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A dynamic model of larval Mexican bean beetle survival as a function of body water balance

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Abstract. This paper presents evidence of the relationship between survival and body water content in the Mexican bean beetle, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae). Results of a simulation model for dynamically describing water balance and survival are compared with experimental data for the Mexican bean beetle feeding on both lima bean and soybean under different variable temperature and moisture regimes.

Key words. *Epilachna varivestis*, simulation, population dynamics.

Introduction

Host plant species and phenology, temperature, and relative humidity have all been recognized as important factors influencing survival of Mexican bean beetle, *Epilachna varivestis* Mulsant (Eddy & McAlister, 1927; Miller, 1930; Sweetman & Fernald, 1930; Howard, 1921; Deitz *et al.*, 1976; Wilson, 1981; Sprenkel & Rabb, 1981; Wilson *et al.*, 1982). However, there are few papers which discuss the relationship between body water content and survival under variable conditions (note review by Wharton & Richards (1978) for lack of quantitative information on this subject). Miller (1930) investigated survival of Mexican bean beetle following exposure to high temperature for 3 h at different relative humidities. He found survival at 73% r.h. of larval Mexican bean bettle to be 100, 96, 89 and 91% at temperature of 37.5, 38.5, 39.5 and 40.5°C, respectively. There was no survival at 42.5°C, regardless of r.h. No measure of body water content was made.

A model for water balance in larval Mexican bean beetle has recently been proposed (Chu *et al.*, 1992), but not tested under variable conditions. The purposes of this paper are to present quantitative information relating larval survival to body water content, and to validate this survival model as well as the underlying water balance model of Chu *et al.* (1992).

Experimental materials and methods

Survival and water balance. All measurements were conducted in two chambers held at 38.5 ± 1 and 39.5 ± 1°C, respectively. Relative humidity was held at 50–70% in both chambers. Larvae were reared in the laboratory (20–27°C, 50–70 r.h.) with an excess of lima bean foliage at all times. Groups of fifty larvae were selected at random and placed into three containers (twenty, twenty and ten individuals) without foliage. Each group of fifty was placed in one of the two chambers for varying time periods. At 38.5°C, exposure times were 1.0, 4.5, 7.5 and 13.5 h, while at 39.5°C, exposure times of 3.0, 4.5 and 5.5 h were used.

After the exposure period, the larvae in the container with ten individuals were weighed, dried, and weighed again to determine percentage body water content (WC). The larvae in the other two containers were placed under favourable laboratory conditions (excess foliage, 20–27°C, 50–70% r.h.), held for 24 h, and survival recorded.

Validation experiment. Four host 'patches' were planted in the glasshouse (Fig. 1), using two crops (lima bean, var. Fordhook; soybean, var. Essex). One-half of each host (one block) was watered daily (dry treatment) and the other half was watered twice daily (wet treatment). Water was applied to soil only. For one set of trials, the temperature in the glasshouse was manipulated to provide a range of 13–32°C (normal temperature), representing a typical early summer diurnal temperature fluctuation. These trials were then repeated with the glasshouse temperature allowed to fluctuate from 23 to 40°C, a not uncommon diurnal range during late July in North Carolina. Temperatures (dry and wet-bulb) were monitored in each plot at 0.5 h intervals. Three replicates (cages, 60 × 60 × 60 cm) were used for each combination of conditions. Two replicates were used for survival estimation, and one for

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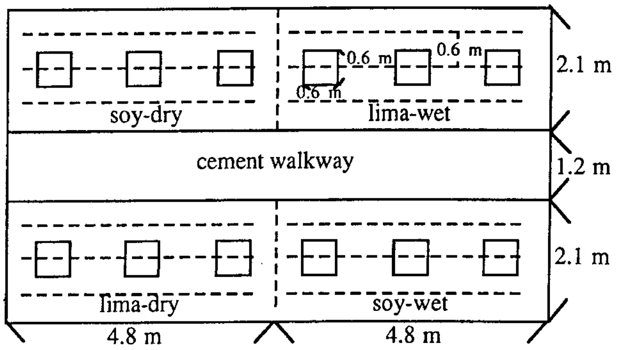

Fig. 1. The experimental plan for the glasshouse validation trials. ----, rows of host plants; □, screen cages.

estimation of water content. A summary of the conditions for each trial is presented in Table 1.

Adult Mexican bean beetles were held in the laboratory (20–30°C, 50–90% r.h., LD 14:10h photocycle) on lima bean. Egg masses were collected daily. At hatching, forty larvae were placed on the top leaves of a plant in the glasshouse and covered with the screen cage. Every 2–4 days the larvae were counted and survival estimated. At three time intervals (days 6, 10 and 14 for normal temperature trials; days 5, 10 and 14 for hot temperature trials), four to six larvae were removed for estimation of water content. These larvae were removed at 3–4 p.m. for the first and third sample, and at 9–10 a.m. for the second. Larvae were wet-weighed, then dried and reweighed. Water content was expressed as per cent wet weight.

