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Effect of temperature on development rates, fecundity & longevity of the groundnut leaf miner, *Aproaerema modicella* (Lepidoptera: Gelechiidae), in India

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Abstract

Threshold temperatures, growth rates and physiological development times were calculated for the egg, larval and pupal stages of the groundnut leaf-miner, *Aproaerema modicella* (Deventer), a key pest of groundnut (*Arachis hypogaea*) and soyabean (*Glycine max*) in India. The life cycle of *Aproaerema modicella* required 660 degree-days (DD) above threshold temperatures (12.4°C for eggs, 11.3° for larvae and 14.7° for pupae). A function fitted to the adult longevity and fecundity data describes the effect of temperature and female age on fecundity. Egg production was greatest at 30°C and declined at lower and higher temperatures. Head capsule width measurements indicated that five larval instars are typical in India. The results obtained are discussed in the context of earlier work.

Introduction

The groundnut leaf miner, *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae), is a key pest of groundnut (*Arachis hypogaea*) and soyabeans (*Glycine max*) throughout Asia (Wightman & Amin, 1988; Shanower *et al.*, 1993). *Aproaerema modicella* was first recorded as a pest of groundnut more than 80 years ago (Maxwell-Lefroy & Howlett, 1909), but many aspects of its biology remain poorly understood. Reported development times for *A. modicella* immature stages and adult longevity differ as much as two-fold (Gujrati *et al.*, 1973; Kapadia *et al.*, 1982). Published values for fecundity are equally disparate (Cherian & Basheer, 1942; Gujrati *et al.*, 1973; Kapadia *et al.*, 1982). The effect of temperature on development and fecundity has not been investigated, and may offer an explanation for the conflicting results of these earlier studies.

Reports in the literature also vary widely concerning the number of larval instars for *A. modicella*. Kapadia *et al.* (1982) reported three, Gujrati *et al.* (1973) and Phisitkul (1985) described four, other authors recorded five (Amin, 1987) and Islam *et al.* (1983) six larval instars for *A. modicella*.

To develop an effective pest management programme for *A. modicella*, its basic biology must be well understood. The experiments described in this paper were designed to relate development rates, fecundity and longevity to temperature. The number of larval instars was also determined to resolve the inconsistencies found in the literature.

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Materials and methods

All experiments were carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), located near Hyderabad (18°N), Andhra Pradesh, peninsular India.

Rearing methods

Experimental insects were taken from laboratory colonies maintained under greenhouse conditions.

Aproaerema modicella larvae were reared and tested on the groundnut variety Kadiri 3 (ICG 799). The colony was maintained by collecting newly emerged moths and introducing them into cages with fresh groundnut plants. Larvae completed development on the same plant on which the eggs had been laid. Cotton wool soaked in sucrose solution (≈10%) was provided for the adults.

Batches of insects were reared at 15, 20, 25, 30 and 35°C, respectively, in Percival temperature cabinets programmed for L:D 12:12 and relative humidity in the range of 62–85%. These data were used to estimate temperature dependent growth and fecundity rates.

Developmental time

Leaflets with a single newly laid egg were placed on moistened filter paper in 120 × 10 mm plastic petri dishes, and reared in temperature controlled incubators. Batches of 80 eggs held under the above conditions were used to calculate the egg development rate.

To determine larval and pupal development times, batches of eggs were held at ambient temperature until they hatched, and then larvae were put into incubators. The number of larvae completing development was not the same at all temperatures; ant predation at 25° reduced the initial number of larvae from 80 to 35. Daily observations were made to record egg incubation, larval survival, pupation and adult emergence times.

To ensure that the use of excised groundnut leaflets would not bias development times, a batch of larvae was reared on whole plants. The plants (Kadiri 3 variety) were grown in the laboratory under a fluctuating temperature regime. Temperatures ranged from 22 to 28°C and daily mean temperatures were between 23.5 and 27°C.

Linear regression was used to calculate development thresholds for each immature stage (Gilbert *et al.*, 1976). The degree-days (DD) required by each stage and the fraction of time spent in each stage, are based on these thresholds.

