

Supercooling Point of Bean Leaf Beetle (Coleoptera: Chrysomelidae) in Minnesota and a Revised Predictive Model for Survival at Low Temperatures

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ABSTRACT Integrated pest management (IPM) programs for the bean leaf beetle, *Cerotoma trifurcata* (Förster), could benefit from an ability to forecast the magnitude and timing of early-season infestations. The objectives of this study were to examine the supercooling point (SCP) of adult *C. trifurcata* as an index of its cold hardiness, monitor overwintering survival, and revise an existing model used to predict the overwintering survival of this pest in wooded areas as a function of low-temperature accumulation. Within a year, the mean SCP of *C. trifurcata* ranged from -8.9 to -6.0°C . Soil temperatures dropped below the lowest mean SCP (i.e., -8.9°C) in only 2 of 11 yr (1994–2004). In-field survivorship studies showed that adult *C. trifurcata* successfully overwintered in Minnesota (34–59% survival). This species survived well in years when the existing model predicted zero or low survival. In contrast, our revised model predicted more closely the overwintering survival of this species in southern Minnesota. However, other overwintering mortality factors should be studied to improve our understanding of how well *C. trifurcata* overwinters in temperate regions.

KEY WORDS *Cerotoma trifurcata*, cold hardiness, winter mortality, modeling

THE BEAN LEAF BEETLE, *Cerotoma trifurcata* (Förster), feeds primarily on cultivated and wild legumes throughout the eastern United States (Kogan et al. 1980). However, when legumes are unavailable, *C. trifurcata* has been documented feeding on nonlegumes, such as cucurbits (Koch et al. 2004a) and several wild herbs (Helm et al. 1983). Damage to cultivated legumes results directly from adult feeding on leaves and pods and indirectly through transmission of plant pathogens (Kogan 1980). In the midwestern United States, *C. trifurcata* has historically been considered a relatively minor pest, occasionally causing economic loss in soybeans (Kogan et al. 1980, Smelser and Pedigo 1992). However, in recent years, the abundance and pest status of *C. trifurcata* has increased (Hutchison et al. 2004, Lam and Pedigo 2004), resulting in a need to evaluate new integrated pest management (IPM) tactics for this pest (Koch et al. 2005, Krell et al. 2005). In particular, the early-season management of overwintered adult *C. trifurcata* has been suggested as an important tactic to reduce population buildup and crop damage (Krell et al. 2004).

Early season management of insect pests can benefit from an ability to forecast the magnitude and timing of infestations. The overwintering survival of insects can be positively correlated to the magnitude of infestations (Leather et al. 1993). In temperate regions, the overwintering survival of an insect relates pri-

marily to its cold hardiness and the protection received at its overwintering site (Leather et al. 1993). Insects with the ability to survive exposure to freezing temperatures are typically classified as freeze tolerant or freeze intolerant (Salt 1961). As the classification implies, freeze-tolerant insects can survive extracellular ice formation (Baust and Rojas 1985); conversely, freeze-intolerant insects cannot, and they avoid ice formation by depressing the freezing point of their body fluids (i.e., supercooling) (Baust and Rojas 1985). The supercooling point (SCP), defined as the temperature at which spontaneous freezing occurs (Zachariassen 1985), along with the time-temperature effect on mortality, has been used as an index of insect cold hardiness (Lam and Pedigo 2000b, Koch et al. 2004b).

Cerotoma trifurcata overwinter as adults in leaf litter in forests and in crop residue in fields (Loughran and Ragsdale 1986, Lam and Pedigo 2000a, b). The cold hardiness of *C. trifurcata* has received some attention (Lam and Pedigo 2000a, b). In a laboratory study, the time for winter-acclimated adults to reach 50% mortality at various temperatures was <12 min at temperatures below -10°C , and >400 h at temperatures greater than -5°C (Lam and Pedigo 2000b). In Iowa, Lam and Pedigo (2000a) modeled the survival of overwintering *C. trifurcata* as a function of cumulative subfreezing daily mean air temperatures. Recently, it was observed that this model may not be suitable for

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C. trifurcata in Minnesota. Early-planted snap beans have been infested with large populations of *C. trifurcata* in years when the model predicts zero or low survival (W.D.H., unpublished data). The objectives of this study were to examine the SCPs of adult *C. trifurcata* as an index of its cold hardiness, monitor the overwintering survival, and revise the model developed by Lam and Pedigo (2000a) to predict the overwintering survival of this pest in wooded areas in southern Minnesota.