In addition, based on the data of Wilson *et al.* (1982), it could be assumed that larvae under normal temperature and wet conditions (low vapour pressure deficit) would have optimum water content for feeding on each host. Based on this assumption, ten larvae of different sizes were chosen at random from the appropriate trials to examine optimum water content as related to body size (weight). Also, four times during the course of the trials, samples of four to seven larvae were selected at random to estimate growth (body weight), to be used as input for validation simulations.

Experimental results

Survival. Under high constant temperatures, after a 4h exposure in either chamber (38.5 or 39.5°C), most of the larvae were moribund, requiring 14–26h to recuperate. Even after this period, a number of the larvae had damage to their mandibles and could not eat properly. However, these larvae were still considered to have survived. The mean survival and water content of larvae after each treatment are presented in Table 2.

Survivals for all glasshouse trials are presented in Fig. 2. Under 'normal' temperatures, there was little effect of either moisture regime or host plant. At high temperatures, however, a host and moisture effect was obvious, with lower survival for 'dry' lima beans compared to 'wet', and almost no survival on soybean, whether wet or dry.

Where survival was low, so was mean water content. At high temperatures, soybean larvae had lower water content than lima bean larvae under the same moisture regime (Table 3).

Table 2. Survival and water content of MBB larvae after exposures to high temperatures.

Temperature (°C)	Exposure (h)	Survival		Water content		
		n	%	*n*	Mean	SD
38.5 ± 1	1.0	40	100	10	0.7727	0.0206
	4.5	40	95	10	0.7541	0.0252
	7.5	40	53	10	0.7286	0.0234
	13.5	40	21	10	0.7211	0.0225
39.5 ± 1	3.0	40	90	10	0.7310	0.0282
	4.5	40	50	10	0.7279	0.0175
	5.5	40	13	10	0.7219	0.0129

Table 1. Summary of temperature and VPD measurements during glasshouse trials.

			Temperature (dry-bulb°C)			VPD (mbars)		
Temp.	Host	Moisture	Mean	SD	Range	Mean	SD	Range
Normal	Lima	Wet	25.3	2.4	18.7–31.5	5.5	2.5	1.2–14.9
		Dry	24.0	2.3	16.8–28.5	3.4	2.2	0.0–16.7
	Soy	Wet	21.5	3.5	15.1–32.0	6.7	3.2	0.0–22.1
		Dry	20.4	3.6	13.2–32.3	6.4	3.6	2.0–21.1
Hot	Lima	Wet	31.1	2.1	26.3–37.8	8.6	2.8	0.0–20.2
		Dry	31.1	2.3	26.8–38.3	10.4	2.6	4.2–26.0
	Soy	Wet	30.3	2.8	22.9–38.0	9.6	4.9	0.0–25.9
		Dry	31.1	2.6	26.0–39.7	10.8	2.8	1.2–25.5

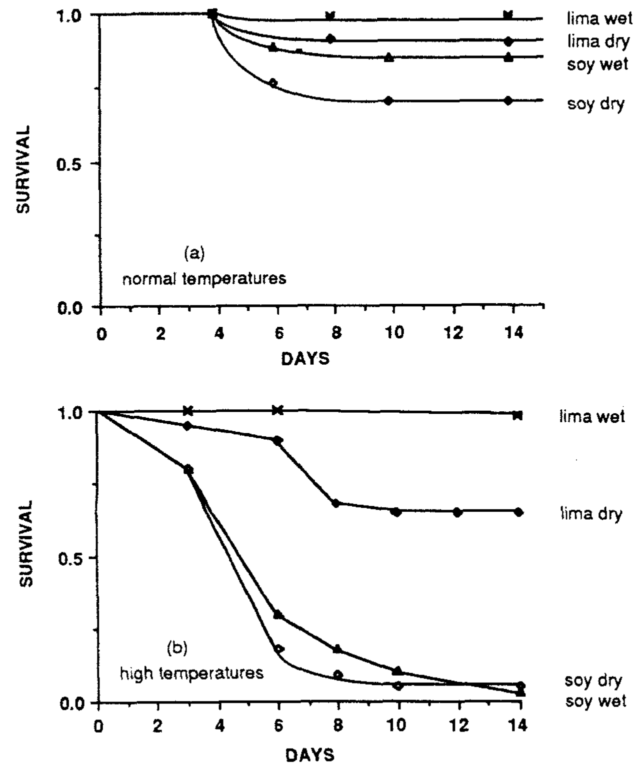

Fig. 2. Observed Mexican bean beetle larval survival, under (a) normal temperatures, and (b) high temperatures.