Fecundity

For fecundity and adult longevity studies, pairs of pupae (male and female) were put into 10 ml plastic screw-top vials containing sucrose-soaked cotton wool as food for emerging adults. The opening of each vial was closed with cheese cloth secured by a rubber band. A fresh groundnut leaflet was provided for oviposition. Leaflets were replaced daily and the number of eggs counted. Only moth pairs producing a minimum of one egg were used to calculate the mean egg production/female. Pupae and adults were held at the same temperatures as the eggs and larvae. Forty-three pairs of adults were tested at 15°C and 81 pairs at 20, 25, 30 & 35°C.

Larval instars

The number of larval instars was determined from head capsule widths of several hundred larvae. Groundnut leaflets containing one-day-old eggs were taken from the colony and held at room temperature on moistened filter paper in petri dishes. The head capsule widths and body lengths of 10 randomly selected larvae were measured daily during the larval period.

Statistical analysis

Analysis of variance (ANOVA) was used to test differences in egg, larval and pupal survivorship and fecundity across temperatures (Zar, 1974). Regression analysis was used to estimate growth and development rates for immature stages, and to estimate development thresholds (Gilbert *et al.*, 1976). The formula of Bieri *et al.* (1983) was generalized and used to describe daily egg production as a function of temperature and female age. This

Table 1. Duration of each life stage at five temperatures, degree-day requirements and development threshold for *Aproaerema modicella*.

Temperature (°C)	Days (mean ± SE)[1]			
	Egg	Larva	Pupa	Adult
15	22.96 ± 0.32 (63)			17.70 ± 8.24 (56)
20	9.13 ± 0.35 (76)	33.87 ± 5.01 (67)	15.11 ± 2.67 (64)	11.41 ± 6.25 (147)
25	4.19 ± 0.19 (79)	6.54 ± 2.89 (35)	7.50 ± 2.45 (34)	12.78 ± 5.09 (143)
30	2.97 ± 0.29 (78)	14.66 ± 2.63 (62)	3.85 ± 1.47 (54)	10.62 ± 5.48 (129)
35	2.79 ± 0.21 (78)	12.33 ± 1.87 (9)	3.89 ± 1.69 (9)	5.47 ± 3.01 (131)
Threshold	12.4°C	11.3°C	14.7°C	3.0°C
Mean developmental period (degree-days)	60.1	327.1	72.3	202.4

[1]Numbers in parentheses refer to number (n) of experimental insects.

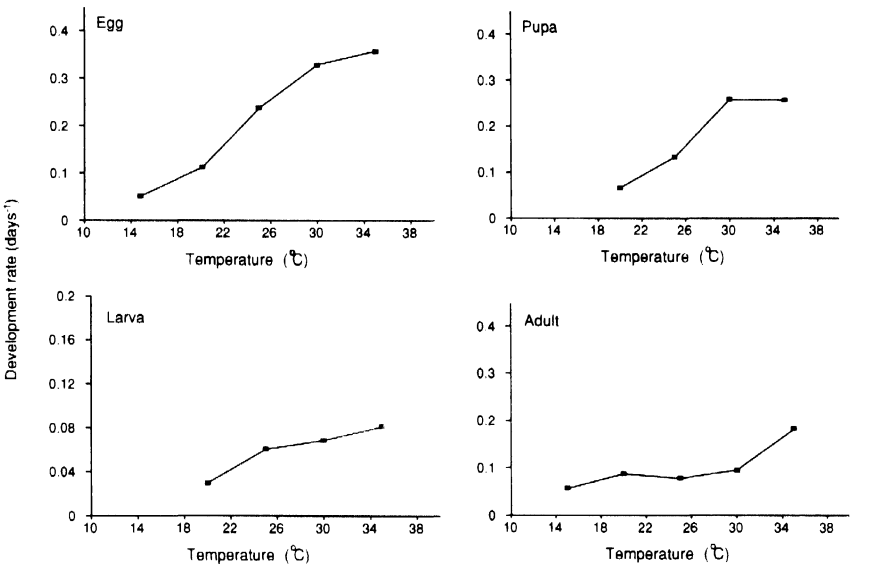

Fig. 1. Development rates (mean) for *Aproaerema modicella* egg, larval and pupal stages and adult longevity.

function was fitted to the oviposition data using multiple regression.