Materials and Methods

SCP Determination. Supercooling points were determined using surface-contact thermometry as described by Carrillo et al. (2004). Adult *C. trifurcata* were immobilized at $\approx 0^{\circ}\text{C}$ for 2 min before thermocouple attachment. Individual insects were attached to 24-gauge copper-constantan thermocouples using a thin layer of high vacuum grease (Dow Corning, Midland, MI) and placed at the center of 19 by 19 by 19-cm polystyrene containers with a starting temperature of $\approx 0^{\circ}\text{C}$. Containers were closed with rubber stoppers and transferred to an ultra-low-temperature freezer (Revco Scientific, Asheville, NC) at -80°C to cool insects at a rate of $\approx 1^{\circ}\text{C}/\text{min}$ (Carrillo et al. 2004). A total of five containers, with two insects per container, were used per cooling period. Multiple consecutive cooling periods were needed to attain the final sample size. Temperatures were recorded with a multi-channel data logger (Personal Daq/56 data acquisition system; Iotech, Cleveland, OH) that transferred data at 1-s intervals through a USB cable into a computer. Data were downloaded to a spreadsheet and graphed as a scatter plot with the SCP visible as the lowest temperature reached before freezing. Freezing was visualized by a sudden increase in temperature during an otherwise decreasing trend, indicating a heat release during the phase change (Lee 1991).

Effect of Season on SCP. In 2004, SCPs were determined at different intervals of time from 20 February to 15 December with sample sizes ranging from 8 to 49 individuals per measurement. Adult *C. trifurcata* (sex not determined) were collected (using a sweep net) from a soybean field at the University of Minnesota Outreach, Research, and Education (UMORE) Park, Rosemount, MN. During the winter months, adults were obtained from the cages described below. Supercooling point data were transformed to the power of 0.25 to improve normality and homogeneity of errors (Box-Cox procedure; MacAnova 2002), and analyzed using analysis of variance (ANOVA; PROC GLM; SAS Institute 1995). Month was the only predictor included in the ANOVA model. Means were separated using the Ryan, Einot, Gabriel, Welch q test. Supercooling points were compared with minimum annual temperatures measured at 1 cm below the soil surface from 1994 to 2004. Temperatures were obtained from the weather station located at the St. Paul campus of the University of Minnesota.

Effect of Acclimation on SCP. The effect of cold acclimation under laboratory conditions was deter-

mined for adult *C. trifurcata* (sex not determined) using the SCP as an index. Adults were collected (using a sweep net) from a soybean field at UMORE Park, Rosemount, MN. Two acclimation regimens were evaluated. In regimen A, the SCP of adults ($n = 15$) collected on 23 August 2004, transferred immediately to a programmable growth chamber (Percival Scientific, Perry, IA) at 5°C , and maintained at that temperature for 24 d was compared with the SCP of adults ($n = 15$) collected on 15 September 2004 and maintained for 1 d at 25°C (i.e., the beetles were collected on different dates from the same location, but the SCPs of both groups were measured simultaneously). In regimen B, adults collected on 1 September 2004 were separated into two groups. The SCP of the first group ($n = 20$) was measured after 1 d at 25°C and compared with the SCP of the second group ($n = 13$), which was measured after 14 d at 5°C followed by 29 d at 10°C (i.e., the beetles were collected on the same date from the same location, but the SCPs of each group were measured on different dates).

