Using Temperature-Mediated Functional Response Models to Predict the Impact of *Coleomegilla maculata*[1] (DeGeer) Adults and 3rd-Instar Larvae on Green Peach Aphids[2,3]

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ABSTRACT

Environ. Entomol. 11: 46–52 (1982)

The effects of temperature and prey density on *Coleomegilla maculata* (DeGeer) feeding on *Myzus persicae* (Sulzer) were determined to quantify their impact on the *C. maculata-M. persicae* interaction. Seven temperatures ranging from 15.6 to 32.2° C were employed in the study. Nine prey densities per temperature and two predator and prey age classes per prey density were also used.

An enzyme kinetic equation was used to describe the change with temperature in the green peach aphid intrinsic rates of increase and the *C. maculata* larval and adult search rates. The larval and adult handling rates were determined to be linearly related to temperature over the range studied. The short-term impact of *C. maculata* adults and 3rd-instar larvae on green peach aphids was simulated by substituting these equations into two aphid growth rate models. Both models predicted that *C. maculata* 3rd-instar larvae and adults would be most effective in reducing the aphid population in temperatures above 29° C.

GPA-CAST is a model that predicts green peach aphid population growth on potato plants (Whalon and Smilowitz 1979b). This model does not include a component quantifying the impact of green peach aphid natural enemies. Smilowitz et al. (1979) showed that natural enemies may have a substantial impact on green peach aphid populations. *Coleomegilla maculata* (DeGeer) is the most abundant green peach aphid natural enemy in Pennsylvania potato fields (Mack and Smilowitz 1980). The feeding rate of *C. maculata* must be determined to quantify its effects on a green peach aphid population. It is also necessary to determine the effects of temperature and prey density on *C. maculata* feeding rate, since *C. maculata* is a long-lived predator that could experience a wide range of temperatures and prey densities in its lifetime.

We have recently developed a temperature-mediated functional response equation which describes the interaction of temperature and a limiting nutrient on poikilothermic activity rates (Mack et al., in press). This equation was also applied to the interaction of temperature and prey density on an insect predator's feeding rate. The purpose of this study was to develop temperature-mediated functional response equations that simulate the effects of both temperature and prey density on the feeding rate of *C. maculata*, and to incorporate them into green peach aphid growth models. These models could then be used to evaluate the influence of temperature on the *C. maculata-M. persicae* interaction. Further, the development of green peach aphid growth models is an important step towards achieving our objective of developing a temperature dependent simulation model of the *C. maculata-M. persicae* interaction.

Materials and Methods

Rearing Procedures

All of the stages and instars of *C. maculata* were separately reared at 22 to 25° C with a 16:8 L/D photoperiod in plastic petri dishes (2.0 by 8.0 cm). *C. maculata* larvae were fed only green peach aphids. Adults were fed green peach aphids and a food supplement[5].

Green peach aphids were reared on Katahdin variety potato plants in large growth chambers. The plants were grown from certified seed pieces planted in 1.89-liter plastic pots with a soil mixture[6].

Experimental Design

Three variables were considered in the study: temperature, predator size, and prey density. Seven temperatures were used: 15.6, 18.3, 21.1, 23.9, 26.7, 29.4, and 32.2° C. These temperatures were employed because they bracketed most field temperatures in Pennsylvania when the predator-prey interaction takes place.

Two predator age classes were used. One- to 2-week-old *C. maculata* adults and 3rd-instar larvae were selected for study because they represented the two most voracious forms of the insect. 4th-instar larvae were not used because they usually pupated prematurely in our preliminary tests.

Nine prey (green peach aphid) densities were employed: 6, 12, 18, 24, 30, 36, 48, 60, and 80 aphids per experimental arena. Two prey age classes were employed to allow *C. maculata* to select from a mixture of prey sizes. Equal numbers of small (1st- to 2nd-instar) and medium (3rd- to 4th-instar) aphids were used at each density. For example, three small and three medium aphids represented a density of six aphids. Both aphid population growth and de-

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[1] Coleoptera: Coccinellidae.