Results

Developmental times and adult longevity

Total immature (egg to adult) development times (y) ranged from 18.9–58.1 days depending on temperature (x) (table 1). The threshold temperature for egg development, based on the regression line $y = -0.2147 + 0.0173x$ ($r^2 = 0.954$; n = 376) was 12.4°C (fig, 1). Eggs required an average of 60 DD to complete development, and approximately 13% of the total development time was spent in the egg stage. Nearly all eggs hatched at 20, 25, 30 and 35°C, respectively. The proportion which successfully hatched at 15°C was significantly lower (0.79) than at the other temperatures (ANOVA; $F_{4,28}=7.23$; $p<0.001$; n=40).

Larval development ranged from 34 days at 20°C to 12.4 days at 35°C (table 1). No larvae survived at 15°C. Despite this, the estimated developmental threshold for larvae was 11.3°C based on the linear equation $y=-0.0429 + 0.0038x$ ($r^2 = 0.892$; n=173) fitted to data from the survivors (fig. 1). Larval development averaged 327 DD or 71% of the total developmental period (table 1). Temperature had a significant effect on larval survivorship (ANOVA; $F_{3,8}=16.15$; $P<0.003$; n=16). Mortality of early instar larvae was high at all temperatures and 100% at 15°C.

Pupal development times ranged from 3.9 days at 30°C to 15.1 days at 20°C (table 1). The threshold temperature for pupal development, calculated from the linear regression equation $y = -0.3267 + 0.0198x$ ($r^2 = 0.808$; n = 161), was 14.7°C (fig. 1). Pupae averaged 72 DD to complete development, equivalent to 16% of the developmental period (table 1). Pupal survivorship was unaffected by temperature (ANOVA; $F_{3,6}=1.72$; $P<0.26$; n=16) being uniformly high (87–100%) at all temperatures.

The larvae reared on whole groundnut plants under a fluctuating temperature regime completed the larval and pupal stages in an average of 23.6 days (range 20–27; n=33). Because of the larval habit of webbing leaflets together it was not possible to determine precisely the date of pupation. The values for combined larval and pupal development fell well within the range recorded from excised leaflets (table 1).

Adult longevity ranged from 17.7 days at 15°C to 5.5 days at 35°C (table 1) with a threshold of 3.0°C, based on the regression equation $y = -0.0195 + 0.0066x$ ($r^2=0.275$; n=606) (fig. 1). Adult longevity averaged 202 DD or about 45% of developmental time. The thermal summation, based on the calculated thresholds of each stadium, was 660 DD.

Fecundity

At 15°C only 15 of the original 43 pairs produced eggs, while 69 of the original 81 pairs produced eggs at 25°C (table 2). The average number of eggs/female was at least 30% higher at 30°C than at other temperatures. A

Table 2. Fecundity of *Aproaerema modicella* at five temperatures.

Temperature	Eggs per female			
	n[1]	Range	Mean[2]	(± SE)
15	15	(1–88)	37.8c	(±6.91)
20	47	(1–160)	42.7bc	(±7.11)
25	69	(1–193)	57.0b	(±6.71)
30	44	(1–248)	87.6a	(±9.85)
35	22	(1–105)	27.1c	(±6.29)

[1]Females producing at least one egg; [2]values within a column followed by the same letter are not significantly different ($P \leq 0.05$) Duncan's Multiple Range Test.