At normal temperatures, the soybean-fed larvae have a slightly higher water content than the lima bean larvae. However, this is misleading, since the larvae were considerably different in size, and optimum water content varied with body weight (Table 4), decreasing as body size increased.

Since there was virtually no difference in vapour pressure deficit or body water content for wet or dry conditions under normal temperature (Table 3), only one estimate of actual body water content was necessary for each host (Table 4).

Lima bean has a higher water content (82.78 ± 2.04%, $n = 27$) than soybean (69.08 ± 4.60%, $n = 27$). In addition, soybean leaves have more and longer tricomes which may interfere with Mexican bean beetle feeding. Thus, water intake may be considerably reduced when feeding on soybean compared with lima bean. This contention is further supported by the reduced larval weight gains under hot, dry conditions (Fig. 3). Under normal temperatures, the weight gains are different for the two hosts, but are not affected by moisture regime. However, at high temperatures the weight gains on wet and dry limas are different, both considerably higher than those on soybean. On soybean, after 14 days the mean larval weight was still less than 5 mg.

These data suggest that the sensitivity of Mexican bean beetle to weather in North Carolina is a combination of decreased water intake on soybean and increased cuticular water loss under conditions of high temperature and low

Table 3. Water content (%) of MBB larvae under various glasshouse 'climates'.*

Temp.	Host	Moisture	Sample 1, day 5–6, 3–4 p.m.	Sample 2, day 10, 9–10 a.m.	Sample 3, day 14, 3–4 p.m.
Normal	Soy	Dry/wet	83.99 ± 1.43 ($n = 5$)	83.33 ± 1.17 ($n = 5$)	81.64 ± 0.91 ($n = 8$)
	Lima	Dry/wet	83.39 ± 0.36 ($n = 5$)	82.65 ± 0.91 ($n = 5$)	78.12 ± 1.30 ($n = 10$)
Hot	Soy	Dry	78.65 ± 0.54 ($n = 5$)	80.60 ± 0.84 ($n = 5$)	–[†]
		Wet	80.75 ± 1.32 ($n = 4$)	83.70 ± 1.32 ($n = 6$)	–
	Lima	Dry	79.48 ± 1.31 ($n = 5$)	80.82 ± 1.59 ($n = 6$)	77.19 ± 1.88 ($n = 8$)
		Wet	81.20 ± 1.62 ($n = 5$)	83.95 ± 0.71 ($n = 8$)	77.14 ± 0.87 ($n = 8$)

* Mean ±standard deviation.

[†] Survival of larvae too low for water content samples.

Table 4. Maximum water content (%) as related to body size. Values are means ±standard deviation.

	Body water content for size*		
Host	Small, 0–15 mg	Medium, 15–30 mg	Large, >30 mg
Lima	83.00 ± 2.14 ($n = 10$)	82.26 ± 1.94 ($n = 8$)	79.01 ± 1.43 ($n = 10$)
Soy	82.18 ± 2.07 ($n = 9$)	80.66 ± 1.96 ($n = 9$)	78.84 ± 1.62 ($n = 8$)

* n = sample size.

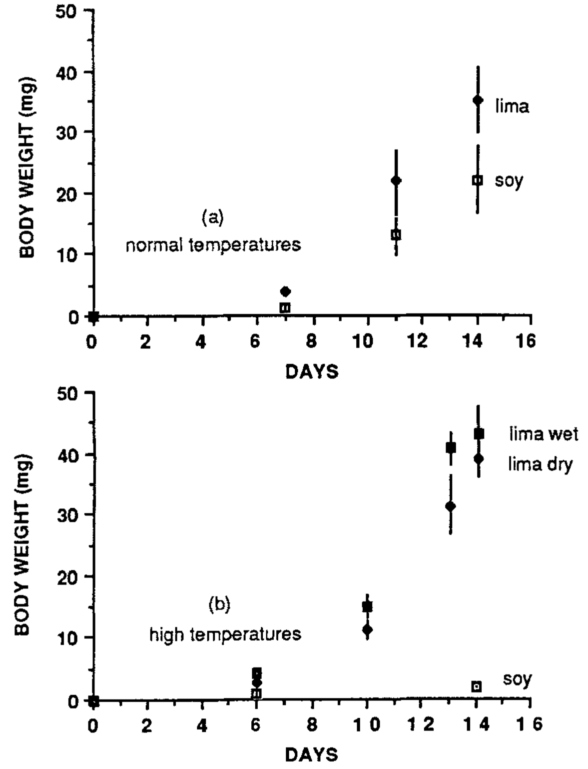

Fig. 3. Observed Mexican bean beetle larval weight gain, under (a) normal temperatures, (b) hot temperatures. Error bars are ±1 standard deviation.

moisture. This hypothesis will be tested by comparison of these data with results of simulation models based on laboratory studies of water input/output, as related to host, temperature, vapour pressure deficit, and larval size.

