

UPPER AND LOWER TEMPERATURE THRESHOLDS FOR DEVELOPMENT OF SIX STORED-PRODUCT BEETLES

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Abstract

Data on the egg, larval, pupal, and egg to adult development for six species of stored-product Coleoptera reared at various constant temperatures were analyzed to estimate the temperatures for maximum (U) and minimum (L) developmental rates. Degree-days (DD) above L required for completing development were also estimated for the different life-stages of each insect species. Temperature thresholds and DD estimates varied among species, and within a species among life-stages. The upper and lower temperature threshold estimates could be used in the field, under variable temperature regimes, for predicting development of the life-stages or seasonal phenology of the six species. Forecasting development or seasonal phenology of the six species in the field is valuable for accurately timing insect sampling programs and control tactics. The adoption of DD methods in integrated management programs for stored-product insects, may depend on the accurate performance of these models in the field, and on the availability of reliable methods for sampling various insect life-stages.

Introduction

The rate of development ($1/\text{developmental time}$) through most insect stages is nonlinear at low and high temperatures, and linear at intermediate temperatures (Fig. 1). Several functions of temperature have been developed to describe the rate of development over the full range of physiologically viable temperatures (Wagner *et al.*, 1984; Logan, 1988). Parameters of these equations are fit to developmental rate data obtained by rearing insects in the laboratory at a series of constant temperatures. Development models are then used in the field, under variable ambient temperatures, for predicting specific phenological events in the insect's life-cycle, such as termination of diapause, egg hatch, pupation, and adult emergence. Predicting the timing of these phenological events is important for accurately scheduling census samples and control tactics (Wagner *et al.*, 1984).

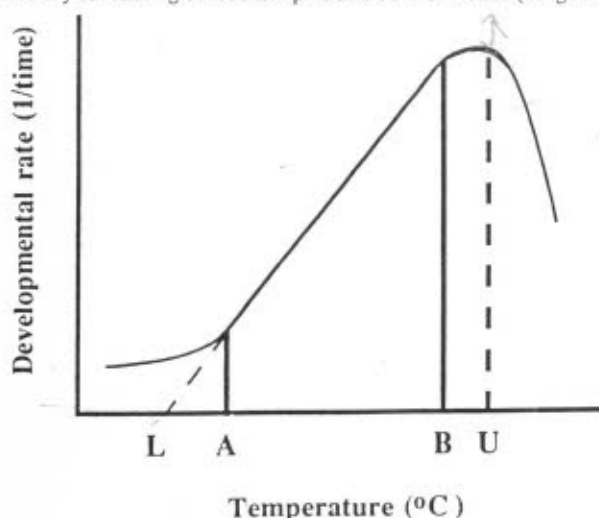


Fig. 1. Nonlinear curve showing the relationship between developmental rate and temperature. L and U are the temperatures where developmental rates are minimum and maximum, respectively. Developmental rates are linear in the temperature range A - B.

Degree-day (DD) methods, which assume a linear relationship between developmental rate and temperature (Fig. 1, range A-B), have been used for predicting developmental times of various life-stages (Giebink *et al.*, 1985; Hutchison *et al.*, 1986; Fielding and Ruesink, 1988), adult emergence (Rummel and Hatfield, 1988; Jones *et al.*, 1989; Sanderson *et al.*, 1989), and seasonal phenology (Eckenrode *et al.*, 1975; Riedl *et al.*, 1976; Levine, 1989) of insect species infesting field and orchard crops. Calculation of a lower temperature threshold (L), below which developmental rate is assumed zero, is essential for accumulating DD. Inclusion of an upper temperature threshold (U), where developmental rate is maximum, in computing DD improves the accuracy of estimates (Higley *et al.*, 1986), because mortality of insects rapidly approaches 100% as temperatures increase above U (Stinner *et al.*, 1974). Assumptions and approximations behind the DD approach and methods for calculating DD from field (ambient or in our case, grain) temperatures were discussed by Pruess (1983) and Higley *et al.* (1986). Higley *et al.* (1986) have also presented a BASIC computer program (DEGDAY) for calculating DD by various methods using field temperatures.