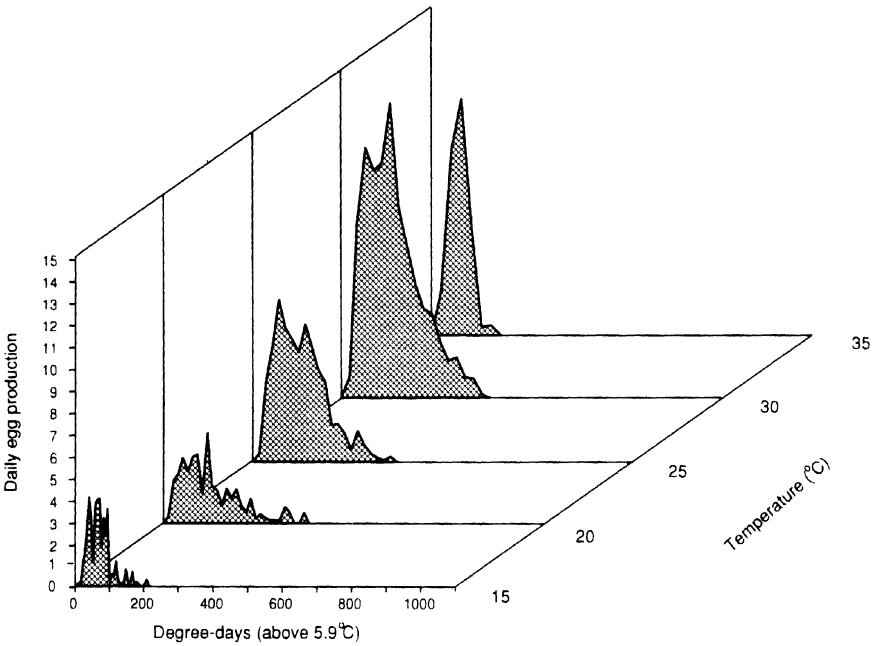

Fig. 2. *Aproaerema modicella* mean daily per-capita egg production at five temperatures.

function describing the effect of temperature and female age on fecundity is summarized below.

The shape of the age-specific patterns for daily egg production is similar across temperatures (fig. 2). Because adult females feed only on soluble carbohydrates, egg production is supported by the fat body accumulated during larval feeding, though energy from carbohydrate ingestion may also be involved. The pattern of oviposition at one temperature (τ) may be described by equation (1) (Bieri *et al.*, 1983):

$$R(a) = R(a)'/\Delta a = \alpha a/\beta^a \quad (1)$$

R is the oviposition rate/DD at female age ($0 < a < 150$), $R(a)'$ is the age specific rate/day (Δa), and α and β are fitted constants. The function can be linearized to obtain:

$$\log R = \log\alpha + \log a - a\log\beta \quad (2)$$

The coefficients may be estimated by multiple regression yielding the following equation:

$$\log R = C_0 + b_1x_1 - x_2\log\beta \quad (3)$$

with variable x_1=log a and x_2=a. Note that the additional coefficient b_1 results, modifying equation (1):

$$R = C_0a^{b1}/\beta^a \quad (4)$$

The coefficients and regression statistics of the multiple regression analysis at the five temperatures are given in table 3. The two best fits were at 25 and 30°C. Combining the data from 25 and 30°C, and assuming a mean of 27.5°C, gave a very close fit ($r^2 = 0.90$). Analysis of variance on this regression was highly significant (ANOVA; $F_{2,35}$=161.92, P<0.001, n=40), indicating that the model gives a satisfactory description of the data. However, the equation needs to fit across all temperatures. Gutierrez & Baumgaertner (1984) showed that the observed patterns of fecundity across all temperatures could be modelled using a ratio of resources acquisition. In this particular case resource acquisition refers to the conversion of the adult fat body tissue into eggs. The ratio utilized is of resource acquisition at temperature (τ) to resource acquisition at the optimum temperature (τ_{opt}) (i.e. equation 4):

Table 3. Results of multiple regression analyses on the effect of age of *Aproaerema modicella* females on fecundity at five temperatures.

Temperture	(°C)	n	C	x_1	x_2	r^2
	15	26	–4.335	–0.405	4.023	0.51
	20	27	–0.260	–0.244	1.447	0.69
	25	22	–0.052	–0.499	2.781	0.92
	30	18	0.851	–0.592	2.882	0.94
	35	7	3.229	–2.447	5.648	0.86
Combined						
	25+30[1]	39	0.432	–0.519	2.704	0.90

[1]Data from both 25° and 30°C combined into a single data set using an assumed mean of 27.5°C.

