PREDICTING BOLL WEEVIL OVERWINTERING SURVIVAL AND SPRING EMERGENCE IN THE ROLLING PLAINS OF TEXAS

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Abstract

A climatic data-based analysis was performed to quantify the overwintering survival and emergence of diapausing boll weevils in the Rolling Plains of Texas. The analysis described four relationships that enabled estimations of 1) the amount of degree-days required for a cohort to begin spring emergence, 2) the amount of degree-days required for the cohort to complete emergence, 3) overwintering survival, and 4) cumulative emergence. Both overwintering survival and emergence were influenced by the day of the year when the weevils were placed in the overwintering habitat (DOY_{in}), the amount of rainfall, and habitat temperatures experienced by the weevils during diapause. Multiple least squares regression analyses describing the degree-days required for the weevils to start emergence (DD_{start}) and the degree-days required for all weevils to emerge (DD_{emerg}) explained 88 and 77% of the variability in the data, respectively. With independent data, 75 and 36% of the variability were explained for DD_{start} and DD_{emerg}, respectively. Multiple regression analysis with DOY_{in}, negative degree-days, rainfall, DD, and their first order interactions explained 99% of the variability in overwintering survival. With independent data, 74% of the variability was explained by the survival function. The spring/summer emergence pattern for the overwintering weevils was described by a sigmoid function that explained 95 and 92% of the variability for the verification data set and the independent data set, respectively.

Introduction

The boll weevil, *Anthonomus grandis* Boheman (Coleoptera: Curculionidae), overwinters as an adult in a state of facultative diapause in most temperate regions of the United States (Brazzel and Newsom 1959). In the Rolling Plains of Texas, boll weevils initiate diapause in early August (Sterling and Adkisson 1974) with spring/summer emergence from overwintering habitats continuing in some cases to mid-August the following year (Carroll and Rummel 1985, Slosser and Fuchs 1991). The proportion of diapausing weevils that successfully overwinter is believed to be dependent on timing of diapause initiation (Fenton and Dunnam 1927, Sterling 1971, Wade and Rummel 1978, Rummel and Carroll 1983), winter severity as reflected by low temperatures and rainfall (Pfrimmer and Merkl 1981, Price et al. 1985, Stone et al. 1990), and by the insulating capacity of the overwintering habitat (Beckham 1957, Bottrell 1983, Bottrell et al. 1972, Carroll et al. 1993, Slosser et al. 1984, Slosser and Fuchs 1991).

A relationship between the timing of diapause initiation and overwintering survival and emergence has been acknowledged by many authors (Calhoun 1931, Sterling 1971, Taft et al. 1973, Hunter and Pierce 1911, Mitchell et al. 1973, Jones and Sterling 1979, Newell and Dougherty 1909, Wade and Rummel 1978, Rummel and Carroll 1983, Stone et al. 1990). However, this relationship has not been included in previous analyses that predict boll weevil overwintering survival and emergence. Winter severity is an im-portant factor affecting boll weevil overwintering biology, but the relationship between winter severity and boll weevil diapause processes is not clearly understood. Mitchell et al. (1973) reported that the duration of diapause was shortest following cold winters. However, Davis et al. (1967) reported that prolonged cool, dry weather delayed overwintering emergence. Pfrimmer and Merkl (1981) described overwintering survivorship as a function of minimum winter temperature and the number of days during which temperatures were 0.0 °C or below. Price et al. (1985) reported that the duration of exposure of weevils to sub-zero temperatures and the interaction between habitat temperature and rainfall significantly affected overwintering survival, but rainfall alone did not affect survival. Stone et al. (1990) reported that cumulative NDD during the longest consecutive number of days with temperatures below -3.9 °C and the interaction between temperature and rainfall best described overwintering survival and emergence, but the effect of cumulative NDD during the entire overwintering period on boll weevil overwintering survival and emergence was not addressed. The role of over-wintering habitat in modifying the microclimate that weevils experienced during diapause has been largely overlooked (Leggett et al. 1988). Jones and Sterling (1979) showed that predicting overwintering survival and emergence based on ambient weather was inaccurate because overwintering habitats differ in their insulating abilities. Parajulee et al. (1995) documented that the amplitude of the daily temperature cycle in three boll weevil overwintering habitats was dampened by 3 to 4 °C when compared with the daily ambient temperature cycle. Sorenson and House (1995) reported that the temperatures in the leaf litter (habitat not specified) in the Missouri Delta were about 5 °C warmer than air temperatures when air temperatures were at or below freezing. Thus, it is apparent that ambient temperature does not accurately reflect biological activities in the leaf litter habitat, and could lead to a biased estimate of overwintering phenology.

