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Temperature-Mediated Development Thresholds of *Sparganothis sulfureana* (Lepidoptera: Tortricidae) in Cranberries

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**ABSTRACT** Larvae of *Sparganothis sulfureana* Clemens frequently attack cranberries, often resulting in economic damage to the crop. Because temperature dictates insect growth rate, development can be accurately estimated based on daily temperature measurements. To better predict *S. sulfureana* development across the growing season, we investigated the temperature range within which *S. sulfureana* larvae can feed and grow. Larvae were reared at 13 constant temperatures ranging from 6.5–38.6 °C. Larval growth rate was determined by the rate of change of larval weight across time. The respective growth rates among these temperatures were modeled using simple linear, cubic, and Lactin nonlinear development functions. These models isolated the lower temperature threshold at which growth became nonzero and the upper temperature at which growth was maximized. All three models were significantly predictive of *S. sulfureana* growth, but the cubic model best represented the observed growth rates, effectively isolating lower and upper thresholds of 9.97 and 29.89 °C, respectively. We propose that these thresholds be used to create a degree-day model of temperature-mediated *S. sulfureana* development.

**KEY WORDS** *Sparganothis sulfureana*, degree-day, developmental model, cranberry, pest management

**Introduction**

*Sparganothis sulfureana* Clemens (Lepidoptera: Tortricidae) is a native, perennial pest of commercial cranberries in Wisconsin, Massachusetts, and New Jersey, which together comprise around 89% of the United States cranberry industry (National Agricultural Statistics Service 2013). Larvae are found in economically damaging numbers across all North American growing regions except Washington and Oregon (Patten and Daniels 2014). Larvae of *S. sulfureana* are polyphagous and can feed on a wide variety of plants, including species in the Ericaceae, Pinaceae, Ulmaceae, Salicaceae, Rosaceae, Apiaceae, Poaceae, Fabaceae, and Asteraceae (Beckwith 1938, Chapman and Lienk 1971). However, Chapman and Lienk (1971) speculated that *S. sulfureana*’s primary hosts are cranberry, *Vaccinium macrocarpon* Aiton, blueberry (*Vaccinium* spp.), and certain species in the Asteraceae. In Wisconsin cranberries, overwintered first-instar larvae emerge from hibernaculae constructed on the bog floor and begin feeding when the plants come out of dormancy in late April (Teixeira and Averill 2006). Overwintered larvae feed on new growth and web leaves and uprights together. Larvae continue developing into mid-June and July (Eck 1990). Moths emerge from July into August and female moths lay eggs in masses of 30–50 eggs (Beckwith 1938, Chapman and Lienk 1971). Second-generation larvae feed preferentially on immature cranberries (Eck 1990), and each larva can destroy three to five berries (Beckwith 1938). Because second-generation larvae feed on berries rather than foliage, they are more damaging to the crop than the overwintered larvae. Additionally, the concealed feeding within the berries provides protection from insecticides, making this generation more difficult to control. Therefore, successful control of the overwintered generation is crucial to keep populations low throughout the growing season.

*S. sulfureana*’s biology makes controlling this pest difficult. The primary cultural controls (e.g. flooding) used in cranberry beds for managing pests do not significantly reduce the number of *S. sulfureana* larvae (Beckwith 1938, Teixeira and Averill 2006). Chemical sprays can be effective on larvae of both generations, but the majority of *S. sulfureana* populations in Massachusetts are resistant to acephate and chlorpyrifos, two commonly used organophosphates; thus, growers are forced to use insecticides with alternative modes of action (Sylvia and Averill 2001, Averill and Sylvia 2013). Spray timing is critical, as many of these compounds must be ingested to be effective. Whatever the management tactic being used, phenology models can refine treatment timings.
Insects are poikilotherms, so their development rate is governed by ambient temperature. Temperature-based phenological models have been created for many insects to track their development across time based on daily weather data (e.g., Stinner et al. 1974, Logan et al. 1976, Harcourt and Yee 1982, Wagner et al. 1984, Lactin et al. 1995). The identification of insect-specific lower and upper temperature thresholds, below or above which the insect does not develop, allows one to calculate heat unit, or degree-day (DD), accumulations based on minimum and maximum daily temperatures (Pruess 1983). Currently, the development thresholds of S. sulfureana are not yet known; thus, the DD accumulations specific to S. sulfureana grow benchmarks (e.g., flight, egg-hatch) have also not yet been articulated. Cockfield et al. (1994) attempted to create a predictive model for S. sulfureana flight. When evaluating their model, they found that the number of calendar days after flight began was actually more accurate than using DDs, but concluded that other equations should be evaluated because of the year-to-year temperature variability. To date, there has not been any other attempt to create a temperature-based model for S. sulfureana.