Untransformed SCP data were analyzed using ANOVA (PROC GLM; SAS Institute 1995), after the Box-Cox procedure was used to determine if transformations of the data were needed to fulfill the assumptions of ANOVA (MacAnova 2002). The presence or absence of acclimation was the only predictor included in the ANOVA model. In addition, SCPs were tested for normality using the Royston (1992) modification to the Shapiro-Wilk W -test (Shapiro and Wilk 1965; PROC UNIVARIATE; SAS Institute 1995). Furthermore, median, mean \pm SE, and range were used to describe the distribution of SCPs for adults after different treatments.

Effect of Winter Conditions on Adult Survival. In-field survivorship experiments were established in autumn of 1983, 1984, 2003, and 2004 and were carried out through spring of the following year. Survivorship data from the 1980s were obtained from experiments conducted by Loughran (1985). In October 1983 and 1984, adult *C. trifurcata* were collected from litter samples from a wooded windbreak at UMORE Park, Rosemount, MN. Litter samples were bagged, brought to the laboratory, and kept refrigerated at 4°C until adults were separated. Adults (sex not determined) were transferred to individual 30 by 30 by 9-cm cages provided with a 4-cm layer of soil and a 5-cm layer of deciduous leaves (1983, 40 beetles per cage; 1984, 44 beetles per cage). Cages consisted of a wooden frame wrapped with fine-mesh metal screen. Caged adults were placed in the field on 1 November, in a wooded location near the St. Paul campus of the University of Minnesota, St. Paul, MN. Twenty-five cages were used to establish the experiment for both winters. Five cages were brought into the laboratory on the first of each month from December to April, and adult survival was assessed after 24 h at room temperature (i.e., $\approx 25^{\circ}\text{C}$). Survival was defined as the presence of movement when adults were prodded with a pair of soft forceps.

In autumn of 2003 and 2004, adult *C. trifurcata* were collected from litter samples and a soybean field, re-

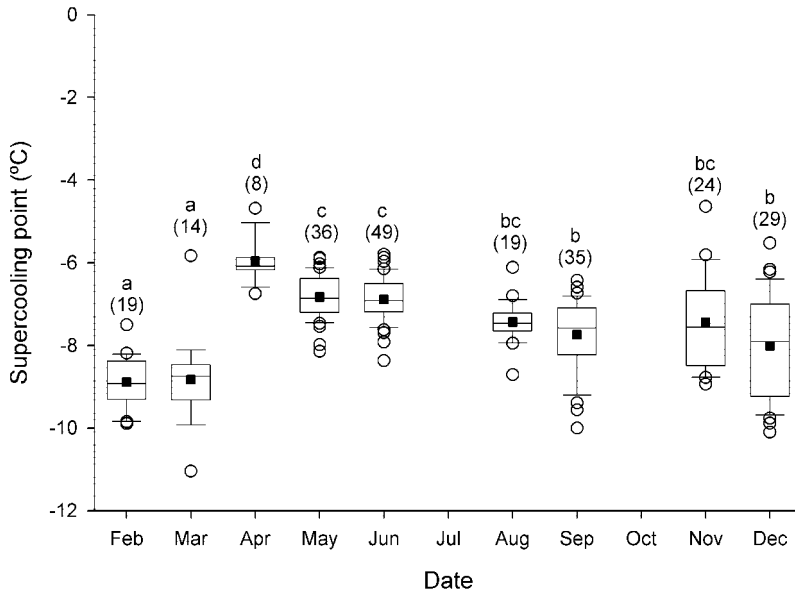


Fig. 1. Seasonal variation of SCPs for field-collected adult *C. trifurcata* from southern Minnesota, 2004. The center bars of the box plots represent the median, the upper and lower ends of the boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, circles represent outliers, and the squares represent the mean. Different lowercase letters above box plots indicate significant differences among mean SCPs ($P < 0.0001$). Numbers in parentheses represent sample size.