Stone et al. (1990) presented a simulation model that predicted overwintering survival and emergence of boll weevils in the Rolling Plains of Texas. Because the relationships were based on a degree-day time-scale, winter severity, and winter rainfall, the predictive value was greater than provided by earlier models. However, ambient temperature data were used, which did not account for the insulating effect of the leaf litter on overwintering survival and emergence. Although observations suggested that emergence was correlated with the time of entry into overwintering habitat, the effect of timing of entry on subsequent diapausing processes was not considered.

The objective of our study was to quantify the effect of climatic data-based variables on boll weevil overwintering survival and spring/summer emer-gence. The approach presented in this paper significantly improves the current understanding of boll weevil overwintering biology because it uses weather data from overwintering habitats and accounts for the effect of time of entry of diapausing weevils into overwintering habitats. This approach also differs substantially from earlier analyses of boll weevil diapause by validating the functional relationships with independent data.

Materials and Methods

Meteorological Data
Daily ambient minimum and maximum temperatures (°C) and rainfall (cm) data were collected from a tall growth shinnery oak, *Quercus havardii* Rydberg, habitat in Stonewall Co., TX from 1978-85. Ambient temperatures from 1978-85 were converted to leaf litter temperatures following the method of Parajulee et al. (1995). Temperature and rainfall during the years 1986-94 were recorded on an hourly basis in the same habitat, but the temperatures were recorded directly from the leaf litter. Hourly leaf litter temperatures and rainfall were also recorded from two other boll weevil overwintering habitats, low shinnery oak brush, and mesquite-grass pasture, in the same locality during 1992-94. Data loggers (CR-21 Micrologger, Campbell Scientific, Inc., Logan, UT) were used to monitor hourly leaf litter temperatures and rainfall. Litter temperatures were recorded at 5, 2.5 and 1.25 cm depths in tall shinnery oak, low shinnery brush and mesquite-pasture habitats, respectively, the litter depths at which most diapausing weevils reside in those habitats (Slosser and Fuchs 1991).

Biological Data
Boll weevils used in this study were obtained from infested squares collected from cotton fields during late summer and early fall from 9 counties (Concho, Dickens, Haskell, Kent, Knox, Motley, Runnels, Stonewall, and Tom Green) in the Rolling Plains of Texas. Weevils were reared in conditions known to induce a high level of diapause (Slosser and Fuchs 1991). Infested squares were incubated in the laboratory at ($\approx$25 °C; the photoperiodic cycle in the

rearing room was programmed to correspond to the natural photoperiod. Upon emergence from squares, adult boll weevils were fed fresh cotton squares and small bolls (< 2.54 cm dia.) obtained from late plantings of cotton. Weevils that emerged during a 1-wk period were combined to form a cohort. Feeding was continued for 2 more weeks, after which cohorts were placed in overwintering cages (77 cm high and 77 cm i.d. at base; 18 by 14 mesh and 0.23 mm wire dia.). A total of 97 cohorts were released during the 15-yr study, with an average of ($\approx$900 weevils per cohort, and ($\approx$6 cohorts per year. Each cohort was inspected every 2 to 7 d starting from mid-January until mid-August to record the number of weevils emerging from overwinter-ing cages. Overwintering survival was calculated separately for each cohort.