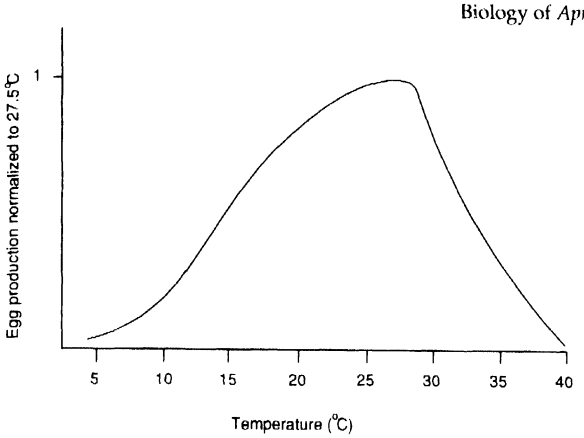

Fig. 3. The relationship between temperature and adult *Aproaerema modicella* fecundity.

$$0<S(t)=\frac{M^*(\tau)-Q_{10}}{M^*_{max}-Q_{10}}<1 \qquad (5)$$

The shape of this function is depicted in figure 3 and has a value between 0 and 1. At less than 5.9°C the supply is insufficient to produce eggs, but at τ_{opt} nearly all demands will be met and egg production maximized.

Combining equations (4) and (5) into one expression (6) gives the per capita egg production rate for individuals of age 'a' under the conditions $S_{(\tau)}$ experienced at time 't'.

$$R_{(\tau)}=S_{(\tau)}C_{10}a^{b1}/\beta^a \qquad (6)$$

Though Q_{10} and consumption rate $M^*_{max}(t)$ in (5) may not be known, Gutierrez & Baumgaertner (1984) have shown that R_0 is a good indicator of the adult assimilation rate. The data suggest that maximum assimilation occurred near 27°C (see above). Hence, $S_{(\tau)}$ may be approximated by function (7) describing a concave function between 5.9 and 27.5°C and a monotonically decreasing function between 27.5 and 40°C. At temperature (τ), $S_{(\tau)}$ is described as follows:

$$S(\tau)=\begin{cases}1-10^{-\lambda(\tau-5.9^\circ C)} & \text{for } 5.9^\circ \le t \le 27.5^\circ C\\ 10^{\lambda(\tau-27.5^\circ C)} & \text{for } 27.5^\circ < t \le 40^\circ C\end{cases} \qquad (7)$$

where $\lambda = 0.17647$ is a fitted constant.

This expression describes the effect of temperature and age of the adult female on per capita egg production.

Larval instars and body size

The relationship between larval body length and head capsule width indicated that five instars were typical for *A. modicella* at ICRISAT (table 4). The data cluster into five relatively distinct groups. The first three clusters showed minimal variation in head capsule widths and were easily differentiated. The body length/head capsule width relationship was more variable in the fourth and fifth instars. Head capsule widths ranged from 0.12 to 0.68 mm and body lengths from 0.56 to 6.4 mm. The correlation between head capsule width and body length was strong (r=0.96). The regression of body length on head capsule width is described by $y = -0.432 + 9.977x$ (n=158).

Table 4. Head capsule widths (mm), head capsule width ratios, and body length (mm) of lab-reared *Aproaerema modicella* larvae.

Instar	Head capsule width				Body length range
	N	Range	Mean+SE	Ratio	
First	40	0.12	0.12		0.48–1.24
Second	26	0.2	0.20	1.67	0.88–2.08
Third	22	0.24–0.28	0.277±0.0103	1.39	1.40–2.96
Fourth	35	0.36–0.48	0.395–0.0425	1.43	2.28–4.88
Fifth	35	0.52–0.68	0.578±0.0349	1.46	3.76–7.16

Discussion

Studies of temperature effects on poikilothermic organisms are common in the literature (e.g. Andrewartha & Birch, 1954; Gilbert *et al.*, 1976; Wagner *et al.*, 1984). Such studies assume that there is a continuous relationship between developmental time, longevity, and fecundity, across temperatures (Hughes, 1963; Gilbert *et al.*, 1976; Curry & Feldman, 1987). The linear or degree-day method used in this study is the most common method for calculating development rates because data are seldom available across the full range of temperatures (Stinner *et al.*, 1974; Gilbert *et al.*, 1976; Wagner *et al.*, 1984).