spectively, at UMORE Park, Rosemount, MN. Adults (sex not determined) were transferred to 34.48 by 34.48 by 12.24-cm cages (2003, 20–21 beetles per cage; 2004, 40 beetles per cage), which were provided with a 10-cm layer of deciduous leaves. Cages consisted of similar materials used in the overwintering studies described above. Caged adults were placed in a wooded area near the place of collection on 15 November 2003 and 21 October 2004. The experiments were initiated with seven and eight cages in the winters of 2003–2004, and 2004–2005, respectively. For the winter of 2003–2004, cages were retrieved from the field on 20 January ($n = 2$), 19 February ($n = 2$), 18 March ($n = 2$), and 28 April ($n = 1$) 2004. For the winter of 2004–2005, cages were retrieved from the field on 18 November ($n = 2$) and 14 December ($n = 2$) 2004 and on 8 February ($n = 2$) and 28 March ($n = 2$) 2005. For all cages, adult survival was assessed as previously described.

Proportionate mortality data were arcsine-square-root-transformed (Southwood and Henderson 2000) and analyzed separately for each winter using ANOVA (PROC GLM; SAS Institute 1995). Month within each winter was the only predictor included in the ANOVA models. Means were separated using the REGWQ test.

Survivorship Model. The predictive survivorship model, developed by Lam and Pedigo (2000a) for overwintering adult *C. trifurcata* in wooded areas ($y = -0.0954x + 13.5486$; hereafter referred to as ISU model [Iowa State University]), was revised to accommodate conditions in southern Minnesota. A linear regression analysis (Arc version 1.06; Cook and Weisberg 1999) of the mean percentage of mortality

versus the cumulative cooling degree-days (CCDDs) was performed for the winters of 1983–1984, 1984–1985, and 2003–2004. Mean percentage of mortality for adults was obtained from the experiments examining the effect of winter temperatures on adult survival as described above. The CCDD was the only predictor used in the regression models because winter temperature has been considered the most important factor affecting overwintering mortality of *C. trifurcata* (Lam and Pedigo 2000a). The CCDD was calculated as:

$$CCDD = \sum_{i=1}^n (Tr - T_{m_i}) * t_i \quad [1]$$

where Tr is the reference (threshold) temperature ($^{\circ}C$), T_m is the measured temperature ($^{\circ}C$; Midwestern Regional Climate Center, Champaign, IL), t is the time interval (i.e., 1 d), and i is the number of observations from 1 to n . To select the appropriate Tr, separate linear regressions of the percentage of mortality versus CCDDs calculated with Tr ranging from -10 to $10^{\circ}C$ (at intervals of $1^{\circ}C$) were performed. From each regression, the residual sum of squares (RSSs) was plotted versus its respective Tr to determine the temperature(s) that yielded the lowest error in the model. When multiple Tr's yielded a similar RSS, the Tr closest to $0^{\circ}C$ was selected. For validation, the resulting revised model was plotted with the observed survival of *C. trifurcata* at UMORE Park, Rosemount, MN, in the winter of 2004–2005.

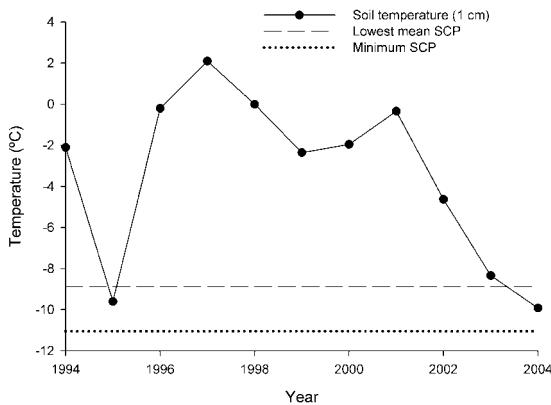


Fig. 2. SCPs of adult *C. trifurcata* plotted with minimum annual temperatures measured at 1 cm below the soil surface. The lowest mean SCP represents the average of 19 individuals collected in February 2004. The minimum SCP represents the lowest value measured for an individual.

