1984

Response of the Western Spruce Budworm (Lepidoptera: Tortricidae) to Temperature and Humidity: Developmental Rates and Survivorship

Norman Reichenbach
Liberty University, nreichen@liberty.edu

Gordon R. Stairs

Table 1. Average duration of peach twig borer life stages

Stage	Day-degrees[a]	Days[b]
Pupa	160	13
Preoviposition adult	28	2
Ovipositing adult	69	—
Egg	92	12
Larva	258	32

[a] Day-degrees calculated at 10°C for lower threshold and 31.1°C for the maximum development rate.
[b] Average number of days for first summer generation under Washington conditions.

spectively. Given the difference between first hatch (119 day-degrees) and egg development time (92 day-degrees), the preoviposition period would require about 28 day-degrees. Bailey (1948) reported preoviposition periods of from 1 to 4 days for adults in the laboratory. Under standard laboratory temperatures 11 to 14 day-degrees would be accumulated each day, giving a range for preoviposition of 11 to 55 day-degrees, which agrees with our estimate.

Larval activity, as determined by shoot flagging, was monitored in 1979 and 1981. First flagging by summer larvae was observed 495 day-degrees after 1 January. The average day-degree total for first flagging was 519 ± 34. First flagging was 295 day-degrees after predicted first adult (Fig. 2) or 260 day-degrees after observed first moth of the summer generation. A total of 166 day-degrees elapsed from first hatch to first flagging. First flagging from larvae of the second summer generation occurred at 1,096 day-degrees on 3 August 1979, with peak activity occurring between 1,194 and 1,222 day-degrees. Flagging of the second summer generation was observed 227 day-degrees after the initiation of egg hatch. In the second summer generation many larvae begin feeding directly on fruit, so flagging was less prevalent. Temperature and water stress of trees can influence flagging to a degree making estimates of this factor more variable than others.

The duration of a generation was determined to be the difference in day-degrees from 50% pupation or 50% emergence in successive generations. The average day-degree accumulations between 50% pupation of the winter and first summer and the first and second summer generations were 565 and 515. The average day-degree accumulations between 50% emergence of the winter and first summer generations, and the first and second summer generations were 608 and 532. From Fig. 2 the predicted day-degrees between 50% emergence of the winter and first summer and first and second summer generations were 612 and 537. Predicted day-degrees between 50% pupation of the winter and first summer and first and second summer generations were 565 and 505. Given the day-degree requirements for development, two complete and a partial third generation of the peach twig borer are possible in Washington in most years.

Table 1 is a summary of proposed day-degree totals for each stage in the peach twig borer life cycle. These values were obtained from the studies reported here or from estimates in the literature. This table can be used to develop a day-degree model predicting stage development of the peach twig borer. A generalized-phenology modeling system proposed by Welch et al. (1978), using the parameters in Table 1 for stage durations and k values of 20 for each stage, provided good agreement with observed data. Such a model may be beneficial by helping improve timing of summer control sprays, thus relinquishing the need for disruptive early-season controls.

Acknowledgment

This research was supported in part by the Washington State Tree Fruit Research Commission grant to Washington State University. Project 6090. Thanks are extended to Lynn O. Smith for technical support in conducting these investigations. Scientific Paper No. 6649

References Cited

Anthon, E. W., J. F. Brunner, and A. H. Retan. 1981. Peach twig borer. Wash. State Univ. Ext. Bull. 0931.

Bailey, S. F. 1948. The peach twig borer. Calif. Agric. Exp. Stn. Bull. 708: 3–56.

Baskerville, G. L., and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514–517.

Brunner, J. F., S. C. Hoyt, and D. P. Carroll. 1982. 1982—Year of the aphid. Proc. Wash. State Hort. Assoc. 78: 143–148.

Jones, L. S. 1935. Observations of the habits and seasonal life history of *Anarsia lineatella* in California. J. Econ. Entomol. 28: 1002–1011.

Price, D. W., and F. M. Summers. 1961. Cyclical changes in numbers of moths and larvae of the peach twig borer in California. J. Econ. Entomol. 54: 933–936.

Rice, R. E., and R. A. Jones. 1975. Peach twig borer: field use of a synthetic sex pheromone. Ibid. 68: 358–360.

Riedl, H., B. A. Croft, and A. J. Howitt. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological-time models. Can. Entomol. 108: 449–460.

Roelofs, W. L., J. Kochansky, E. Anthon, R. E. Rice, and R. Cardé. 1975. Sex pheromone of the peach twig borer, *Anarsia lineatella*. Environ. Entomol. 4: 580–582.

Sardi, D. S. 1966. The peach twig borer, *Anarsia lineatella* Zell. (Lepidoptera: Gelechiidae), in the Okanagan and Similkameen valleys of British Columbia. J. Entomol. Soc. B.C. 63: 19–22.

Summers, F. M. 1955. The peach twig borer. Calif. Agric. Exp. Stn. Circ. 499.

Tamaki, G. 1973. Spring populations of the green peach aphid on peach trees and the role of natural enemies in their control. Environ. Entomol. 2: 186–191.

Welch, S. M., B. A. Croft, J. F. Brunner, and M. F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Ibid. 7: 482–494.

Received for publication 11 October 1983; accepted 6 January 1984.