[2] *Myzus persicae* (Sulzer) (Homoptera: Aphididae).

[3] Authorized for publication on 23 October 1980 as paper no. 6122 in the journal series the Pa. Agric. Exp. Stn. Received for publication 4 December 1980.

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[5] Formula 57®, CRS Food Service and Supply Company, St. Paul, MN 55119.

[6] Jiffy Mix®, Jiffy Products of America, West Chicago, Ill.

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pletion due to predation were allowed to occur during each 24-h experimental period.

A Youden square (Montgomery 1976) was used as the experimental design. Each cell in the Youden square (Fig. 1) represented a 1-week period in a growth chamber at a fixed temperature. All 18 predator-prey combinations (two predator sizes by nine prey densities) were run in each of the three chambers within this 1-week period. The entire experiment was repeated so that six replicates were obtained for each predator-prey combination.

Experimental Arena

Arenas (Fig. 2) were made by gluing a piece of 4-mil clear polyurethane (35.6 by 45.7 cm) to a plastic petri dish bottom (2.0 by 15.0 cm). A three-leaf potato stem section was used as the surface (ca. 600 cm^2) to be searched by each predator. Each 17.8- to 22.9-cm section had three equally sized leaves. Wilting was prevented by placing the cut end of the stem into a plastic bottle filled with Coon's (1959) NPK solution.

Green peach aphids were placed on the stem section by introducing a potato leaflet with a known number of aphids onto the lowest leaf of the stem. Thus, the aphids were nonrandomly distributed on the stem section. This method was designed to simulate late-season field conditions where most green peach aphids occur on the lowest leaves (Mack and Smilowitz 1981).

TIME	CHAMBER		
	1	2	3
1	7	1 (15.6)	3
2	1	2 (18.3)	4
3	2	3 (21.1)	5
4	3	4 (23.9)	6
5	4	5 (26.7)	7
6	5	6 (29.4)	1
7	6	7 (32.2)	2

FIG. 1.—Youden square, which was used as the experimental design. Time was the blocking variable, and chambers were replicates. The number in each cell represents the coded temperature used in the study. Numbers in parentheses indicate the actual temperatures in °C.

FIG. 2.—Experimental arena.

Each predator was put on the top leaf of the stem and allowed to feed for 24 h in a 16:8 L/D photoperiod. Only one predator was placed in each arena. Predators that were employed in the study were starved for 24 h at 23.8 to 25.6° C before use. Before the placement of the predator on the plant, the stem sections were misted with water. This helped maintain a moderate humidity (60 to 90%) and also acted as a water supply for the predator. After 24 h, each *C. maculata* was removed, and all remaining aphids were counted and the size differentiated.

Green peach aphid counts were converted to biomass estimates for use in data analysis (Table 1). A population growth rate model was fitted to the data. The equation was:

$$\frac{dA}{dt} = r \cdot A - \frac{(1/T_h) \cdot A \cdot P}{\left(\frac{1}{a \cdot T_h}\right) + A} \qquad (1)$$

where r = intrinsic rate of increase (h^{-1}), A = green peach aphid biomass (g/area), 1/T$_h$ = handling rate (g/predator · h), a = search rate (area/predator · h), P = *C. maculata* density (predators/area), and t = time (h). This equation was composed of an exponential growth model for aphids minus predator feeding. An exponential growth model was employed because Whalon and Smilowitz (1979b) found that an exponential growth model described at least 74% of the total variation in green peach aphid means over time in 14 of 15 data sets from 3 years' field research. A temperature-mediated functional response equation (Mack et al., in press) was the predator feeding model incorporated into equation 1. Prey biomass rather than numbers was used in equation 1 because it converted the varying age classes and numbers of aphids counted at t = 24 into a single number. Biomass consumed rather than numbers has been extensively employed in feeding rate equations used by ecologists (e.g., Williams 1980).

