

AN ABSTRACT OF THE THESIS OF

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Air temperatures and soil temperatures at the surface, two inches, and four inches under a grass cover were recorded over a 93 day period. These data were used along with other temperature data from bare soil in the construction of three sets of models for the prediction of maximum and minimum daily temperatures at several depths below bare and grass-covered soils. The model set having the most accurate predictions was used in conjunction with models for predicting the temperature-dependent postdiapause development of the western cherry fruit fly, *Rhagoletis indifferens* Curran.

Postdiapause developmental rates of *R. indifferens* pupae collected from Albany, Oregon and Zillah, Washington were determined under constant temperature conditions. Mean times until adult emergence from Albany puparia and Zillah puparia exposed to the same constant temperature were found to be significantly different ($\alpha = .01$) for all temperatures tested (15.5°C., 19.5°C., and 25.5°C.). Mean times until adult emergence from Zillah puparia held in moist sand at 15.5°C. and in dry sand at 15.5°C. were also found to be significantly different ($\alpha = .01$). Thus, geographical location and presence or absence of moisture were implicated

as factors which may affect the accuracy of the postdiapause development models.

Albany puparia were exposed to two alternating temperature regimes to determine if the mean time of adult emergence under alternating temperature conditions can be predicted using constant temperature developmental rate data. The observed mean time of emergence from puparia exposed to a regime with extreme temperature changes was found to be significantly different ($\alpha = .01$) from the expected mean time of emergence. No significant difference ($\alpha = .01$) was found between observed and expected mean times of emergence from puparia exposed to the other regime, in which temperatures more closely simulated those found in the field.

Albany puparia from which no emergence occurred were dissected to determine the developmental stages of their contents. These data were used in an attempt to determine the upper and lower temperature thresholds for postdiapause development. Thirty degrees C. was established as the upper threshold. A lower threshold was not clearly shown, although the data suggest that it is greater than 6°C.

Four models of the postdiapause development of R. indifferens were constructed and evaluated for accuracy of predictions of the times of several levels of adult emergence from an experimental abandoned orchard in Albany, Oregon. The models predict temperature-dependent postdiapause development based on soil temperatures predicted by the soil temperature model set. Three of the models predict postdiapause development on the basis of day-degree relationships. The predictions of the fourth model are based upon a nonlinear temperature-dependent developmental rate

function. This model predicted the times of adult emergence with mean errors of ca. two days per year. Thus, it was found to likely be more accurate than other models reported here and elsewhere for the prediction of the times of various levels of emergence of the adult western cherry fruit fly.

SIMULATION OF POSTDIAPAUSE DEVELOPMENT OF THE WESTERN CHERRY FRUIT FLY,
RHAGOLETIS INDIFFERENS CURRAN, AND ITS APPLICATION TO PREDICTING
THE TIME OF ADULT EMERGENCE

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SIMULATION OF POSTDIAPAUSE DEVELOPMENT OF THE WESTERN CHERRY FRUIT FLY,
RHAGOLETIS INDIFFERENS CURRAN, AND ITS APPLICATION TO PREDICTING
THE TIME OF ADULT EMERGENCE

I. Introduction

The western cherry fruit fly, Rhagoletis indifferens Curran, is currently the most important pest of the sweet cherry, Prunus avium L., and the sour cherry, Prunus cerasus L., in western North America (Ali-Niazee 1974). Current management practices are based upon the application of insecticides to kill the newly-emerged adult flies prior to oviposition. The timing of the insecticide application is a critical part of the effective management of this pest. Application of insecticide too late after adult emergence may result in a cherry crop infested with R. indifferens larvae and thus unacceptable for canning and undesirable as fresh fruit. This may result in a considerable economic loss to the grower. Insecticide applications made too far in advance of adult emergence may not result in effective control, making a larger number of applications necessary. This is both ecologically and economically undesirable. Thus, a method for accurately predicting the time of emergence of adult R. indifferens would be a valuable tool for the management of this pest.

The objectives of the research reported here were to refine the day-degree model and to develop a model using a nonlinear developmental rate function for the prediction of various levels of adult western cherry fruit fly emergence from an abandoned orchard in Albany, Oregon. The Albany orchard was selected for this research because emergence data were available for this site, and because these data had been used in related modeling efforts. Several emergence experiments were

conducted to obtain data for establishing the nonlinear developmental rate function and for testing assumptions associated with the development models. The models were constructed, coded in FORTRAN, and evaluated for accuracy of predictions.

A set of soil temperature models was a component part of the above models to predict soil temperatures for use in the developmental predictions. Several sets of soil temperature models were constructed to predict daily maximum and minimum temperatures at several depths below both grass-covered and bare soils from observed daily maximum and minimum air temperatures. Model sets were coded in FORTRAN and evaluated for accuracy of predictions; the most accurate was used with the development models.

II. Literature Review

A. Taxonomy

The family Tephritidae is distributed throughout the temperate, subtropical, and tropical areas of the world. The Tephritidae are divided into two groups (Bateman 1972). One group is represented by nondiapausing, multivoltine, polyphagous species inhabiting tropical and subtropical regions. The second group, which includes the genus Rhagoletis, is represented by generally univoltine and monophagous (oligophagous) temperature zone species which diapause in the pupal stage.

A number of species in the genus Rhagoletis are economically important pests because of the characteristic feeding of the larval stages in the pulp of developing fruit (Wasbauer 1972). The cherry-infesting species of the genus Rhagoletis include the European cherry fruit fly, R. cerasi L., the black cherry fruit fly, R. fausta (Osten Sacken), the (eastern) cherry fruit fly, R. cingulata (Loew), and the western cherry fruit fly, R. indifferens Curran. R. cerasi is found only in Europe while the other three species are found only in North America. R. fausta is found in both eastern and western North America (Frick et al. 1954). R. cingulata is found east of Iowa while R. indifferens is found in the Pacific Northwest and parts of California, Colorado, and Montana (AliNiazee 1973).

B. Biology

Emergence of the adult western cherry fruit fly usually begins near the first week in June and ends in mid-July in the Willamette Valley (Jones 1945). Mating occurs mostly on the host fruit shortly after

emergence (Brown 1978) and oviposition follows after a preoviposition period of seven to ten days (Johansen 1971). The eggs hatch after five to seven days and the larvae feed on the pulp of the developing fruit. After two to three weeks, the third instar larvae drop from the fruit and burrow into the soil (Johansen 1971). Pupation occurs in the soil at depths ranging from the surface to six inches, depending in part on the cultivation practices (AliNiazee 1974, Frick et al. 1954).

Shortly after pupation most of the insects enter diapause, which ends sometime during the winter after an exposure to low temperatures (Frick et al. 1954). Postdiapause development resumes with the onset of higher springtime temperatures. Although the western cherry fruit fly is primarily univoltine, approximately one percent of the population completes the pupal stage without the low temperature exposure (Brown 1978) and a small number may not emerge until the second season (Jones 1935, 1937).

C. Pest Status and Control Techniques

The western cherry fruit fly was first reported in the Pacific Northwest at Stayton, Oregon in 1908 and has since become the most important pest of Prunus avium L., the sweet cherry, and Prunus cerasus L., the sour cherry, in western North America (AliNiazee 1974). The economic threshold is extremely low; growers are currently advised to apply organophosphate insecticides at the onset of adult emergence (Anon. 1978). Most growers continue to apply the insecticides at eight to ten day intervals until just prior to harvest (AliNiazee 1978). The goal of this control effort is to kill the adult flies before oviposition occurs. The timing of the insecticide application is critical; premature

insecticide applications may be ineffective against the later emerging flies, and late applications may allow fruit damage by flies emerging and ovipositing before the control effort. AliNiazee (1978) has demonstrated a substantial savings in spray costs when the criterion for timing insecticide applications is the time of adult fly emergence in individual orchards rather than the commonly used calendar spray schedule. However, few growers have monitored fly emergence in the past due to the lack of dependable and facile sampling techniques.

Several methods have been used for determining the time of adult fly emergence for the proper timing of the control effort. Devices for monitoring emergence include ground emergence cages and aerial traps. The use of ground emergence cages is time-consuming and inconvenient, however, so aerial traps are preferred. Several types of aerial traps have recently been shown to be effective for monitoring adult fly emergence as part of a control program directed towards the reduction of insecticide applications (AliNiazee 1978).

A phenology model based upon a day-degree (thermal unit) summation has also been shown to be a useful tool for determining the time of adult fly emergence (AliNiazee 1976). The day-degree sum approximates the amount of heat available for the insect's development on the basis of maximum and minimum daily temperatures. The day-degree method can be used either by itself or in conjunction with the monitoring program. If accurate in predicting the time of adult emergence, it can be useful for determining the most effective time for starting the monitoring program. Much time could be saved by placing and monitoring aerial traps only immediately prior to the time of adult emergence predicted on the basis of the day-degree sum. This would be especially important

if the monitoring program involved a large number of orchards distributed over a large area. Moreover, if a fruit fly population is known to exist in an orchard, the emergence prediction might be used as the sole criterion for timing the insecticide applications. This would eliminate the time and expense associated with the monitoring program.

AliNiazee (1976) used a basic equation (average daily temperature minus a threshold) to accumulate day-degrees for predicting the time of emergence of the adult western cherry fruit fly. Predictions were found to be more accurate when the average daily soil temperatures at the five centimeter depth were used in the computations rather than the average daily air temperatures. Chiang and Sisson (1968) also found day-degree predictions for egg development of the northern corn rootworm, Diabrotica longicornis, to be more accurate when the average daily soil temperatures were used rather than the average daily air temperatures. The day-degree totals for corn rootworm egg development were more variable when the average daily air temperatures were used due to the moderating effect of vegetation on the soil temperatures; development under bare soil occurred after fewer air temperature day-degrees than development under soil covered with vegetation. Therefore, a day-degree index, scaled up or down depending on the presence or absence of vegetation, was proposed.

The depth at which the insects are found in the soil may also be an important factor contributing to the variability in day-degree predictions. Boyce (1934) found the median emergence time of the walnut husk fly, R. completa, to be ten days earlier from pupae at the three inch depth than from pupae at the twelve inch depth. Thus, the presence of vegetation and the distribution of the insects in the soil are implicated as factors

which might affect the accuracy of predictions of the time of emergence of a subterranean insect.

D. Temperature-Dependent Developmental Rate Models

A number of models have been proposed for the temperature-dependent development rate processes of poikilothermic organisms. Perhaps the most basic of these is the day-degree model, based upon the assumption that the developmental rate is proportional to temperature. Shelford (1930) gives a detailed history of early work in this field; this is summarized below.

The day-degree concept is based upon the principles developed by the early phenologists, who studied periodic biological phenomena as related to weather and climate. In 1735, Reamur, a French naturalist, advocated the use of sums of daily mean temperatures for estimating the time of plant maturation. Reamur's method of thermal summation is based upon the assumption that a constant amount of heat energy is required for a given amount of development in a poikilothermic organism.

A century after Reamur's work, de Candolle realized that development cannot take place at some low temperatures, so the thermal summation should involve only those temperatures at which development is able to proceed. This idea was further developed by Oettingen, who applied the term "threshold" to the lowest temperature at which development could be perceived. He also assumed a direct proportionality between temperatures above this threshold and the corresponding developmental rates.

Several methods were introduced for the determination of the threshold temperature for use in the thermal summations. In Oettingen's method

products of the time until development was completed at a constant temperature and the difference between this constant temperature and the threshold temperature were computed for a variety of assumed threshold temperatures. The threshold resulting in the products with the least variation was chosen as the most accurate. Another method based directly upon the assumed linear relationship between developmental rate and temperature was later introduced by Reibisch. In this method, the threshold was determined by extrapolation of a line passing through two observed temperature-developmental rate coordinates. The intercept of this line on the temperature axis is the threshold, the temperature at which the developmental rate is assumed to be zero.

As mentioned above, the thermal summation method is based upon the assumption that a constant amount of heat energy is required for a given amount of development in a poikilothermic organism. An approximation of the amount of heat energy to which the organism is exposed is realized through the use of the day-degree. A widely used equation for the computation of day-degrees is:

$$DD = \frac{TMAX + TMIN}{2} - TLO \quad (1)$$

where DD is the daily day-degree total, TMAX is the maximum daily temperature, TMIN is the minimum daily temperature, and TLO is the lower threshold temperature (Arnold 1960). Equation (1) provides an approximation of the area under the daily temperature wave and above the threshold; however, this approximation is reasonably accurate only if the daily minimum temperature is greater than or equal to the threshold temperature. Equation (1) does not provide an accurate approximation of the area under the daily temperature wave if the daily minimum temperature is less than

the threshold temperature (Arnold 1960). Furthermore, the use of equation (1) involves the implicit assumption that the minimum temperature on the following day is equal to the minimum temperature on the day for which the day-degrees are being computed (Sevacherian et al. 1977).

Several methods have been introduced to correct for the inherent errors associated with the use of equation (1) when the daily minimum temperature is less than the threshold temperature. Lindsey and Newman (1956) developed a method which computes the area under the temperatures wave and above the threshold temperature using the equation for an isosceles triangle. As indicated in figure 1, the height of the triangle is equal to the difference between the maximum temperature and the lower threshold temperature. The length of the triangle's base corresponds to the proportion of the daily period during which the temperature wave is above the threshold temperature. The basic day-degree equation would approximate this area as nil since the average temperature is equal to the lower threshold. Arnold (1960) introduced another method which corrected for the residual area below the threshold temperature and under a sine curve, used as an approximation of the temperature wave.

However, both of the above methods utilize equation (1) for computations when the daily minimum temperature is greater than or equal to the threshold temperature. Allen (1976) introduced a method for computing the area under a sine wave, used as an approximation of the area under the temperature wave. This method allows the use of both lower and upper threshold temperatures, thus enabling the computation of both heating and cooling day-degrees (corresponding to areas between both thresholds and below the lower threshold, respectively).

Other methods have been introduced which are not based on the implicit assumption, associated with the use of equation (1), that the minimum on the next day is equal to the minimum on the day for which the day-degrees are being predicted. The method of day-degree computation introduced by Sevacherian et al. (1977) avoids this assumption by computing day-degrees for twelve-hour periods between successive maximum and minimum temperatures. Thus, the day-degrees for one day are computed by summing the day-degrees computed for two twelve-hour periods; the first period starts at the current day's minimum and ends at the current day's maximum while the second period starts at the current day's maximum and ends at the next day's minimum. Approximations provided by the equations based upon a 24-hour period and two 12-hour periods are presented in figure 2. The sine wave method developed by Allen (1976) also computes day-degrees for twelve-hour periods.

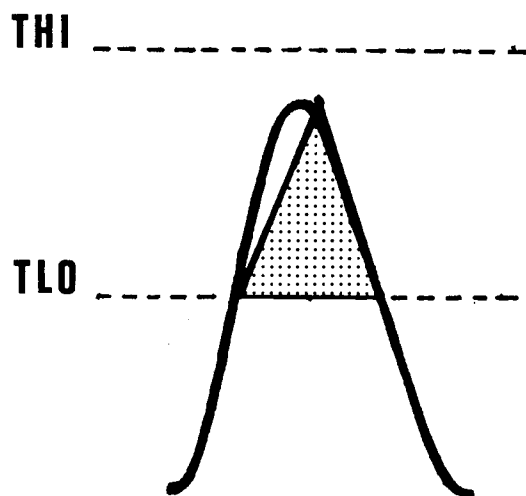


Figure 1. Approximation of the area under a daily temperature wave and above a lower threshold (TLO) provided by the triangulation method. (THI is an upper threshold.)