Response of the Western Spruce Budworm (Lepidoptera: Tortricidae) to Temperature and Humidity: Developmental Rates and Survivorship

NORMAN G. REICHENBACH AND GORDON R. STAIRS

Department of Entomology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210

Environ. Entomol. 13: 611–618 (1984)

ABSTRACT Developmental rates of embryos, larvae, and pupae of the western spruce budworm, *Choristoneura occidentalis*, were determined over temperatures ranging from 10 to 31°C and RHs ranging from 10 to 100%. Humidity had a trivial influence on developmental rates of all these life stages, whereas temperature had major effects. Several nonlinear developmental rate models and a cubic polynomial model were fit to the data, all of which adequately described the data for each life stage. Development was minimal below 10°C for all stages, and maximum rates occurred from 26 to 29°C, depending upon sex and life stage. At temperatures above 29°C, the rates decreased sharply. Low temperatures induced melanin production in over 30% of the larvae and pupae. Survival of embryos and pupae was determined over temperatures and humidities as noted above. Embryonic survivorship decreased at the temperature extremes and as the humidity decreased. Survival was highest near 22°C and 100% RH. Pupal survivorship decreased at both temperature and humidity extremes. Rates were highest near 23°C and 75% RH. Survivorship of diapausing larvae decreased at the humidity extremes (10 and 100% RH) and decreased with the length of time in diapause (7 versus 9 months).

TEMPERATURE AND HUMIDITY affect a large variety of physiological processes; hence, the microclimate selected by an insect becomes a multidimensional question that is dependent on the life stage and physiological state (Willmer 1982). Optimal conditions may therefore be difficult to define because, for example, developmental rates, fecundity, and survivorship may each have different temperature and humidity optima. Optimal conditions for outbreaks of spruce budworm have been implicated by field investigations to be warm and dry summers (Morris 1963). The impact and quantification of these environmental factors (warmth and dryness) upon the spruce budworm are necessary to delineate optimal conditions and to verify whether these factors may be causative agents or simply correlated with outbreak conditions. Here we examine how temperature and humidity affect developmental rates and survivorship of different life stages of the western spruce budworm (WSB), *Choristoneura occidentalis* Freeman. In addition, several nonlinear equations are examined with regard to their adequacy in modeling developmental rate data.

Materials and Methods

WSB were obtained from the Forest Sciences Laboratories, Corvallis, Oreg., and were reared on McMorran's artificial diet (McMorran 1965). Throughout the experiments a photoperiod of LD 12:12 was maintained. From six to seven different temperatures in the range of 10 to 31°C were used in the experiments. RHs were maintained by using saturated salt solutions; for 7 to 12% RH, pc hydroxide; 43% RH, potassium carbonate; 7 sodium chloride; 100% RH, distilled water span 1977). Salt solutions were placed i plastic crispers (18 by 9 by 8 cm) with sealed by using stopcock grease and polye tubing around the rim of the crisper. The bers were allowed to equilibrate to the in temperature for at least 1 wk. The air spac containers was kept to a minimum by using volume of the saturated salt solution. Pe plastic sheets with depressions were po above the salt solutions, and individual egg or pupae were placed in each depression. the food in the 1-oz. (ca. 30-ml) plastic cu larvae, humidity could not be controlled larval experiments and was assumed to be b 90 and 100% RH. The larvae used in the ments on developmental rates at constant t atures were in diapause for at least 3 mor fore experimentation. The larvae were re cups with initially four larvae per cup an the 4th instar were separated to one larva p Animals were checked twice daily at the temperatures (>25°C) and once daily at al temperatures.

Diapausing larvae were kept at 0 and 5 at the four different humidities mentioned Half of the larvae were removed to 20°C to survival rates after 7 months, and the oth were removed after 9 months (length of t diapause coded 0 or 1, respectively, in the sis).

Table 1. Parameter estimates (followed by SD) for the developmental rate equation by Logan et al. (1976) for larvae and embryos of the WSB

Model parameters	Embryos	Larvae (males)	Larvae (females)
alpha	0.245	0.097	0.111
	0.023	0.279	0.420
k	15.060	30.024	32.028
	1.023	33.724	40.818
rho	0.158	0.213	0.201
	0.014	0.181	0.201
tm	27.179	31.915	30.589
	0.562	9.324	6.677
dt	0.718	6.140	6.253
	0.351	28.608	25.200
tb	5.00	5.00	5.00

See appendix for the equation.

To assess color changes due to temperature, tan-colored larvae (3rd instar) reared at 20°C were placed at 15, 20, and 25°C. These animals were checked again as 6th-instar larvae and pupae and were classified into two categories: (1) normal, light brown to having some black pigmentation; and (2) black, markedly darker or having much more black pigment both ventrally and dorsally than did the normal ones.

Both mechanistic and empirical statistical models for developmental rates by Logan et al. (1976), Sharpe and DiMichele ([1977], as modified by Schoolfield et al. [1981]), Stinner et al. (1974), and Taylor ([1982], a truncated Gaussian distribution) were examined, as well as a third-order polynomial model, $y = b_0 + b_1(x) + b_2(x^2) + b_3(x^3)$. The nonlinear models were fit by using Marquardt's algorithm in the Statistical Analysis System (SAS; Proc Nlin; partial derivatives for these models are given in the appendix). Empirical multifactor models were used to examine the effects of temperature and humidity on developmental rates and survivorship through the use of a stepwise regression procedure which maximizes the R^2 value (SAS; Proc stepwise using the Max*r* option). Discrete variables such as sex were coded 0 or 1 as noted above and used as dummy variables in the analyses. The number of factors included in the model was contingent upon when the reduction in the error sums of squares (ESS) was no longer compensated by the reduction in the degrees of freedom for the ESS, as indicated by a stable or increasing mean square error term.