The predicted overwintering survival of *C. trifurcata* from the ISU and revised models was compared at three locations in Minnesota (Crookston, Morris, and Waseca) and three locations in Iowa (Mason City, Ames, and Leon) from 1 October to 1 April from 1974 to 2004 (i.e., 30 winters). Historical air temperatures were obtained from the Midwestern Regional Climate Center, Champaign, IL, and used to calculate a CCDD for each location. Predicted proportionate survival at each location was arcsine-square-root-transformed and analyzed using ANOVA (PROC GLM; SAS Institute 1995). Model (i.e., ISU and revised), location, and their interaction were included as predictors in the ANOVA model. Means were separated using the REGWQ test.

Results and Discussion

Effect of Season on SCP. The mean SCP of adult *C. trifurcata* differed significantly through time ($F = 21.19$; $df = 8,224$; $P < 0.0001$; Fig. 1). The mean SCP ranged from -8.9°C in February to -6.0°C in April 2004 (Fig. 1). It appeared that adult *C. trifurcata* were

able to adjust their SCPs in response to seasonal changes; however, the magnitude of this change was not as discernible as it has been observed for other insect species (e.g., Koch et al. 2004b, Carrillo and Cannon 2005). According to Boiteau et al. (1980) and Lam and Pedigo (2000b), the threshold temperature that causes a significant increase in mortality in *C. trifurcata* is between -10 and -5°C . Although we did not conduct studies on the lower lethal temperature (i.e., the temperature that causes a particular percentage of mortality at a constant time of exposure), it seems that the mean SCP is the absolute threshold temperature between death and survival. However, individuals can experience some mortality at temperatures above this point (Bale 1996). Nevertheless, it seems that a mean SCP of -8.9°C could confer *C. trifurcata* protection from freezing temperatures and mortality in their overwintering microhabitat. From 1994 to 2004, minimum annual soil temperatures at 1 cm below the soil surface dropped below the lowest mean SCP in only 2 of 11 yr (Fig. 2). However, these soil temperatures and the temperature of the soil surface under leaf litter reported by Lam and Pedigo (2000b) never reached the minimum SCP (-11.0°C) observed in this experiment (Fig. 2), suggesting that a fraction of the population may not experience freezing. Furthermore, the depth of snow and leaf litter may have a strong insulating effect on microclimate at the soil surface (Leather et al. 1993, Lam and Pedigo 2000a, b).

Effect of Acclimation on SCP. Cold acclimation and gut-content evacuation before overwintering have been considered important factors increasing the supercooling capacity of freeze-intolerant insects (Sømme 1982, Baust and Rojas 1985). Lam and Pedigo (2000b) hypothesized that *C. trifurcata* adults may depress their SCPs by clearing their guts, as observed by the presence of excreta pellets, during acclimation at low temperature. However, the extent of supercooling in *C. trifurcata* has not been reported in the literature. In this study, SCPs were significantly affected by cold acclimation in regimens A ($F = 4.88$; $df = 1,28$; $P = 0.0356$) and B ($F = 14.41$; $df = 1,31$; $P = 0.0006$; Table 1). In particular, the mean SCP for cold-acclimated adults was significantly depressed by

Table 1. SCP comparison for laboratory-acclimated versus nonacclimated *C. trifurcata* adults

Comparison ^a	<i>n</i>	Median (°C)	Mean \pm SE (°C) ^b	Range (°C) min, max	Shapiro-Wilk (W-value) ^c	<i>P</i> ^d
Regimen A		-7.46				
Nonacclimated	15		$-7.43 \pm 0.14\text{a}$	-10.45, -6.49	0.97	0.864
Acclimated	15	-8.02	$-8.10 \pm 0.27\text{b}$	-8.34, -6.43	0.96	0.762
Regimen B		-7.61				
Nonacclimated	20		$-7.97 \pm 0.22\text{a}$	-10.00, -6.74	0.92	0.097
Acclimated	13	-9.05	$-9.29 \pm 0.26\text{b}$	-11.07, -7.78	0.98	0.960

^a Regimen A indicates a comparison of beetles collected on 23 Aug. 2004 and maintained for 1 d at 5°C versus beetles collected on 15 Sept. 2004 and maintained for 1 d at 25°C . Regimen B indicates a comparison of beetles collected on 1 Sept. 2004, with some of them measured after 1 d at 25°C versus others measured after 14 d at 5°C followed by 29 d at 10°C .

