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

Follow this and additional works at: http://digitalcommons.liberty.edu/bio_chem_fac_pubs

Recommended Citation
Reichenbach, Norman and Stairs, Gordon R., "Response of the Western Spruce Budworm (Lepidoptera: Tortricidae) to Temperature and Humidity: Developmental Rates and Survivorship" (1984). Faculty Publications and Presentations. 77.
http://digitalcommons.liberty.edu/bio_chem_fac_pubs/77
Response of the Western Spruce Budworm (Lepidoptera: Tortricidae) to Temperature and Humidity: Developmental Rates and Survivorship

NORMAN G. REICHHENBACH and GORDON R. STAIBS

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

ABSTRACT: Developmental rates of embryos, larvae, and pupae of the western spruce budworm were determined at 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 20 to 29°C, depending upon sex and life stage. At temperatures above 26°C, the rates decreased sharply. Low temperatures induced melanosis in over 50% 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 33°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).

Table 1. Average duration of peach twig borer life stages

<table>
<thead>
<tr>
<th>Stage</th>
<th>Day-degree totals</th>
<th>Days*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pupa</td>
<td>160</td>
<td>12</td>
</tr>
<tr>
<td>Preoviposition adult</td>
<td>29</td>
<td>2</td>
</tr>
<tr>
<td>Postoviposition adult</td>
<td>69</td>
<td>2</td>
</tr>
<tr>
<td>Egg</td>
<td>581</td>
<td>32</td>
</tr>
<tr>
<td>Larva</td>
<td>239</td>
<td>32</td>
</tr>
</tbody>
</table>

*Day-degree calculated at 10°C for lower threshold and 31°C for the upper threshold.

Average number of days for first summer generation under Washington conditions.

Acknowledgment

This research was supported in part by the Washington State Tree Fruit Research Commission award a Washington State University. Project 6969. Thanks are extended to L. M. Owen-Smith for technical support in conducting these investigations. Scientific Paper No. 683.

References Cited


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

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 identified in part by the Washington State Tree Fruit Research Commission grant to a model may be developed in part by the Washington State Tree Fruit Research Commission grant project 6090.
Table 1. Parameter estimates (followed by SD) for the developmental rate equation by Logan et al. (1976) for larvae and embryos of the WSB.

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>Embryos Larvae (males) Larvae (females)</th>
</tr>
</thead>
<tbody>
<tr>
<td>alpha</td>
<td>0.245 (0.097) 0.093 (0.370) 0.420 (0.220)</td>
</tr>
<tr>
<td>k</td>
<td>10.060 (30.024) 36.028 (30.024) 1.023 (33.724) 40.818 (30.024)</td>
</tr>
<tr>
<td>rho</td>
<td>0.215 (0.213) 0.201 (0.201) 0.201 (0.201) 0.201 (0.201)</td>
</tr>
<tr>
<td>m</td>
<td>27.179 (0.105) 36.069 (0.105) 36.069 (0.105) 36.069 (0.105)</td>
</tr>
<tr>
<td>d</td>
<td>0.718 (6.140) 0.203 (6.140) 0.203 (6.140) 0.203 (6.140)</td>
</tr>
<tr>
<td>b</td>
<td>0.00 (5.00) 0.00 (5.00) 0.00 (5.00) 0.00 (5.00)</td>
</tr>
</tbody>
</table>

SAS appendix for the equation.

To assess color changes due to temperature, tann-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 (1980), were fitted to the data in a similar fashion to those employed in the Study of Biological System Analysis (SAS; Proc: Funct). Equations in the text are followed by the simple size, R^2, and the SDs of the model’s parameter, save the intercept, in the order they appear in the model. The following abbreviations are used in the models: y = developmental rate (ljdays); p = arc sine square root of the proportion survived; t = temperature in °C; H = RH, x = 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.

\[ y = 0.0054 + 0.018(h) + 0.0007(t') \]

(54, 0.39, 0.005, 0.0008, 0.00002)

