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

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Table 1. Average duration of peach twig borer life stages

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

* Day-degrees calculated at 10°C for lower threshold and 31.1°C for the maximum development rate.

* 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 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.

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

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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, potassium hydroxide; 43% RH, potassium carbonate; 75% RH, sodium chloride; 100% RH, distilled water (span 1977). Salt solutions were placed in plastic crispers (18 by 9 by 8 cm) with sealed by using stopcock grease and poly tubing around the rim of the crisper. The containers were allowed to equilibrate to the temperature for at least 1 wk. The air space containers was kept to a minimum by using volume of the saturated salt solution. Per plastic sheets with depressions were placed above the salt solutions, and individual eggs or pupae were placed in each depression. The food in the 1-oz. (ca. 30-ml) plastic cups was placed in each depression. The larvae used in the experiments on developmental rates at constant temperatures were in diapause for at least 3 months before experimentation. The larvae were reared with initially four larvae per cup and the 4th instar were separated to one larva per cup. Animals were checked twice daily at the temperatures (>25°C) and once daily at all temperatures.

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

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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 0.023	0.097 0.279	0.111 0.420
k	15.060 1.023	30.024 33.724	32.028 40.818
rho	0.158 0.014	0.213 0.181	0.201 0.201
tm	27.179 0.562	31.915 9.324	30.589 6.677
dt	0.718 0.351	6.140 28.608	6.253 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 Maxr 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 (percent, 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 than 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 Fncat).

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 temperatures are of long duration.

The only mechanistic model based upon physical principles (Sharpe and DiMichele 1977) produced very large SDs associated with parameters estimated (Table 2). The polynomial model produced adequate predictions without beyond the range of the data (Fig. 1) must therefore be collected over the entire for which model predictions are required because of Logan et al. (1976) produced good predictions because it adequately modeled the of high temperature, had small SDs for the parameter estimates (generally), and usually did require a large number of iterations to converge a solution. The truncated Gaussian distribution model was the easiest nonlinear model to fit only disadvantage of this model was its prediction at temperatures above the maximum developmental rate. The model assumes a symmetric response around the point where development is maximal and this was not verified by the Mortality may be great if these high temperatures 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

The differences between the models would produce a minimal amount of error relative to the multitude of factors that affect the temperature which the insect is exposed. Fourier series, sending different temperature regimes (Taylor 1981) in conjunction with three developmental models (polynomial, Logan et al. [1976], as truncated Gaussian) were used to predict the time to complete pupal development beginning in 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*				
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 ⁻³
14,738.3	—	0.002	0.192	2.0 × 10 ⁻³
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.

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

Fig. 1. Developmental rate models and data (means $\pm$ 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.

Environmental temperatures were in or below the zone where the developmental rates were linear ($<28^{\circ}\text{C}$). 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 lar-

vae, $\chi^2 = 8.82$, $P = 0.003$; linear and quadratic trends in the pupae, $\chi^2 = 5.82$, $P = 0.02$ at 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 necessarily indicate that the pupae would be dark. The induction of pigment can be caused by a variety of factors, including photoperiod and color of the microhabitat (Hazel and West 1979, 1983), and temperature induced dark pigment formation. Dark pigment would increase the absorption of solar radiation and consequently increase the internal temperature of the larvae or pupae at the ambient temperature (Shepard 1958, West 1982). The induction of dark pigment may be adaptive to increasing developmental rates; development could be completed within a shorter time that were cooler than usual.

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

$$p = -2.244 + 0.294(t) - 1.429(h) - 0.000 + 0.191(t^*h) - 0.004(h^*t^2) \\ (77, 0.87, 0.040, 0.545, 0.001, 0.060, 0.001)$$

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

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

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

Model ^a	Embryos		Larvae				Pupae	
	R^2	Iterations	R^2	Iterations	R^2	Iterations	R^2	Iterations
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 et al. (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.

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 ($R^2 = 0.45$).

$$p = 0.951 - 0.258(h) + 0.003(t^*h) - 0.00006(t^*h^2) - 0.000005(t^*h^2) \quad (4)$$

(37, 0.45, 0.008, 0.0008, 0.00002, 0.000002)

There were no significant differences in the sur-

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	Poly-nomial	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).

$$T(t) = \bar{T} - \frac{a_1}{2} \cos\left(\frac{2\pi}{365}t + \phi\right) - \frac{a_2}{2} \cos(2\pi t). \text{ Fourier equation}$$

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.

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

survivorship of the different sexes of the pupae. At the temperature and humidity extremes (15 to 31°C and 10 and 100% RH), the survivorship of the pupae decreased (Fig. 3). Low temperature affected pupal survivorship less than did the high temperatures, but as noted above, both temperature and humidity explained only 45% of the variability; consequently, other factors including genetic components might be important in determining pupal survivorship.

Maximum survival rates and developmental times for the embryos were at 22 and 29°C, respectively. Therefore, even though development can occur rapidly at 29°C, the survival rates at this temper-

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

Temp (°C)	Life stage	Sample size (n)	% of total where dark pigment induction occurred
15	Larvae*	46	45.8
15	Pupae	39	30.5
20	Larvae*	45	6.7
20	Pupae	37	63.1
25	Larvae*	44	0.0
25	Pupae	39	7.7

* 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 conditions because they are mobile and can thermoregulate both behaviorally (Shepard 1958) and through melanin production at low temperatures. The pupae are also insensitive to adverse weather conditions. They may produce melanin at low temperatures which might offset the slow development rates imposed by the low temperature by increasing the amount of solar radiation absorbed. Hence the population would decline in numbers due to low fecundity and embryo survivorship, but would stabilize at an endemic population mode because of the high survivorship of the remaining larvae and pupae.

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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):

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

where r = universal gas constant (1.987 cal deg⁻¹ mol⁻¹), ρ , ha , hl , th , and th are parameters to be estimated, and t = temperature (°K)

quantities repeated in the partial derivatives

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

$$z = (\rho \cdot t / 298) \cdot ha / r \cdot (1/298 - 1/t)$$

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

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

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

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

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

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

Equation 10 in Logan et al. (1976):

$$r(t) = \alpha \cdot ((1/(1 + k \cdot \exp(-\rho \cdot t))) - \exp((t - tm)/dt))$$

where t = temperature (°C) above some base temperature, and α , k , ρ , tm , and dt are parameters to be estimated, and $q = 1 + k \cdot \exp(-\rho \cdot t)$

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

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

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

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

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

Equation 1 in Stinner et al. (1974):

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

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

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

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

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

if $t > topt$, $q = 1 + \exp(k1 + k2 \cdot (2 \cdot topt - t))$

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

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

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

Taylor (1982) (truncated Gaussian distribution):

$$r(t) = rm \cdot \exp(-0.5 \cdot ((t - tm)/to)^{**2})$$

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

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

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

$$\frac{\partial r(t)}{\partial to} = rm \cdot (t - tm) \cdot to^{**} - 3 \cdot q$$

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