Shade temperatures in peninsular India range from 9 to 42°C, though cropping season air temperatures are more moderate and range from 18 to 32°C (ICRISAT, 1988). At low temperatures *A. modicella* completed its life cycle in 80 days while at higher temperatures only 23 days were required. A physiological time scale (DD above a threshold temperature) accounts for differences in development rate due to temperature. When development in physiological time was compared across temperatures, the differences were not large. The total *A. modicella* life cycle required 660 DD with only a 60 DD difference between the longest and shortest development times.

Earlier reports gave the following developmental times for eggs, larvae and pupae; 3, 9.3, and 5 days (Gujrati *et al.*, 1973) and 7.5, 18.5, and 9.9 days (Kapadia *et al.*, 1982). Temperatures in these studies were not controlled so from these earlier data it is impossible to calculate temperature dependent development rates. Data from these earlier studies fall within the range reported here (table 1) and it is likely that the discrepancies in reported development times were due to temperature variations. Valley & Wheeler (1976) reported similar developmental times for a related species, *Stomopteryx palpilineella* (Chambers).

Temperature influenced survival in immature stages, of *A. modicella*, especially the larval stage. Hatching was lowest at 15°C. Larval mortality was high at all temperatures and 100% at 15°C. The low rate of hatching and high larval mortality indicated the sensi-

tivity of these stages to extreme temperatures. At mid-range temperatures (25 and 30°C) survivorship was generally between 40 and 70%.

Temperature did not influence the viability of pupae. Emergence from the pupal stage was uniformly high (82–100%) at all temperatures. Adult longevity, however, was affected by temperature. Adults at 25 and 30°C lived approximately 50% longer than at 15, 20 and 35°C in terms of physiological time units. These differences are important because they indicate that females at these temperatures have longer ovipositional periods than females at other temperatures.

Females at 15 and 35°C lived equivalent physiological time periods and produced statistically similar numbers of eggs (table 2), although the real time was three times longer at 15°C (table 1). Mean daily egg production was similar at 25, 30 and 35°C (fig. 2), but because adults survived fewer days at 35°C, average egg production was lower. Egg production was highest at 30°C followed by 25°C and fell significantly at both lower and higher temperatures. This result could be predicted from the model proposed by Gutierrez & Baumgaertner (1984).

The data suggest a relationship between oviposition and temperature. At high temperatures daily egg production is high but adult longevity is short, while at low temperatures, adults live considerably longer but egg production is severely reduced. Under mid-range conditions (25 and 30°C), the optimum is reached; adults live relatively longer and egg production is maximized.

Ambient temperatures were not reported in three earlier studies measuring *A. modicella* fecundity (Cherian & Basheer, 1942; Gujrati *et al.*, 1973; Kapadia *et al.*, 1982) and the large differences in egg production reported may have been due to differences in technique, temperature and/or larval feeding regime.

Dyar (1890) was the first to note that head capsule width between successive instars increased by a constant factor for a given species. Gujrati *et al.* (1973) reported the following larval head capsule widths: first instar 0.07 mm, second instar 0.14 mm, third instar 0.21 mm and fourth instar 0.28 mm, respectively. Head capsule widths of the first two instars were smaller and larger than the width of the first instar reported here. The ratio of head capsule widths between successive lepidopteran instars is usually about 1.4 (Wigglesworth, 1972). The ratio of head capsule widths between first and second instars reported by Gujrati *et al.* (1973) was 2, higher than expected. Head capsule width ratios in this study were between 1.39 and 1.67 (table 4).

A second discrepancy is that Gujrati *et al.* (1973) reported head capsule widths for only four instars. The largest head capsule measured (0.28 mm), was equivalent to the width of the third instar head capsule in the present study (table 4). Valley & Wheeler (1976) measured head capsule widths for the slightly smaller, related species, *S. palpilineella*. This species has only four larval instars, but the ranges reported are very close to the values reported here for *A. modicella*.

Accurate information on the biology of *A. modicella* is a prerequisite for developing an effective pest management programme against this important and widespread groundnut pest. The results of the experiments described here have resolved much of the confusion over development times, fecundity and number of larval instars.

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References

Amin, P.W. (1987) Insects pests of groundnuts in India and their management. pp. 219–233 *in* Veerabhadra Rao, M. & Sithnanatham, S. (*Eds*) *Plant protection in field crops.* Hyderabad, India, Plant Protection Association of India.