The objective of this study was to determine the specific lower and upper temperature thresholds for S. sulfureana development, with the ultimate goal of creating a DD model that can aid cranberry growers and consultants in managing this pest.

Materials and Methods

Most studies of insect developmental temperature thresholds have measured the amount of time that it takes a neonate to become a pupa at a given temperature. However, such methods do not take into account physiological differences between generations in bivoltine species. Diapausing arthropods often have a higher temperature threshold at the end of diapause (Tauber and Tauber 1976), and there are many other biochemical changes that take place that help an insect survive the winter (Zachariassen 1985). Therefore, in order to ensure that our temperature thresholds were accurate at determining when the overwintered larvae are emerging, we used field-collected overwintered larvae for the lower threshold study. Because S. sulfureana overwinters as a first-instar larva, we needed to calculate growth rate directly as a function of weight gain rather than the time from egg to pupa. Additionally, many studies calculate the instar-specific growth rates, but the total number of instars for S. sulfureana has not been determined. For this reason, we calculated an overall larval growth rate per temperature, as we could not ensure that we began with larvae that were all the same instar.

Insect Collections. Larvae (N = 218) were obtained in a variety of ways. To ensure that our study accurately incorporated any physiological differences between generations, overwintered, field-collected, larvae were used for the lower temperatures (<15°C). These larvae were collected from commercial cranberry marshes of the ‘Ben Lear’ and ‘Stevens’ varieties in central Wisconsin in 2012 and 2013 by sweep net and visually scanning for webbed uprights. Larvae used for the mid temperatures (17.8 and 22.4°C) were collected from insect-damaged berries in commercial cranberry fields in 2012. Larvae placed at the high temperatures (>25°C) were reared from eggs laid by the first-generation moths in the laboratory. Laboratory-reared larvae were used for the high temperature experiments because second-generation larvae are the ones that would be exposed to the warmest temperatures in the field during the middle of the summer. Larvae were weighed individually and placed in glass microcosms. All the larvae were mid-instars.

Experimental Conditions. Larvae were placed in growth chambers with a photoperiod of 16:8 (L:D) h. HOBO weather loggers (Onset, Bourne, MA) were placed in each incubator to track the actual temperature in the chamber. Larvae were placed individually in microcosms that were constructed by gluing a layer of mesh or pollination cloth over one end of a 5.1-cm-long x 2.5-cm-diameter glass tube (2012) or a 6.5-cm-long x 2.5-cm-diameter clear acrylic tube (2013). Stems of two cranberry uprights were wrapped tightly with foam wrapping and placed snugly in the top of a green plastic water vial. The outside of the upper portion of each water vial was wrapped in more foam wrapping and inserted into the open end of the glass or acrylic tube, allowing the cranberry uprights to project upward inside the tube (Fig. 1). Table-like bases were constructed that could hold 15 microcosms each (Fig. 1). Each base had holes drilled into the top surface that allowed the microcosms to stand upright with the water vials hanging underneath. All cranberry uprights were from field-collected plants of the ‘Stevens’ variety kept in the greenhouse to avoid the possibility of pesticide contamination. Water and uprights were replaced as needed.

Temperature Thresholds. In 2012, overwintered larvae were placed at 6.5, 7.8, 9.4, and 11.2°C based on previous work estimating that the lower threshold was around 10°C (C.R.R-S., unpublished data). Larvae were removed and weighed weekly. To determine the upper development temperature threshold, larvae were placed at 26.6, 29.1, 32.8, and 35.6°C and were weighed every two to three days because of their expected rapid growth rate. Mid-range temperatures were 17.8 and 22.4°C and larvae at these temperatures were also weighed every two to three days. In 2013, overwintered larvae were placed at 6.6, 9.2, and 13.3°C to provide further resolution for the lower threshold. Between 11 and 21 larvae were placed in each temperature. Differences in the initial number of replicates per temperature were due to the number of larvae that were available at that time. Furthermore, when there were extra larvae, larvae that died early in the experiment were replaced with additional replicate(s) at that temperature.