Model development and validation

Survival. If survival (S) is plotted against body water content (WC), without regard to temperature, the relationship (Fig. 4) can be approximated by a sigmoid function of the form:

$$S = 1/1 + \exp\left[-a\,(\mathrm{WC} - b)\right]$$

where a, b = parameters to be estimated

The parameters a and b were estimated using nonlinear regression (PROC NLIN; SAS Institute, 1985), yielding

$$S = 1/1 + \exp\left[-331.14\,(\mathrm{WC} - 0.7273)\right]$$

To test goodness-of-fit, predicted S was regressed against observed S. The r^2 was equal to 0.95, the slope was not different from 1, nor the intercept different from zero.

From a biological perspective, it is important to recognize the narrow range over which survival goes from essentially zero to 100%, a range of only 0.72–0.76, or a change of only 4% in total body weight.

Model validation under variable conditions. Two basic simulation approaches were used, treating the variables as either constant or stochastic, to obtain predicted values for water content and survival. Both of the simulation models are written in FORTRAN and may be obtained from the authors.

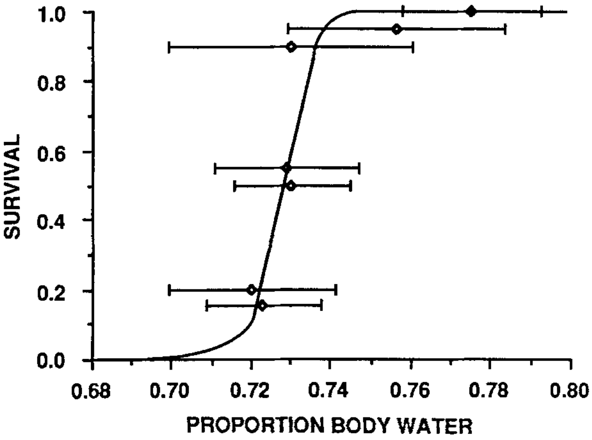

Fig. 4. Observed and predicted survival versus Mexican bean beetle larval body water content. Error bars are ±1 standard deviation; □, observed, — — —, predicted.

In all simulations it was assumed that only water balance affected survival. Two input data sets were used. The first includes the actual dry and wet bulb temperatures from the glasshouse experiment, taken at 0.5 h intervals. The second data set consists of growth (weight gain) data for Mexican bean beetle larvae from the glasshouse trials. These data were used by fitting the simplest function which adequately described the data for estimates of body weight between measurement intervals.

Under normal temperatures, linear functions could be fitted to growth, but at high temperatures, exponential functions were necessary for lima fed Mexican bean beetle. The equations used are presented in Table 5.

For both simulation models it was assumed there were no effects of moulting and no drinking of free water. If the simulated body water content exceeded the maximum water content allowable, the body water content was set at the maximum. The actual equations used for evaporative water loss (EWL), frass water loss (FWL), time between defecations (Tf), and water gain (WG) are all detailed in Chu *et al.* (1992). For the stochastic simulation model, the variables treated as random were initial water content, EWL, WG, Tf and FWL. All variables except Tf were assumed normally distributed. For the stochastic model, eighty larvae were simulated for 14 days for each glasshouse trial condition. Fig. 5 contains a flow chart for the simulation models. A listing of the variables and their symbols used in the simulations is given in Table 6.

The weather data, including dry and wet bulb temperatures recorded at 0.5 h intervals for a given trial (14 days) are read into the program, starting at the time when larvae were placed on the plants.

For the stochastic version of the model, a random

Table 5. Models used to mimic growth (wet weight, BW) of MBB larvae in glasshouse trials.

Host	Temp.	Moisture	Equation
Lima	Normal	Wet and dry	$BW = 0.23 + 0.32*day$, for $day \leqslant 7$ $BW = -29.8 + 4.6*day$, for $day > 7$
Soybean	Normal	Wet and dry	$BW = 0.25 + 0.107*day$, for $day \leqslant 7$ $BW = -19.3 + 2.9*day$, for $day > 7$
Lima	Hot	Wet	$BW = 0.6188*\exp(0.3223*day)$, for $day < 13$ $BW = 43$ (mg), for $day = 14$
Lima	Hot	Dry	$BW = 0.5793*\exp(0.3030*day)$
Soybean	Hot	Wet and dry	$BW = 0.10 + 0.15*day$