Survival rates (percents, *p*; for embryos on a per-egg-mass basis, *n* ranging from 2 to 111, mean = 36, $n = 2{,}772$; for pupae based on 12 animals, and diapausing larvae based on 2 to 60 larvae, mean = 34, $n = 538$) were converted, using an arc sine $\sqrt{p}$ transformation. Weights of $n/0.25$ were then used in a weighted least-squares procedure. Both untransformed and transformed data were analyzed and showed that the probability statements concerning the parameters in the model were altered very little; hence, the arc sine square root transformation was used primarily to keep the model predictions within the bounds of 0 and 100% rather then being necessary to stabilize the variances and normalize the data.

The data for insect color change was analyzed by using a weighted least-squares approach to the analysis of categorical data (Grizzle and Koch [1969]; in SAS, Proc Funcat).

Equations in the text are followed by the sample size, R^2, and the SDs of the model's parameters, save the intercept, in the order they appear in the model. The following abbreviations are used in the models: y = developmental rate (1/days); p = arc sine square root of the proportion survived; t = temperature in °C; h = RH, s = sex (coded 0 for females and 1 for males).

Results and Discussion

Developmental rates (y) for the embryos were primarily affected by temperature and at low temperatures (<15°C), the rates were also influenced by humidity.

$$y = 0.054 + 0.018(h) + 0.0007(t^2) - 0.00002(t^3) \quad (1)$$
$$(54,\ 0.89,\ 0.006,\ 0.00008,\ 0.000002)$$

At temperatures below 15°C only embryos at the high humidities survived, and even here the survival rates were very low (<10%). Consequently the data were pooled over all humidities in fitting the five developmental rate models, all of which adequately described the data (Tables 1 and 3). Development of the embryos proceeded in a nonlinear fashion indicating enzyme inactivation at both high and low temperatures (Sharpe and DiMichele 1977). The rate was maximum at 29°C. Above 29°C, developmental rates dropped rapidly; below 10°C, development proceeded very slowly; and between 18 and 28°C, the rates were linear.

Developmental rates (y) for larvae were different for the two sexes as indicated by the interaction term between sex and temperature (t^*s) and were not affected by changes in humidity.

$$y = 0.091 - 0.018(t) + 0.001(t^2) - 0.00002(t^3) + 0.0002(t^*s) \quad (2)$$
$$(428,\ 0.87,\ 0.002,\ 0.00008,\ 0.000001,\ 0.00002)$$

Separate nonlinear models were fit to the data for each sex, all of which adequately described the data (Tables 1 and 3). The developmental rates for male larvae reached a maximum at 27°C and then decreased sharply above this temperature. Between 15 and 25°C, the rates were linear. At temperatures below 10°C, development occurred at a slow rate. For female larvae the maximum rate of development occurred at 26°C; otherwise, the female larvae developed in a manner similar to the males.

Developmental rates for pupae were not affected by changes in humidity, nor were the rates statistically different for males and females. Therefore the data were pooled in the developmental rate models (Tables 2 and 3). Pupae developed very slowly below 10°C, and the rates reached a maximum at 29°C. Between 15 and 28°C, the rates were linear. Above 29°C, the rates decreased rapidly (Fig. 1).

All five developmental rate models described the data for each life stage adequately, though some were difficult and expensive to use in estimating the parameters, as indicated by the number of iterations required to fit the model (Table 3; Fig. 1). The 0 variances associated with some of the parameter estimates were due to the algorithm finding a minimum residual sums of squares in an *N*-dimensional space where one or more variables could be fixed. In addition, mean developmental rates are often used in fitting nonlinear models (Logan et al. 1976, Schoolfield et al. 1981). Using mean values may produce different parameter estimates than when using the individual data points as is usually done in standard regression model fitting procedures. In all cases, though, the models adequately described the data and the additional computing expense (generally 3-fold or more) may not compensate for the loss in accuracy by using mean developmental rates in estimating the model parameters.

Comparison of the models using only R^2 values shows that all of the models explain similar proportions of the variability, even though models with more parameters will generally explain more of the variability in the data than models with fewer parameters (Table 3). In general, the choice of which nonlinear model to use is largely a matter of preference, because the model predictions differ primarily at the high temperature extremes mortality may be high if these temperatu of long duration.

The only mechanistic model based up physical principles (Sharpe and DiMichel produced very large SDs associated with rameters estimated (Table 2). The poly model produced adequate predictions wit not beyond the range of the data (Fig. 1 must therefore be collected over the entir for which model predictions are require model of Logan et al. (1976) produced go dictions because it adequately modeled the of high temperature, had small SDs for the eter estimates (generally), and usually did quire a large number of iterations to conve a solution. The truncated Gaussian distri model was the easiest nonlinear model to f only disadvantage of this model was its pred at temperatures above the maximum de mental rate. The model assumes a symmet sponse around the point where developm maximal and this was not verified by the Mortality may be great if these high tempe are of long duration so that this inconsistenc the data may have a trivial effect when usi model to estimate life stage duration in the