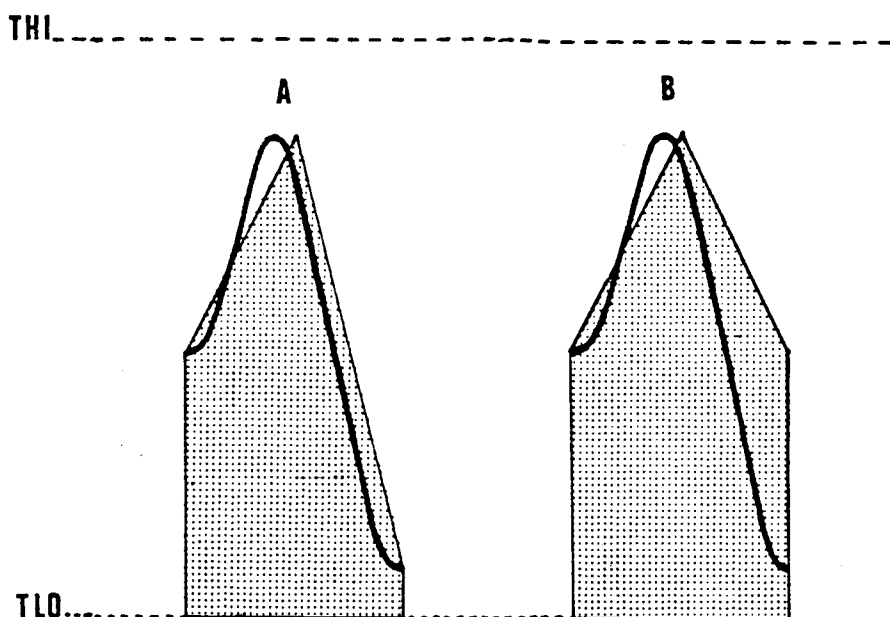


Figure 2. Approximations of the area under a daily temperature wave and above a lower threshold (TLO) provided by day-degree equations based upon (A) two 12-hour periods and (B) one 24-hour period. (THI is an upper threshold.)

Even if the method used in the day-degree computations is able to provide an accurate approximation of the area under the temperature wave, accurate predictions of the amount of development completed may often not be obtained due to the assumption that the development rate is proportional to temperature. Extreme departures from the assumed linear relationship of development rate to temperature often occur in both the high and low temperature ranges, resulting in inaccurate predictions of the day-degree model (Stinner et al. 1974). At low temperatures the linear day-degree relationship underestimates the developmental rate while at high temperatures the developmental rate is overestimated. This "lack of fit" often causes significant errors in day-degree model predictions, especially if the ambient temperatures regularly vary outside of the intermediate temperature range. Shelford

(1917) was the first to point out that these departures from the linear day-degree relationship were rather general and deserved a more adequate interpretation than had been offered at that time. The generality of the nonlinear relationship between temperature and developmental rates of poikilothermic organisms has since been demonstrated by Sharpe and DeMichele (1977) who fit a nonlinear model to temperature-developmental rate data for Tetrahymena pyriformis, a protozoon, Escherichia coli, a bacterium, Chlorella sorokinian, an alga, Drosophila melanogaster, a fly, Pseudatomoscelis seriatus, a fleahopper, Zea mays, corn, Pinus taeda, pine, and Gossypium hirsutum, cotton.

Although the assumed linear relationship of developmental rate to temperature is not an adequate description of the observed relationship at high and low temperatures, the day-degree model is widely used in entomology for a number of purposes, including the timing of insecticide applications (eg. AliNiazee 1976), crop damage forecasting (eg. Apple 1952), predicting development at different localities (eg. Baker and Miller 1978), studies of climatic limits to species distributions (eg. Messenger 1959), and population dynamics studies (eg. Morris and Fulton 1970). The day-degree approach has also been used in studies of other insects belonging to the genus Rhagoletis, including the European cherry fruit fly, R. cerasi (Baker and Miller 1978), the black cherry fruit fly, R. fausta, and the (eastern) cherry fruit fly, R. cingulata (Jubb and Cox 1974), the apple maggot, R. pomonella (Lathrop and Dirks 1945), and the walnut husk fly, R. completa (Boyce 1934). In these and other studies, the day-degree model has been found to be a useful tool for predicting the temperature-dependent development of insects in spite of its inherent limitations.

Two possible explanations exist for the adequate performance of the day-degree model. First, the relationship between developmental rate and temperature is approximately linear at intermediate temperatures. Thus, the day-degree model provides a fairly accurate description of the relationship at intermediate temperatures, and will often perform well if the ambient temperatures do not fluctuate outside of this range (Stinner et al. 1974). Second, even if the ambient temperatures fluctuate outside of the intermediate range of temperatures, the errors in developmental rate predictions may be compensatory. That is, the underestimation of development at low temperatures by the day-degree model may be negated by the overestimation of development at high temperatures, thus resulting in accurate day-degree model predictions.

In other cases, the day-degree model has been found to be inadequate for the prediction of temperature-dependent poikilotherm development (eg. Stinner et al. 1974). A number of empirical nonlinear models have been proposed with the objective of providing a good fit to the observed relationship between developmental rate and temperature. Although originally formulated to describe the relationship between temperature and the rate of a chemical reaction, the equations of van't Hoff and Arrhenius have been used as models of the temperature-developmental rate relationship (eg. Peairs 1927). Belehradek (1926) developed an exponential equation as a model for the observed relationship. Janisch (1932) proposed the equation of a catenary curve, Davidson (1944) proposed the logistic equation, and Eubank et al. (1973) proposed the equation of a parabola as models of the temperature-developmental rate relationship. Stinner et al. (1974) developed a sigmoid function as a model for the observed relationship.

Other workers have realized the advantages of models having a more theoretical basis and have attempted to deduce model structures from assumptions involving the physiological processes occurring in a poikilothermic organism in response to temperature. Pradhan (1946) utilized the law of compound interest, and an analogy between growth by cellular division (which follows the law of compound interest) and the development of the poikilothermic organism, to develop a model which has a partly theoretical basis. Logan et al. (1976), following arguments advanced by Pradhan, developed a partly theoretical model in which the temperature-developmental rate relationship is conceptualized as consisting of two phases. Phase one is characterized by a monotonically increasing developmental rate corresponding to temperatures increasing from a lower threshold to an optimum temperature for development; this phase is based on the law of compound interest as used by Pradhan. Phase two relates the observed precipitous decline in developmental rate to temperatures increasing from the optimum to the lethal, maximum temperature. After equations were formulated for these two phases, the mathematical technique of matched asymptotic expansions was used to obtain a solution for the entire range of temperatures. In this technique, the equations describing the behaviour of the two phases are added, and the common limit of the two phases are subtracted from this sum (Wollkind et al. 1978).

Sharpe and DeMichele (1977) have developed another model of poikilotherm development based upon assumptions involving developmental control enzymes. The developmental rate of the poikilothermic organism is assumed to be regulated by the reaction rate of a single control enzyme, which can exist in two inactive states, due to high and low temperature inactivation,

and one active state. The compensating effect of high and low temperature enzyme inactivation incorporated into the model effectively establishes a low temperature threshold for development and a reduced rate of development at high temperatures.

E. Soil Temperature Models

Soil temperatures have yearly cycles due to seasonal changes and diurnal cycles due to diurnal variation in insolation; soil temperatures also change with respect to depth. Several models have been proposed for the prediction of soil temperatures based upon these characteristics. Fourier series describe the cyclic nature of the temperature wave as a function of time (eg. Carson 1963). Other models have been proposed which predict the soil temperature as a function of time and depth using a one-dimensional heat flow equation (eg. Fluker 1958). Hasfurther and Burman (1974) developed a model which predicts soil temperatures from past values of observed air temperatures using Fourier series and the one-dimensional heat flow equation.

The use of the heat flow equation in predicting soil temperatures involves the assumption that the soil is homogeneous and its physical properties are invariant with time and depth (Qashu and Zinke 1964). Since this assumption is invalid if the soil is cultivated or covered by vegetation, Bonham and Fye (1970) used a statistical model, rather than the model based on the heat flow equation, for the prediction of soil temperatures under these conditions. They utilized linear regression models for the prediction of the daily average soil temperatures at various depths using either the daily average air temperature

or the daily average soil surface temperature as the independent variable. These models were found to adequately predict temperatures in cultivated soil.

Although factors such as moisture, color, and other physical characteristics influence soil temperature, Crabb and Smith (1953) claim that the factor having the greatest influence on soil temperature is vegetation. They emphasize that vegetation not only influences the soil temperature directly by shading the soil surface, but also influences the soil temperature indirectly by markedly influencing the soil color, organic content, porosity, permeability, aeration, and moisture content at different depths. Qashu and Zinke (1964) also described the influence of vegetation on soil temperature in terms of the direct effect of reduced insolation at the soil surface and the indirect effects of continually changing soil properties.

Vegetation provides a surface for absorption of incoming solar radiation, thereby reducing the amount of insolation reaching the soil surface. The amount of reduction depends on the "leaf area index", the ratio of the whole leaf area to the soil surface area (van Eimern 1969). If the vegetation is sufficiently dense, a layer of still air may be formed, thus insulating the soil surface (Angus 1969). The effect of vegetation is twofold; it reduces the amount of direct insolation at the soil surface, thereby reducing the amount of heat received by the soil, and it retards radiation, thereby reducing the loss of heat from the soil surface. Thus, the maximum daily soil temperature is reduced and the minimum daily soil temperature is increased under a soil surface covered with vegetation, in comparison to soil temperatures under a bare soil surface (Li 1926).

III. MATERIALS AND METHODS

A. Soil and Air Temperatures

Soil and air temperatures were recorded at a site on the Entomology Farm, Oregon State University from March 18, 1978 to May 11, 1978 and from May 28, 1978 to July 4, 1978. Soil temperatures at the surface, and at two and four inch depths were recorded every two hours by YSI Precision Thermistors connected to a Rustrak chart recorder. Air temperatures were recorded by a Bendix hygrothermograph housed in a white, louvered wooden shelter which was placed upon clay pot holders sitting on the soil surface. Both the thermistors and the hygrothermograph were located in the southwest quadrant and within the drip-line of an Italian prune tree, Prunus sp. A dense growth of Lolium perenne L., perennial ryegrass, with small amounts of Holcus lanatus L., velvet grass, and Crepis setosa Haller f., rough hawksbeard, covered the site during this period.

Maximum and minimum (max-min) soil and air temperature data for the same time period were obtained from the Hyslop Farm Field Station, Corvallis, Oregon. Max-min soil temperatures were recorded at two and four inch depths below bare soil; max-min air temperatures were recorded from a shaded area about two inches above the soil surface. The soils at Hyslop Farm and the Entomology Farm have a silt loam texture.

B. Soil Temperature Models

The soil and air temperature data sets from the Entomology Farm and Hyslop Farm were used to construct models for the prediction of soil

temperatures under bare and grass-covered soils. Three sets of regression models were constructed using least-squares regression methods (Neter and Wasserman 1974). The three sets of regression models represent successive levels of development in the evolution of the soil temperature model structure.

Each model set includes six regression models for the prediction of temperatures under grass-covered soil and four regression models for the prediction of temperatures under bare soil. Daily max-min temperatures under grass-covered soil are predicted for the surface, two, and four inch depths. Daily max-min temperatures under bare soil are predicted for the two and four inch depths. Models for the prediction of surface temperatures of bare soil were not constructed as surface temperature data for bare soil were not available. Thus, a total of thirty regression models were constructed; three model sets, each containing regression models for predicting daily max-min temperatures at the surface, two and four inch depths under grass-covered soil, and at the two and four inch depths under bare soil.

The ability of the models to accurately predict soil temperatures was evaluated by summing the absolute values of the difference between observed temperatures and temperatures predicted in the model runs. The presence of autocorrelated variables in the models precluded the usual use of F and R^2 statistics for model evaluation. The same data set was used in both model construction and evaluation, so the results of the model evaluation do not necessarily indicate how accurate model predictions will be for another year, when conditions may be different. However, the results from the model evaluations are useful for comparisons between the three soil temperature model sets.

C. Sources of Puparia

Puparia used in emergence experiments were collected from an abandoned orchard southwest of Albany, Oregon and at an orchard in Zillah, Washington¹. Puparia from the Albany orchard were collected in July, 1977 and stored at 3°C. until the start of emergence experiments. Puparia from the Zillah orchard were collected on April 1, 1978 and stored at 4.5°C. until September 8, 1978; they were then transferred and stored at 3°C. until the start of emergence experiments. All puparia received at least 210 days of chilling before they were used in emergence experiments.

D. Determination of Postdiapause Development Rates Under Constant Temperature Conditions

Puparia from both collection sites were placed in petri dishes and exposed to several constant temperature treatments in darkened growth chambers to determine postdiapause development rates.

Puparia from the Albany orchard were exposed to 13°C., 28°C., 30°C., and 32°C. constant temperature treatments. One group of 135 puparia was exposed to 13°C. while three other groups of 100 puparia were exposed to 28°C., 30°C., and 32°C. The data from these emergence experiments were used along with other emergence data to establish a nonlinear function relating postdiapause developmental rate to temperature.

Puparia from the Zillah orchard were exposed to constant temperature treatments so comparisons could be made between the developmental rates

¹ Puparia were collected from the Zillah orchard by technicians from the Yakima Agricultural Research Lab, Yakima, Washington.

of puparia from the two sites. Puparia from the Zillah orchard were also exposed to both moist and dry conditions to determine the effect of moisture on developmental rate. One group of 100 puparia was exposed to 19.5°C. Three other groups of 100 puparia were surface sterilized and transferred to sterile petri dishes containing fine sand. The puparia were surface sterilized by immersion in .4% methyl benzethonium chloride for five minutes followed by two rinses in sterile distilled water. One group of puparia was exposed to 25.5°C. while the other two groups were exposed to 15.5°C. The sand in one of the 15.5°C. treatment dishes was kept moistened with sterile distilled water while the sand in the other two dishes was kept dry.

The numbers of male and female flies emerging each day were recorded for each treatment. The mean development time was computed for each treatment by multiplying that proportion of the total number of flies emerging on each day by the number of days elapsed since the start of the experiment, and summing these products over all days. The mean developmental rate was computed by taking the reciprocal of the mean number of days until emergence for each treatment.

E. Determination of Postdiapause Developmental Rates Under Alternating Temperature Conditions

Puparia collected from the Albany orchard were exposed to two alternating temperature regimes to determine postdiapause developmental rates under these conditions. Alternating temperature environments were realized in the laboratory by transferring the puparia between darkened constant temperature growth chambers; this alleviated the growth chamber shortage and avoided problems which may have arisen if the chambers had to be reset while experiments were in progress.

One hundred and thirty puparia were exposed to a four week temperature regime which alternated weekly between 15.5°C. and 28°C. Following this, the puparia were stored at 19.5°C. until emergence was completed. Another 100 puparia were exposed to an alternating temperature regime consisting of eight-hour daytime temperatures and sixteen-hour nighttime temperatures. The nighttime temperatures increased from 3°C. to 13°C. to 19.5°C. as the experiment progressed. The daytime temperature varied between 3°C., 13°C., 19.5°C., 25.5°C., and 28°C. The temperature was constant during any one daytime or nighttime period in this experiment. The schedule of temperatures for this experiment is listed in Appendix A.