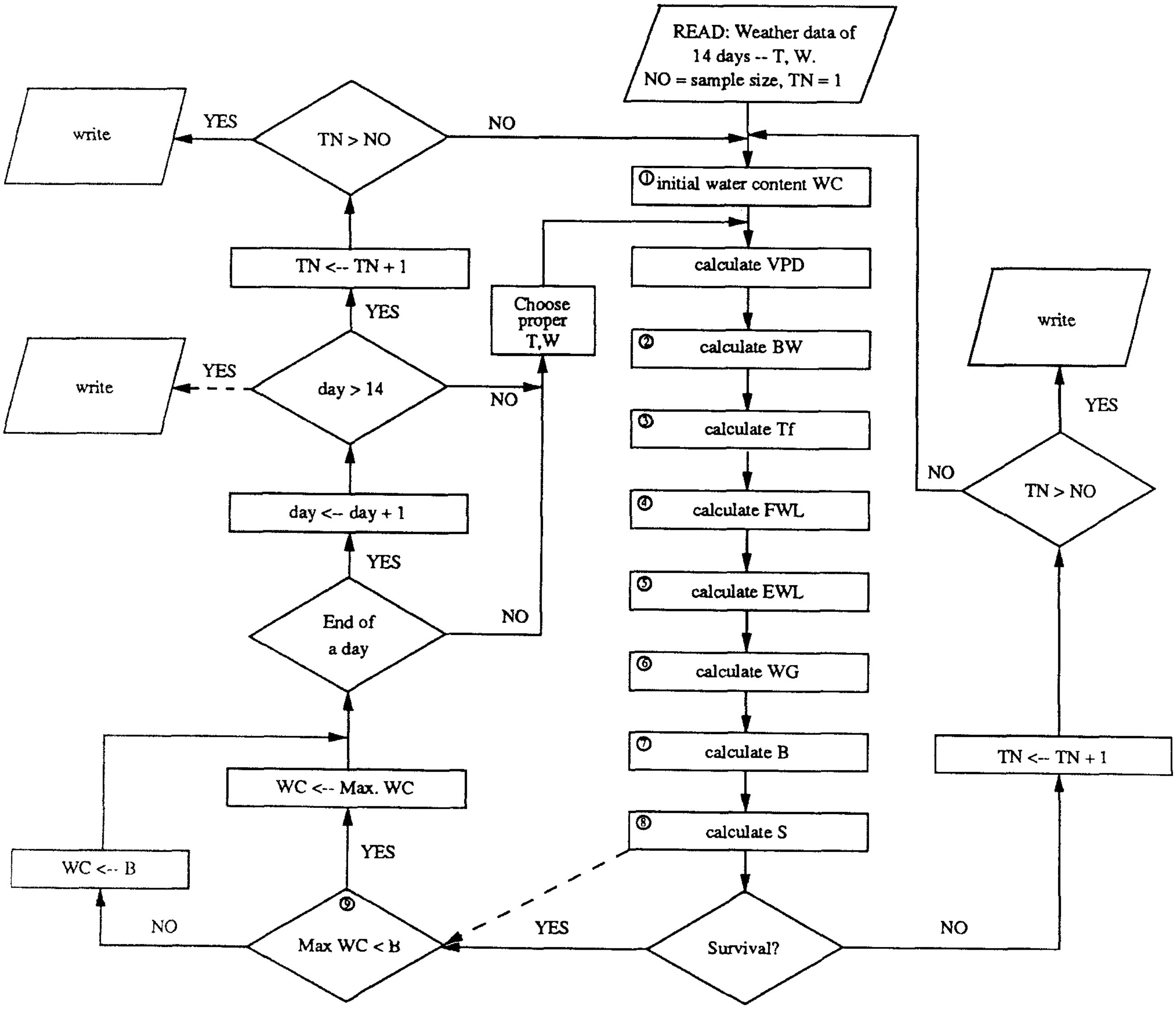

Fig. 5. Flow chart for simulation models of water balance in larval Mexican bean beetle (– – –>, deterministic model only).

Table 6. Definition of symbols used in the simulation equations.

