 702 pp.
- Scriber, J. M., 1978. The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: An ecological consideration. *Entomol. exp. & appl.* 24: 694-710.
- Scriber, J. M., 1979. Post-ingestive utilization of plant biomass and nitrogen by Lepidoptera: Legume feeding by the southern armyworm. *J. N.Y. Ent. Soc.* 87: 141-153.
- Scriber, J. M., 1984. Host plant suitability, pp. 159-202. In R. T. Cardé & W. J. Bell (eds.), *Chemical Ecology of Insects*, London, Chapman & Hall Ltd., 524 pp.
- Scriber, J. M. & F. Slansky Jr., 1981. The nutritional ecology of immature insects. *Ann. Rev. Entomol.* 26: 183-211.
- Shields, E. J. & J. A. Wyman, 1984. Responses of variegated cutworm (Lepidopteran: Noctuidae) to various light levels. *Ann. Entomol. Soc. Am.* 77: 152-154.
- Shorey, H. H. & R. L. Hale, 1965. Mass rearing of the larvae of nine noctuid species on a simple artificial medium. *J. Econ. Entomol.* 58: 522-524.
- Slansky, F., Jr., 1982. Insect nutrition: An adaptationists' perspective. *Florida Entomol.* 65: 45-71.
- Slansky, F. Jr. & P. P. Feeny, 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol. Monogr.* 47: 209-228.
- Soo Hoo, C. F. & G. Fraenkel, 1966. The selection of food plants in a polyphagous insect, *Prodenia eridania* (Cramer). *J. Ins. Physiol.* 12: 693-709.
- Thompson, J. N., 1983a. Selection of plant parts by *Depressaria mutilifida* (Lep., Oecophoridae) on its seasonally restricted host plant, *Lomatium grayi* (Umbelliferae). *Ecol. Entomol.* 8: 203-211.
- Thompson, J. N., 1983b. The use of ephemeral plant parts on small host plants: How *Depressaria leptotaeniae* (Lepidoptera: Oecophoridae) feeds on *Lomatium dissectum* (Umbelliferae). *J. Am. Ecol.* 52: 281-291.
- Waldbauer, G. P., 1964. The consumption, digestion and utilization of solanaceous and non-solanaceous plants by larvae of the tobacco hornworm, *Protoparce sexta* (Johan) (Lepidoptera: Sphingidae). *Entomol. exp. appl.* 7: 253-269.
- Waldbauer, G. P., 1968. The consumption and utilization of food by insects. *Adv. Ins. Physiol.* 5: 229-289.
- Wint, G. R. W., 1981. The effect of foliar nutrients upon the growth and feeding of a Lepidopteran larva, pp. 301-320. In J. A. Lee, *et al.*, (eds.), *Nitrogen as an Ecological Factor*. London, Blackwell Scientific Publications, 470 pp.

Accepted: November 27, 1984