Emergence data from these alternating temperature treatments were recorded following the same procedures used in the constant temperature experiments.

F. Dissections of Puparia

Puparia collected from the Albany orchard and used in constant temperature emergence experiments were dissected to determine the developmental stages of the pupae that did not emerge as adult flies. Puparia from the 13°C., 28°C., 30°C., and 32°C. emergence experiments reported here, and the 15.5°C., 17°C., 21°C., 22°C., and 25.5°C. emergence experiments of Van Kirk (1979), were dissected. The contents of the puparia were classified as: live and undeveloped pupae, if they were turgid and of a uniform yellow coloration; dead pupae if they were not turgid or had a brown or black discoloration without any well-developed adult features; or dead pharate adults, if they had well-developed adult features such as compound eyes, legs, body coloration and setae.

G. Day-Degree Models

Three day-degree models² (DD1, DD2, and DD3) which summed daily day-degrees through time and computed a weighted mean number of day-degrees were developed and coded in FORTRAN for use on the OS3 operating system. All of the models computed day-degrees for the surface (for grass-covered soil only), two inch, and four inch depths based upon max-min temperatures predicted by the third soil temperature model set. The models differ only in the equations used for the day-degree computations.

The day-degree models were run using daily max-min air temperature data sets for the years 1973 to 1977; model runs for each year were started on March 1. Air temperature data sets for 1976 and 1977 were from a hygrothermograph located in the Albany orchard. Since air temperature data were not collected from the Albany orchard in 1973, 1974, and 1975, air temperature data from the Hyslop Farm Field Station, located ca. 2.6 miles west of the Albany orchard, were used in model runs for those years. These air temperature data were collected from ca. four feet above the soil surface and are assumed to approximate sufficiently the air temperatures in the Albany orchard.

DD1 and DD2 were run three times for each year's temperature data set using three different lower temperature thresholds, 8.33°C., 10.00°C., and 11.67°C., established by Van Kirk (1979). DD3 was run twice for each year's temperature data set using two of the lower temperature thresholds,

² To facilitate this presentation, all postdiapause development models which utilize day-degree computations will be referred to as day-degree models; the model which does not utilize day-degree computations will be referred to as the postdiapause development model.

8.33°C. and 10.00°C. An upper temperature threshold of 27.00°C. was used for all runs of DD2 and DD3.

The accuracy of the day-degree models in predicting the mean time of adult fly emergence was evaluated on the basis of adult emergence records obtained using ground emergence cages in the Albany orchard (AliNiazee, unpublished data). The sums of the weighted mean number of daily day-degrees from the start of the model runs (March 1) to the observed mean time of adult emergence in the Albany orchard were computed for 1973 to 1977. The means and coefficients of variation of the yearly sums, and the sums of the absolute values of the deviations of the sums from their means were computed and used as criteria in the evaluation of the models and in the selection of the lower temperature threshold.

H. Postdiapause Development Model

A postdiapause development model which utilized a nonlinear temperature-dependent postdiapause developmental rate function was developed and coded in FORTRAN for use on the OS3 operating system. The model predicts the proportion of postdiapause development completed each day on the basis of soil temperatures predicted by soil temperature model set three.

The postdiapause development model was run using the same max-min air temperature data sets used for the day-degree model runs. The model was run twice for each year's temperature data set using an upper temperature threshold of 30°C. and two lower temperature thresholds, 7°C. and 9°C. The accuracy of the postdiapause development model in predicting the mean times of adult fly emergence was evaluated using the same

emergence data as were used in evaluating the day-degree models. The absolute values of the difference between the predicted mean times of emergence and the observed mean times of emergence were computed and used for the comparison of the accuracy of the postdiapause development model predictions with the accuracy of the day-degree model predictions.

IV. RESULTS AND DISCUSSION

A. Soil Temperature Models

The soil temperature models were constructed using observed soil and air temperatures. However, when model runs are made, soil temperatures are predicted from previously predicted soil temperatures and, in some models, observed air temperatures. Thus, the soil temperature models take the form of linear difference equations.

Soil temperature model set one (ST1) is presented in table 1. In these models, today's minimum temperature at a given depth is predicted using yesterday's minimum temperature predicted for that depth and today's measured minimum air temperature. The same type of relationship is used in predicting maximum soil temperatures. The regressions were computed with both maximum and minimum temperatures in the same data set. Thus, the parametric relationship between maximum temperatures was assumed to be equivalent to that between minimum temperatures.

Soil temperature model set two (ST2) is presented in table 2. Models for predicting maximum temperatures and minimum temperatures were constructed with separate data sets; the above assumption was not made. Two types of variables, one representing the past state, the other a heat input, are used for predictions. Today's minimum temperature at a given depth is predicted using yesterday's maximum temperature predicted for that depth, which represents the past state. The heat input is represented by the difference between today's minimum temperature predicted for the upper adjacent depth and the past state. The same type of relationship is used in predicting maximum temperatures.

Table 1. Soil temperature model set one (ST1).

Models for grass-covered soil

Today's min. soil surface temp. = $2.889 + .576 \times \text{today's min. air temp.} + .286 \times \text{yesterday's min. soil surface temp.}$

Today's min. two inch soil temp. = $2.622 + .278 \times \text{today's min. air temp.} + .565 \times \text{yesterday's min. two inch soil temp.}$

Today's min. four inch soil temp. = $1.797 + .159 \times \text{today's min. air temp.} + .729 \times \text{yesterday's min. four inch soil temp.}$

Today's max. soil surface temp. = $2.889 + .576 \times \text{today's max. air temp.} + .286 \times \text{yesterday's max. soil surface temp.}$

Today's max. two inch soil temp. = $2.622 + .278 \times \text{today's max. air temp.} + .565 \times \text{yesterday's max. two inch soil temp.}$

Today's max. four inch soil temp. = $1.797 + .159 \times \text{today's max. air temp.} + .729 \times \text{yesterday's max. four inch soil temp.}$

Models for bare soil

Today's min. two inch soil temp. = $1.483 + .453 \times \text{today's min. air temp.} + .534 \times \text{yesterday's min. two inch soil temp.}$

Today's min. four inch soil temp. = $1.425 + .202 \times \text{today's min. air temp.} + .734 \times \text{yesterday's min. four inch soil temp.}$

Today's max. two inch soil temp. = $1.483 + .453 \times \text{today's max. air temp.} + .534 \times \text{yesterday's max. two inch soil temp.}$

Today's max. four inch soil temp. = $1.425 + .202 \times \text{today's max. air temp.} + .734 \times \text{yesterday's max. four inch soil temp.}$

Table 2. Soil temperature model set two (ST2)

Models for grass-covered soil

Today's min. soil surface temp. = $2.454 + .820 \times \text{yesterday's max. soil surface temp.} + .602 \times (\text{today's min. air temp.} - \text{yesterday's max. soil surface temp.})$

Today's min. two inch soil temp. = $1.345 + .903 \times \text{yesterday's max. two inch soil temp.} + .758 \times (\text{today's min. soil surface temp.} - \text{yesterday's max. two inch soil temp.})$

Today's min. four inch soil temp. = $.263 + .977 \times \text{yesterday's max. four inch soil temp.} + .857 \times (\text{today's min. two inch soil temp.} - \text{yesterday's max. four inch soil temp.})$

Today's max. soil surface temp. = $-1.160 + 1.125 \times \text{today's min. soil surface temp.} + .891 \times (\text{today's max. air temp.} - \text{today's min. soil surface temp.})$

Today's max. two inch soil temp. = $.324 + .975 \times \text{today's min. two inch soil temp.} + .699 \times (\text{today's max. soil surface temp.} - \text{today's min. two inch soil temp.})$

Today's max. four inch soil temp. = $.300 + .985 \times \text{today's min. four inch soil temp.} + .748 \times (\text{today's max. two inch soil temp.} - \text{today's min. four inch soil temp.})$

Models for bare soil

Today's min. two inch soil temp. = $.239 + .765 \times \text{yesterday's max. two inch soil temp.} + .368 \times (\text{today's min. air temp.} - \text{yesterday's max. two inch soil temp.})$

Today's min. four inch soil temp. = $.885 + .932 \times \text{yesterday's max. four inch soil temp.} + .778 \times (\text{today's min. two inch soil temp.} - \text{yesterday's max. four inch soil temp.})$

Today's max. two inch soil temp. = $-2.327 + 1.277 \times \text{today's min. two inch soil temp.} + .897 \times (\text{today's max. air temp.} - \text{today's min. two inch soil temp.})$

Today's max. four inch soil temp. = $.515 + .936 \times \text{today's min. four inch soil temp.} + .700 \times (\text{today's max. two inch soil temp.} - \text{today's min. four inch soil temp.})$

Soil temperature model set three (ST3) is presented in table 3. A variable representing the soil temperature gradient was used in addition to the two types of variables used for predictions in model set two. This variable is the difference between the past temperatures at the lower adjacent depth and the depth for which predictions are being made.

Mean absolute deviations of observed soil temperatures from soil temperatures predicted by ST1, ST2, and ST3 are presented in table 4. The mean absolute deviations for models in ST3 are smaller than those for models predicting the same dependent variables in ST1. Mean absolute deviations for seven of the ten models in ST3 are less than those for models predicting the same dependent variables in ST2; in one of the models they are greater and in two others they are equal. Thus, the predictions of ST3 were determined to be more accurate than those of ST1 or ST2.

The models in ST3 are structured to include the salient features of a soil temperature system controlled by heat fluxes. Soil temperature changes are the result of a system of heat fluxes driven by absorbed shortwave solar radiation and longwave radiation (Cochran 1969). Soil surface temperatures follow a cycle having a minimum at about sunrise and a maximum during the middle of the afternoon. The soil surface temperature increases from the minimum to the maximum due to the influx of shortwave solar radiation which is converted to heat energy upon striking the soil surface. A downward soil temperature gradient results from this soil surface heating; this results in a heat flux into the soil. A heat flux from the soil surface into the air is also present due to longwave radiation from the soil surface into the air and the latent heat removed from the soil surface with the evaporation of water.

Table 3. Soil temperature model set three (ST3)

Models for grass-covered soil

Today's min. soil surface temp. = $1.435 + .890 \times \text{yesterday's max. soil surface temp.} + .511 \times (\text{today's min. air temp.} - \text{yesterday's max. soil surface temp.}) + .662 \times (\text{yesterday's max. two inch soil temp.} - \text{yesterday's max. soil surface temp.})$

Today's min. two inch soil temp. = $1.086 + .918 \times \text{yesterday's max. two inch soil temp.} + .705 \times (\text{today's min. soil surface temp.} - \text{yesterday's max. two inch soil temp.}) + .308 \times (\text{yesterday's max. four inch soil temp.} - \text{yesterday's max. two inch soil temp.})$

Today's min. four inch soil temp. = $.263 + .977 \times \text{yesterday's max. four inch soil temp.} + 8.57 (\text{today's min. two inch soil temp.} - \text{yesterday's max. four inch soil temp.})$

Today's max. soil surface temp. = $-3.427 + 1.256 \times \text{today's min. soil surface temp.} + .786 \times (\text{today's max. air temp.} - \text{today's min. soil surface temp.}) + 1.652 \times (\text{today's min. two inch soil temp.} - \text{today's min. soil surface temp.})$

Today's max. two inch soil temp. = $.250 + .978 \times \text{today's min. two inch soil temp.} + .694 \times (\text{today's max. soil surface temp.} - \text{today's min. two inch soil temp.}) + .224 \times (\text{today's min. four inch soil temperature} - \text{today's min. two inch soil temp.})$

Today's max. four inch soil temp. = $.300 + .985 \times \text{today's min. four inch soil temp.} + .748 \times (\text{today's max. two inch soil temp.} - \text{today's min. four inch soil temp.})$

Models for bare soil

Today's min. two inch soil temp. = $-1.698 + 1.055 \times \text{yesterday's max. two inch soil temp.} + .260 \times (\text{today's min. air temp.} - \text{yesterday's max. two inch soil temp.}) + 1.979 \times (\text{yesterday's maximum four inch soil temp.} - \text{yesterday's max. two inch soil temp.})$

Today's min. four inch soil temp. = $.885 + .932 \times \text{yesterday's max. four inch soil temp.} + .778 \times (\text{today's min. two inch soil temp.} - \text{yesterday's max. four inch soil temp.})$

Today's max. two inch soil temp. = $-2.893 + 1.300 \times \text{today's min. two inch soil temp.} + .877 \times (\text{today's max. air temp.} - \text{today's min. two inch soil temp.}) + .447 \times (\text{today's min. four inch soil temp.} - \text{today's min. two inch soil temp.})$

Today's max. four inch soil temp. = $.515 + .936 \times \text{today's min. four inch soil temp.} + .700 \times (\text{today's max. two inch soil temp.} - \text{today's min. four inch soil temp.})$

Table 4. Mean absolute deviations of observed soil temperatures from soil temperatures predicted by soil temperature model sets one, two, and three (°C.).

<u>Soil temperature model set one</u>				
Depth	<u>Grass-covered soil</u>		<u>Bare soil</u>	
	Maximum temperature	Minimum temperature	Maximum temperature	Minimum temperature
Surface	1.94	1.06	-	-
Two Inches	2.15	1.51	2.98	1.84
Four Inches	2.25	1.80	3.20	1.84

<u>Soil temperature model set two</u>				
Depth	<u>Grass-covered soil</u>		<u>Bare soil</u>	
	Maximum temperature	Minimum temperature	Maximum temperature	Minimum temperature
Surface	1.27	0.58	-	-
Two Inches	0.98	0.51	1.52	2.00
Four Inches	0.79	0.58	1.23	1.86

<u>Soil temperature model set three</u>				
Depth	<u>Grass-covered soil</u>		<u>Bare soil</u>	
	Maximum temperature	Minimum temperature	Maximum temperature	Minimum temperature
Surface	1.34	0.51	-	-
Two Inches	0.98	0.45	1.44	1.55
Four Inches	0.79	0.47	1.12	1.41

As the afternoon passes, the angle of incidence of the solar radiation decreases and the amount of solar radiation intercepted and converted to heat energy at the soil surface decreases. The soil surface temperature increases until the decreasing heat input to the soil surface equals the heat loss due to longwave radiation and latent heat of evaporation from the soil surface.

The heat loss from the soil surface is only partially compensated for by the upward heat flux from the lower soil depths along the thermal gradient. The amount of compensation decreases as the lower depths become cooler as the night progresses. The soil surface temperature decreases until the early morning solar radiation warms the soil surface sufficiently to balance the heat loss.

Since heat fluxes downward through the soil during the day and upward through the soil during the night, the soil temperatures below the surface follow cycles much like the soil surface temperature cycle. However, the amplitudes of the temperature cycles decrease with increasing depth due to the expenditure of the heat energy as it passes through the soil. Also, the maximum and minimum soil temperatures are delayed with increasing depth due to the time required for heat to flux through the soil.

Modifications of the soil temperature models were motivated by the recognition of variables, and relationships among the variables, which increased the realism of the models as representations of the above features of the soil temperature system. ST3 represents the end product in the evolution of the soil temperature model structure.