Symbol	Units	Definition
WC_0	decimal	Initial body water content
WC	decimal	Body water content
BW	mg	Body weight
Tf	min	Time between excretion
FWL	%/excretion	Frass water loss
EWL′	%/min	Evaporative water loss rate
EWL	%/excretion	Evaporative water loss
WG′	%/min	Water gain rate
WG	%/excretion	Water gain
B	decimal	Water balance
S	decimal	Survival probability
Max.WC	decimal	Maximum body water content
T	°C	Dry-bulb temperature
W	°C	Wet-bulb temperature
RH	decimal	Relative humidity
VPD	mbars	Vapour pressure deficit
DAY	days	Time after start of simulation
RANi	decimal or real number	*i*th random number

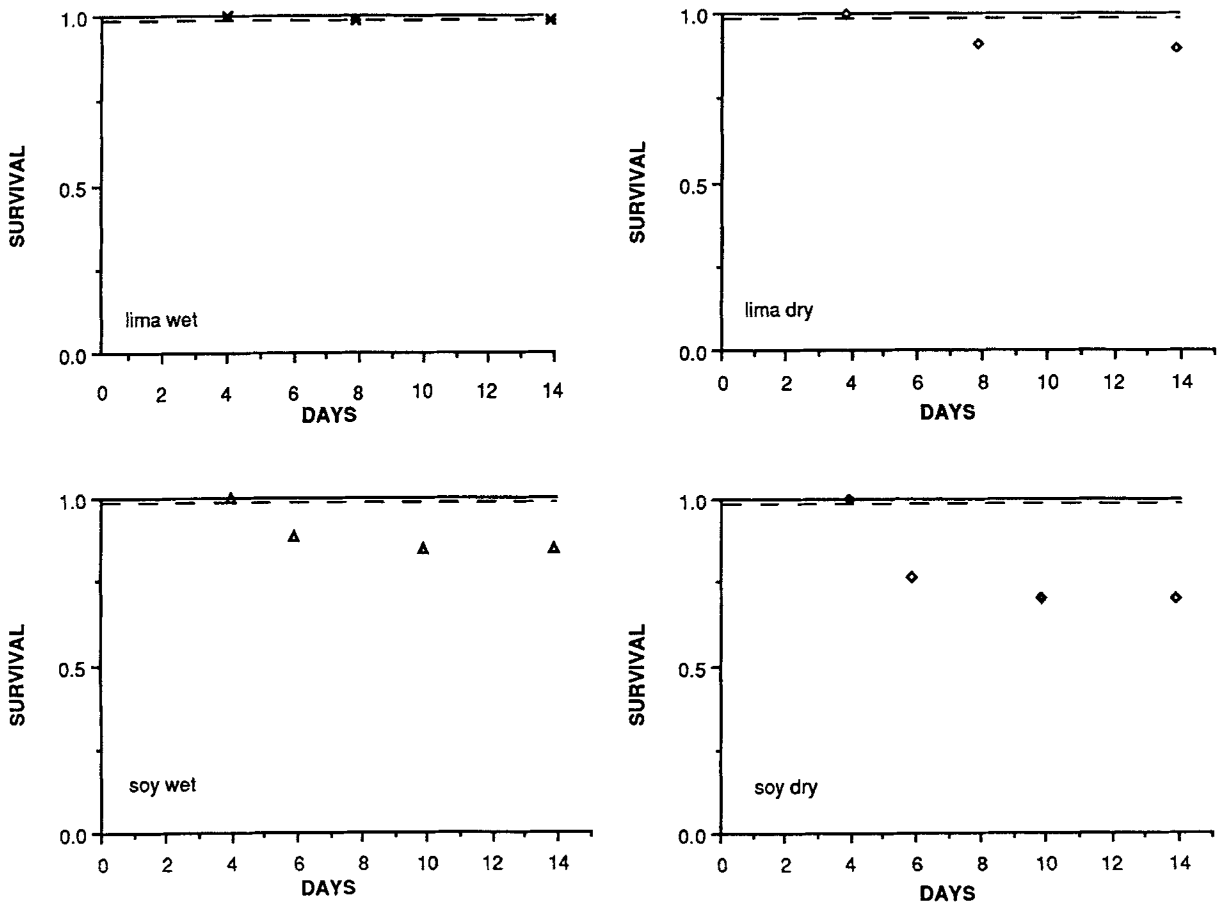

Fig. 6. Observed and predicted survival (– – – –, deterministic; ——, stochastic) under normal temperature.

number generator was necessary. We used the linear congruential generator described by Dohse (1982).

In the program, estimates of the mean and standard deviation for initial water content, EWL and WG, were obtained from actual data.

Vapour pressure deficit. The saturation vapour pressure, E_s (T), for temperatures, T, from 1 to 42°C are read into the program as an array, and actual vapour pressure deficit (VPD), calculated according to Lowry (1969) using constants and equations from Brooker (1967).

Survival. The probability of survival was calculated as function of body water content, as described earlier. In the stochastic model, this survival probability was then compared with a random number generated from U (0,1). If the random number was larger than the survival probability, the larva died; otherwise, it remained alive.

Maximum body water content. Since the optimal body water content is related to body size (mg), in the simulations the maximum body water content was changed as a function of body weight, and was defined as the optimal body water content plus one standard deviation. Maximum body water content was set at 85.14, 84.20 and 80.44% for small, medium and large larvae on lima, respectively, and, similarly, 84.25, 82.62 and 80.46% for larvae on soybean.