The differences between the models woul duce a minimal amount of error relative multitude of factors that affect the temperat which the insect is exposed. Fourier series senting different temperature regimes (' 1981) in conjunction with three development models (polynomial, Logan et al. [1976], a truncated Gaussian) were used to predict th to complete pupal development beginning f July. All three functions estimated similar for completion of pupal development when

Table 2. Parameter estimates (followed by SD) for the developmental rate models for pupae of the WSB

Developmental rate model[a]				
1	2	3	4	5
rho	*tm*	*topt*	alpha	b_0
0.1748	29.270	29.000	0.187	0.054
0.006	0.186	—	0.002	0.018
tl	*tv*	*c*	*k*	b_1
288.547	10.500	0.192	6.926	−0.013
0.006	0.181	0.001	0.388	0.003
th	*rm*	*k1*	rho	b_2
304.604	0.181	4.210	0.262	0.001
1.128	0.001	0.060	0.009	0.0001
ha		*k2*	*tm*	b_3
2,543.45	—	−0.242	21.698	-2.54×10^{-5}
14,738.3	—	0.002	0.192	2.0×10^{-6}
hl			*dt*	
−49,833.0	—	—	0.146	—
4,798.4	—	—	0.000	—
hh			*tb*	
829,049.9	—	—	10.000	—
2.02×10^{10}	—	—	—	—

See appendix for the developmental rate models.
[a] (1) Sharpe and DiMichele (1977), as modified by Schoolfield et al. (1981); (2) truncated Gaussian (Taylor 1982); (3) Stinne (1974); (4) Logan et al. (1976); (5) cubic polynomial.

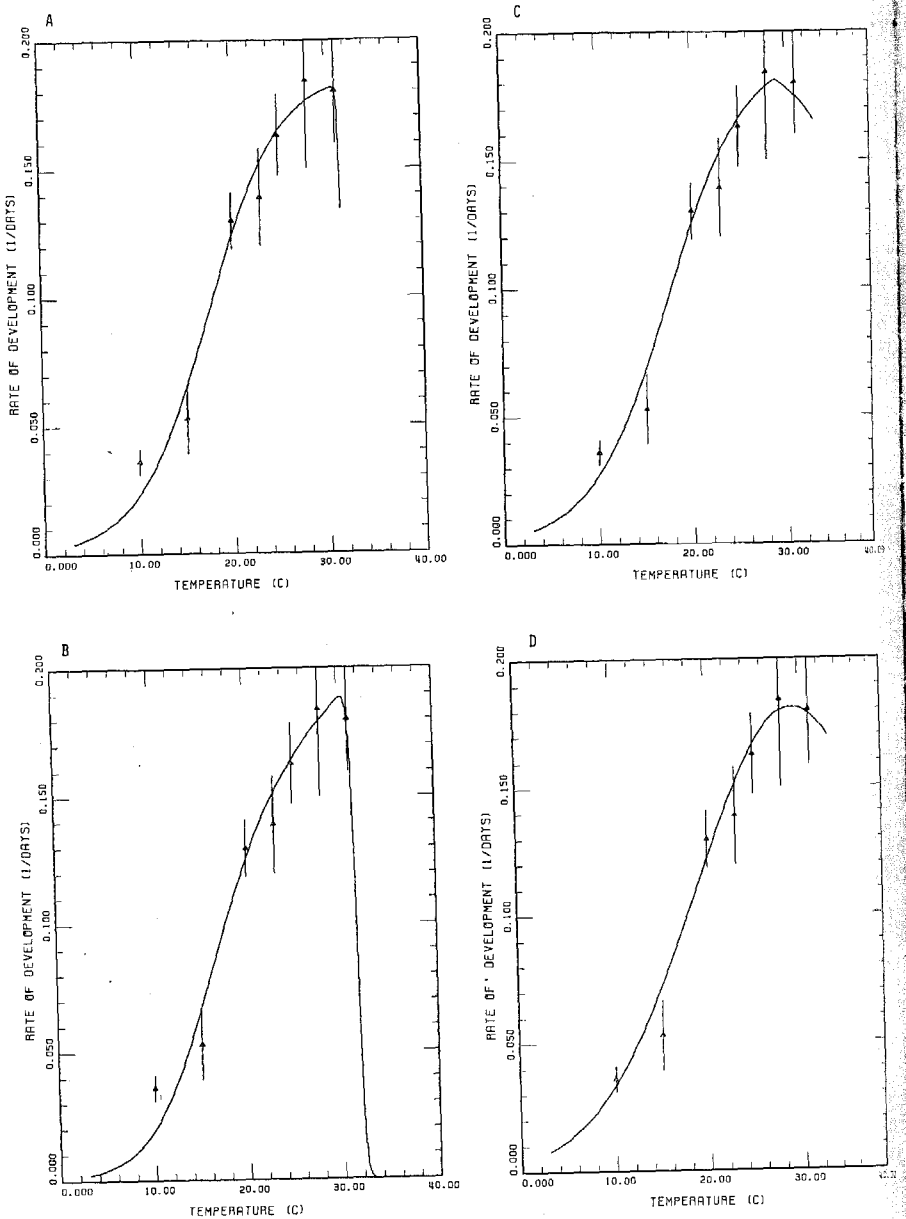

Fig. 1. Developmental rate models and data (means ± 1 SD) for pupae of the WSB. (A) Logan et al. (1976); (B) Sharpe and DiMichele (1977); (C) Stinner et al. (1974); (D) Taylor (1982); (E) cubic polynomial.

ronmental temperatures were in or below the zone where the developmental rates were linear (<28°C). When the environmental temperatures were above 28°C, greater differences occurred, but here mortality may be high (Table 4). Therefore, the equations currently available are adequate to model insect developmental rates, and future efforts should be directed toward modeling the temperature function with regard to microclimatic influences.