At temperatures below 15°C only embryos at very humidities survived, and even here the survival rates were very low (<10%). Consequently, the data were pooled over all humidities in fitting the five Taylor (1980) mixed models. All of what 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 25°C, developmental rates dropped rapidly. Below 10°C, developmental processes were altered very little; hence, the arc sine square root of the proportion survived; \( t = \text{temperature in °C}; \ H = \text{RH}; \ x = \text{sex (coded 0 for females and 1 for males).} \)

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 to the developmental rate models (Tables 2 and 3). Pupae developed very slowly below 10°C, and the rates reached a maximum at 25°C. Between 15 and 25°C, the rates were linear. Above 20°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). There were no parameters associated with some of the parameter estimates were due to the algorithm finding a minimum residual sums of squares in an 1-dimensional space where one or more variables could be fixed. In addition, the 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 it 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 portions of the variability, even though models with more parameters will generally give better distribution of the variability in the data 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 temperatures of long duration.

The only mechanistic model based upon physical principles (Sharpe and DiMichele produced very large SDs associated with parameters estimated (Table 2). The only model produced adequate predictions at temperatures beyond the range of the data. Eq. 1 must therefore be collected over the entire range for which model predictions are required of Logan et al. (1976) produced good predictions because it adequately modeled the data and was used for completion of pupal development. The truncated Gaussian model was the easiest nonlinear model to fit only disadvantage of this model was its pred temperature at temperatures above the maximum developmental rate. The model assumes a symmetrical response around the point where development maximal and this was not verified by the Mortality may be great if these high temperature are of long duration so that this inconsistency the data may have a trivial effect when using model to estimate life stage duration in the difference between the model would duce a minimal amount of error relative magnitude of factors that affect the temperature which the insect is exposed. Fourier series fitting different temperature regimes (Taylor 1981) in conjunction with three development models (polynomial, Logan et al. (1976), as truncated Gaussian) were used to predict pupal development beginning July. All three functions estimated similar for completion of pupal development when
SPRUCE BUDWORM DEVELOPMENT

Reichenb ach and Stairs: Spruce Budworm Development

Vac, \( z^2 = 8.82, \quad P = 0.003 \), linear and quadratic trends in the pupae, \( z^2 = 5.82, \quad P = 0.02 \) at 4.88, \( P = 0.03 \), respectively; Table 5). Near the developmental maxima were most evident at temperatures of 15°C, to 35°C of the pupae darkened at 15°C and above, respectively. Dark larvae did not necessary indicate that the pupae would be dark. The temperature of pigments can be caused by a variety of factors, including photoperiod and color of the habitat (Hazel and West 1979, 1983), an extensive pigment induced by the ambient temperature of the larvae of pupae in the ambient temperature (Shepard 1985, W 1982). The induction of dark pigment is adaptive to increasing developmental rates: development could be completed within a temperature range that were cooler than usual.

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

\[
p = -2.244 + 0.294(t^2) - 1.429(h) - 0.001 \\
(10, 0.57, 0.040, 0.545, 0.001, 0.060, 0.01)
\]

Survivorship decreased toward the extremes of temperature range (10°C and 35°C), with no embryos surviving at 35°C, and increased to a plateau at 20°C. 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 development function with regard to microclimatic influences.

The number of dark larvae and pupae increased as the temperature decreased (linear trend in larvae)

Table 3. Comparison of developmental rate equations using the proportion of the variability in the data explained by the model (R²) and the relative difficulty and cost of fitting the model as indicated by the number of iterations required to estimate the constants in the equations:

<table>
<thead>
<tr>
<th>Stage</th>
<th>Eggs</th>
<th>Larvae</th>
<th>Pupae</th>
</tr>
</thead>
<tbody>
<tr>
<td>R²</td>
<td>( \mu )</td>
<td>Iterations</td>
<td>R²</td>
</tr>
<tr>
<td>0.990</td>
<td>0.099</td>
<td>50</td>
<td>0.989</td>
</tr>
<tr>
<td>0.991</td>
<td>0.099</td>
<td>4</td>
<td>0.991</td>
</tr>
<tr>
<td>0.991</td>
<td>0.099</td>
<td>2</td>
<td>0.991</td>
</tr>
<tr>
<td>0.991</td>
<td>0.099</td>
<td>14</td>
<td>0.991</td>
</tr>
<tr>
<td>0.991</td>
<td>0.099</td>
<td>1</td>
<td>0.991</td>
</tr>
</tbody>
</table>