There is extensive literature on the temperature-dependent development of stored-product Coleoptera (see Hagstrum and Milliken, 1988; Kawamoto *et al.*, 1990; Subramanyam and Hagstrum, in press) and Lepidoptera (e.g., Burges and Haskins, 1965; Savov, 1973; Cox *et al.*, 1981). However, only a few studies (Savov, 1973; Kawamoto *et al.*, 1990; Subramanyam and Hagstrum, in press), involving three species, reported estimates of U, L, or DD.

In this paper, we present estimates of U and L for egg, larval, pupal, and egg to adult development of six species of stored-product Coleoptera. In addition, for the developmental stages of each species, we also estimated DD above L required for completing development. Equations for estimating U, L, and DD and associated standard errors (SE) are given for the benefit of researchers interested in developing DD models for stored-product insect species not included here. We realize, and emphasize, that the temperature thresholds and DD estimates have biological validity only if they can satisfactorily predict insect development or phenology in the field. Hence, before widescale adoption, any model should be evaluated (validated) with independent field data.

Materials and Methods

Insect species and temperature-development data - Temperature thresholds and DD were estimated for the following insect species: rusty grain beetle, *Cryptolestes ferrugineus* (Stephens); flat grain beetle, *Cryptolestes pusillus* (Schoenherr); sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.); lesser grain borer, *Rhyzopertha dominica* (F.); red flour beetle, *Tribolium castaneum* (Herbst); and confused flour beetle, *Tribolium confusum* (Jacquelin duVal). Data on the mean egg, larval, pupal, and egg to adult developmental times for the six species reared on various diets at a series of constant temperatures were compiled by Hagstrum and Milliken (1988) from published literature. Data for eggs or pupae reared on diets of < 12% and > 12% moisture contents were pooled, because diet moisture did not influence the temperature-dependent development of each of these stages (Hagstrum and Milliken, 1988). Larval and egg to adult development of *O. surinamensis*, *C. ferrugineus*, and *Tribolium* spp. were significantly different at the two moisture levels (Hagstrum and Milliken, 1988). Therefore, the development data at each moisture level for these two stages were analyzed separately. For some species, especially at < 12% moisture content, there was limited or no information on the temperature-dependent development of the larval and egg to adult stages.

Estimating U - U for the developmental stages of each species was estimated using the algorithm of Stinner *et al.* (1974):

$$R_T = A / [1.0 + \exp (K1 + \{K2 \cdot T^*\})] \quad (1)$$

where, R_T = developmental rate at temperature T (in °C); A = maximum R_T [1.0 + exp (K1 + {K2*U})]; U = temperature where developmental rate is maximum; K1 and K2 are empirical constants; and T^* = T for T < U, or T^* = (2U) - T for T > U. The parameters K1, K2, A, and U and associated SE were estimated using the derivative-free (DUD) regression method (Ralston and Jennrich, 1978) of PROC NLIN procedure (SAS Institute, 1987). For the developmental stages of some species (*C. ferrugineus* and *R. dominica* larval development, and *C. ferrugineus* and *O. surinamensis* egg to adult development on diets of < 12% moisture content), U was inaccurately determined because the experimental temperature range was not high enough to span U.

Estimating L - L for each species and developmental stage was estimated by fitting a simple regression line to developmental rates (Y) that were linearly related to temperatures (X) using the PROC REG procedure (SAS Institute, 1987). The variation in developmental rates in the linear portion of the curve is less compared with the variation in the nonlinear portions of the curve (Campbell *et al.*, 1974). However, there was considerable variation in the developmental rates in the linear portion of the curve in our study, because data were derived from various sources. Therefore, before fitting a linear regression to the data, we used Cook's distance (which indicates the

influence of an individual observation on the regression slope), and an outlier test (Weisberg 1980) to delete an observation that did not conform to the linear model. The coefficient of determination (R^2) was not used as a criterion, because data can be manipulated to obtain a high R^2 (Weisberg 1980). The regression line was extrapolated to the "X"-axis, and L and approximate SE for L (SE_L) were estimated (Campbell *et al.*, 1974) as

$$L = (-I) / S \quad (2)$$

$$SE_L = R / S \sqrt{1/n + [(L - \bar{X})^2 / \sum (X_i - \bar{X})^2]} \quad (3)$$

where, I = y-intercept, S = slope, R = root mean square residual error, n = number of "X"- "Y" pairs used in the regression (i.e., number of cohorts), X_i = average temperature experienced by the i^{th} cohort, and \bar{X} = mean of all temperatures.