The number of dark larvae and pupae increased as the temperature decreased (linear trend in larvae, $x^2 = 8.82$, $P = 0.003$; linear and qu trends in the pupae, $x^2 = 5.82$, $P = 0.02$ ar 4.48, $P = 0.03$, respectively; Table 5). Near of the larvae developed melanin at 15°C, to 35% of the pupae darkened at 15 and respectively. Dark larvae did not necessar dicate that the pupae would be dark. The tion of pigment can be caused by a var factors, including photoperiod and color of t crohabitat (Hazel and West 1979, 1983), an temperature induced dark pigment forn Dark pigment would increase the absorba solar radiation and consequently increase t ternal temperature of the larvae or pupae the ambient temperature (Shepard 1958, W 1982). The induction of dark pigment mi adaptive to increasing developmental rates development could be completed within s that were cooler than usual.

Survival rates for the embryos and pupae significantly affected by both temperature ar midity, as indicated in the following equati embryonic survivorship (p):

$$p = -2.244 + 0.294(t) - 1.429(h) - 0.00 + 0.191(t^*h) - 0.004(h^*t^2)$$
$$(77, 0.87, 0.040, 0.545, 0.001, 0.060, 0.0$$

Survivorship decreased toward the extremes temperature range (10 and 31°C), with no ar surviving at 34°C, and increased to a plate humidity increased (Fig. 2). Survivorship wa in the plateau region which ranged from 28°C and 50 to 100% RH. The width of this indicates that, within certain limits, the em are able to adjust to a wide variety of tempera and humidities, whereas beyond these limit vivorship drops off rapidly (Fig. 2).

The dead embryos were fully formed an parently died just before hatching. Morris Fulton (1970) showed that high humidity was ical for successful emergence from the egg. deaths recorded here may have been prim due to the inability of the larvae to rupture egg.

Table 3. Comparison of developmental rate equations using the proportion of the variability in the data expla by the model (R^2) and the relative difficulty and cost of fitting the model as indicated by the number of iterations requ to find estimates to the constants in the equations

Model[a]	Embryos		Larvae ♂		Larvae ♀		Pupae	
	R^2	Iterations	R^2	Iterations	R^2	Iterations	R^2	Iter- ation
1	0.990	50	0.990	81	0.990	103	0.985	35
2	0.991	4	0.991	6	0.991	7	0.984	4
3	0.991	2	0.991	7	0.991	13	0.984	36
4	0.993	14	0.993	34	0.993	42	0.984	8
5	0.991	—	0.991	—	0.991	—	0.984	—

[a] (1) Sharpe and DiMichele (1977), as modified by Schoolfield et al. (1981); (2) truncated Gaussian (Taylor 1982); (3) Stinner e 1974); (4) Logan et al. (1976); (5) cubic polynomial.

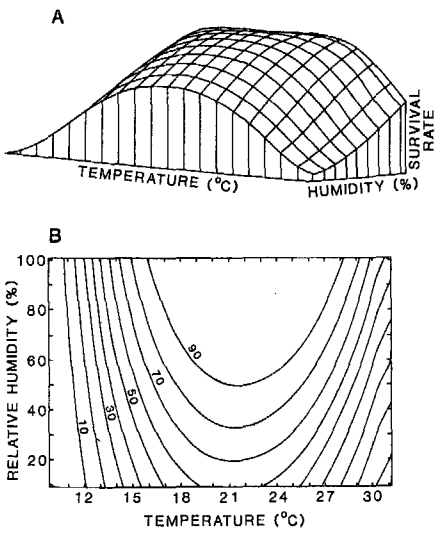

Fig. 2. (A) Response surface of equation 3 for the effect of temperature and humidity on the survivorship of the egg life stage in the WSB. (B) Contour plot of equation 3. Contours represent the percent survivorship in relation to temperature and RH.

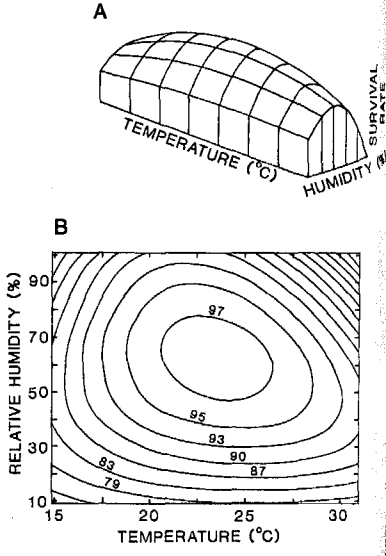

Fig. 3. (A) Response surface of equation 4 for t effect of temperature and humidity on the survivors of pupae in the WSB. (B) Contour plot of equation Contours represent the percent survivorship in relat to temperature and RH.