Statistical Analysis. Individual replicates were removed from the data set if the larva did not live long enough to be weighed at least three times to ensure there was enough statistical power to calculate an accurate growth rate. If a larva pupated, the previously
recorded weight was removed because weight drops before pupation. Additionally, because we were using field-collected samples, any larva that was parasitized was removed from the analysis, although we could only determine parasitism if the larva survived to pupate. In 2012, the field-collected larvae were not reared to adults, so there was an unknown level of parasitism, but in 2013, the larvae were reared and parasitized individuals were removed. Of the 54 larvae used in 2013, 14 were parasitized and thus removed from the analysis. Any larva not showing signs of parasitism remained in the analysis. All larvae at temperatures greater than 25°C were reared from eggs in the laboratory, so there were no parasitoids in that population. To determine the growth rate at each temperature, a linear regression model was fit for each individual larva, where larval mass was regressed against time (R Core Team 2013). If there was no significant evidence to suggest that the slope of the regression was nonzero, the growth rate of the larva was determined to be zero. The slope terms (growth rates) for the larvae at each temperature were averaged to give the representative rate at that temperature.

**Model Fitting.** We analyzed the fit of three models (linear, cubic, and Lactin [Lactin et al. 1995]) to best describe the relationship between growth rate and temperature. The linear model is often used to determine the number of DDs needed for development (e.g. Tobin et al. 2001, Kontodimas et al. 2004). Because we measured growth rate directly, as a function of weight gain rather than the inverse of developmental time, the linear model equation could not be used to calculate DDs directly. Likewise, the cubic and Lactin models could not be used to directly predict developmental time. Instead, in order to create a DD model for *S. sulfureana*, we used each model to determine the upper and lower developmental thresholds. These thresholds could then be used to calculate DDs separately. Model fitting was done using the Gauss (for the linear and cubic models) or Marquardt (for the Lactin model) iterative methods (PROC GLM or PROC NLIN, SAS Institute Inc. 2013).

**Linear Model.** The linear equation was as follows:

\[ r(T) = a(T) + b \]  

(1)

where \( r(T) \) is the growth rate (mg/d), \( T \) is temperature (°C), and \( a \) and \( b \) are fitted parameters. The x-intercept corresponds to the lower temperature threshold. An upper threshold cannot be calculated using this model.

**Cubic Model.** The cubic model, also known as the Harcourt Equation (Harcourt and Yee 1982, Briere and Pracros 1998, Kontodimas et al. 2004), was the following:

\[ r(T) = a(T^3) + b(T^2) + c(T) + d \]  

(2)

where \( T \) is temperature (°C) and \( a, b, c, \) and \( d \) are empirical constants. The lower and upper thresholds were determined by calculating the x-value at the “peak” and “trough” of the 3rd-order polynomial (cubic) function.

**Lactin Model.** The third equation selected was a nonlinear model developed by Lactin et al. (1995). This model was selected over other nonlinear models.
because it allowed for the direct calculation of a lower and upper temperature threshold. The equation used was:

\[
 r(T) = e^{\rho T} - e^{\left(\rho T_{\text{max}} - \frac{T_{\text{max}} - T}{\Delta}\right)} + \lambda
\]  

where \( T \) is temperature (°C), \( T_{\text{max}} \) is the lethal temperature, \( \rho \) is the rate of increase to the optimum temperature, \( \Delta \) is the difference between \( T_{\text{max}} \) and the optimal temperature for development, and \( \lambda \) allows for the equation to cross the x-axis (Lactin et al. 1995, Briere and Pracros 1998, Tobin et al. 2001, Kontodimas et al. 2004). However, because our units of rate were not 1/time, the parameters lost their biological meaning and were regarded as purely empirical constants. The lower threshold was calculated by solving for the x-intercept and the upper threshold was determined by solving for the x-value at the peak of the curve.

Results and Discussion

The temperature in each growth chamber and the average larval growth rate at each temperature were determined empirically (Table 1). Most of the variation in the temperature in each growth chamber was due to temperature fluctuation as the lights turned on and off. Many larvae had growth rates that were not significantly different from zero, especially at the lower temperatures and very highest temperature. At temperatures below 15°C, 60% had no measurable growth, whereas at temperatures above 15°C, only 24% had zero growth. Interestingly, at the highest temperature (38.6°C), 69% of larvae had growth rates equivalent to zero. The growth rate of each larva (including zero growth where applicable) was included in the average growth rate for a given temperature. In 2013, when larvae were reared to adults to determine if they were parasitized, there were 6, 5, and 3 parasitized larvae that were removed from the analysis at 6.6, 9.2, and 13.3°C, respectively.