Estimating DD from constant temperature-developmental rate data - DD (from time, $t = 0$) and approximate SE for DD (SE_{DD}) required for completing egg, larval, pupal, and egg to adult development were estimated (Campbell *et al.*, 1974) as follows:

$$DD = I / S \quad (4)$$

$$SE_{DD} = SE_S / S^2 \quad (5)$$

where, SE_S = standard error of the regression slope.

The 95% confidence intervals for temperature thresholds and DD estimates have little statistical meaning, because standard errors of these estimates are approximately determined (Campbell *et al.*, 1974).

Estimating DD from field temperatures - Several techniques, ranging from simple to complex, exist for computing DD from field temperatures (see Higley *et al.*, 1986). Some techniques estimate DD using only L, and other techniques estimate DD using both U and L.

For example, DD for a given day (DD^*) is calculated as the difference between the average daily temperature (T_i) and lower temperature threshold (L). DD^* are computed by summing ($T_i - L$) over successive increments of time (hours or days) as

$$DD^* = \sum (T_i - L) \Delta t \quad (6)$$

where, Δt is a day ($t = 1$), half-day ($t = 0.5$), or any suitable interval of time when temperatures were measured (e.g., hourly [$t = 0.042$]); and T_i is the average temperature during the time interval. Development is assumed to be completed when $DD^* \geq DD$ (Equation 4).

Results

Estimates of U for egg, larval, pupal, and egg to adult development when reared on diets of < 12% or > 12% moisture content are summarized in Table 1. Estimates of U varied among species, and within a species among life-stages. At > 12% moisture content, the maximum difference in U (highest U - lowest U) among the species for egg, larval, pupal, and egg to adult development was 8.4, 4.5, 4.1, and 2.8 °C, respectively. Except for *T. castaneum*, U estimates for larval development of *C. ferrugineus* and egg to adult development of *C. ferrugineus*, *R. dominica*, *T. confusum*, and *T. castaneum* were higher when reared on diets of < 12% than on diets of > 12% moisture content. In general, *C. ferrugineus* had the highest U for all developmental stages compared with the other species. *T. castaneum* had the second highest U for development of eggs, larvae, and pupae compared with the remaining four species. Estimates of U for development of the immature stages of *C. pusillus* were similar. For all species, estimates of U among different life-stages did not follow any trend. However, U estimates were higher for insects reared on diets of < 12% than on diets of > 12% moisture.

Estimates of L for various life-stages of each species are summarized in Table 2. L varied among the species. Except for *C. ferrugineus*, L was different for different developmental stages of a species. Difference between the lowest and highest L among species for the egg, larval, pupal, and egg to adult development was 6.1, 7.7, 4.7, and 9.5 °C, respectively. Except for *O. surinamensis*, L for the larval development of *C. ferrugineus*, and egg to adult development of *C. ferrugineus* and *Tribolium* spp. was lower when insects were reared on diets of < 12% than on diets of > 12% moisture. In general, for each developmental stage, estimates of L were highest for *Tribolium* spp.

Table 1. Estimated upper temperature thresholds (mean $U \pm SE$) for egg (E), larval (L), pupal (P), and egg to adult (EA) development of six stored-product beetles, reared on diets of low (< 12%) or high (> 12%) moisture content (M.C.).

Stage	M.C. (%)	Insect species					
		<i>C. ferrugineus</i>	<i>C. pusillus</i>	<i>O. surinamensis</i>	<i>R. dominica</i>	<i>T. castaneum</i>	<i>T. confusum</i>
E ^a	Both	40.0±0.5	33.5±1.3	32.2±0.4	31.6±0.3	36.7±0.3	35.1±0.2
L ^b	<12	40.6±0.0	ND ^g	ND	ND	ND	ND
L ^c	>12	37.0±2.4	33.9±1.3	32.5±0.9	34.3±0.0	35.4±0.5	32.5±0.3
P ^d	Both	38.1±0.4	33.9±0.4	35.6±0.4	ND	36.7±0.7	36.0±1.0
EA ^e	<12	40.0±0.0	ND	36.0±0.0	ND	32.5±1.6	33.7±1.1
EA ^f	>12	36.7±1.1	36.6±1.5	34.0±0.9	34.2±1.1	34.1±0.6	33.1±0.7

^a 10-32 observations in the temperature range 17-40 °C (see Hagstrum and Milliken, 1988), were fitted to the nonlinear model of Stinner *et al.* (1974). R^2 among species ranged from 0.94-0.99.