In contrast to the data on embryo survivorship ($R^2 = 0.87$), the survivorship of the pupae to temperature and humidity was much more variable ($R^2 = 0.45$).

$$p = 0.951 - 0.258(h) + 0.003(t^*h) - 0.00006(t^{2*}h) - 0.000005(t^*h^2) \quad (4)$$
$$(37,\ 0.45,\ 0.008,\ 0.0008,\ 0.00002,\ 0.000002)$$

There were no significant differences in the sur-

vivorship of the different sexes of the pupae t the temperature and humidity extremes (15 a 31°C and 10 and 100% RH), the survivorship the pupae decreased (Fig. 3). Low temperatu affected pupal survivorship less than did the hi temperatures, but as noted above, both tempe ture and humidity explained only 45% of the va ability; consequently, other factors including g netic components might be important determining pupal survivorship.

Maximum survival rates and developmental ra for the embryos were at 22 and 29°C, respectiv Therefore, even though development can occ rapidly at 29°C, the survival rates at this temp

Table 4. Comparison of the time calculated to complete pupal development, using different developmental rate equations under three temperature regimes (represented by fourier series); the first temperature regime (1) includes temperatures below the zone where the developmental rates are linear, the second regime (2) is in the linear zone, and the last regime (3) includes temperatures above the linear zone

Fourier series	Temp (°C)		Pupal developmental time (days)		
	Maximum	Minimum	Polynomial	Logan et al.	Gaussian
1	17.3	8.2	17.4	18.6	16.7
2	27.3	11.8	8.4	8.5	8.4
3	32.0	14.1	7.4	10.2	7.4

Time accumulation began on Julian day 181 (1 July).

$T(t) = \bar{T} - \frac{a_2}{2}\cos\left(\frac{2\pi}{365}t + \phi\right) - \frac{a_1}{2}\cos(2\pi t)$. Fourier equation parameters ($\bar{T}$, a_1, a_2, ϕ) from Taylor (see Table 2 in Taylor [1981]); (1) 3.1, 9.1, 21.2, −0.4097; (2) 10.0, 16.1, 21.7, −0.3030; (3) 12.5, 19.3, 23.4, −0.2565.

Table 5. Induction of dark pigment in larvae and pu of the WSB in relation to temperature; initial color of larvae (3rd instar) was tan

Temp (°C)	Life stage	Sample size (n)	% Of animals where dark pigment induction occurred
15	Larvae[a]	46	45.8
15	Pupae	39	30.5
20	Larvae[a]	45	6.7
20	Pupae	37	35.1
25	Larvae[a]	44	0.0
25	Pupae	39	7.7

[a] Sixth instar.

ature were not high, ranging from 20 to 60%, depending upon the humidity. Consequently a variety of factors must be considered when evaluating the effects of temperature and humidity upon the embryos. In pupae, maximum development occurs at 29°C, whereas survivorship was highest near 23°C. Here again, the shortest time spent within this life stage may not be optimal when considering other factors such as survivorship.

The survivorship of the diapausing larvae kept at different temperatures and humidities and then removed on two different dates indicated that humidity and length of time in diapause had significant effects on larval survivorship, whereas temperature (0 or 5°C) did not.

$$p = 0.072 + 0.039(h) - 0.469(\text{date}) - 0.0003(h^2) \quad (5)$$
$$(16,\ 0.95,\ 0.004,\ 0.048,\ 0.00003)$$

Both high and low humidities decreased the survivorship of the diapausing larvae, and the larvae retained for a longer time in diapause also showed increased mortality.

Embryo survivorship in relation to weather conditions may be an important factor in the initiation or the collapse of an outbreak. Under favorable temperature conditions, a large number of eggs can be produced (Regniere 1983) and the embryos would have high survivorship. As noted above, maximum developmental rates at 29°C do not favor high survivorship, so that optimal conditions would not be at this high temperature, but rather in the zone around 25°C without unusual fluctuations. In this zone, egg production is maximum (135 eggs per female [Reichenbach, unpublished data]), embryo survivorship is high, and foliage production of the current year would not be destroyed or retarded (McKnight 1967). Once the 2nd-instar larvae break diapause, it is unlikely that any but the most extreme temperature and humidity conditions would directly impose mortality. The larvae are mobile and can move to habitats with favorable microclimates (Wellington 1949). If there is a large number of late-instar larvae, the population would probably not decline during the pupal stage due to adverse weather conditions, because pupal survivorship is relatively insensitive to temperature and humidity (survival rates were greater than 70% from 15 to 30°C and from 10 to 100% RH.).

Consequently, if relatively stable temperatures around 25°C prevail, there might be a dramatic increase in the number of spruce budworms surviving, leading to epidemic populations. Conversely, if weather conditions are outside the optimal zone (ca. 25°C) or unusual temperature fluctuations occur, the fecundity of the adults (Regniere 1983) and survivorship of the embryos is greatly reduced and the production of new foliage may be reduced or destroyed (McKnight 1967). All of these factors might contribute to a rapid collapse of the population to an endemic level. Again, the larvae could tolerate adverse weather conditi because they are mobile and can thermoregul both behaviorally (Shepard 1958) and throu melanin production at low temperatures. The p pae are also insensitive to adverse weather con tions. They may produce melanin at low temp atures which might offset the slow developmen rates imposed by the low temperature by incre ing the amount of solar radiation absorbed. Hen the population would decline in numbers due low fecundity and embryo survivorship, but wou stabilize at an endemic population mode becau of the high survivorship of the remaining larv and pupae.

Acknowledgment

We thank the Ohio State University for use of the computing facilties, and R. Smith for his assistance the laboratory.

References Cited

Grizzle, J. S., J. Starmer, and G. Koch. 1969. Ana ysis of categorical data by linear models. Biometri 25: 489–504.