A nonlinear least-squares fit for each data set was computed by numerically integrating equation 1 with FORTRAN subroutine RKF45 (Forsythe et al. 1977), passing this to subroutine VA05A (Powell 1968), and repeating the process until a minimized residual sum of squares occurred. The search and handling rates were the only parameters to be estimated in equation 1. The intrinsic rate of increase and its change with temperature was independently estimated from the results of a laboratory study similar to this predator study. The differences between the studies were that (a) there were no predators, (b) three replicates at each density were employed, and (c) only six temperatures were used in the intrinsic increase experiment.

The observed mean intrinsic rate of increase at each temperature served as an input to a nonlinear regression program fitting a simplified Eyring and Urry (1975) equation to the data. This equation was a basic component of our temperature-mediated functional response equation. The simplified Eyring and Urry (1975) equation was:

$$r = \frac{C \cdot \mathrm{temp} \cdot e^{(-u1/\mathrm{temp})}}{1 + D \cdot e^{(-u2/\mathrm{temp})}} \qquad (2)$$

where r = intrinsic rate of increase, temp = temperature (° C), and C, D, u1, and u2 are constants. A discussion of this equation and its parameters can be found in Eyring and Urry (1975). Equation 2 was also fitted to the *C. maculata* adult and larval search rates obtained from the fit of equation 1 to the data. Linear models were fitted to the larval and adult handling rates. These models represent a linear approximation to the curves generated by equation 2. They were used because an optimum temperature for the handling rates was not reached, and a decrease in rate beyond the optimum temperature did not occur. Thus, a nonlinear equation such as the Eyring and Urry equation was not needed, since there was no deviation from a linear increase in the handling rates.

Table 1.—Green peach aphid biomass estimates

Aphid size	$\bar{x} \pm S_{\bar{x}}$[a] (g/aphid)
Small	0.0000430 ± 0.0000296
Medium	0.0001628 ± 0.0000453
Large	0.0002720 ± 0.0000439

[a] Mean ± SE of the mean. Based on weighing three replicates of 50 aphids per replicate.

Results

Intrinsic Rates of Increase

The intrinsic rates of increase changed with temperature in a nonlinear manner (Fig. 3). The rates ranged from 0.0139688/h at 21.1° C to a low of 0.0074033/h at 32.2° C. These rates were greater than the value used by Whalon and Smilowitz (1979a) in GPA-CAST. This may have been due to the short length of time used to determine the intrinsic rates of increase, since no medium sized aphids could have molted to adults and died of old age in 24 h. The change in the intrinsic rates of increase with temperature concurs with Whalon and Smilowitz (1979a), who reported that green peach aphids developed the fastest at 19.7° C and more slowly at temperatures above 24.5° C. Equation 2 accurately described the change in the increase rates with temperature, and was thus in agreement with theory (Mack et al., in press). A Kolmogorov-Smirnov test (Barr et al. 1979) failed to indicate that the residuals from the fit of equation 2 to the data were not normally distributed, so equation 2 was both a statistically and biologically acceptable model. The predicted rates from equation 2 were used as the intrinsic rates of increase in equation 1. These rates were used because we believe equation 2 provides a biologically acceptable description of the change of many poikilothermic activity rates with temperature (Mack et al., in press).

Fit of Equation 1 to the Data

Equation 1 satisfactorily described the change in the aphid population with time when the aphid population was also being attacked by a *C. maculata* larva (Table 2) or by a single adult (Table 3).The r^2 values from the fit of equation 1 to data from aphid populations attacked by a *C. maculata* larva ranged from 0.97 at 15.6 and 23.9° C to 0.81 at 32.2° C. When equation 1 was fitted to data from green peach aphid populations attacked by an adult *C. maculata*, the r^2 values ranged from 0.98 at 15.6° C to 0.80 at 32.2° C. Thus, the poorest fits of equation 1 for both the larval and adult data occurred at 32.2° C. This may have been caused by the aphids' behavioral response to the high temperature. More aphids were observed on the plastic sides and top of the arena at 32.2° C than at the other temperatures. These aphids would have acted as a refuge population, since the *C. maculata* larvae and adults appeared to primarily search the potato stem section and not the container. Equation 1 could not be ex-