^b Means within a regimen followed by different letters are significantly different ($P < 0.05$; SAS Institute 1995).

^c Test for normality, $0 < W\text{-value} \leq 1$.

^d Probability that the observed data came from a normal distribution.

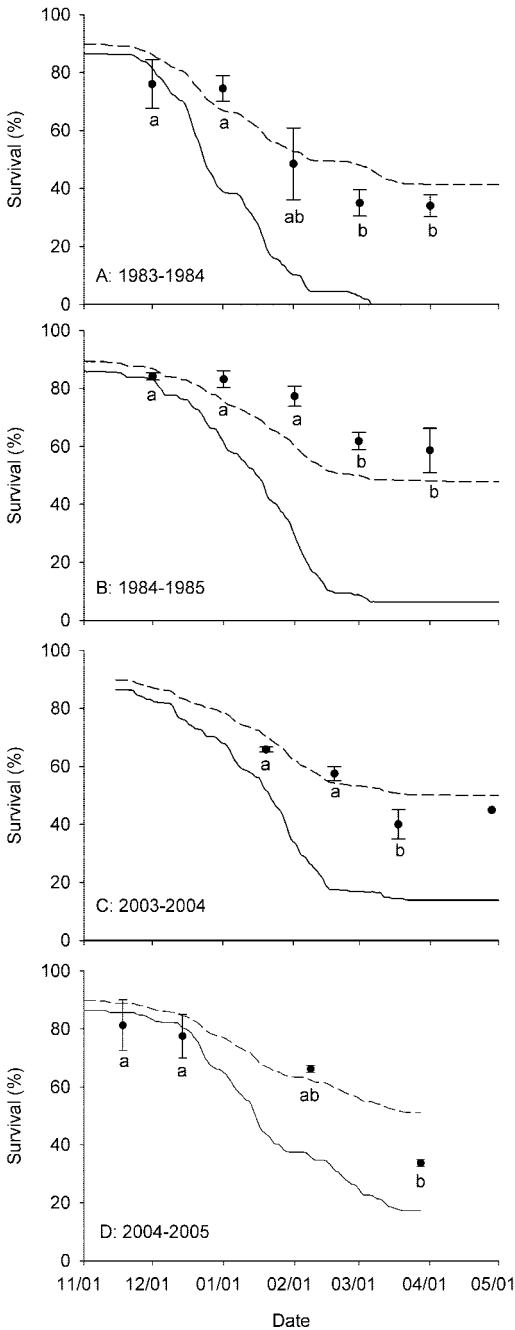


Fig. 3. Observed (mean \pm SE; ●) and predicted (ISU model, solid line; revised model, dashed line) percentage of overwintering survival of *C. trifurcata* in southern Minnesota. The lines for the revised model were based on data from A, B, and C. Means followed by the same lowercase letters are not significantly different ($P > 0.05$). For the winter of 2003–2004, the last mortality estimate was based on a single replication; therefore, it was not included in the ANOVA model.

0.67 and 1.32°C in regimens A and B, respectively (Table 1). As suggested by Lam and Pedigo (2000b), this depression of SCPs was possibly associated with

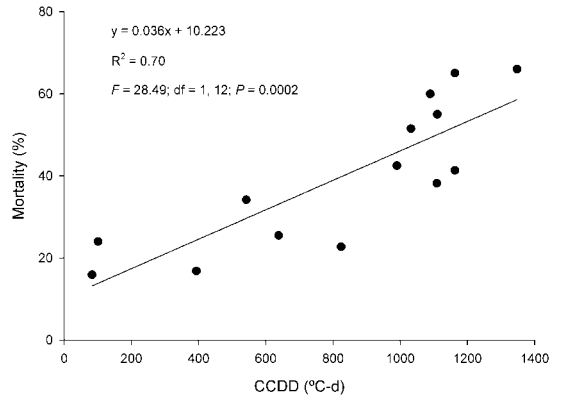


Fig. 4. Regression analysis of percentage of survival of *C. trifurcata* versus the CCDDs calculated with a threshold temperature of 3°C.

gut clearing, indicated by the abundance of excreta pellets produced by the adults.