Greenspan, L. 1977. Humidity fixed points of binar saturated aqueous solutions. J. Res. Natl. Bur. Sta dards. A. Phys. Chem. 81A: 89–96.

Hazel, W., and D. West. 1979. Environmental cor trol of pupal color in swallowtail butterflies (Lep doptera: Papilioninae) *Battus philenor* (L.) and *Pa pilio polyxenes* F. Ecol. Entomol. 4: 393–400.

1983. The effect of larval photoperiod on pupal col our and diapause in swallowtail butterflies. Ibid. 8 37–42.

Logan, J., D. Wollkind, S. Hoyt, and L. Tanigoshi 1976. An analytical model for description of tem perature dependent rate phenomena in arthropods Environ. Entomol. 5: 1133–1140.

McKnight, M. 1967. Ecology of the western spruce budworm, *Choristoneura occidentalis* Freemar (Lepidoptera: Tortricidae) in Colorado. Ph.D. dissertation, Colorado State University, Fort Collins.

McMorran, A. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. 97: 58–62.

Morris, R. [editor]. 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31: 1–332.

Morris, R., and W. Fulton. 1970. Models for the development of *Hyphantria cunea* in relation to temperature and humidity. Ibid. 70: 1–60.

Regniere, J. 1983. An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 115: 1371–1382.

Schoolfield, R., P. Sharpe, and C. Magnuson. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J. Theor. Biol. 88: 719–731.

Sharpe, P., and D. DiMichele. 1977. Reaction kinetics of poikilotherm development. Ibid. 64: 649–670.

Shepard, R. 1958. Factors controlling the internal temperature of spruce budworm larvae, *Choristoneura fumiferana* (Clem.). Can. J. Zool. 36: 779–786.

Statistical Analysis Systems Institute, Inc. 1979. SAS user's guide: statistics. SAS Institute, Raleigh, N.C.

Stinner, R., A. Gutierrez, and G. Butler. 1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106: 519–524.

Taylor, F. 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1–23.

1982. Sensitivity of physiological time in arthropods to variation of its parameters. Environ. Entomol. 11: 573–577.

Wellington, W. 1949. The effects of temperature and moisture upon the behavior of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). II. Responses of larvae to gradients of evaporation. Sci. Agric. 29: 216–229.

Willmer, P. 1982. Microclimate and the environmental physiology of insects, pp. 1–57. *In* J. Treherne and V. Wigglesworth [eds.], Advances in insect physiology. Vol. 16. Academic Press, Inc., New York.

Received for publication 2 November 1983; accepted 6 January 1984.

Appendix

Models and their partial derivatives (written in a form useable in SAS or fortran algorithms) for use in nonlinear regression model fitting procedures such as Marquardt's algorithm.

Equation 17 in Sharpe and DiMichele (1977), as modified by equation 4 in Schoolfield et al. (1981):

$$r(t) = \frac{\text{rho}*T/298*\exp(ha/r*(1/298 - 1/t))}{1 + \exp(hl/r*(1/tl - 1/t)) + \exp(hh/r*(1/th - 1/t))}$$

where r = universal gas constant (1.987 cal deg^{-1} mol^{-1}), *rho, ha, hl, tl,* and *th* are parameters to be estimated, and t = temperature (°K)

quantities repeated in the partial derivatives

$$q = 1 + \exp(hl/r*(1/298 - 1/t))$$
$$z = (\text{rho}*t/298)*ha/r*(1/298 - 1/t)$$

$$\frac{\partial r(t)}{\partial \text{rho}} = t/298*\exp(ha/r*(1/298 - 1/t))*q** - 1$$

$$\frac{\partial r(t)}{\partial ha} = (1/298 - 1/t)*\text{rho}*t/(298 + r)* \cdot\exp(ha/r*(1/298 - 1/t))*q** - 1$$

$$\frac{\partial r(t)}{\partial hl} = (1/r*(1/tl - 1/t)* \cdot\exp(hl/r*(1/tl - 1/t)) - z)*q** - 2$$

$$\frac{\partial r(t)}{\partial tl} = (hl/r*tl** - 2* \cdot\exp(hl/r*(1/tl - 1/t)) - z)*q** - 2$$

$$\frac{\partial r(t)}{\partial hh} = (1/r*(1/th - 1/t)* \cdot\exp(hh/r*(1/th - 1/t)) - z)*q** - 2$$

$$\frac{\partial r(t)}{\partial th} = (hh/r*th** - 2* \cdot\exp(hh/r*(1/th - 1/t)) - z)*q** - 2$$

Equation 10 in Logan et al. (1976):

$$r(t) = \text{alpha}*((1/(1 + k*\exp(-\text{rho}*t))) - \exp((t - tm)/dt))$$

where t = temperature (°C) above some base temperature, and alpha, *k, rho, tm,* and *dt* are parameters to be estimated, and $q = 1 + k*\exp(-\text{rho}*t)$

$$\frac{\partial r(t)}{\partial \text{alpha}} = 1/q - \exp((t - tm)/dt)$$

$$\frac{\partial r(t)}{\partial k} = -\text{alpha}*\exp(-\text{rho}*t)*q** - 2$$

$$\frac{\partial r(t)}{\partial \text{rho}} = \text{alpha}*k*\exp(-\text{rho}*t)*t*q** - 2$$

$$\frac{\partial r(t)}{\partial tm} = \text{alpha}/dt*\exp((t - tm)/dt)$$

$$\frac{\partial r(t)}{\partial dt} = \text{alpha}*(t - tm)*dt** - 2* \cdot\exp((t - tm)/dt)$$