Data Analysis
Cumulative degree-days (DD > 6.1 °C), negative degree-days (NDD < 0.0 °C), and rainfall were calculated for each cohort from the day of the year when a cohort was placed in an overwintering cage (DOY_{in}) to when the first weevil emerged from overwintering (DOY_{start}), and from DOY_{in} to the completion of emergence (DOY_{end}). The threshold for DD was obtained from Curry et al. (1980) while the threshold for NDD was estimated from Slosser et al. (1995) as the highest chilling temperature at which mortality occurred to diapausing weevils. DD, NDD, and rainfall from DOY_{in} to DOY_{start} will hereinafter be referred to as DD_{start}, NDD_{start}, and $Rain_{start}$, respectively. DD and rainfall from DOY_{in} to DOY_{end} will hereinafter be referred to as DD_{Tot} and $Rain_{Tot}$, respectively. There were no NDD after the start of spring emergence. DD and rainfall between DOY_{start} and DOY_{end} are referred to as DD_{emerg} and $Rain_{emerg}$.

Of 97 cohorts released over the 15 overwintering seasons, 21 had one or no weevils emerging the following spring. Data from the remaining 76 cohorts were used in the overwintering survival analysis. Of those 76 cohorts, 20 had limited emergence (< 10 individuals) for which consistent patterns were not obtainable. Only the 56 remaining cohorts were used in the emergence timing and emergence profile analyses.

The 76 cohorts used in the overwintering survival analysis, and the 56 cohorts used to estimate spring emergence were each divided into a parameterization-verification data set, and a validation data set. Both data sets had cohorts representing three levels of DOY_{in} (low, medium, and high levels, representing early, mid-, and late cohorts), and two levels each of NDD_{start} and $Rain_{start}$ (low and high levels), the variables found to have the greatest association with overwintering survival and emergence in the subsequent analyses. This division resulted in 31 and 25 cohorts for the DD_{start}, DD_{emerg}, and emergence profile verification and validation data sets, respectively, and 45 and 31 cohorts for the survival verification and validation data sets, respectively.

An iterative nonlinear multiple least squares regression procedure (JMP®, SAS Institute 1994) was used to quantify the relationships between DD_{start} and DOY_{in}, NDD_{start}, and $Rain_{start}$. The significance of each term was determined using a backward step-wise elimination procedure (Draper and Smith 1981; JMP®, SAS Institute 1995). The 100% emergence point, DD_{Tot}, was calculated by first determining the duration of emergence, DD_{emerg}, and then adding DD_{start} to DD_{emerg}. The DD_{emerg} function was thus a component of the DD_{Tot} function. The approach used to quantify the relationship between DD_{start} and the climatic variables was also used to quantify the relationship between DD_{emerg} and DOY_{in}, NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, and DD_{start}. Overwintering survival was estimated using a survival function, $S = e^{-\alpha}$, where (= f(DOY_{in}, NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, DD_{start}, DD_{Tot}), with a non-linear iterative regression used to derive parameter estimates, with the significance of each term assessed as described previously. Emergence profile data were fit using the following sigmoidal function (Stinner et al. 1975):

$$E_i = (1 - z)^{-z\beta}, \ \alpha \geq 1, \ \beta \geq 0$$

where $z = (DD_{Tot} - \min(\max(DD_{start}, DD_i), DD_{Tot})/DD_{emerg}$; E_i = cumulative proportional emergence on the ith DOY, DD_i = cumulative degree-days (> 6.1 °C) for the ith DOY accumulated from DOY_{in}; (and (= f(DOY_{in}, NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, DD_{start}, DD_{Tot}). An iterative procedure was used to derive parameter estimates, with the significance of each parameter assessed as described previously.