Modelling results and discussion

For the deterministic model, output was printed only when the body water content was less than the maximum. When this occurred, time, T, W, VPD, BW, EWL, FWL, WG, B and SR were printed.

For the stochastic version, the above variables plus Tf were printed for those time periods when actual measurements of body water content were made. In addition, at the end of each simulation, the daily survival rate was printed.

The predicted values from both simulations and the corresponding observed survivals under normal temperatures are presented in Fig. 6 for normal temperatures and Fig. 7 for high temperatures. For all trials, the simulation results present a pattern similar to the observed. By day 14, the end of the trials, errors in prediction are less than 10%, except in the soybeans under normal temperatures, where the survivals are 10–25% over-estimated. In this situation, it is possible that predation by spiders (not considered in the model) was involved. Also, larvae tended to be more widely dispersed in soybean than lima, and sampling error could also be involved.

If we examine predicted versus observed water content

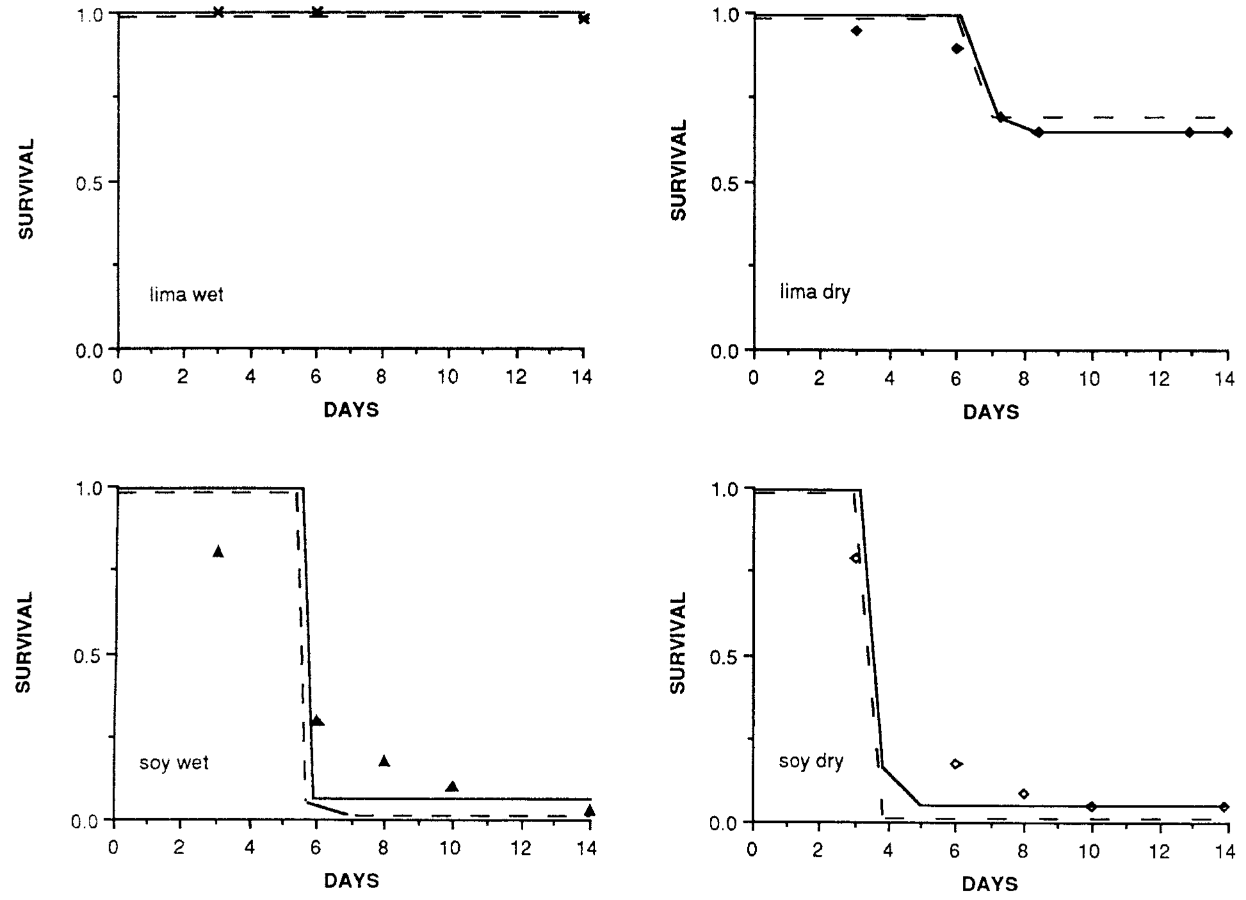

Fig. 7. Observed and predicted survival (– – – –, deterministic; ——, stochastic) under hot temperatures.