Equation 1 in Stinner et al. (1974):

$$r(t) = c/(1 + \exp(k1 + k2*t))$$

where topt = temperature (°C) at which the maximum developmental rate occurs, t = temperature (°C) for $t <$ topt, $t = 2*\text{topt} - t$ for $t >$ topt, c, $k1$, and $k2$ are parameters to be estimated, and if $t <$ topt, $q = 1 + \exp(k1 + k2*t)$

$$\frac{\partial r(t)}{\partial c} = 1/q$$

$$\frac{\partial r(t)}{\partial k1} = -c*\exp(k1 + k2*t)*q** - 2$$

$$\frac{\partial r(t)}{\partial k2} = -c*\exp(k1 + k2*t)*t*q** - 2$$

if $t >$ topt, $q = 1 + \exp(k1 + k2*(2*\text{topt} - t))$

$$\frac{\partial r(t)}{\partial c} = 1/q$$

$$\frac{\partial r(t)}{\partial k1} = -c*q** - 1$$

$$\frac{\partial r(t)}{\partial k2} = -c*q** - 1*(2*\text{topt} - t)$$

Taylor (1982) (truncated Gaussian distribution):

$$r(t) = rm*\exp(-0.5*((t - tm)/tv)**2)$$

where t = temperature (°C), *rm, tm,* and *tv* are parameters to be estimated, and $q = \exp(-1/2*((t - tm)/tv)**2)$

$$\frac{\partial r(t)}{\partial rm} = q$$

$$\frac{\partial r(t)}{\partial tm} = rm*tv** - 2*(t - tm)*q$$

$$\frac{\partial r(t)}{\partial tv} = rm*(t - tm)**2*tv** - 3*q$$

Information to Contributors

Environmental Entomology is published during February, April, June, August, October, and December. Publication in the journal is generally limited to members of the Entomological Society of America. Contributions report on the interaction of insects with the biological, chemical, and physical aspects of their environment. Specifically, articles report on ecology and population dynamics; host preference; basic studies of pheromones, attractants, repellents, gland secretions, and venoms; the interaction of insects with other organisms; basic studies of the discovery, characteristics, and activity of microbial insecticides, viruses, and other insect pathogens; pesticide selectivity; and physiologic responses to the environment.

All papers are reviewed by scientists qualified to judge the validity of the research. Acceptance or rejection, however, is the decision of the subject editor. Acceptance of papers is based solely on their scientific merit. Appeal of a rejected manuscript should be made to the *Environmental Entomology* Editorial Board via the managing editor. Accepted manuscripts are published approximately in the order they are received.

In addition to research papers, *Environmental Entomology* publishes Letters to the Editor, interpretive articles in a Forum section, and articles that describe new entomological techniques. The same guides apply to these as to research articles.

For more detailed instructions concerning the preparation and submission of manuscripts, consult the "Publications Policies and Guide for Authors" printed in the March 1984 issue of the *Bulletin*

Manuscript Preparation. Type all manuscripts double spaced, with 1½-inch margins, on one side of 8½ by 11 inch nonerasable bond paper. Underscore only to denote italic type. Do not underscore headings. Number pages consecutively, beginning with the title page. Begin each of the following on a separate page and arrange in this order: Title page, abstract, text, acknowledgment, references cited, footnotes, tables, figure legends, and running head. Submit the original manuscript and two copies to:

Managing Editor
Entomological Society of America
4603 Calvert Road
College Park, MD 20740

Do not submit a new manuscript directly to the subject editor.

Title Page. Include the following: (1) Complete name and address to whom galley proofs should be sent in the upper right corner; (2) the journal title "Environmental Entomology" in the upper left corner; (3) a complete and informative title that includes order and family names in parentheses; (4) complete author name(s) and affiliation(s), including complete address and ZIP code.

Abstract. Abstracts should be an informative digest of the significant contents and the main conclusions of the research.

References Cited. Citations in the text should be by last name of author and date and refer to a reference listed alphabetically by author in References Cited. The format should conform to the style in recent issues.

Tables. Keep tables to a minimum. Type all parts of each table double spaced, with each table starting a new page.

Illustrations. Submit original drawings on illustration board no larger than 11 by 15 inches. Photographs must be on glossy paper. Separate parts of the same figure must be mounted together on illustration board and arranged to use space efficiently. Figures must be numbered and marked with author's name on the back. Figures will be returned after publication *only* at an author's request.

Style Conventions. When first mentioned, a plant or animal should include the full scientific name and the author of the zoological name unabbreviated (except for Linnaeus [L.] and Fabricius [F.]). Use only common names approved by the Entomological Society of America. Otherwise, the manuscript should conform to the guidelines established by the latest edition of the *Council of Biology Editors Style Manual.*

Proofs and Reprints. Page proofs and a reprint order will be sent to the author after a manuscript is typeset. All changes in proof, except for printer's and editorial errors, will be charged to the author.

Charges. Authors will be assessed page charges to cover publication expenses, in addition to reprint charges and author changes. Member authors who are retired and not affiliated with any institution may publish five pages a year free of page charges. Member authors who are employed, but have no grants or funds for publication may request a partial waiver of page charges. This request must be made when a manuscript is submitted.