When presenting the results, estimated values refer to those derived when parameterizing the above relationships (verification cohorts), and predicted values refer to those obtained for independent (validation) cohorts. Coefficients of multiple determination (R^2) were calculated based on residuals of observed and estimated/predicted values for DD_{start}, DD_{emerg}, survival, and emergence profile data.

Results

The 15-yr average monthly NDD, rainfall, and DD showed seasonal trends which delineated the year into three broad periods corresponding to the time of entry into winter habitat (late Aug. - late Nov.), overwintering (Dec. - Feb.), and overwintering emergence (early Mar. - late July). All of the NDD were accumulated during the overwintering period, with the exception of a small amount in March. The total NDD accumulated by each overwintering cohort in the study ranged from 0 (a mild winter) to 31.4 (a cold winter) ($\bar{x}$ = 9.5). Both rainfall and DD were highest during the time of entry into winter habitat and overwintering emergence months, and the lowest during overwintering months. On average, 42% of the total rainfall during diapause occurred before the start of weevil emergence ($Rain_{start}$). $Rain_{start}$ ranged from 3.3 to 44.5 cm ($\bar{x}$ = 17.7 cm), while $Rain_{emerg}$ ranged from 12.2 to 35.5 cm ($\bar{x}$ = 24.9 cm). The DD required for the start of

overwintering emergence ranged from 250 to 1198 DD ($\bar{x}$ = 634 DD), while the DD required to complete emergence ranged from 1321 to 2497 DD ($\bar{x}$ = 1856 DD). Overwintering survival ranged from 0 to 50%, with a mean of 11% for the 76 cohorts.

The step-wise non-linear multiple regression analysis indicated that DD_{start} was best estimated as a function of DOY_{in} and NDD_{start} (Fig. 1A, Table 1), with 88% of the variability explained. When the resulting equation was used to predict DD_{start} for the validation data cohorts, 75% of the variability in the data was explained (Fig. 1B). Similarly, the multiple regression analysis indicated that DD_{emerg} was best estimated as a function of DOY_{in}, NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, and DD_{start} (Fig. 2A, Table 1), with 77% of the variability explained. When used to predict DD_{emerg} for the validation data cohorts, the resulting equation explained 36% of the variability in the data (Fig. 2B). Overwintering survival was best estimated as a function of DOY_{in}, NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, DD_{start}, and DD_{Tot} (Fig. 3A, Table 1), with 99% of the variability explained. When the multiple regression equation was used to predict survival for the validation data, 74% of the variability in the data was explained (Fig. 3B). Cumulative proportional emergence (Figs. 4 A and B) was best estimated as a function of NDD_{start}, $Rain_{start}$, $Rain_{emerg}$, DD_{start}, and DD_{Tot} (Table 1), with 95% of the variability explained for the verification data set, and 92% of the variability explained for the validation data set.

Discussion

Time of entry of the diapausing boll weevils into overwintering habitat appears to influence both overwintering survival and the timings of spring/summer emergence. Weevils that were placed in the overwintering habitat later in the season experienced a lower overwintering mortality compared to those placed in the habitat earlier in the season. Brazzel and Newsom (1959) documented a steady decline in fat content in diapausing weevils through the overwintering period, suggesting that stored lipids serve as a source of energy during diapause. Also, the early cohorts primarily feed on squares (flower buds) and/or small bolls and thus accumulate significantly less triglyceride fatty acids compared to latter cohorts that feed on medium and large bolls (Lambremont et al. 1964). The higher the level of triglycerides in diapausing weevils, the greater the overwintering success (Lambremont et al. 1964). The physical condition of weevils that initiate diapause at different times of the season appears to be a major determinant of the timings of emergence, with the assumption that diapause is a metabolite-mediated and hormonally controlled system, as contrasted with a strictly heat unit controlled system (Wilson et al. 1994). The notion of early diapausing cohorts initiating overwintering emergence earlier and late diapausing cohorts later (Newell and Dougherty 1909, Rummel and Carroll 1983, Stone et al. 1990, Wade and Rummel 1978), appears to be a

plausible phenomenon from a biological standpoint, because weevils from cohorts that enter overwintering habitat earlier in the season may deplete their fat reserves earlier which would force them to emerge earlier or die. The higher mortality of early diapausing weevils can also be attributed to the early diapausing cohorts spending more time in the overwintering habitat, which exposes such weevils to biotic and abiotic mortality factors for a longer period of time than weevils in latter cohorts (Price et al. 1985).