Andrewartha, H.G. & Birch, L.C. (1954) *The distribution and abundance of animals.* 782 pp. Chicago, University of Chicago Press.

Bieri, M., Baumgaertner, J., Bianchi, G., Delucchi, V. & von Arx, R. (1983) Development and fecundity of pea aphid (*Acyrthosiphon pisum* Harris) as affected by constant temperature and by pea varieties. *Mitteilungen der Schweizerschen Entomologischen Gesellschaft* **56,** 163–171.

Cherian, M.C. & Basheer, M. (1942) Studies on *Stomopteryx nerteria* Meyr: a pest of groundnut in the Madras Presidency. *Madras Agricultural Journal* **30,** 379–381.

Curry, G.L. & Feldman, R.M. (1987) *Mathematical foundations of population dynamics.* 246 pp. College Station, Texas, Texas A & M University Press.

Dyar, H.G. (1890) The number of molts of lepidopterous larvae. *Psyche* **5,** 420–422.

Gilbert, N., Gutierrez, A.P., Fazer, B.D. & Jones, R.E. (1976) *Ecological relationships.* 156 pp. New York, W.H. Freeman and Co.

Gujrati, J.P., Kapoor, K.N. & Gangrade, G.A. (1973) Biology of soybean leaf miner, *Stomopteryx subsecivella* (Lepidoptera: Gelechiidae). *Entomologist* **106,** 187–191.

Gutierrez, A.P. & Baumgaertner, J.U. (1984) Multitrophic models of predator-prey energetics: I. Age-specific energetics models—pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae) as an example. *Canadian Entomologist* **116,** 924–932.

Hughes, R.D. (1963) Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *Journal of Animal Ecology* **32,** 393–426.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) (1988) *Annual report 1987.* Patancheru, A.P. 502 324, India.

Islam, W., Ahmed, K.N., Nargis, A. & Islam, U. (1983) Occurrence, abundance and extent of damage caused by insect pests of groundnuts (*Arachis hypogaea*). *Malaysian Agricultural Journal* **54,** 18–24.

Kapadia, M.N., Bharodia, R.K. & Vora, V.J. (1982) Biology and estimation of incidence of groundnut leaf miner, *Stomopteryx subsecivella* Zell. (Gelechiidae: Lepidoptera). *Gujarat Agricultural University Research Journal* **8,** 37–39.

Maxwell-Lefroy, H. & Howlett, F.M. (1909) *Indian insect life: a manual of the insects of the plain (tropical India).* 786 pp. reprinted 1971. New Delhi, Today and Tomorrows' Publishers.

Phisitkul, S. (1985) The biology and natural enemies of the leafminer, *Aproaerema modicella* Deventer (Lepidoptera: Gelechiidae) on groundnut (*Arachis hypogaae* L.). PhD thesis, University of the Philippines, Los Banos, The Philippines.

Shanower, T.G., Wightman, J.A. & Gutierrez, A.P. (1993) Biology and control of the groundnut leafminer, *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae). *Crop Protection*. **12,** 3–10.

Stinner, R.E., Gutierrez, A.P. & Butler, G.D. (1974) An algorithm for temperature-dependent growth rate simulation. *Canadian Entomologist* **106,** 519–524.

Valley, K. & Wheeler, A.G. (1976) Biology and immature stages of *Stomopteryx palpilineella* (Lepidoptera: Gelechiidae), a leafminer and leaftier of crownvetch. *Annals of the Entomological Society of America* **69,** 317–324.

Wagner, T.L., Wu, H., Sharpe, P.J.H., Schoolfield, R.M. & Coulson, R.N. (1984) Modeling insect rates: A literature review and application of a biophysical model. *Annals of the Entomological Society of America* **77,** 208–225.

Wigglesworth, V.B. (1972) *The principles of insect physiology*. 7th edn. 544 pp. London, Chapman & Hall.

Wightman, J.A. & Amin, P.W. (1988) Groundnut pests and their control in the semi-arid tropics. *Tropical Pest Management* **34,** 218–226.

Zar, J.H. (1974) *Biostatistical analysis*. 620 pp. Englewood Cliffs, New Jersey, Prentice-Hall.

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