(1) Shepard and D'Amicile (1977), as modified by Schoolfield et al. (1981); (2) truncated Gaussian (Taylor 1982); (3) Stinner = Stinner and Logan et al. (1970); (5) cubic polynomial.
In contrast to the data on embryo survivorship ($R' = 0.87$), the survivorship of the pupae to temperature and humidity explained only 45% of the variation. Here is a large number of late-instar larvae, the survival rates at this temperature and humidity explained only 45% of the variation. Consequently, other factors including environmental conditions might be important in determining pupal survivorship.

Maximum survival rates and developmental times for the embryos were 22 and 28°C, respectively. Therefore, even though development occurred rapidly at 29°C, the survival rates at this temperature 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 period 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 then increased on two different dates indicated that humidity and length of time in diapause had significant effects on larval survivorship, whereas temperature (0 or 30°C) did not.

$$p = 0.072 + 0.003(k - 0.49)(\text{date})$$

(16, 0.08, 0.004, 0.048, 0.00003)

Both high and low humidities decreased the survival of the diapausing larvae, and the larvae reared 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 of the collapse of an outbreak. Under favorable temperature conditions, a large number of eggs can be produced (Regniere 1985) and the embryos would have high survivorship. As noted above, minimum developmental rates at 20°C do not favor high survivorship, so that optimal conditions would not be at this high temperature, but rather the zone around 25°C without unusual fluctuations in this zone, egg production is maximum [20 eggs per female (Reichenbach, unpublished data)]. In addition, high, and moderate pupal survivorship is high, and foliage production of the current year would not be decreased or reduced (McKnight 1967). Once the first-instar larvae break diapause, it is unlikely that they will be at 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 100 to 200 RH). Consequently, if relatively stable temperatures around 20°C prevail, there might be a dramatic increase in the number of spruce budworms surviving, leading to epidemic population increases. Conversely, if weather conditions are outside the optimal zone (ca. 25°C) or unusual temperature fluctuations occur, the fecundity of the adults (Regniere 1985) 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 conditions because they are mobile and can thermoregulate both behaviorally (Shepard 1958) and through melanin production at low temperatures. The larval survival rates imposed by the low temperature by increasing the amount of solar radiation absorbed. Here, the population would decline in numbers due to low survivorship and embryo survivorship, but would stabilize at an endemic population mode because of the high survivorship of the remaining larvae and pupae.

**Acknowledgment**

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

**References Cited**


Recieved for publication 2 November 1982; accepted 6 January 1984.

Appendix

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

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

$$r(t) = \frac{\rho_0 * T/298 * \exp(\alpha(ha/r^*(1/298 - 1/t))}{1 + \exp(hh/r^*(1/t - 1))}$$

where $\rho_0$ is universal gas constant ($1.987 \text{cal} \cdot \text{deg}^{-1} \cdot \text{mol}^{-1}$), $rh$, $ha$, $hb$, $t$, and $s$ are parameters to be estimated, and $t$ = temperature ($\degree{C}$).

quantities repeated in the partial derivatives

$$q = 1 + \exp(hl/r^*(1/298 - 1/t))$$

$$s = (rho_0 T/298 hha/r_*(1/298 - 1/t))$$

$$\partial r(t)/\partial ha = \frac{\rho_0 * T/298 * \exp(\alpha(ha/r^*(1/298 - 1/t))}{1 + \exp(hh/r^*(1/t - 1))}$$

$$\partial r(t)/\partial hb = \exp(hh/r^*(1/t - 1)) * \exp(\alpha(ha/r^*(1/298 - 1/t)))$$

$$\partial r(t)/\partial s = 1$$

$$\partial r(t)/\partial th = \exp(hh/r^*(1/t - 1)) * \exp(\alpha(ha/r^*(1/298 - 1/t)))$$

Taylor (1982) (truncated Gaussian distribution

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

where $t$ = temperature ($\degree{C}$), $rm$, $tm$, and $st$ are parameters to be estimated, and $q = \exp(\alpha(ha/r^*(1/298 - 1/t)))$.

Equation 10 in Logan et al. (1976):