Temperature during diapause affected both overwintering survival and spring/summer emergence. The higher the temperature above the lower threshold of boll weevil activity, the higher the overwintering survival, and earlier the initiation of overwintering emergence. Conversely, the greater the degree-days below 0.0 °C, the lower the overwintering survival and later the initiation of emergence. Jones and Sterling (1979) similarly reported earlier initiation of emergence and an extended emergence pattern under a mild weather condition compared to a severe winter. Davis et al. (1967) documented a delay in emergence of overwintered weevils under an extended period of cool weather, while Mitchell et al. (1973) reported an extended emergence following a mild winter. Results of our study showed that winter severity, measured in terms of NDD_{start}, significantly affected timing of overwintering emergence. An increased amount of NDD_{start} delayed the start of spring emergence, while a milder winter favored the weevils to start spring emergence earlier, with the duration of emergence being longer.

Price et al. (1985) found lower overwintering survival associated with lower pre-emergence rainfall. Our analyses showed that rainfall during diapause significantly affected overwintering survival and spring/summer emergence (Table 1). Results of our analyses also indicated that increased rainfall during diapause contributed to higher overwintering survival. A simultaneous occur-rence of both high temperature and high rainfall was more conducive for overwintering survival than the occurrence of either situation alone. Leggett and Fye (1969) reported that only 7% of the diapausing weevils survived to emerge when weevils were exposed to dry conditions compared to 37% emergence under wet conditions. Pfrimmer and Merkl (1981) reported almost complete elimination of boll weevils from the state of Mississippi during 1962-63 due to a simultaneous occurrence of cold temperatures and dry conditions. Henneberry et al. (1990) reported an increased overwintering survival and extended emergence of weevils under moist conditions compared to dry conditions.

Boll weevil overwintering emergence patterns can be predicted with consider-able accuracy, but greater knowledge of factors affecting boll weevil over-wintering survival and the time to completion of overwintering emergence is required for these to be predicted accurately. Although the data base used for these analyses is possibly the largest of its kind, it is somewhat limited when considering the wide range of temperature, rainfall, and times of entry into overwintering habitat represented. Nonetheless, the derived relationships should serve as the best available tools to predict boll weevil overwintering survival and spring/summer emergence within the limits of the climatic range used for parameterization-verification. The present study offers a significant improvement in our understanding of boll weevil overwintering biology. While previous studies used ambient weather to explain weevil activity in the leaf litter, this study treated each cohort independently in calculating weather related parameters, with the time of entry into overwintering habitat one of the most important factors. The present study also placed emphasis on validating the functional relationships with independent data, a process which has been largely neglected in previous studies.

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Table 1. Coefficients of parameters estimated for start of overwintering emergence (DD_{start}), duration of overwintering emergence (Dd_{emerg}), overwintering survival, and emergence pattern functions.