The past temperature variable of ST3 represents the past state, upon which the effect of a given heat input to the soil temperature

system depends. A large temperature change will occur only if there is a relatively large difference between the past state and the input. Without a difference there will be no gradient to allow a heat flux and consequently no change in the state of the system.

The input is from the depth immediately above the depth for which the temperature is being predicted, except for the case of the soil surface which receives its input from the air. The effect of the past state is incorporated by using the difference between the current temperature at the upper depth and the past state as the input variable. The maximum temperature at the upper depth represents the intensity of heat which may contribute to a downward heat flux to the lower (and cooler) depth at which the temperature is being predicted. The minimum temperature at the upper depth represents the low intensity of the heat which may allow an upward heat flux from the next lower (and warmer) depth at which the temperature is being predicted.

The past temperature gradient between the next lower depth and the depth at which the temperature is being predicted represents the capacity of the lower depth to act as a heat sink or source and thus affect the heat flux at the current time step. The heat flux is upward if the minimum temperature is being predicted and downward if the maximum temperature is being predicted. A large gradient between the past minimum temperatures might allow a larger amount of heat to flux to the lower, colder depth rather than remaining at the upper depth during the period of heat influx. A large gradient between the past maximum temperatures may indicate that a smaller amount of heat will be available at the lower depth during the period of heat loss.

The identification of air temperature as an independent variable in the model of the relationship between the minimum air and soil temperatures seems realistic since the cool morning air results in the loss of heat from the soil surface, thereby reducing its temperature. Surely, the soil surface temperature also affects the air temperature but air temperature seems best identified as the independent variable. It is not so apparent whether the air temperature should be considered the input (independent variable) or the response variable in the model of the relationship between maximum air and soil temperatures; the warm soil undoubtedly influences the air temperature as it radiates heat. However, the identification of air temperature as an input in the maximum soil temperature model and the minimum soil temperature model need not imply a causal relationship between these variables. In general, the response variable need not be dependent causally on the independent variable in any regression model. Moreover, in some applications, as when temperature (the response) is estimated from the height of mercury (the independent variable) in a thermometer, the independent variable is actually dependent causally on the dependent variable (Neter and Wasserman 1974). The above identification of inputs is justified since it increases the facility of the model due to the ease of collection and availability of air temperature data sets in comparison to soil temperature data sets, and results in sufficiently accurate model predictions.

The accuracy of soil temperature model set three predictions compares favorably with the accuracy of predictions of other soil temperature models. Standard deviations of differences between observed soil temperatures and those predicted by ST3 are presented along with the percent of predictions within $\pm 2.0^{\circ}\text{C}$. of observed soil temperature in table 5.

Table 5. Standard deviations of differences between observed soil temperatures and those predicted by ST3 and percent of predictions within $\pm 2.0^{\circ}\text{C}$. of observed soil temperatures.

Depth	<u>Grass-covered soil</u>				<u>Bare soil</u>			
	Maximum temperature		Minimum temperature		Maximum temperature		Minimum temperature	
Surface	1.71 ¹	82 ²	0.65	99	-		-	
Two inches	1.25	88	0.55	100	1.90	72	1.87	68
Four inches	1.00	93	0.58	100	1.46	84	1.72	73

¹ Standard deviation of differences between observed and predicted soil temperatures.

² Percent of predicted soil temperatures within $\pm 2.0^{\circ}\text{C}$. of observed soil temperatures.

Predicted soil temperatures are within $\pm 2.0^{\circ}\text{C}$. of 88% of the observed maximum temperatures under grass-cover, 100% of the observed minimum temperatures under grass-cover, 78% of the observed maximum temperatures under bare soil, and 71% of the observed minimum temperatures under bare soil.

The linear regression models of Bonham and Fye (1970) for predicting daily average soil temperatures in the winter from daily average air temperatures were accurate to within $\pm 2.78^{\circ}\text{C}$. The model of Fluker (1958), which predicts the daily average soil temperature as a function of time and depth, was accurate to within $\pm 2.0^{\circ}\text{C}$. for predictions at depths from two to twelve inches. However, this model was constructed and validated using a five-year average of daily average soil temperatures. By using a five-year average of daily average soil temperatures for validation, the fluctuations of soil temperatures are reduced, thereby possibly reducing the errors in the model predictions in comparison to those that might occur if soil temperatures during any one year were used for validation. The model of Hasfurther and Burman (1974), which predicts the daily average soil temperature from past values of daily air temperatures, was constructed and validated using "smoothed" temperature data. Temperature data sets were "smoothed" by taking ten day moving averages; this removed extreme fluctuations in the temperature data. The predicted temperatures were usually within $\pm 1.67^{\circ}\text{C}$., but occasionally deviated as much as 3.33°C . from the "smoothed" observed temperatures.

Deviations of temperatures predicted by the models of Fluker (1958) and Hasfurther and Burman (1974) from observed soil temperatures would

be expected to be greater than deviations from these averaged observed temperatures. However, the model of Hasfurther and Burman (1974) was validated with a different data set than that with which it was constructed. Thus, the validation of this model was more rigorous than that of the other models, including those constructed as part of this research. While direct comparisons are not facilitated, soil temperature model set three seems likely to be as accurate as these other models.

The current research was focused on the development of models to predict the emergence times of the western cherry fruit fly from the abandoned Albany orchard, which had an undisturbed grass cover. Thus, soil temperature predictions for use in the development model predictions were made using the soil temperature models for grass-covered soil. However, by also using the models for bare soil conditions, predictions of emergence times from commercial orchards which often have bare soils due to cultivation might also be made.

Ryegrass is common in the cherry orchards of the Willamette Valley of Oregon; cultivation is used in the spring to remove this growth as soon as the soil is sufficiently dry (personal communication, Dr. G. D. Crabtree, O.S.U. Department of Horticulture). Therefore, if the time of emergence from a commercial orchard is to be predicted, the soil temperature models for grass-covered conditions could be used for predictions prior to the time of first cultivation. Since commercial orchards are kept free of grass for the remainder of the season, the soil temperature models for bare soil conditions could be used thereafter.

The construction of the soil temperature models was justified due to the cost in time and equipment associated with the collection of soil temperatures from several depths, which would be required for developmental predictions in the absence of predicted soil temperatures. Also, it may be possible to make sufficiently accurate soil temperature predictions for a number of orchards using readily available regional air temperature data.

B. Postdiapause Developmental Rates Under Constant Temperature Conditions

Emergence data from constant temperature emergence experiments with puparia from Albany and Zillah are presented in Appendices B and C. Adult emergence from puparia collected at the Albany orchard was observed from the 13°C. and 28°C. treatments. Emergence also occurred from puparia initially exposed to the 32°C. treatment, but not until transfer to 19.5°C. prior to dissection. No emergence was observed from puparia in the 30°C. treatment. Adult emergence from puparia collected at the Zillah orchard was observed from the 15.5°C. (both the moist and dry treatments), 19.5°C, and 25.5°C. treatments.

Mean times until emergence and developmental rates are presented for all treatments (except 32°C. which is discussed later) in table 6. Significant differences ($\alpha = .01$)³ between the mean times until emergence of adult flies from puparia collected at the Albany and Zillah orchards and exposed to the same temperatures were found for all constant temperature treatments. These differences in developmental rates between pupae from the two locations suggest that the postdiapause

³ All statistical comparisons of means are based upon the t-statistic.

Table 6. Mean times of adult emergence from puparia collected at the Zillah and Albany orchards and incubated at various temperatures after chilling.

Collection site	Incubation temp. (°C.)	Number of days in chilling	Mean number of days until emergence ¹	Standard deviation ²	Developmental rate (day ⁻¹)
Albany	13.0	450	87.85	3.95	.0114
Zillah ³	15.5	360	61.24 a	2.05	.0163
Zillah ⁴	15.5	360	64.22 a	2.36	.0156
Albany ⁵	15.5	280	76.71 a	1.96	.0130
Zillah	19.5	250	52.74 b	4.27	.0190
Albany ⁵	19.5	360	46.99 b	3.74	.0213
Zillah	25.5	360	27.70 c	2.00	.0361
Albany ⁵	25.5	525	23.56 c	2.65	.0425
Albany	28.0	410	30.20	4.87	.0331

¹ Means followed by the same letter are significantly different ($\alpha = .01$) on the basis of a t-test; comparisons were made only between treatments at the same temperature.

² Standard deviation of the number of days until emergence.

³ Emergence from moist sand.

⁴ Emergence from dry sand.

⁵ Emergence data from Van Kirk (1979).

development models, which were constructed using data from the Albany pupae, might not be appropriate for the prediction of development of pupae from other locations.

As mentioned before, the puparia were not collected from the Zillah orchard until April 1. Postdiapause development may have already started before these puparia were collected and transferred to cold storage. However, if this did occur, it is not likely the cause of the differences between the mean times of emergence of puparia from the two collection sites.

The mean times until adult emergence from the Zillah puparia in the 19.5°C. and 25.5°C. treatments were greater than those from the Albany puparia in the same treatments. If postdiapause development had occurred in the Zillah pupae prior to collection, the subsequent mean times until emergence from the constant temperature treatments would be shortened. Postdiapause development would have reduced the differences found in the means of the above treatments. Thus, at 19.5°C. and 25.5°C. differences apparently exist between the developmental rates of pupae from the two sites, although the values found here may be somewhat conservative.

However, since the mean times until adult emergence from Zillah puparia in the 15.5°C. treatment (in dry sand) was shorter than that from the Albany puparia in the same treatment the above argument does not apply. Any postdiapause development occurring in the Zillah puparia prior to collection would have increased the difference between the means rather than decreasing the differences as above. Thus, differences

between mean times until emergence from Zillah and Albany puparia were not clearly established for the 15.5°C. treatment.

Boller and Bush (1974) found that the number of days until 50% emergence, and the number of days between first and 50% emergence, were different for some of the samples of Rhagoletis cerasi puparia collected from fourteen European countries. A tendency for the slope of the cumulative emergence curves to become less steep with decreasing latitude of the sample location was noted. Baker and Miller (1978) found that the effect of constant temperature treatments on the post-diapause development of R. cerasi pupae varied between samples collected from Austria, Czechoslovakia, Switzerland, and Italy. Italian flies were last to emerge from all temperatures while the Swiss flies were first to emerge from almost all temperatures. The day-degree totals for first, 10%, 50%, and 90% emergence were also found to differ between puparia collected from the different locations.

Zillah, Washington is ca. 200 miles northwest of Albany, Oregon. While the distance between the two locations is not very great, selective pressures may be different enough to give rise to the differences in developmental rates observed in this experiment.

Brown (1978) found that the mean time until adult emergence decreased as the chilling time was increased between 75 and 192 days; from 200 to 316 days (the longest treatment) this value levelled off. All puparia used in the research reported here had been chilled for over 200 days before being used in emergence experiments so the effect of a short chilling time was eliminated. However, as indicated in table 6, puparia were chilled for over 316 days; this was due to the limited availability of growth chambers.

Frick (1957) found that increasing chilling time from ca. 200 days to ca. 500 days resulted in increased mortality. However, no effect on developmental time was indicated. It is assumed that chilling times in excess of 316 days did not affect the developmental times reported here. However, the possibility exists and suggests the need for further study.

Relative humidity was approximately equal within any constant temperature treatment to which the Albany and Zillah puparia were exposed. Thus, it is not a causal factor of the differences found between developmental rates of the puparia from the two locations. However, the presence or absence of moisture was found to have a significant effect on developmental rate, at least at 15.5°C. A significant difference ($\alpha = .01$) was found between the mean times until adult emergence from the Zillah puparia exposed to the 15.5°C., moist sand treatment and the Zillah puparia exposed to the 15.5°C., dry sand treatment. The mean time of emergence was approximately three days earlier from the puparia held in moist sand than that from puparia held in dry sand, as indicated in table 2.

In the emergence experiments conducted by Van Kirk (1979) and those reported here, relative humidity was not a controlled factor as it was assumed not to affect developmental rate. While moisture has been demonstrated to affect developmental rate, this does not necessarily imply that relative humidity has an effect. However, the possibility exists and its implications deserve mention.

If relative humidity has a large effect on developmental rate, it might be necessary to include it as a factor in the postdiapause developmental model in order to obtain accurate predictions. However,

this would be quite costly, in terms of data acquisition for both constructing and running the model. These costs must be weighed against the possible benefits associated with improved accuracy of the predictions of this more complex model. As will be discussed later, the predictions of the postdiapause development model which does not include moisture or relative humidity as factors affecting developmental rate are sufficiently accurate. Thus, the costs associated with a more complex model do not appear justified.

C. Postdiapause Developmental Rates Under Alternating Temperature Conditions

Emergence data from alternating temperature emergence experiments with the Albany puparia are presented in Appendix D. Statistical comparisons of observed mean times of emergence from puparia exposed to these alternating temperature regimes and expected mean times of emergence were made using a t-test. Expected mean times of emergence were computed on the basis of an assumption of the day-degree and postdiapause development models, that the proportion of development completed during any time interval is a function of the temperature and the length of the time interval. Again, this is based on the thermal summation concept, that a certain amount of heat energy (represented in this experiment by the temperature-time treatment) is required for a certain amount of development. Moreover, the proportion of development completed during any time interval is assumed to be independent of the amount of development already completed. For example, the observed mean time until adult emergence is ca. 30 days at 28°C., so

one half of the development would be completed during any 15 day time interval at 28°C., under these assumptions.

Both alternating temperature experiments had constant temperature exposures at 19.5°C. following the alternating temperature exposures; this was done to avoid complications due to alternating temperature exposures during the emergence period. Expected mean times until emergence after transfer to 19.5°C. were computed by multiplying the number of days at each temperature in the alternating temperature regime (excluding the 19.5°C. treatment) by the developmental rates determined for each temperature from the constant temperature emergence experiments. The sum of these products is subtracted from one to determine the expected proportion of development not completed at the time of transfer to 19.5°C. This difference is multiplied by the total number of days until the mean time of emergence at a constant 19.5°C. to determine the expected number of days until the mean time of emergence after transfer to 19.5°C. following the alternating temperature exposures.

The data used in the computations of the above quantities and the comparisons of the expected number of days until mean time of emergence after transfer to 19.5°C. with the observed number of days are presented in tables 7 and 8. In the first experiment where the puparia were exposed to a four week temperature regime which alternated weekly between 15.5°C. and 28°C., the observed mean time of emergence after transfer to 19.5°C. was significantly less than ($\alpha = .01$) the expected mean time of emergence. However, in the second experiment where the puparia were exposed to several eight-hour daytime and sixteen-hour nighttime temperatures, there was no significant difference ($\alpha = .01$) between observed and expected mean times of emergence.

Table 7. Determination of expected proportions of development completed under two alternating temperature regimes.

Alternating Temperature Treatment #1

Temp. (°C.)	Length of exposure (days)	Developmental rate (day ⁻¹) ¹	Proportion of development completed ²
15.5	14	.0131	.1834
28.0	14	.0331	.4634
Total	28		.6468

Alternating Temperature Treatment #2

Temp. (°C.)	Length of exposure (days)	Developmental rate (day ⁻¹) ¹	Proportion of development completed ²
3.0	5.33	--	--
13.0	14.00	.0114	.1596
19.5	11.67	.0213	.2486
25.5	1.33	.0424	.0564
28.0	0.67	.0331	.0222
Total	33.00		.4868

¹ Developmental rates determined under constant temperature conditions; all developmental rate data (except for 28°C. treatment) are from Van Kirk (1979).