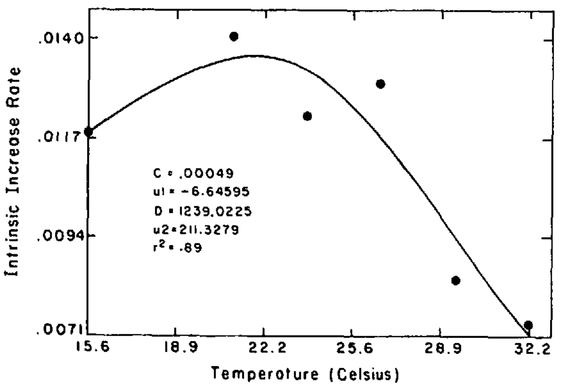

FIG. 3.—Fit of equation 2 to the mean intrinsic increase rates per hour from green peach aphids reared at six temperatures. C, D, u1, and u2 are the estimated parameters.

pected to fit these data since it did not contain a prey refuge term (Whittaker 1975).

Modeling the Change in Handling Rates with Temperature

Both the larval and the adult handling rates increased linearly with temperature. *C. maculata* larvae (Fig. 4) had a higher handling rate at low temperatures than the adults. The adult handling rate (Fig. 5) was greater at temperatures above 27.5° C. The predicted handling rates for both the larvae and the adults were in the range of feeding rates reported in the literature for various coccinellids. For example, a handling rate of 0.000544 g/predator · h equalled 48 large green peach aphids handled per day. This was similar to the feeding rate of 50.3 aphids per day for *Coccinella septempunctata*[7] L. (Balduf 1935), and the 46 *Toxoptera graminum* (Rond.)[8] per day eaten by *Hippodamia convergens*[7] Guerin (Nielson and Currie 1960).

Modeling the Change in Search Rates with Temperature

The larval (Fig. 6) and the adult (Fig. 7) search rates changed with temperature in a nonlinear manner. Both search rates increased linearly with temperature for a large portion of their observed responses. This linear portion concurs with Frazer and Gilbert (1976), who found that the search rates for *Coccinella californica*[7] Mannerheim and *Coccinella trifasciata*[7] Mulsant were linearly related to temperature. Equation 2 satisfactorily described the relationship between the larval and adult search rates with temperature, and thus concurred with theory (Mack et al., in press). A Kolmogorov-Smirnov test failed to indicate that the residuals from the fit of equation 2 to the larval and adult search rates were not normally distributed. Thus, equation 2 was both a biologically and a statistically acceptable model.

Discussion

It is now possible to simulate the impact of *C. maculata* 3rd-instar larvae on a green peach aphid population by substituting the intrinsic rate model and the larval search and handling rate models into equation (1). We obtain:

$$\frac{dA}{dt} = r \cdot A - \frac{(1/T_h) \cdot A \cdot P}{\left(\frac{1}{a \cdot T_h}\right) + A} \qquad (3)$$

where: A = green peach aphid biomass (g/area); r = $(0.00049 \cdot \text{temp} \cdot e^{[6.64595/\text{temp}]})/(1 + 1239.0225 \cdot e^{[-211.3279/\text{temp}]})$; $1/T_h = 0.0003720 + 7.493\text{E-}06 \cdot \text{temp}$; a = $(0.01541 \cdot \text{temp} \cdot e^{[-34.71839/\text{temp}]})/(1 + 9386.6584 \cdot e^{[-297.5601/\text{temp}]})$; P = *C. maculata* larval density; and temp = temperature (°C).

By using equation 3, the growth of a green peach aphid population at a given temperature that is also being attacked by a *C. maculata* larva can be represented by a three-dimensional surface. A surface can be generated for any temperature within the range studied. For example, the seven response surfaces obtained from the temperatures used in the experiment are illustrated in Fig. 8. The shape of each surface is a function of the temperature, the length of time the aphid population is allowed to grow, and the initial green peach aphid density. The simulations used to generate each surface were run

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[7] Coleoptera: Coccinellidae.
[8] Homoptera: Aphididae.