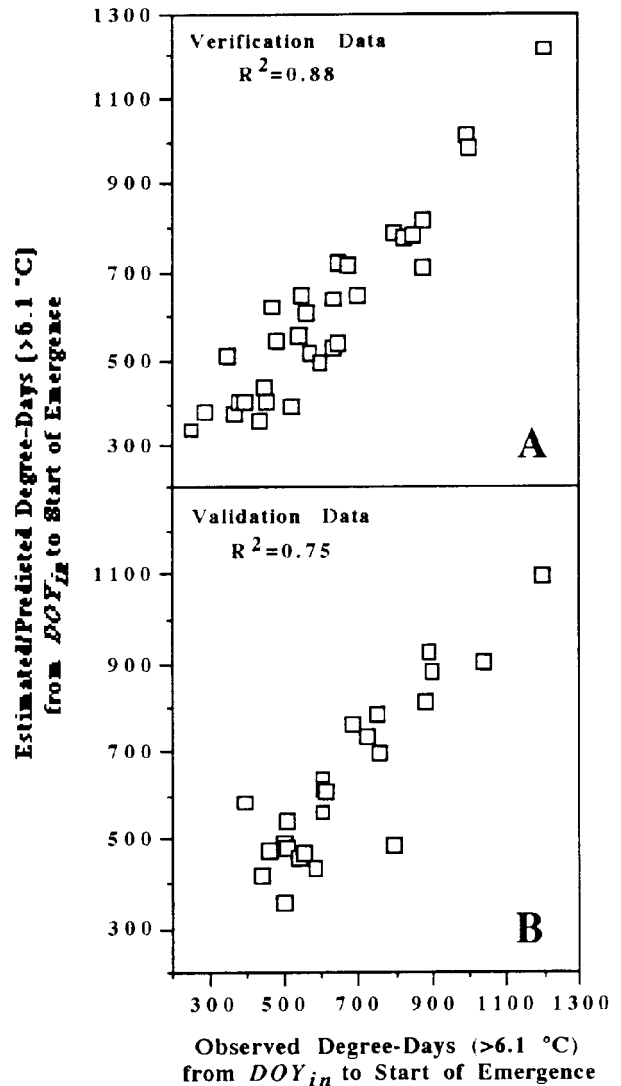| Parameters	DD_{start}	DD_{emerg}	Survival	Emergence a	β
constant	9870.764	-1656.022	157.176096	1.325048	-1.226434
DOY_{in}	-52.960	12.519	-0.321596	–	–
$DOY_{in}2$	0.072	–	–	–	–
NDD_{start}	4.129	-728.982	2.853521	-0.042594	-0.030622
$NDD_{start}2$	–	0.593	–	–	–
$Rain_{start}$	–	47.693	2.409182	0.042162	–
$Rain_{start}2$	–	-1.107	–	–	–
$Rain_{emerg}$	–	292.354	-4.246774	0.033196	0.018358
$Rain_{emerg}2$	–	2.783	0.014985	–	–
Dd_{start}	–	3.814	0.082759	-0.002933	-0.001252
DD_{Tot}	–	–	-0.125060	0.000726	0.001364
$DD_{Tot}2$	–	–	0.000008	–	–
DOY_{in} x NDD_{start}	–	2.254	-0.008982	–	–
DOY_{in} x $Rain_{start}$	–	–	-0.008867	–	–
DOY_{in} x $Rain_{emerg}$	–	-1.219	0.009735	–	–
DOY_{in} x DD_{start}	–	-0.011	-0.000222	–	–
DOY_{in} x DD_{Tot}	–	–	0.000248	–	–
NDD_{start} x $Rain_{start}$	–	–	0.013642	–	–
NDD_{start} x $Rain_{emerg}$	–	-2.485	–	–	–
NDD_{start} x DD_{start}	–	0.172	-0.000576	–	–
$Rain_{start}$ x $Rain_{emerg}$	–	–	-0.020175	–	–
$Rain_{start}$ x DD_{start}	–	0.052	-0.000429	–	–
$Rain_{start}$ x DD_{Tot}	–	–	0.000433	–	–
$Rain_{emerg}$ x DD_{start}	–	-0.110	0.000515	–	–
R^2	0.88	0.77	0.99	0.95	
n	31	31	45	661	