² Expected proportions of development completed are computed by multiplying the length of exposure by the constant temperature developmental rate.

Table 8. Computations and comparisons of expected mean number of days until emergence at 19.5°C., following exposure to two alternating temperature treatments.

Treatment number	Proportion of development not completed ¹	Expected mean number of days until emergence ²	Observed mean number of days until emergence ³
1	.3532	16.60	11.41* (5.42)
2	.5132	24.09	26.75 (7.33)

¹ Expected proportion of development not completed during the alternating temperature treatments.

² Expected mean number of days until emergence after transfer to 19.5°C. from the alternating temperature treatments; computed by multiplying the total number of days until emergence from a constant 19.5°C. treatment (46.99 days) by the expected proportion of development not completed in the alternating temperature treatments.

³ Observed mean number of days until emergence at 19.5°C. following transfer from the alternating temperature treatments. Observed means followed by an asterisk are significantly different ($\alpha = .01$) from expected means on the basis of a t-test. Values in parentheses are standard deviations.

The implications of the results of the first experiment with regard to the day-degree and postdiapause development models are not clear. In the normal application of the models, the postdiapause development of pupae is being predicted under field conditions, where temperature changes are more gradual than those used here. The abrupt change to a high temperature, from 15.5°C. to 28°C., may have altered the developmental processes of the pupae. However, the observed mean time of emergence was less than the expected mean time of emergence; it would seem more likely that the developmental rate would be decreased due to the possible injurious effects of the abrupt temperature change. The temperature regime used in the second experiment may not have had such an effect, since temperature changes were not as extreme and exposures to high temperatures were shorter.

Numerous reports of the accelerating and decelerating effects of alternating temperatures on poikilotherm development appear in the literature. Hagstrum and Hagstrum (1970) listed 26 species of insects in which development was claimed to be accelerated or decelerated by alternating temperature, in comparison to expected developmental rates determined from constant temperature exposures. Messenger and Flitters (1959) claimed that the developmental rates of Dacus dorsalis, the oriental fruit fly, Dacus cucurbitae, the melon fly, and Ceratitis capitata, the Mediterranean fruit fly, were increased when temperatures varied in the lower ranges and were decreased when temperatures varied in the upper ranges. However, their analysis was based upon day-degree computations which do not provide an accurate representation of the developmental rate-temperature relationship in these temperature ranges. This may have resulted in a misinterpretation of the data

since temperatures varied into the high and low ranges, but expected day-degree totals were for constant temperatures in the median range.

Ryan (1941) found a number of other reported accelerations or decelerations of development under alternating temperatures to be due to misinterpretations of data. Several causes for misinterpretation were implicated, including the assumption of a linear developmental rate-temperature relationship, the assumption that no development is taking place at low temperatures, the use of extreme temperatures which may have resulted in injury and impairment of the developmental processes, and a general disregard for the statistical significance of observed differences. Thus, the effect of alternating temperatures on poikilotherm development is not clear.

In models of temperature-dependent development of poikilothermic organisms, the generally accepted equation for computing the development under variable temperatures during the time interval $[0, t]$, dt is

$$dt = \int_0^t r[\psi(\tau)] \delta\tau$$

where $\psi(\tau)$ denotes the temperature at time τ and $r(k)$ denotes the developmental rate at temperature k (Curry et al. 1978). The function $r(k)$ is determined from constant temperature developmental rate data. Thus, the use of the above equation involves the assumption that developmental rates under variable temperature regimes can be predicted using a function based upon developmental rates determined under constant temperatures (ie. there are no significant accelerating or decelerating effects associated with alternating temperatures). To increase the tractability of the calculations, the equation is normally

converted to a discrete form and solved using iterations over short time intervals (as is done in the postdiapause development model reported here).

The accuracy of predictions of models based upon the above equation has been amply demonstrated (eg. Stinner et al. 1975). This suggests that accelerations or decelerations of development under variable temperature regimes either are not occurring or are not significant enough to affect the accuracy of predictions.

D. Dissections of Puparia

The data from dissections of puparia collected from the Albany orchard and exposed to various constant temperature treatments after chilling are presented in table 9. These data were utilized in an attempt to establish the upper and lower temperature thresholds for the postdiapause development of the western cherry fruit fly. These thresholds could not be determined from the adult emergence data alone. Partial postdiapause development may have occurred in some of the high and low temperature treatments but these treatment conditions may not be suitable for complete development to the emerged adult stage. Thus, postdiapause development might not be detected by using adult emergence as the sole criterion for determining its occurrence. Under variable temperature regimes, these high and low temperature conditions may allow considerable development to occur. The high and low temperature thresholds are therefore important data for the construction of an accurate postdiapause development model.

In most cases, the groups of puparia in different treatments were exposed either to the treatment temperature or the temperature at which

Table 9. Developmental stages of the contents of puparia collected from the Albany orchard and dissected after various temperature treatments.

Incubation temp. (°C.)	Length of exposure ¹	Number of days in storage ²	% emerged adults	% dead pharate adults	% live and undeveloped pupae	% dead pupae
6.0 ³	363	88	8.3 ⁴	13.8	6.4	71.5
9.0 ³	363	88	0	33.9	0	66.1
13.0	123	14	14.8	31.1	3.7	50.4
15.5 ³	106	206	47.7	8.3	0	44.0
17.0	106	206	39.4	3.7	0	56.9
19.5	228	--	77.0	5.0	0	18.0
21.0	106	206	45.9	10.1	1.8	42.2
22.0	215	45	21.0	25.0	1.0	53.0
25.5	95	--	8.3	10.2	1.9	87.6
28.0	109	53	10.0	22.0	10.0	58.0
30.0	122	50	0	0	21.0	79.0
32.0	106	175	4.0 ⁵	7.0	0	89.0

¹ Number of days at incubation temperature.

² Puparia were stored at 25.5°C. after the 6, 9, and 25.5°C. treatments prior to dissection; all others were stored at 19.5°C.

³ Puparia for these dissections were from experiments conducted by Mr. Jim Van Kirk, Department of Entomology, Oregon State University.

⁴ Adults emerged after transfer to 25.5°C.

⁵ Adults emerged after transfer to 19.5°C.

they were stored prior to dissection for different time periods. Since the length of exposure may affect the percentages of puparia in the different classes, comparisons were made only between groups of pupae having approximately the same exposure times.

The 30°C. treatment was continued for 122 days; following this the puparia were transferred to 19.5°C. and dissected after 50 days. No development was evident in any of the dissected puparia from this treatment. However, 21% of the puparia contained pupae which appeared to be alive and undeveloped, possibly in a state of aestivation. Pupal aestivation has been reported in Rhagoletis lycopersella in response to adverse conditions (Smyth 1960). The 30°C. treatment may also be inducing the western cherry fruit fly to aestivate to avoid the possibly harmful effects of the high temperature during postdiapause development.

The 28°C. treatment was continued for 109 days; following this the puparia were transferred to 19.5°C. and dissected after 53 days. Development had occurred during the 28°C. treatment as indicated by the adults that emerged from 10% of the puparia. The dissections revealed another 22% of the puparia contained pupae which had developed to the pharate adult stage. Ten percent of the puparia contained pupae which appeared to be alive and undeveloped, again possibly in aestivation.

In comparison to the 28°C. and 30°C. treatments, which had 10% and 21% apparent pupal aestivation, respectively, the 25.5°C. treatment had only 1.9%. The puparia from this treatment were dissected after 94 days at 25.5°C.; the reduction in percent aestivation was thus not due to a longer treatment time, which may have allowed increased mortality of these aestivating pupae. Furthermore, the relative humidity was

approximately equal (ca. 40%) in the three treatments, thus eliminating this as a factor. However, an interaction between temperature and humidity may be effecting the high percentage of pupae apparently in aestivation from the 28°C. and 30°C. treatments. The pupae in aestivation may have been able to develop to the adult stage and emerge if the relative humidity had been higher; a positive developmental rate would have been obtained for the pupae in the 30°C. treatment. This has been assumed not to have occurred. Thirty degrees centigrade was therefore selected as the upper temperature threshold for the postdiapause development of the western cherry fruit fly, since development was observed in puparia from the 28°C., but not the 30°C. treatment.

However, 30°C. should not be considered as the upper temperature limit for pupal survival. Adult flies emerged after a mean of 49.5 days from 4% of the puparia exposed to 19.5°C., following the previous treatment of 106 days at 32°C. The mean number of days until adult emergence following transfer to 19.5°C. from the 32°C. treatment is not significantly different ($\alpha = .01$) from the mean number of days until emergence at 19.5°C. without the previous exposure to 32°C. If postdiapause development had occurred at 32°C., the proportion of development completed would be expected to reduce the time until emergence after transfer to 19.5°C. in comparison to the time until emergence at 19.5°C. without any previous exposure to temperatures allowing development. Thus, while postdiapause development apparently does not occur at 32°C., the pupae are able to survive (possibly by aestivating) and development proceeds when they are transferred to a lower temperature.

The data from the 6°C. and 9°C. treatments were used in an attempt to establish the lower temperature threshold for postdiapause development.

Adult flies emerged from puparia exposed to 25.5°C., following a previous exposure of 363 days at 6°C.; however, adult emergence was later than that from puparia exposed to 25.5°C. without any previous exposure to temperatures allowing development (personal communication, Mr. Jim Van Kirk, Department of Entomology, Oregon State University). Thus, postdiapause development apparently did not occur at 6°C. in the pupae that completed development and emerged at 25.5°C. Again, if postdiapause development had occurred at 6°C., the time until emergence after transfer to 25.5°C. would be reduced in comparison to the time until emergence at 25.5°C. without any previous exposure to temperatures allowing development.

The data from the 9°C. treatment indicated that postdiapause development may have occurred, as indicated by the large percentage (33.9) of pupae that developed to the pharate adult stage. However, this development may have occurred after transfer to 25.5°C. rather than during the 9°C. treatment. If the postdiapause development was assumed to have occurred during the 9°C. treatment, the developmental rate could still take a wide range of values since the pupae could have developed to the pharate adult stage and died at any time during the 363 days at 9°C.

Since the available evidence did not clearly indicate the appropriate lower temperature threshold, the postdiapause development model was run using both a 7°C. and a 9°C. lower temperature threshold. The threshold associated with the most accurate model predictions was selected as the appropriate threshold. In all postdiapause development model runs, an upper temperature threshold of 30°C. was used.

E. Day-degree models

The FORTRAN coding for the main subroutine of the day-degree models is presented in Appendix E. The model codings differ only in the subroutine used for the day-degree computations; therefore, the FORTRAN coding for the main subroutine is presented only once. The three subroutines which are called by the main subroutine for day-degree computations in the three day-degree models are presented in Appendix F.

The operations performed by the FORTRAN program are executed in a stepwise fashion; thus the models will be described in such a fashion. Initially, the location and first and last dates for the current model run are input to be used for the output identification. The maximum soil temperatures at the surface, two, and four inch depths on the day preceeding the first day for the current model run, and the postdiapause developmental sums at these depths (if the current run is a continuation of a previous run for the same location), are input to be used as initial conditions. The number of days for the current run and the number of days before the location was first cultivated, during which vegetation covered the soil, are input to determine which models of soil temperature model set three (ST3) will be used to predict soil temperatures on different dates. The successive dates for the current run and the observed minimum and maximum air temperatures on these dates are input for use in ST3 soil temperature predictions.

At this point, the subroutine for the day-degree computations from the predicted soil temperatures at each depth is called from the main program. Day-degrees are computed from each day's predicted max-min soil temperatures and are summed through time. DD1, DD2, and DD3 are

equivalent except for this subroutine. The equations used in the subroutines of DD1, DD2, and DD3 are presented in table 10.

Day-degree model one (DD1) utilizes the basic day-degree equation with computations based on a 24-hour period. No upper threshold is identified.

The triangulation method of Lindsey and Newman (1956) is used in DD2 and DD3 to provide a more accurate approximation of the area under the temperature wave when the minimum temperature is less than the lower temperature threshold. An upper temperature threshold of 27°C. is also used in these two models. DD2 and DD3 differ in the method used for approximations when the maximum temperature exceeds the upper temperature threshold. The DD2 and DD3 approximations of the area bounded by the temperature wave and the upper and lower temperature thresholds are presented in figure 3. The models also differ in that DD2 computes daily day-degrees for two 12-hour periods while DD3 computes daily day-degrees for a 10-hour period from the minimum to the maximum and a 14-hour period from the maximum to the minimum. Thus, the skewness of the daily temperature wave is accounted for in DD3.

After the computations of day-degrees at each depth, control returns to the main program where a weighted sum of day-degrees for the upper soil column is computed for each day's predictions. Model output consists of the run identification, dates, daily day-degrees and sums for each depth, and the weighted sums.

The equations from soil temperature model set three used for predicting soil temperatures and the method used for computing the weighted sum of daily day-degrees depend upon whether the soil was cultivated on or before the current time step for predictions. If the

Table 10. Equations used in day-degree models one, two and three.

Day-degree model one

- A. If the maximum temperature is less than or equal to the lower threshold:
daily day-degrees = 0
- B. If the maximum temperature is greater than the lower threshold:
daily day-degrees = $\frac{\text{maximum temperature} + \text{minimum temperature}}{2} - \text{lower threshold}$

Day-degree model two

- A. If the maximum temperature is less than or equal to the lower threshold:
daily day-degrees = 0
- B. If the maximum temperature is greater than the lower threshold, less than or equal to the upper threshold, and:
 - 1. The minimum temperature is less than the lower threshold;
day-degrees for 12 hours = $\frac{(\text{maximum temperature} - \text{lower threshold})^2}{4 \times (\text{maximum temperature} - \text{minimum temperature})}$
 - 2. The minimum temperature is greater than or equal to the lower threshold;
day-degrees for 12 hours = $\frac{1}{2} \times \left(\frac{\text{maximum temperature} + \text{minimum temperature}}{2} - \text{lower threshold} \right)$
- C. If the maximum temperature is greater than the upper threshold, the upper threshold is used in the above equations in lieu of the maximum temperature.