^b 4 observations in the temperature range 25-40 °C were used. $R^2 = 0.93$.

^c 5-20 observations in the temperature range 20.0-40.0 °C were used. $R^2 = 0.81-0.99$.

^d 12-23 observations in the temperature range 17.0-42.0 °C were used. $R^2 = 0.94-0.99$.

^e 4-7 observations in the temperature range 25-40 °C were used. $R^2 = 0.71-0.91$.

^f 5-14 observations in the temperature range 22.5-42.0 °C were used. $R^2 = 0.67-0.91$.

^g ND = no data.

Table II. Estimated lower temperature thresholds (mean L_{50} SE) for egg (E), larval (L), pupal (P), and egg to adult (EA) development of six stored-product beetles, reared on diets of low (< 12%) or high (> 12%) moisture content (M.C.).

Stage	M.C. (%)	Insect species*					
		<i>C. ferrugineus</i>	<i>C. pusillus</i>	<i>O. surinamensis</i>	<i>R. dominica</i>	<i>T. castaneum</i>	<i>T. confusum</i>
E ^a	Both	15.1±0.9 (20.0-40.0)	13.2±1.5 (17.0-33.0)	12.8±2.0 (16.0-32.5)	16.7±0.8 (22.0-34.1)	18.9±0.6 (22.2-35.0)	15.8±0.4 (17.0-34.0)
L ^b	<12	13.2±5.2 (25.0-40.0)	ND ^g	9.5±0.4 (20.0-35.0)	ND	14.0±2.5 (25.0-35.0)	9.9±4.8 (22.5-32.5)
L ^c	>12	15.7±1.3 (22.5-35.0)	9.7±3.3 (21.0-37.5)	9.7±2.8 (20.0-35.0)	14.0±3.9 (25.0-33.0)	17.0±1.9 (22.5-37.5)	17.4±0.6 (22.2-32.5)
P ^d	Both	15.4±0.9 (21.1-37.8)	14.8±1.2 (20.0-37.5)	14.2±1.5 (18.0-36.0)	18.9±1.4 (25.0-28.0)	18.0±0.7 (20.0-32.5)	16.9±0.6 (20.0-34.0)
EA ^e	<12	8.1±7.1 (25.0-40.0)	ND	12.7±7.3 (25.0-30.0)	ND	8.1±7.7 (25.0-32.5)	8.4±3.8 (25.0-32.5)
EA ^f	>12	15.5±3.7 (22.5-35.0)	14.2±4.1 (22.5-32.5)	8.8±6.8 (22.5-37.5)	13.2±6.6 (27.0-33.0)	17.6±1.3 (24.0-32.5)	18.3±3.1 (24.0-32.5)

* For each species and stage, the range of temperatures, where developmental rates were linear, is given in parenthesis.

^a 9-27 observations were used to describe the developmental rates that were linearly related to temperatures. $R^2 = 0.93-0.99$.

^b 4-6 observations were used. $R^2 = 0.84-0.99$.

^c 4-15 observations were used. $R^2 = 0.95-0.98$.

^d 3-20 observations were used. $R^2 = 0.94-0.99$.

^e 3-5 observations were used. $R^2 = 0.88-0.95$.

^f 4-11 observations were used. $R^2 = 0.77-0.97$.

^g ND = no data.

Table III. Estimated degree-days (mean $DD \pm SE$) for egg (E), larval (L), pupal (P), and egg to adult (EA) development of six stored-product beetles, reared on diets of low (< 12%) or high (> 12%) moisture content (M.C.).