Table 2.—Fit (r^2) of equation (1) to data from green peach aphid populations attacked by a *C. maculata* 3rd-instar larvae

Temp (°C)	N[a]	Handling rate (× 10^{-4})[c] (g/predator · h)	Search rate[c,d] (area/predator · h)	r^2
15.6	9	5.0139	0.028331	0.97
18.3	8[b]	5.1071	0.050911	0.95
21.1	9	5.3350	0.049060	0.94
23.9	9	5.4569	0.076452	0.97
26.7	8[b]	5.1705	0.119597	0.94
29.4	9	6.2085	0.085123	0.87
32.2	9	6.2771	0.093401	0.81

[a] Number of means used in the analysis. Each mean represented an average of the total biomasses of aphids found after 24 h from a given initial green peach aphid density. There were six observations per mean.
[b] Means from the largest aphid density were not used in the analysis because they were outliers due to aphids escaping from the arena before t = 0.
[c] Parameters estimated with nonlinear regression.
[d] Part of total surface area (ca. 600 cm²) traversed/h by a *C. maculata* larva. For example, a search rate of 0.093401 = 56.04 cm²/h traversed by a predator.

Table 3.—Fit (r^2) of equation 1 to data from green peach aphid populations being attacked by a *C. maculata* adult

Temp (°C)	N[a]	Handling rate (× 10^4)[c] (g/predator · h)	Search rate[c,d] (area/predator · h)	r^2
15.6	9	1.2783	0.0441012	0.98
18.3	9	4.0714	0.0415470	0.95
21.1	9	3.3734	0.0637324	0.88
23.9	8[b]	6.3536	0.0651344	0.89
26.7	9	3.5194	0.0953376	0.95
29.4	8[b]	5.1461	0.0907769	0.91
32.2	8[b]	8.7240	0.0764922	0.80

[a–d] See respective footnotes to Table 2.

for 72 h, since the purpose of this study was to develop green peach aphid growth models that could be used to develop a simulation model of the *C. maculata-M. persicae* interaction. The aphid population at 32.2° C (Fig. 8G) decreased when a low initial aphid density was used and increased gradually when an initial aphid density of 8.2 mg per area was employed. The aphid population grew more rapidly at temperatures less than 24° C (Fig. 8A–D) than at temperatures above 29° C (Fig. 8F, G). This was especially noticeable at the initial aphid density of 8.2 mg per area. Thus, temperature greatly influenced the simulated population dynamics of the green peach aphid. This was caused by two factors; (a) the green peach aphid intrinsic rate of increase was greatest at temperatures between 18.9 and 24° C, and (b) the larval handling rate linearly increased with temperature. Comparable results were obtained for the *C. maculata* adult simulations. These results were similar to those reported by Frazer and Gilbert (1976) for coccinellids feeding on *Acyrthosiphon pisum* (Harris)[8] and by Skuhravy and Novak (1966, cited by Hagen and van den Bosch [1968]) for coccinellids feeding on bean aphids[9].

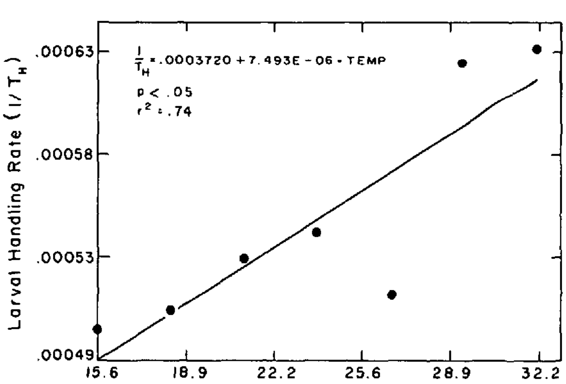

FIG. 4.—Relationship between larval handling rate per hour and temperature.