Day-degree model three

- A. If the maximum temperature is less than or equal to the lower threshold:
Day-degrees for 12 hours = 0
- B. If the maximum temperature is greater than the lower threshold, less than or equal to the upper threshold, and:
 - 1. the minimum temperature is less than the lower threshold;
day-degrees for 12 hours = $\frac{(\text{maximum temperature} - \text{lower threshold})^2}{4 \times (\text{maximum temperature} - \text{minimum temperature})}$

(Table 10, continued)

2. the minimum temperature is greater than or equal to the lower threshold;
 day-degrees for 12 hours = $\frac{1}{2} \times \left(\frac{\text{maximum temperature} + \text{minimum temperature}}{2} - \text{lower threshold} \right)$

C. If the maximum temperature is greater than the upper threshold and:

1. the minimum temperature is less than the lower threshold;
 day-degrees for 12 hours = $\frac{(\text{maximum temperature} - \text{lower threshold})^2}{4 \times (\text{maximum temperature} - \text{minimum temperature})} - \frac{(\text{maximum temperature} - \text{upper threshold})^2}{4 \times (\text{maximum temperature} - \text{minimum temperature})}$
2. the minimum temperature is greater than or equal to the lower threshold, and less than the upper threshold;
 day degrees for 12 hours = $\frac{1}{2} \times \left(\frac{\text{maximum temperature} + \text{minimum temperature}}{2} - \text{lower threshold} \right) - \frac{(\text{maximum temperature} - \text{upper threshold})^2}{4 \times (\text{maximum temperature} - \text{minimum temperature})}$
3. the minimum temperature is greater than or equal to the upper threshold;
 day-degrees for 12 hours = $\frac{\text{upper threshold} - \text{lower threshold}}{2}$

D. If the day-degrees were computed for the period from the minimum temperature to the maximum temperature;
 day-degrees for the period = $(20/24) \times \text{day-degrees for the 12-hour period.}$

E. If the day-degrees were computed for the period from the maximum temperature to the minimum temperature;
 day-degrees for the period = $(28/24) \times \text{day-degrees for the 12-hour period.}$

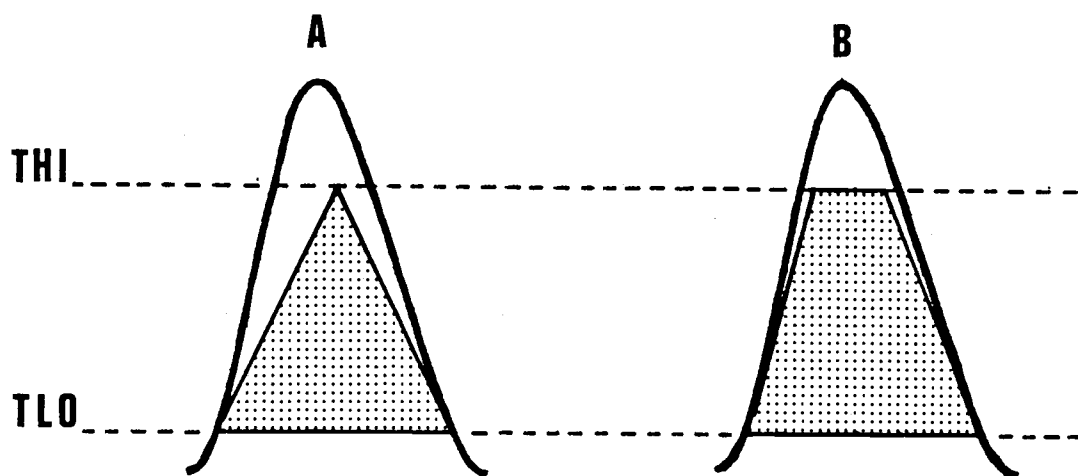


Figure 3. Approximations of the area bounded by the daily temperature wave and the upper (THI) and lower (TLO) thresholds provided by (A) day-degree model two and (B) day-degree model three.

soil was not cultivated on or before the current time step, the equations for predicting temperatures under grass-covered soil are used. The weighted sum of daily day-degrees is computed by multiplying the daily day-degrees for the surface, two, and four inch soil depths by the proportions of puparia estimated to be within certain ranges about these depths. The daily day-degrees for the soil surface are multiplied by the proportion of puparia estimated to be within the top inch of soil; the daily day-degrees for the two inch depth are multiplied by the proportion of puparia estimated to be within the one to three inch range of soil depths; the daily day-degrees for the four inch depth are multiplied by the proportion of puparia estimated to be below the three inch depth. The above products are summed to establish an estimate of daily day-degrees for the portion of the uncultivated soil column where cherry fruit fly puparia are found. Estimates of the proportions of puparia within each range of depths in uncultivated soil were obtained from Frick et al. (1954).

If the soil was cultivated on or before the current time step for predictions, the equations for predicting soil temperatures under bare soil are used. Since no predictions of surface temperatures of bare soil are made, the weighted sum of daily day-degrees is based only upon the daily day-degrees for the two and four inch soil depths. The daily day-degrees for the two inch depth are multiplied by the proportion of puparia estimated to be within the top three inches of soil; the daily day-degrees for the four inch depth are multiplied by the proportion of puparia estimated to be below the three inch soil depth. The above products are summed to establish an estimate of daily day-degrees for the portion of the cultivated soil column where cherry fruit fly

puparia are found. Estimates of the proportions of puparia within each range of depths in cultivated soil were obtained from AliNiazee (1974).

The method for weighting the daily day-degrees at each depth was utilized in the day-degree models because it provided a facile index for predictions which incorporated differences in the distribution of pupae in the soil due to grass-control practices in the commercial orchard.

An upper threshold of 27°C. was selected for use in DD2 and DD3 on the basis of the observed developmental rate-temperature curve. This threshold is not the temperature threshold at which development is stopped due to extreme heat as is used in the postdiapause development model. The upper threshold in the day-degree models is used only to minimize errors of the day-degree computations which occur when the developmental rates at high temperatures are overestimated by the linear day-degree relationship. The upper threshold was selected in an attempt to balance the overestimation of developmental rates by the day-degree model at high temperatures below the threshold with the underestimation of developmental rates by the day-degree model at temperatures above the threshold where development can still occur, but is predicted as nil.

The yearly sums accumulated up to the observed mean times of adult emergence from the Albany orchard during the years 1973 to 1977 were used in developing the criteria for the day-degree model predictions. The mean of the yearly day-degree totals for a given day-degree model-threshold combination is used as the criterion for its predictions of the mean time of adult emergence. In the operation of the day-degree model, the first day on which the computed day-degree total exceeds the mean of

the yearly day-degree totals is the predicted day for the mean time of emergence.

The yearly day-degree totals should be equal, if the models are accurately predicting postdiapause development and if the assumed starting date (March 1) is correct. Assuming that March 1 is the correct starting date, the inequality of the yearly day-degree totals may be due to assumptions of the day-degree model, including the assumed linear relationship between developmental rate and temperature, which may result in errors in the developmental predictions. Alternatively, the estimated parameters (eg. upper and lower temperature thresholds) may not be correct, or the formulas used in day-degree computations may not be providing an accurate representation of the area under the temperature wave.

The temperature threshold resulting in the most accurate day-degree model predictions may be estimated by comparing the coefficients of variation of the yearly day-degree totals computed using different temperature thresholds (Arnold 1959). This method was used to establish the day-degree model-temperature threshold combination resulting in the most accurate predictions of the mean time of adult emergence from the Albany orchard.

The yearly day-degree totals at the observed mean times of adult emergence from the Albany orchard are presented in table 11 for DD1, DD2, and DD3. Day-degree totals were computed using lower temperature thresholds of 8.33°C., 10.00°C., and 11.67°C. for DD1 and DD2; 8.33°C. and 10.00°C. were used for DD3. Means and coefficients of variation of the yearly day-degree totals are also shown.

Table 11. Day-degree totals above different lower thresholds for day-degree models one, two, and three at the mean time of adult emergence from the Albany orchard.

Day-Degree Model One

Threshold (°C.)

Year	8.33	10.00	11.67
1973	423.70	294.06	193.04
1974	460.57	308.19	191.26
1975	414.50	295.30	206.65
1976	433.58	282.36	168.47
1977	397.77	248.95	147.48
Mean	426.02	285.77	181.38
Coefficient of variation	5.49	7.88	12.89

Day-Degree Model Two

Threshold (°C.)

Year	8.33	10.00	11.67
1973	431.27	306.16	208.97
1974	464.46	320.41	210.16
1975	425.13	306.56	217.57
1976	442.50	298.93	188.33
1977	390.09	263.23	165.27
Mean	430.69	299.06	198.06
Coefficient of variation	6.32	7.18	10.76

Day-Degree Model Three

Threshold (°C.)

Year	8.33	10.00
1973	433.69	308.64
1974	467.18	323.15
1975	427.57	309.07
1976	444.15	300.60
1977	391.65	264.77
Mean	432.85	301.25
Coefficient of variation	6.36	7.29

The coefficients of variation of the yearly day-degree totals of DD1 and DD2 with the 11.67°C. lower threshold are large, relative to those of the other model-threshold combinations, indicating that they are not likely to predict the time of emergence as accurately as the other model-threshold combinations. These results are corroborated by the comparisons of the differences in days between the predicted mean times of emergence (based on the means of the yearly day-degree totals) and the observed mean times of emergence from the Albany orchard during the five year period. These are presented along with their sums, standard deviations, and the sums and means of absolute values in table 12.

The sums of the absolute values of differences between predicted and observed mean times of emergence were 18 and 16 days for the DD1-11.67°C. and the DD2-11.67°C. combinations, respectively. All of the other model threshold combinations resulted in sums of ten days, except the DD2-8.33°C. combination which resulted in a nine day sum.

The total number of days associated with late predictions exceed those associated with early predictions for all models except those utilizing the 11.67°C. threshold. This is indicated by the sums of positive and negative errors. The standard deviations of these signed errors are of the same magnitude for all models except those utilizing the 11.67°C. threshold. The larger coefficients of variations, larger sums of absolute deviations, and larger standard deviations of signed errors of the models utilizing the 11.67°C. threshold indicate that these are the least accurate for predicting emergence. However, these data do not clearly indicate differences between the accuracies of the other model-threshold combinations. The DD2-10°C. combination was selected for

Table 12. Days between mean time of emergence predicted using means of the yearly day-degree totals and mean times of emergence observed in the Albany orchard.¹

<u>Day-Degree Model One</u>			
Threshold (°C.)			
Year	8.33	10.00	11.67
1973	0	+1	+2
1974	+3	+2	+1
1975	-2	+1	+7
1976	0	-1	-2
1977	-5	-5	-6
$\Sigma x ^2$	10	10	18
Σx^3	-4	-2	2
$\Sigma x /n^4$	2.0	2.0	3.6
S_x^5	2.95	2.79	4.83

<u>Day-Degree Model Two</u>			
Threshold (°C.)			
Year	8.33	10.00	11.67
1973	0	+1	+1
1974	+2	+2	+1
1975	-1	+1	+6
1976	+1	-1	-2
1977	-5	-5	-6
$\Sigma x $	9	10	16
Σx	-3	-2	0
$\Sigma x /n$	1.8	2.0	3.2
S_x	2.70	2.79	4.42

<u>Day-Degree Model Three</u>		
Threshold (°C.)		
Year	8.33	10.00
1973	0	+1
1974	+2	+2
1975	-1	+1
1976	+1	0
1977	-5	-5
$\Sigma x $	10	10
Σx	-3	-1
$\Sigma x /n$	2.0	2.0
S_x	2.70	2.77

¹ A positive sign indicates an early prediction while a negative sign indicates a late prediction.

² Sum of absolute values of days.

³ Sum of days.

⁴ Mean of absolute values of days.

⁵ Standard deviation of days.

further refinement for the predictions of other levels of emergence, although the other model-threshold combinations are likely to perform equally well.

While the day-degree models were constructed and validated with regard to the prediction of the mean time of adult emergence, predictions of the times of other emergence levels are required for the timing of control activities. The predictions of the times of initial emergence levels, such as first, 10%, and 25% emergence, are especially important since premature insecticide applications may not be effective against the later emerging flies, and late insecticide applications may result in fruit damage by flies emerging and ovipositing before the insecticide application. Thus, criteria were developed for the prediction of the times of the first, 10%, and 25% emergence levels by the DD2-10°C. threshold combination.

The same procedures were used for developing the criteria for the prediction of these other emergence levels as were used for mean time of emergence. Table 13 presents the yearly day-degree totals at the time of first, 10%, and 25% emergence levels in the Albany orchard. The means of these totals are used as the criteria for the prediction of the time of occurrence of the emergence levels. Thus, the first day on which the day-degree total exceeds 214.52 is the predicted day for first emergence; 224.62 day-degrees are associated with 10% emergence, and 271.80 day-degrees are associated with 25% emergence. The days between predicted and observed times of occurrence of the emergence levels in the Albany orchard are presented along with summary statistics in table 14. Mean errors of 2.2, 3.0, and 1.6 days are associated with

Table 13. Day-degree totals for the DD2-10°C. threshold combination at the times of the first, 10%, and 25% emergence levels at the Albany orchard.

Year	Emergence level		
	first	10%	25%
1973	218.00	239.55	300.06
1974	211.82	224.36	255.22
1975	238.12	247.99	282.41
1976	211.97	214.33	266.14
1977	192.70	196.88	255.16
\bar{x}	214.52	224.62	271.80

Table 14. Days between times of emergence predicted by the DD2-10°C. threshold combination and observed times of emergence in the Albany orchard.¹

Year	Emergence Level		
	first	10%	25%
1973	0	+2	+2
1974	-1	-1	-2
1975	+2	+2	+1
1976	-3	-4	-1
1977	-5	-6	-2
$\Sigma x ^2$	11	15	8
Σx^3	-7	-7	-2
$\Sigma x /n^4$	2.2	3.0	1.6
s_x^5	2.70	3.58	1.82

¹ A positive sign indicates an early prediction while a negative sign indicates a late prediction.

² Sum of absolute values of days.

³ Sum of days.

⁴ Mean of absolute values of days.

⁵ Standard deviation of days.

predictions of first, 10%, and 25% emergence levels, respectively, using the above criteria for predictions.

The method used in evaluating the accuracy of predictions of the day-degree models is not very rigorous, since the same data set was used in the model construction as was used in the evaluation procedure. However, this method facilitated comparisons between models developed as part of this research, and between others which have been proposed for predicting the time of emergence of the western cherry fruit fly. These comparisons will be discussed later, along with the postdiapause development model evaluation.

F. Postdiapause Development Model

The FORTRAN coding for the postdiapause development model is presented in Appendix G. The operations performed by the postdiapause development model are the same as those described for the day-degree models up through the predictions of the daily max-min soil temperatures by ST3. From this point, the daily max-min soil temperatures at the various depths are input to a subroutine which computes the successive two-hourly temperatures using a skewed sine wave function which varies between the successive predicted max-min soil temperatures. The sine wave function is skewed so there is a ten-hour period between the predicted minimum and maximum soil temperatures and a fourteen-hour period between the predicted maximum and minimum soil temperatures. The algorithm thereby simulates the progression of fluctuating temperatures in the soil.

The sequences of two-hourly temperatures at each depth are input to a subroutine which computes and sums the predicted proportion of

postdiapause development completed during each of the two hour periods. Developmental predictions are based upon a non-linear postdiapause developmental rate function. The model output consists of the run identification, dates, observed max-min air temperatures, predicted max-min soil temperature for each depth, predicted proportions of postdiapause development completed on each day at each depth, and the sums of the predicted proportions of postdiapause development completed at each depth since March 1.

Postdiapause developmental rates of Albany puparia exposed to 13°C., 26.7°C.⁴, and 28°C. are presented in table 15 along with postdiapause developmental rates at 15.5°C., 17°C., 19.5°C., 21°C., 22°C., and 25.5°C. determined by Van Kirk (1979). These were used as a data set for the development of the non-linear postdiapause developmental rate function mentioned above. A least squares fit of the natural logarithm of postdiapause developmental rates to temperatures from 13°C. to 22°C. was used as an empirical description of the relationship between postdiapause developmental rates and temperatures in the low to medium range; this had an R^2 of .96. A least squares fit of postdiapause developmental rates to a quadratic function of temperatures from 19.5°C. to 28°C. was used as an empirical description of the relationship between postdiapause developmental rates and temperatures in the medium to high range; this had an R^2 of .93. The two models predict the same developmental rate at ca. 20.4°C., so the first model is used for predictions at temperatures less than or equal to 20.4°C. while the second model is used for predictions at temperatures greater than 20.4°C. Postdiapause

⁴ Emergence data for 26.7°C. from AliNiazee (unpublished data).