Effect of Winter Conditions on Adult Survival. Mean percentage of survival significantly decreased over time for the winters of 1983–1984 ($F = 7.20$; $df = 4,20$; $P = 0.0009$), 1984–1985 ($F = 8.23$; $df = 4,20$; $P = 0.0004$), 2003–2004 ($F = 16.11$; $df = 2,3$; $P = 0.0249$), and 2004–2005 ($F = 9.77$; $df = 3,4$; $P = 0.0260$; Fig. 3). However, the observed mean percentage of survival at the end of the winters ranged from 34% in March 2005 to 59% in April 1985 (Fig. 3), indicating that a high percentage of beetles may survive to infest early-planted crops (Koch et al. 2004a, 2005). This relatively high percentage of survival may have resulted from the protection conferred by the overwintering microhabitat and by the intrinsic cold tolerance of *C. trifurcata* (e.g., Lee and Denlinger 1991, Leather et al. 1993).

Survivorship Model. The ISU model appears to be useful for predicting *C. trifurcata* survival in Iowa (Lam and Pedigo 2004). However, this model underestimated survival of adult *C. trifurcata* in Minnesota in all years studied (Fig. 3). For example, in the winter

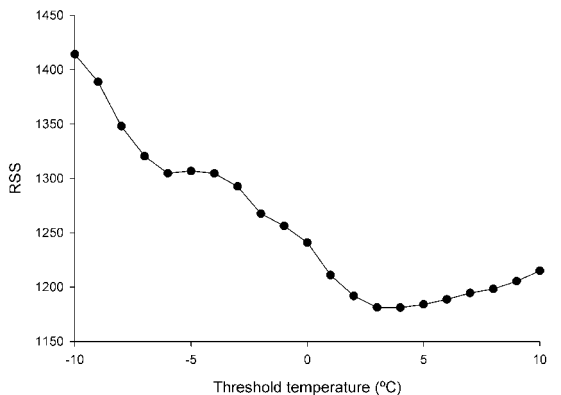


Fig. 5. Relationship between the RSS and various threshold temperatures used to calculate the CCDDs.

Table 2. Predicted overwintering survival of *C. trifurcata* adults based on air temperature from 1 Oct. to 1 April for 30 winters (1974–2004) at different locations in Minnesota and Iowa

State/location	Coordinates (degree, min)		Mean \pm SE survival (%) (min, max)		Probability of zero percent survival	
	Latitude	Longitude	ISU model	Revised model	ISU model	Revised model
Minnesota						
Crookston	47, 47'	96, 35'	0.1 \pm 0.1 (0, 2.6)	23.4 \pm 2.3 (0, 46.0)	0.97	0.03
Morris	45, 34'	95, 52'	2.4 \pm 0.9 (0, 20.3)	32.5 \pm 2.2 (8.6, 51.6)	0.77	0
Waseca	44, 04'	93, 31'	6.8 \pm 1.8 (0, 27.7)	40.4 \pm 2.0 (16.0, 55.9)	0.60	0
Iowa						
Mason City	43, 09'	93, 11'	13.6 \pm 2.7 (0, 46.4)	47.1 \pm 1.7 (28.7, 63.4)	0.37	0
Ames	42, 01'	93, 48'	29.3 \pm 3.3 (0, 56.9)	57.0 \pm 1.6 (36.7, 70.7)	0.07	0
Leon	40, 43'	93, 37'	39.0 \pm 3.0 (7.7, 65.5)	62.0 \pm 1.3 (46.7, 73.9)	0	0

Location, model, and the interaction location by model were significantly different ($P < 0.0001$).