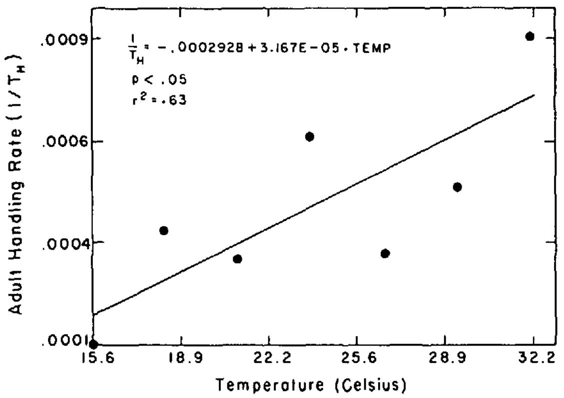

FIG. 5.—Relationship between adult handling rate per hour and temperature.

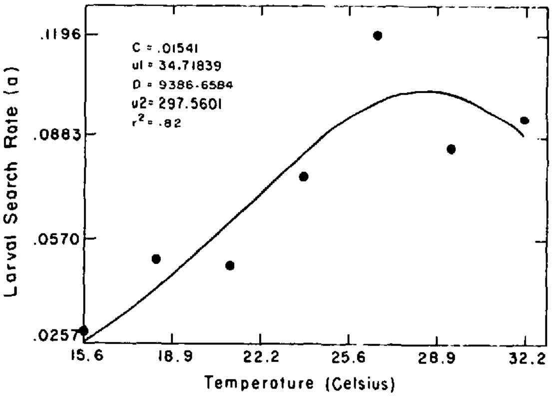

FIG. 6.—Fit of equation 2 to the larval search rates. C, D, u1, and u2 are the estimated parameters.

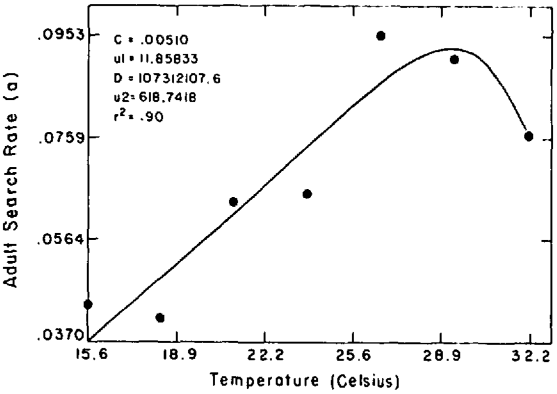

FIG. 7.—Fit of equation 2 to the adult search rates. C, D, u1, and u2 are the estimated parameters.

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[9] *Aphis fabae* Scopoli (Homoptera: Aphididae).