Fig. 1. Relationship between degree-days (>6.1 °C) accumulated by a cohort from the day of year when the weevils were placed in the overwintering habitat (DOY_{in}) to when weevils began to emerge from overwintering habitat and A) estimated cumulative degree-days (verification data), and B) predicted degree-days (validation data).
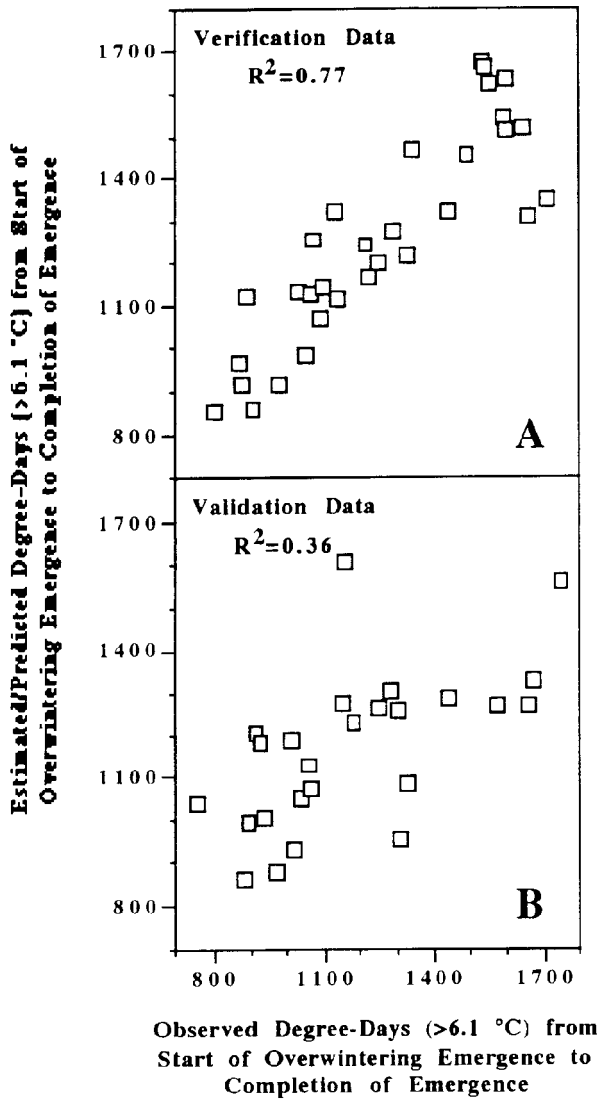
Fig. 2. Relationship between degree-days (>6.1 °C) accumulated by a cohort from the day of year when the weevils initiated emergence from overwintering habitat to completion of emergence and A) estimated cumulative degree-days (verification data), and B) predicted degree-days (validation data).
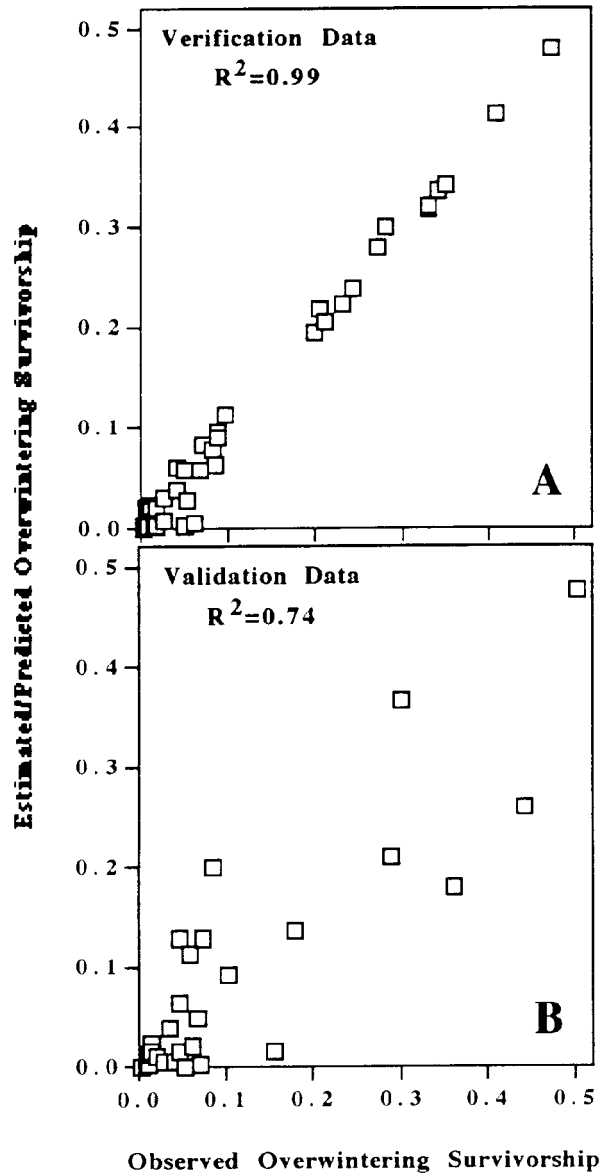