(Table 7), during normal temperatures, the predicted water content was within the confidence limits (95%) in all but two of the twelve observations. In those two cases, both the deterministic and stochastic results were only slightly higher than the upper confidence limit. At high temperatures, both models tended to overestimate the body water content, but with one exception (soybean, dry), by only 1–1.5%. There are two possible explanations for these over-estimations. First, under hot temperatures, the body water content could be changing so rapidly that small errors in measurement time could produce large differences in predicted body water content. Second, at temperatures less than 37°C, water gain may be overestimated. In practice, since the area eaten by larvae was difficult to estimate exactly, measurements may have been biased by overestimation. At high temperatures (>37°C), larvae tend to move around a great deal and spend little time feeding. Given the functional form used to relate water intake to temperature, slight errors in either temperature or parameter estimates could produce large differences in water intake, and thus body water content.

With few discrepancies, both the deterministic and the stochastic models mimicked both water balance and survival over a wide range of conditions. However, sensitivity analyses (Chu, 1987) suggest that the stochastic model is more stable than the deterministic, particularly under higher temperatures, but both models agree reasonably with the observed data, except for soybean-fed larvae under dry, normal temperatures. For this particular case, it would appear that mortality other than water-stress induced mortality was involved, since simulated and actual body water content were both high (implying a lack of water stress), yet mortality was observed (perhaps due to spider predation).

In measuring water gain from leaf area eaten, it was difficult to estimate this physical area, and these measurements could have been biased by overestimation. This may explain the higher simulated values for body water content at high temperatures, compared with the observed values. Additionally, the model used to simulate water gain assumes no water gain at temperatures higher than 37°C, since that temperature limit minimized the residual sum of squares for the available data. Sensitivity analyses (Chu, 1987) suggests that no water gain above 37°C may be too strong an assumption, since a 1°C increase caused the simulated survival rate on day 5 to drop to 0%; all larvae died when subjected to temperatures above 38.1°C for only 3.5 h in the simulation. However, from laboratory

Table 7. Predicted and observed body water content for larval MBB under various glasshouse 'climates'.

			Body water content		
Climate	Host	Day	Observed range*	Deterministic model range†	Stochastic model range†
Hot/wet	Lima	5	0.780–0.844	0.851	0.851
		10	0.826–0.853	0.842	0.842
		14	0.754–0.789	0.787–0.803	0.785–0.804
	Soy	5	0.782–0.833	0.843	0.843
		10	0.811–0.863	0.843	0.843
		14	–	–	–
Hot/dry	Lima	5	0.769–0.821	0.805–0.847	0.801–0.851
		10	0.777–0.839	0.851	0.851
		14	0.735–0.809	0.804	0.804
	Soy	5	0.776–0.797	0.843	0.727–0.811
		10	0.790–0.823	0.843	0.843
		14	–	–	–
Normal/wet	Lima	5	0.827–0.841	0.851	0.851
		10	0.809–0.844	0.842	0.842
		14	0.756–0.807	0.804	0.804
	Soy	6	0.812–0.868	0.843	0.843
		10	0.810–0.856	0.843	0.843
		14	0.799–0.834	0.826	0.826

* Based on 95% confidence limit.

† Predicted range over the 1 h sampling interval. Where the simulated body water content did not change during the interval, only one value is given.

data (Chu *et al.*, 1992), there was 21% survival after 13.5 h at *c.* 38 ± 1°C.

It is suspected from the above that water loss also was overestimated. Considering that the evaporative water loss (EWL) is the major component at high temperatures for total water loss, and the fact that there is a weak but positive correlation between EWL and body water content ($r = 0.046$) in Wilson's (1981) data, the possibility of body water content affecting EWL, particularly at low body water content levels, cannot be dismissed. Further experimentation in this area is necessary to determine the form of the relationship, if any.

To complete a water relations component for Mexican bean beetle dynamics, it will also be necessary to include the impact of drinking, moulting, and adult reproduction, in addition to estimating EWL for eggs, pupae and adults, and FWL for adults. However, given the models, extreme sensitivity to temperature, it simply may not be feasible to directly include this water balance model in a population dynamics simulator, due to a lack of temperature data of sufficient accuracy from the field. This is particularly true when one recognizes that virtually nothing is known about Mexican bean beetle movement in response to water stress. Nevertheless, the use of these simulation models to provide estimates of survival under variable durations of high temperatures should provide rough ranges of physical measures (temperature and vapour pressure deficit) within which it is possible for the Mexican bean beetle to survive, and beyond which local populations cannot exist.

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