Table 15. Postdiapause developmental rates of Albany puparia exposed to various constant temperature treatments.

Temperature (°C.)	Mean number of days until emergence	Developmental rate (day ⁻¹)
13.0	87.85	.0114
15.5 ¹	76.71	.0130
17.0 ¹	61.94	.0161
19.5 ¹	46.99	.0213
21.0 ¹	31.66	.0316
22.0 ¹	29.38	.0340
25.5 ¹	23.56	.0425
26.7 ²	25.43	.0393
28.0	30.20	.0331

¹ Data for these temperatures are from Van Kirk (1979).

² Data for 26.7°C. are from AliNiazee (unpublished data).

developmental rates are set equal to zero for temperatures less than a lower threshold or greater than an upper threshold. Thus, an empirical description of the temperature-dependent postdiapause developmental rate relationship was obtained for the entire temperature range. The function is presented in figure 4 with a lower threshold of 9°C. and an upper threshold of 30°C.

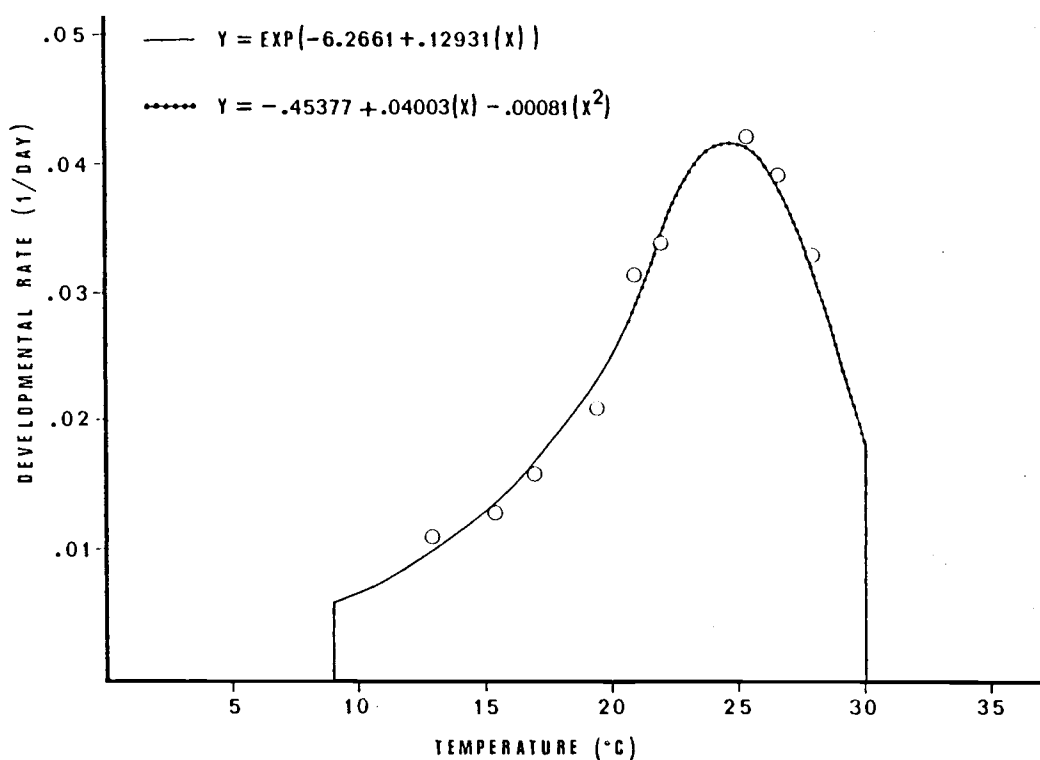


Figure 4. Temperature-dependent postdiapause developmental rate function used in the postdiapause development model.

The sums of predicted postdiapause development are usually different at the different depths due to differences in the predicted soil temperatures. The method used in the day-degree models to weight the day-degrees at each depth was used in the postdiapause development model to weight the predicted proportions of development at each depth.

However, this is not performed by the FORTRAN program since an alternative weighting method was being investigated at the time the program was written.

The alternative weighting method is based upon the assumption that postdiapause development is able to begin on March 1 in pupae at all depths. In this method, the number of days between March 1 and the predicted mean time of emergence (when the sum of predicted proportions of development equals one) would be computed for each depth. The mean time until emergence for the entire soil column could then be predicted by weighting the predicted number of days until the mean time of emergence at each depth by the estimated proportion of puparia found at those depths.

This method was used and predictions were compared to those resulting from the use of the method that weighted the sums of the predicted proportions of development at each depth by the proportions of puparia found at those depths. No differences were found between model predictions when a 9°C. lower threshold was used. The mean times of emergence predicted by the postdiapause development model differed by only one day in two of the five model runs using a 7°C. lower threshold. Moreover, one prediction was one day earlier while the other was one day later, so the mean yearly errors of model predictions were equivalent for both of the weighting methods. Since the weighting method used in the day-degree models would be simpler to incorporate into the FORTRAN program and results in predictions which are nearly equivalent to those obtained through the use of the more complex method based on the assumption of the same starting date for predictions at each depth, it was selected for further use.

The days between mean times of emergence predicted by the postdiapause development model using a 7°C. and a 9°C. lower threshold and observed mean times of emergence in the Albany orchard are presented along with summary statistics in table 16. The postdiapause development model was run for each year using both a 7°C. and a 9°C. lower threshold. The totals of the absolute values of calendar day deviations for model runs using the 7 and 9°C. thresholds were 26 and 9 days, respectively, indicating that the use of the 9°C. lower threshold resulted in more accurate model predictions.

As previously discussed, the predictions of the times of occurrence of the initial emergence levels are important for timing control activities. Therefore, a method was developed for predicting the times of occurrence of the first, 10%, and 25% emergence levels with the postdiapause development model.

The number of days from the observed times of the first, 10%, and 25% emergence levels until the observed mean times of emergence in the Albany orchard during the years 1973 to 1977 are presented in table 17. The means of the number of days for all years are also shown for each emergence level. The mean number of days between the first emergence and the mean time of emergence was ca. 12 for the years 1973 to 1977; the mean was ca. 11 days between 10% emergence and the mean time of emergence, and ca. 5 days between 25% emergence and the mean time of emergence. These means were used to determine the appropriate weighted sums of the proportions of development predicted by the postdiapause development model for predicting the times of the first, 10%, and 25% emergence levels. Table 18 presents the weighted sums from the postdiapause development model runs using the 9°C. lower threshold for the

Table 16. Days between mean times of emergence predicted by the post-diapause development model using two lower postdiapause developmental threshold temperatures and mean times of emergence observed in the Albany orchard.¹

Year	Threshold temperature (°C.)	
	7	9
1973	+4	0
1974	+7	+3
1975	+7	0
1976	+8	+1
1977	0	-5
$\Sigma x ^2$	26	9
Σx^3	26	-1
$\Sigma x /n^4$	5.2	1.8
S_x^5	3.27	2.95

¹ A positive sign indicates an early prediction while a negative sign indicates a late prediction.

² Sum of absolute values of days.

³ Sum of days.

⁴ Mean of absolute values of days.

⁵ Standard deviation of days.

Table 17. Days from first, 10%, and 25% emergence until mean time of emergence at the Albany orchard.

Year	Emergence level		
	first	10%	25%
1973	12	9	5
1974	12	10	7
1975	10	9	5
1976	18	16	4
1977	10	9	3
\bar{x}	12.4	10.6	4.8

Table 18. Postdiapause development model weighted sums of predicted proportions of development completed at the mean time of the first, 10%, and 25% emergence levels.

Year	Emergence level		
	first	10%	25%
1973	.777	.802	.897
1974	.776	.788	.899
1975	.768	.795	.938
1976	.832	.847	.926
1977	.767	.782	.916
\bar{x}	.784	.803	.915

years 1973 to 1977. These weighted sums are the predicted proportions of development completed at each soil depth, multiplied by the proportions of puparia found within ranges about these depths, as previously discussed. The weighted sums for the first, 10%, and 25% emergence levels are those that were predicted at 12, 11, and 5 days before the mean time of emergence predicted by the postdiapause development model. The means of these weighted sums are used as the criteria for the prediction of the time of the first, 10%, and 25% emergence levels by the postdiapause development model. When the weighted sum of predicted postdiapause development is equal to .784, first emergence is predicted; a weighted sum of .803 is used for 10% emergence and .915 is used for 25% emergence. As before, a weighted sum of 1.00 is used for the mean time of emergence.

The days between the predicted and observed times of the first, 10%, and 25% emergence levels are presented along with summary statistics in table 19. The means of the deviations for all years indicate that the method used for predicting the times of the first, 10%, and 25% emergence levels results in fairly accurate predictions with mean yearly deviations of 1.8 days for first emergence, 2.0 days for 10% emergence, and 1.6 days for 25% emergence.

The time of first emergence is dependent on the size of the population. Thus, the observed accuracy of predictions of first emergence by the postdiapause development model (and the day-degree model) may not be achieved when predictions are made for populations of different sizes from those observed in the Albany orchard. However, these data do provide criteria for comparison of the postdiapause development model to other models which were evaluated with the same data set.

Table 19. Days between times of emergence predicted by the postdiapause development model and observed times of emergence in the Albany orchard.

Year	Emergence level		
	first	10%	25%
1973	-1	-1	-3
1974	-2	-2	0
1975	-1	-1	+1
1976	0	+1	+3
1977	-5	-5	+1
$\Sigma x ^2$	9	10	8
Σx^3	-9	-8	2
$\Sigma x /n^4$	1.8	2.0	1.6
S_x^5	1.92	2.19	2.19

¹ A positive sign indicates an early prediction while a negative sign indicates a late prediction.

² Sum of absolute values of days.

³ Sum of days.

⁴ Mean of absolute values of days.

⁵ Standard deviation of days.

The postdiapause development model predictions are slightly more accurate than those of the DD2-10°C. threshold combination, which was selected as a representative of the day-degree models. Upon first inspection, the differences in accuracy do not appear significant enough to be used as criteria for the selection of the most accurate model; for first, 10%, and mean time of emergence the postdiapause development model was an average of only 0.4, 1.0, and .2 days per year, respectively, more accurate than the day-degree model. However, the postdiapause development model was constructed (at least for predicting the mean time of emergence) without reference to the data set used in the evaluation of the accuracy of its predictions. The day-degree model was constructed and evaluated using the same data set. The more rigorous evaluation of the postdiapause development model allows a greater confidence in the accuracy of the evaluation.

The accuracy of the postdiapause development model predictions compares favorably with the accuracy of predictions of the day-degree model used by Van Kirk (1979). This day-degree model utilized the basic day-degree equation with two inch soil temperature data from the Hyslop Farm Field Station; the method of Arnold (1960) was used to correct for errors resulting from minimum temperatures being less than the lower threshold. The same data were used for evaluation of the accuracy of this model as were used for determining the accuracy of the postdiapause development model; these data were also used in the model construction. Means of the absolute values of differences between predicted and observed times of the first and 50% emergence levels were 4.4 and 5.5 days per year, respectively. Thus, the postdiapause development model predictions were more accurate by greater than two

days per year for first emergence and are likely more accurate by greater than three days per year for the mean time of emergence (exact comparisons were not made at the 50% emergence level).

AliNiazee (1976) used the basic day-degree equation with soil temperature data from the two inch depth at the Hyslop Farm Field Station to predict emergence times from the Albany orchard in 1973, 1974, and 1975. The means of the absolute values of differences between the predicted and observed times of the first and 50% emergence levels were 1.0 and 0.67 days per year, respectively. A comparison of these results to the results of the postdiapause development model evaluation is difficult since 1976 and 1977 data were not included in the construction and evaluation of the above model.

As previously mentioned, the postdiapause development model is based upon the assumption that the rate of postdiapause development of the western cherry fruit fly is dependent only upon temperature. This assumption is likely invalid. Moisture has been implicated as a factor affecting developmental rate; other factors may also have an effect. However, even with these factors possibly affecting developmental rate, and thus possibly contributing to the inaccuracy of the postdiapause development model predictions, the model predicted the times of first emergence, 10% emergence, 25% emergence, and the mean time of emergence from the Albany orchard with mean errors of only ca. two days per year. The seven to ten day preoviposition period seems long enough to accomodate errors of this magnitude. Thus, the minor impact of factors other than temperature does not justify efforts to include them in the model. The postdiapause development model appears to be a promising tool for use in the management of the western cherry fruit fly.

V. SUMMARY

Air temperatures and soil temperatures at the surface, two inches, and four inches under a grass cover were recorded over a 93 day period. These data were used along with other air temperature data and soil temperature data from two and four inch depths under bare soil for the construction of three sets of soil temperature models. Each model set predicts maximum and minimum soil temperatures at the surface, two inches and four inches under grass-covered soil and at two inches and four inches under bare soil. The three sets of soil temperatures models were evaluated for accuracy of predictions. The model set with the most accurate predictions was selected for use in conjunction with models of the temperature-dependent postdiapause development of the pupal stage of the western cherry fruit fly.

Puparia collected from Albany, Oregon and Zillah, Washington were exposed to several constant temperature treatments after cold storage to determine postdiapause developmental rates. Significant differences ($\alpha = .01$) were found between the mean times until adult emergence from Albany and Zillah puparia exposed to the same constant temperatures (15.5°C., 19.5°C., and 25.5°C.). A significant difference ($\alpha = .01$) was also found between the mean times until adult emergence from Zillah puparia held in moist sand at 15.5°C. and in dry sand at 15.5°C.

Albany puparia were exposed to two alternating temperature treatments to determine if mean times of adult emergence after transfer to 19.5°C. could be predicted on the basis of the length of exposure to each temperature and the developmental rate at each temperature, determined from constant temperature emergence experiments. The first

treatment consisted of a four week temperature regime which alternated weekly between 15.5°C. and 28°C. A significant difference ($\alpha = .01$) was found between the observed mean time until adult emergence after transfer to 19.5°C. and the expected mean time until adult emergence. The second treatment consisted of a sequence of eight-hour daytime temperatures and sixteen-hour nighttime temperatures, both of which changed as the experiment progressed. No significant difference ($\alpha = .01$) was found between the observed mean time until adult emergence after transfer to 19.5°C. and the expected mean time until adult emergence.

Albany puparia from the constant temperature emergence experiments reported here, and from the constant temperature experiments of Van Kirk (1979) were dissected; the contents were classified either as live and undeveloped pupae, dead pupae, or dead pharate adults. These data were used in an attempt to determine the upper and lower threshold temperatures for the postdiapause development of the western cherry fruit fly. Thirty degrees C. was established as the upper developmental threshold. A lower developmental threshold was not clearly shown, although the data suggest that it is greater than 6°C.