Fig. 3. Relationship between observed overwintering survivorship and A) estimated overwintering survivorship (verification data), and B) predicted overwintering survivorship (validation data).

Cumulative Proportional Emergence (y-axis)

A — Verification Data

1.00
0.75
0.50
0.25
0.00

B — Validation Data

1.00
0.75
0.50
0.25
0.00

x-axis: 0, 500, 1000, 1500, 2000, 2500, 3000

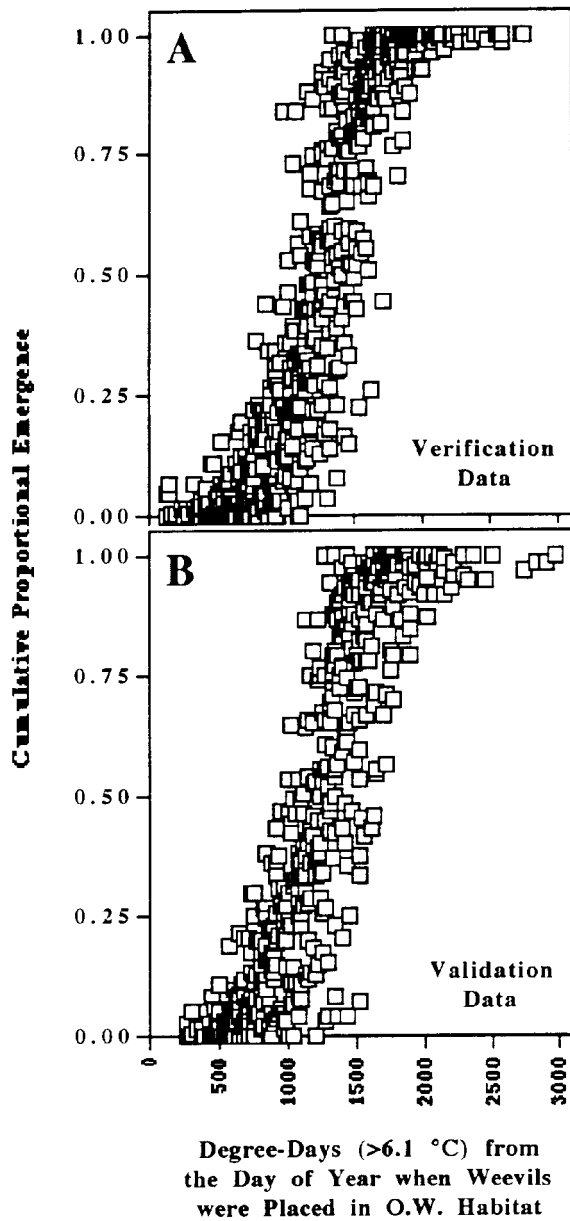**Degree-Days (>6.1 °C) from the Day of Year when Weevils were Placed in O.W. Habitat**

Fig. 4. Observed cumulative emergence plotted against DD (>6.1 °C) from the day of the year when weevils were placed in the overwintering habitat for A) verification data, and B) validation data.