Stage	M.C. (%)	Insect species					
		<i>C. ferrugineus</i>	<i>C. pusillus</i>	<i>O. surinamensis</i>	<i>R. dominica</i>	<i>T. castaneum</i>	<i>T. confusum</i>
E	Both	66.6 \pm 2.7	71.1 \pm 4.4	68.6 \pm 6.4	85.1 \pm 4.2	41.3 \pm 1.8	73.6 \pm 1.9
L	<12	598.4 \pm 93.6	ND ^a	510.2 \pm 7.7	ND	453.7 \pm 43.1	607.9 \pm 130.6
L	>12	259.1 \pm 18.5	435.5 \pm 46.0	357.1 \pm 24.8	426.3 \pm 23.5	242.5 \pm 21.1	256.0 \pm 11.3
P	Both	72.5 \pm 3.4	75.5 \pm 3.6	89.9 \pm 4.7	48.9 \pm 7.9	64.4 \pm 3.9	81.3 \pm 4.4
EA	<12	841.0 \pm 219.8	ND	552.5 \pm 132.8	ND	822.4 \pm 156.1	908.3 \pm 140.9
EA	>12	359.2 \pm 61.6	493.1 \pm 82.8	620.4 \pm 112.4	685.9 \pm 162.3	299.4 \pm 21.0	293.1 \pm 48.2

^a ND = no data.

and *R. dominica*, lowest for *O. surinamensis*, and intermediate for *Cryptolestes* spp. Across all species and stages, L was higher for egg and pupal development than for larval and egg to adult development.

DD above L required for completing development varied among species, and within a species among the life-stages. Differences in DD among species and stages is a consequence of unequal L. Based on DD, the immature stages of each species, with the exception of *R. dominica*, can be arranged in the following descending order: larva > pupa > egg. Larval stages of *C. ferrugineus* and *Tribolium* spp., reared on diets of < 12% moisture required about two times more DD to complete development compared with insects reared on diets of > 12% moisture. About two to three times more DD were required for completing egg to adult development of *C. ferrugineus* and *Tribolium* spp. on diets of < 12% moisture compared with similar development on diets of > 12% moisture. However, diet moisture had a slight effect on the DD required for completing larval and egg to adult development of *O. surinamensis*.

Discussion, Conclusions, and Recommendations

Differences in temperature thresholds among species and stages are attributable to differences in enzyme-catalyzed reaction rates regulating growth, and influence of temperature on these rates (Higley *et al.*, 1986). Temperature thresholds vary among insect life-stages (Sanborn *et al.*, 1982; Giebink *et al.*, 1985), and within a life-stage among different instars (Hutchison *et al.*, 1986). This suggests that temperature thresholds are dynamic and change with insect age (Howe, 1967).

Within a species, developmental thresholds also vary among populations occupying different geographical regions (Campbell *et al.*, 1974). Because temperature-dependent developmental rate data in our study were derived from various sources, the thresholds calculated for the species are representative of different populations, and of populations reared on different diets. Therefore, these thresholds may be applicable in calculating DD for predicting development of the six species in various stored-commodities.

Howe (1965) reported that the minimum temperature for epidemic increases of the six species studied here was between 21 and 23 °C. He stated that the lower temperature threshold for egg to adult development was 3-5 °C below this temperature range. Our estimates of L for egg to adult development of *Tribolium* spp. were within the 3-5 °C range below 21-23 °C. However, for the remaining species estimates of L for the same development were about 8-12 °C below the 21-23 °C range. Our estimates were lower than those suggested by Howe (1965), because L in our study was estimated by extrapolating developmental rate curve to the "X"-axis.

L for insects reared on diets of < 12% moisture were lower than those reared on diets of > 12% moisture content. L and DD are negatively correlated (Campbell *et al.*, 1974). Therefore, according to Equation 6, developmental stages that have very low L require more DD to complete development. Hagstrum and Milliken (1988) reported that low moisture of diet prolonged larval development of these six species. Low moisture content of diet may have affected the rate of feeding of larvae or efficiency with which larvae can assimilate and convert their diet into biomass (Hagstrum and Milliken, 1988). Estimates of U for egg to adult development of *Tribolium* spp., *R. dominica*, and *O. surinamensis* fell in the optimum temperature ranges reported for these species by Howe (1965). However, estimates of U for *Cryptolestes* spp. were higher than those reported by Howe (1965).