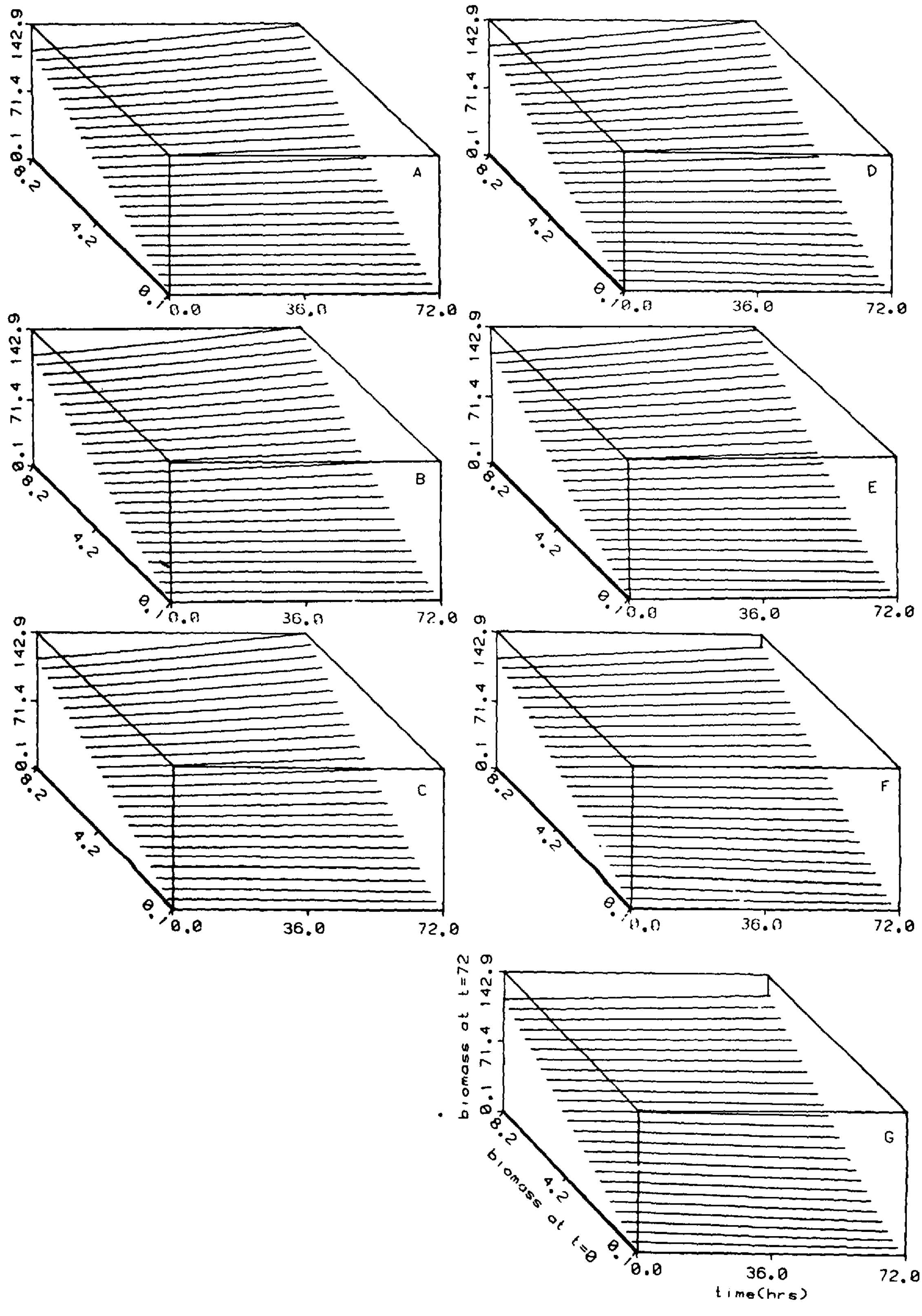

FIG. 8.—Simulation of the growth of a green peach aphid population being attacked by a *C. maculata* 3rd-instar larva. The growth is affected by time (h), the initial aphid density (mg), and temperature (° C). A = 15.6, B = 18.3, C = 21.1, D = 23.9, E = 26.7, F = 29.4, and G = 32.2°C.

McLeod (1937, cited by Hagen and van den Bosch [1968]) reported that a green peach aphid parasite was also most effective at warmer temperatures.

Thus, the two green peach aphid growth models with *C. maculata* predation added qualitatively agree with the literature. These models are important because for the first time, the interaction of temperature and aphid density on *C. maculata* feeding has been quantified and used to simulate the impact of *C. maculata* on green peach aphid populations. However, these models are limited in their use to time periods where the larval and adult *C. maculata* populations are constant. We have recently remedied this by coupling these equations with some *C. maculata* population growth equations in a FORTRAN-based simulation model. Our future studies will be directed toward the improvement and evaluation of this simulation model.

Acknowledgment

We gratefully acknowledge the assistance of A. Bower and G. Hanley in data collection and in rearing the predators. We also thank B. A. Bajusz for her assistance with the statistical design and analysis, and E. S. Nolan for his help with the computer graphics. Finally, we thank Richard Craig, Larry Hull, and Frederick Williams for their critical reviews of the manuscript.

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