The linear, cubic, and Lactin models were fit to our empirical data (Fig. 2A–C), and model parameters were determined for each (Table 2). For the linear model (Fig. 2A), the fit was initially relatively poor (R² = 0.427), but past work has suggested that the removal of growth data deriving from extremely high temperatures may be necessary for the linear fit (Logan et al. 1991, López et al. 2001, Aghdam et al. 2009). This type of data removal is done primarily to provide a better fit among the lower and mid-range temperatures, thereby allowing for a better estimate of the x-intercept of the line (i.e., the lower growth threshold). When the two highest temperatures, 32.8°C and
38.6°C, were excluded, the linear model had a good fit (R² = 0.574).

The cubic model was highly predictive of larval growth rate and incorporated all data (R² = 0.914; Fig. 2B). The upper threshold isolated by the model was very similar to what our data suggested (the model predicted 29.89°C and our highest growth rate was observed at 29.1°C). The lower threshold, determined by finding the x-value at the trough of the curve, was 9.97°C (Table 2). Although there was some growth at 9.2°C and 9.4°C, 45% of the larvae did not have significant growth at those temperatures. This is not surprising because at the lower threshold, the relationship between temperature and growth rate is curvilinear or asymptotic; thus, there will always be a very small amount of growth measurable at temperatures below the model’s threshold. Therefore, even if some growth was observed at those temperatures, at a field-scale, growth occurring at temperatures below the lower threshold would be relatively trivial.

The Lactin model was also a good fit (R² = 0.913; Fig. 2C); however, the predicted thresholds were different from what our data suggested. The upper threshold calculated by this model was higher than expected. The model predicted the upper threshold to be 32.06°C, but the highest rate observed was at 29.1°C and we saw a decrease in growth rate by 32.5°C. Additionally, the lower threshold predicted by this model, 8.34°C, was likely an underestimate because we did not observe any growth at 7.8°C and most of the larvae did not have positive growth rates until temperatures were above 11.2°C.

All three models were similarly predictive of growth rate as a function of temperature, but they differed in their respective predictions of growth thresholds. For the upper threshold, the linear model could not predict a threshold, the cubic model predicted the upper threshold to be 29.89°C, and the Lactin model predicted the threshold to be 32.06°C. In Wisconsin, summer temperatures often go above 30°C, so it is important that the selected model accurately reflect the upper threshold for the S. sulfureana. The cubic model prediction is closer to the temperature at which we observed the highest growth rate. Regarding the lower threshold, the linear and Lactin models both had similar predictions (~8.4°C), which may be a bit too low; as the majority of the larvae did not have growth rates significantly above zero until 11.2°C. Moreover, 10 of the 15 larvae did not have significantly positive growth rates even at 13.3°C. This number might be slightly inflated due temperature fluctuations in the growth chamber (SD = 1.05°C), but it also indicates that even at this temperature many larvae may have limited mobility due to the cold. Based on this information, the lower threshold predicted by the cubic model (9.97°C) is the most reasonable. Other agricultural pests, including the codling moth Cydia pomonella L. (Lepidoptera: Tortricidae) also have a lower temperature threshold of 10°C (Riedl et al. 1976, Pitcairn et al. 1992).

Altogether, the larval growth data and cubic model fit support our conclusion that S. sulfureana development is a predictable function of temperature between 9.97°C and 29.89°C. We further suggest that when using these thresholds within a model for DD accrual, the intermediate “cut-off” in the daily computation of DDs should be used rather than the commonly used horizontal or vertical cut-offs. The reason for this is that while the developmental rate does decline significantly at temperatures above the upper threshold, the decline is gradual and does not drop to zero immediately, as would be indicated by the vertical cut-off. Having identified these thresholds, future work should focus on determining the number of DDs associated with developmental benchmarks, such as the initiation of flight, oviposition, egg hatch, and larval development. With this information, we will be able to compile a complete phenology model for S. sulfureana to allow for predictions of each life stage event, which will improve the timing of insecticide applications and other nonchemical treatment methods in cranberries.

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