If lower or upper thresholds for different stages of a species are approximately similar, then a single value can be used in DD calculations (Welch *et al.*, 1981). However, one should be aware of the assumptions and limitations of DD models. DD models may work well in predicting development of the six species studied here, because development of these species is dependent on temperature to a greater extent than moisture or nutritional quality of diet (Hagstrum and Milliken, 1988).

DD models may work well in areas where the field temperatures do not fall below L or exceed above U. However, DD models may overestimate development if some undetectable development occurs below or close to L. Nevertheless, depending on daily and seasonal changes in temperature in a given region, DD models could more accurately predict development than the complex nonlinear models. Hochberg *et al.* (1986) found that DD models were more accurate than nonlinear models in predicting development of the pea aphid and alfalfa aphid in the field.

Inclusion of U in DD calculations may improve the accuracy of estimates. However, if temperatures in the field fluctuate about U, DD methods may underestimate development, because temperature fluctuations about U increase developmental rate of insects (Hagstrum and Leach, 1973; Walker *et al.*, 1988). Therefore, inclusion or exclusion of an upper cut-off point in computing DD must be based on the relative accuracy that can be achieved in predictions.

When predicting development of stored-product insects in the field, it is important to measure temperature experienced by insects, such as the grain temperature instead of the ambient temperature. The simplest approach is to measure average temperature per day based on the minimum and maximum grain temperatures ($(\text{minimum} + \text{maximum})/2$). Because temperature of stored-commodities (e.g., grain) fluctuate very little with respect to daily changes in ambient temperature (Longstaff and Banks, 1987), the magnitude of errors when computing DD from grain temperatures will be minimal.

Seasonal phenology of insect pests can be also expressed on a DD scale by relating catch of insects (e.g., adults in probe traps, sticky traps, or grain samples) to DD computed using estimates of L and U for the egg to adult development. Number of insects caught on each sampling date is expressed as a cumulative percentage of the total catch. Plotting cumulative percentage of catch ("Y") on DD ("X") yields a sigmoidal curve, which is linearized by transforming percentage of catch to probit scale, and DD to log scale. From this linear curve, DD required for a fixed percentage of catch (usually 50%) of a species trapped in different locations can be compared. This method can be used to compare dates for 50% catch based on DD with calendar dates (Levine 1989). Critical phenological events, such as peak egg hatch, emergence, and oviposition identified on a DD scale (e.g., Riedl *et al.*, 1976) could be used to accurately time insect sampling programs and control tactics.

In describing seasonal phenology, the date of first catch (e.g., Jones *et al.*, 1989) is normally used as a starting point for accumulating DD. This procedure was applied to insect species (e.g., onion maggots and codling moth) that have two to three generations during a growing season (Eckenrode *et al.*, 1975, Riedl *et al.*, 1976). A similar procedure was employed to describe the adult emergence of apple maggots (Jones *et al.*, 1989) and navel orangeworm (Sanderson *et al.*, 1989), and egg hatch (larval emergence) of the codling moth (Riedl *et al.*, 1976). Herms *et al.* (1990) used this procedure to compare the relative efficiencies of two sampling methods in describing the seasonal phenology of five species of phytophagous Hemiptera infesting mature honeylocust.

DD methods can be used for predicting insect phenological events that have occurred in the past, and for forecasting future events. In addition, demographic statistics such as age-specific fecundity and survival could be also expressed on a DD scale (Elliott *et al.*, 1988). However, the performance of DD models in predicting phenological events must be tested in the field, i.e., predicted and observed events must be compared. An indifference band method (Welch *et al.*, 1981) could be used to determine DD model failure rate in the field. DD models are suitable for use in the field, if phenological events can be predicted within 10-15% of the observed events.

This paper and a paper by Subramanyam and Hagstrum (in press) presented U and L estimates for a total of seven species of stored-product beetles. These estimates could be used in developing DD models for the seven species. However, the use of DD methods in integrated management programs for stored-product insects will depend on the accurate performance of models in the field, and on the availability of reliable methods for detecting and estimating various insect life-stages.

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