of 1984–1985, the ISU model predicted only 6% survival when the observed survival was 59% (Fig. 3B). Thus, we concluded that the ISU model is not suitable for predictions of overwintering survival in southern Minnesota. Therefore, we revised the ISU model using overwintering mortality data from Minnesota (Fig. 4, A–C). The resulting model followed the form:

$$y = 0.036 [\pm 0.0067]x + 10.223 [\pm 6.1612]$$

where y is the overwintering mortality of *C. trifurcata* and x is the CCDD calculated with a threshold temperature (Tr) of 3°C. Values for Tr of 3 and 4°C yielded the lowest RSS; however, a Tr of 3°C was selected because it was the closest temperature to 0°C (Fig. 5). The revised model provided a good fit to the data used for parameter estimation (Fig. 3, A–C). In addition, the revised model appeared to predict well the overwintering mortality of *C. trifurcata* during the independent validation year until 8 February (Fig. 3D). However, by 28 March 2005, the survival predicted by the revised model (51%) was considerably greater than the observed (34%; Fig. 3D). This discrepancy may be a result of other biotic (e.g., pathogens) or abiotic (e.g., rainfall and freeze-thaw cycles) factors during late winter and early spring, not included in our model, which could contribute to the overwintering mortality of this species.

The consistently lower percentages of survival predicted by the ISU model compared with the revised model (Fig. 3) could be explained by the different methods used to assess overwintering mortality between the two studies. Lam and Pedigo (2000a) estimated mortality by sampling the natural population (i.e., not in cages) of beetles in their overwintering sites through time and compared that to the initial density of beetles at the beginning of winter. In our study, mortality through winter was estimated based on a known initial density of beetles in cages. Therefore, Lam and Pedigo (2000a) could have overestimated mortality because of temperature because beetles could have been exposed to other mortality factors (e.g., predation by small mammals), whereas our methods likely excluded them. Although our revised model could underestimate mortality in some years (e.g., Fig. 3D), it seems that our estimates may follow more closely the overwintering mortality of *C. trifur-*

cata under natural conditions in southern Minnesota, as indicated by the damage observed in early-planted snap beans in years when the ISU model predicts zero or low *C. trifurcata* overwintering survival (W.D.H., unpublished data). Thus, mortality factors excluded by the cages may be less important in southern Minnesota than in Iowa. The importance of these additional mortality factors may account for the high percentage of missing beetles (16.1–65.6%) reported by Lam and Pedigo (2000a).

The predicted percentage of survival of overwintering *C. trifurcata* significantly increased with decreasing latitude ($F = 100.36$; $df = 5,348$; $P < 0.0001$; Table 2). In addition, the percentage of survival predicted by the ISU model was significantly lower than that predicted by the revised model ($F = 620.47$; $df = 1,348$; $P < 0.0001$; Table 2). This trend also was observed when both models were used to predict the percentage of survival in our field studies (Fig. 3). Furthermore, the interaction of location and model also was significant ($F = 7.80$; $df = 5,348$; $P < 0.0001$).

A model that predicts overwintering mortality based on a single “most important” factor may fail in years when other generally “less important” factors vary outside their range from the years used to develop the model. Therefore, future work is required to determine additional factors such as predation, precipitation, and freeze-thaw cycles, which could influence mortality of overwintering *C. trifurcata* during late winter or early spring months in Minnesota. In addition, mortality of *C. trifurcata* at other latitudes should be examined to determine the suitability of the model.

In conclusion, our results show that adult *C. trifurcata* successfully overwinters in southern Minnesota despite the limited capacity to seasonally depress their SCP. In addition, this species survives well in years when the ISU model predicts zero or low survival. Our revised model predicts more closely the overwintering survival of this species in southern Minnesota and may allow for more informed early-season management decisions. However, failure of the model to accurately predict the overwintering survival of this species may occur in years when other factors become more influential. A better understanding of how well

C. trifurcata overwinters in temperate regions should aid in its early-season IPM.

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