Three day-degree models were constructed for the prediction of the mean time of adult emergence of the western cherry fruit fly. Emergence data from an abandoned orchard in Albany, Oregon were used in the construction and evaluation of these models. The day-degree models utilized three different sets of equations for the computation of day-degrees from maximum and minimum soil temperatures predicted by the soil temperature model set. Several lower temperature thresholds were evaluated with the three day-degree models. The model utilizing a set of day-degree equations which corrected for errors associated with

minimum temperatures below a lower threshold of 10°C., and which compensated for errors associated with maximum temperatures exceeding an upper threshold of 27°C., was selected as the day-degree model for predicting the times of adult emergence from the Albany orchard. Criteria were established for the predictions of the times of the first, 10%, and 25% emergence levels using this day-degree model.

A postdiapause development model which utilized a nonlinear temperature-dependent postdiapause developmental rate function was constructed for the prediction of the times of several emergence levels of the western cherry fruit fly from the Albany orchard. A skewed sine-wave function was used to compute successive two-hourly temperatures based on the maximum and minimum temperatures predicted by the set of soil temperature models. The successive two-hourly temperatures were used by the developmental rate function for predicting the proportion of development completed during the time intervals. The accuracy of the predictions of the postdiapause development model compared favorably with the accuracy of predictions of other models developed as part of this research, and other models reported elsewhere.

Other factors in addition to temperature, including exposure to moisture as revealed in this research, may have an effect on developmental rate. These other factors may adversely affect the accuracy of the postdiapause development model, since temperature is used as the sole determinant of developmental rate. However, the postdiapause development model was found to be sufficiently accurate in spite of these possible sources of error.

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APPENDICES

Appendix A

Schedule of eight-hour daytime and sixteen-hour nighttime temperature treatments for alternating temperature emergence experiment.¹

Day	Daytime temp. (°C.)	Nighttime temp. (°C.)
1	13	3
2	13	3
3	13	3
4	13	3
5	13	3
6	3	3
7	3	3
8	19.5	13
9	19.5	13
10	19.5	13
11	19.5	13
12	13	13
13	13	13
14	13	13
15	19.5	13
16	19.5	13
17	19.5	13
18	19.5	13
19	13	13
20	13	13
21	13	13
22	13	13
23	25.5	19.5
24	25.5	19.5
25	25.5	19.5
26	25.5	19.5
27	19.5	19.5
28	19.5	19.5
29	19.5	19.5
30	19.5	19.5
31	19.5	19.5
32	28	19.5
33	28	19.5

¹ Puparia were exposed to 19.5°C. from day 34 until emergence was completed.

APPENDIX B

Emergence of adults from puparia collected at the Albany orchard and exposed to several constant temperature treatments after chilling.

Temperature (°C.)	Day ¹	Females ²	Males ³	Total ⁴
13.0	84	3	2	5
	85	1	-	1
	86	2	1	3
	87	3	1	4
	89	2	-	2
	91	-	1	1
	92	2	-	2
	95	1	-	1
	98	1	-	1
26.7 ⁵	23	2	5	7
	24	28	26	54
	25	25	25	50
	26	16	14	30
	27	2	1	3
	28	3	1	4
	29	2	3	5
	32	3	-	3
	38	-	1	1
	42	1	1	2
28.0	23	1	-	1
	25	1	-	1
	26	-	1	1
	27	-	1	1
	30	1	-	1
	31	-	1	1
	32	-	1	1
	35	-	1	1
	36	1	-	1
	37	-	1	1
32.0 ⁶	147	1	-	1
	156	1	1	2
	163	1	-	1

¹ Day after transfer from chilling on which adult emergence occurred.

² Number of females emerged.

³ Numbers of males emerged.

⁴ Total number of adults emerged.

⁵ Data from AliNiazee (unpublished data)

⁶ Puparia were transferred to 19.5°C. after 106 days.

APPENDIX C

Emergence of adults from puparia collected at the Zillah orchard and exposed to several constant temperature treatments after chilling.

Temperature (°C.)	Day ¹	Females ²	Males ³	Total ⁴
15.5 ⁵ (moist)	58	1	-	1
	59	3	1	4
	61	2	3	5
	62	1	2	3
	63	2	-	2
	65	1	1	2
15.5 ⁶ (dry)	61	3	1	4
	62	2	2	4
	63	2	2	4
	64	2	-	2
	65	1	4	5
	66	3	-	3
	67	1	-	1
	68	1	3	4
19.5	47	2	1	3
	48	1	-	1
	49	2	1	3
	50	5	1	6
	51	3	2	5
	52	2	1	3
	53	1	1	2
	54	3	-	3
	55	1	-	1
	57	1	-	1
	58	-	1	1
	59	2	-	2
	60	2	-	2
	61	-	1	1
	62	-	1	1
25.5	26	5	3	8
	27	4	4	8
	28	3	1	4
	29	1	3	4
	30	1	-	1
	31	-	1	1
	35	-	1	1

(Appendix C , continued)

-
- 1 Day after transfer from chilling on which adult emergence occurred.
 - 2 Number of females emerged.
 - 3 Number of males emerged.
 - 4 Total number of adults emerged.
 - 5 The sand in this treatment dish was kept moistened with sterile distilled water.
 - 6 The sand in this treatment dish was kept dry.

APPENDIX D

Emergence of adults from puparia collected at the Albany orchard and exposed to two alternating temperature treatments after chilling.

Temperature	Day ¹	Females ²	Males ³	Total ⁴
Alternating ⁵	34	3	1	4
	35	2	2	4
	36	5	3	8
	37	3	4	7
	38	5	1	6
	39	3	1	4
	40	1	3	4
	41	-	2	2
	42	1	1	2
	43	-	1	1
	47	1	-	1
	48	2	-	2
	49	1	-	1
	50	1	-	1
	52	1	-	1
	61	-	1	1
Alternating ⁶	51	1	-	1
	52	1	-	1
	54	1	1	2
	55	1	-	1
	56	2	1	3
	57	2	2	4
	58	1	-	1
	60	-	1	1
	62	-	1	1
	64	1	1	2
	72	1	-	1
	75	-	1	1
	77	-	1	1

¹ Day after transfer from chilling on which adult emergence occurred.

² Number of females emerged.

³ Number of males emerged.

⁴ Total number of adults emerged.

⁵ Temperature treatments alternated weekly between 15.5°C. and 28°C. for four weeks, then puparia were exposed to 19.5°C. until emergence was complete.

⁶ See Appendix A for temperature treatment schedule.

APPENDIX E

FORTRAN coding for the main subroutine of the day-degree models.

```

PROGRAM DEGREE
  DIMENSION LOCATION(6), DATES(3), DATE(150), ATMIN(150), ATMAX(150),
    CSTSMIN(150), STSMAX(150), ST2MIN(150), ST2MAX(150), ST4MIN(150),
    CST4MAX(150), DDS(150), DD2(150), DD4(150), SUMS(150), SUM2(150),
    SUM4(150), SUM(150)
10  FORMAT(6A4, 1X, 3A8)
  READ(60, 10) LOCATION, DATES
25  FORMAT(3F6, 2)
  READ(60, 25) STSMAX(1), ST2MAX(1), ST4MAX(1)
30  FORMAT(I3, 1X, I3)
  READ(60, 30) NDGRASS, NDAYS
  NDGRASS=NDGRASS+1
  NDAYS=NDAYS+1
40  FORMAT(10(F4, 2, 2F2, 0))
  READ(60, 40) (DATE(I), ATMIN(I), ATMAX(I), I=2, NDAYS)
  DO 1 I=2, NDGRASS
    ATMIN(I)=5./9.*(ATMIN(I)-32.)
    ATMAX(I)=5./9.*(ATMAX(I)-32.)
    STSMIN(I)=1.4352+.09006*STSMAX(I-1)+.66233*(ST2MAX(I-1)-
    CSTSMAX(I-1))+.51055*(ATMIN(I)-STSMAX(I-1))
    ST2MIN(I)=1.0864+.91793*ST2MAX(I-1)+.30801*(ST4MAX(I-1)-
    CST4MAX(I-1))+.70453*(STSMIN(I)-ST2MAX(I-1))
    ST4MIN(I)=26.324+.97723*ST4MAX(I-1)+.85749*(ST2MIN(I)-ST4MAX(I-1))
    STSMAX(I)=3.4273+1.2562*STSMIN(I)+1.6516*(ST2MIN(I)-
    CSTSMIN(I))+.78558*(ATMAX(I)-STSMIN(I))
    ST2MAX(I)=24.051+.97751*ST2MIN(I)+.22415*(ST4MIN(I)-
    CST2MIN(I))+.69377*(STSMAX(I)-ST2MIN(I))
    ST4MAX(I)=29.981+.98538*ST4MIN(I)+.74772*(ST2MAX(I)-ST4MIN(I))
1  CONTINUE
  K=NDGRASS+1
  DO 2 I=K, NDAYS
    ATMIN(I)=5./9.*(ATMIN(I)-32.)
    ATMAX(I)=5./9.*(ATMAX(I)-32.)
    STSMIN(I)=0.
    ST2MIN(I)=1.6981+1.0551*ST2MAX(I-1)+1.9786*(ST4MAX(I-1)-ST2MAX
    C(I-1))+.25933*(ATMIN(I)-ST2MAX(I-1))
    ST4MIN(I)=8.8526+.9323*ST4MAX(I-1)+.77791*(ST2MIN(I)-ST4MAX(I-1))
    STSMAX(I)=0.
    ST2MAX(I)=2.8927+1.2999*ST2MIN(I)+.44783*(ST4MIN(I)-ST2MIN(I))
    C+.87671*(ATMAX(I)-ST2MIN(I))
    ST4MAX(I)=5.1471+.93634*ST4MIN(I)+.70016*(ST2MAX(I)-ST4MIN(I))
2  CONTINUE
  CALL DDAYS(NDAYS, STSMIN, STSMAX, DDS, SUMS)
  CALL DDAYS(NDAYS, ST2MIN, ST2MAX, DD2, SUM2)
  CALL DDAYS(NDAYS, ST4MIN, ST4MAX, DD4, SUM4)
  DO 3 I=2, NDGRASS
    SUM(I)=.603*SUMS(I)+.387*SUM2(I)+.01*SUM4(I)
3  CONTINUE
  DO 4 I=K, NDAYS
    SUM(I)=.635*SUM2(I)+.365*SUM4(I)
4  CONTINUE
45  FORMAT(1H1, 5X, 6A4, 5X, 3A8)
  WRITE(61, 45) LOCATION, DATES
50  FORMAT(1H0, 10X, #SOIL SURFACE#, 16X, #TWO INCH DEPTH#, 14X,
  C#FOUR INCH DEPTH#, 15X, #ALL DEPTHS#)
  WRITE(61, 50)
55  FORMAT(1H0, 1X, #DATE#, 5X, #DAY-DEGREES#, 6X, #SUM#, 8X, #DAY-DEGREES#, 6X
  C, #SUM#, 8X, #DAY-DEGREES#, 6X, #SUM#, 10X, #WEIGHTED MEAN#)
  WRITE(61, 55)
60  FORMAT(1H0, F5, 2, 8X, F5, 2, 6X, F7, 2, 2(10X, F5, 2, 6X, F7, 2), 10X, F7, 2)
  WRITE(61, 60) (DATE(I), DDS(I), SUMS(I), DD2(I), SUM2(I), DD4(I), SUM4(I)
  C, SUM(I), I=2, NDAYS)
  CALL EXIT
  END

```

APPENDIX F

Three subroutines used in day-degree models one, two, and three, respectively.

```

SUBROUTINE DDAYS(NDAYS,STXMIN,STXMAX,DDX,SUMX)
  DIMENSION STXMIN(150),STXMAX(150),DDX(150),SUMX(150)
  TLO=10.
  SUMX(1)=0.
  DO 1 I=2,NDAYS
    DDX(I)=(STXMIN(I)+STXMAX(I))/2.-TLO
    IF(DDX(I) .LT. 0.) DDX(I)=0.
    SUMX(I)=SUMX(I-1)+DDX(I)
1 CONTINUE
  RETURN
  END

SUBROUTINE DDAYS(NDAYS,STXMIN,STXMAX,DDX,SUMX)
  DIMENSION STXMIN(150),STXMAX(150),DDX(150),SUMX(150)
  TLO=10.
  THI=27.
  SUMX(1)=0.
  DO 1 I=2,NDAYS
    DDX(I)=0.
    STXMAX=STXMAX(I)
    DO 2 J=1,2
      IF(J .EQ. 1) STXMIN=STXMIN(I)
      IF(J .EQ. 2) STXMIN=STXMIN(I+1)
      IF(STXMAX .GT. THI) STXMAX=THI
      IF(STXMAX .LT. TLO) STXMAX=TLO
      IF(STXMIN .GE. TLO) DHD=.5*((STXMAX+STXMIN)/2.-TLO)
      IF(STXMIN .LT. TLO) DHD=((STXMAX-TLO)**2.)/(4.*(STXMAX-STXMIN))
      DDX(I)=DDX(I)+DHD
2 CONTINUE
    SUMX(I)=SUMX(I-1)+DDX(I)
1 CONTINUE
  RETURN
  END

SUBROUTINE DDAYS(NDAYS,STXMIN,STXMAX,DDX,SUMX)
  DIMENSION STXMIN(150),STXMAX(150),DDX(150),SUMX(150)
  TLO=10.
  THI=27.
  SUMX(1)=0.
  DO 1 I=2,NDAYS
    DDX(I)=0.
    STXMAX=STXMAX(I)
    IF(STXMAX .LT. TLO) STXMAX=TLO
    DO 2 J=1,2
      IF(J .EQ. 1) STXMIN=STXMIN(I)
      IF(J .EQ. 2) STXMIN=STXMIN(I+1)
      IF(STXMAX .LE. THI) GO TO 3
      IF(STXMIN .GT. THI) DHD=.5*(THI-TLO)
      IF(STXMIN .LE. THI .AND. STXMIN .GE. TLO) DHD=(.5*((STXMAX+STXMIN)
C/2.-TLO))-(((STXMAX-THI)**2.)/(4.*(STXMAX-STXMIN)))
      IF(STXMIN .LT. TLO) DHD=((STXMAX-TLO)**2.)-((STXMAX-THI)**2.))/
C(4.*(STXMAX-STXMIN))
      GO TO 4
3 IF(STXMIN .GE. TLO) DHD=.5*((STXMAX+STXMIN)/2.-TLO)
      IF(STXMIN .LT. TLO) DHD=((STXMAX-TLO)**2.)/(4.*(STXMAX-STXMIN))
4 IF(J .EQ. 1) DHD=(20./24.)*DHD
      IF(J .EQ. 2) DHD=(28./24.)*DHD
      DDX(I)=DDX(I)+DHD
2 CONTINUE
    SUMX(I)=SUMX(I-1)+DDX(I)
1 CONTINUE
  RETURN
  END

```


APPENDIX G

FORTTRAN coding for the postdiapause development model.

```

PROGRAM DEVELOP
DIMENSION LOCATION(6), DATES(3), DATE(150), ATMIN(150), ATMAX(150),
CSTSMIN(150), STSMAX(150), ST2MIN(150), ST2MAX(150), ST4MIN(150),
CST4MAX(150), STS(150,12), ST2(150,12), ST4(150,12),
PCDEV5(150), PCDEV2(150), PCDEV4(150), SUMS(150), SUM2(150), SUM4(150)
10 FORMAT(6A4,1X,3A8)
READ(60,10) LOCATION,DATES
20 FORMAT(1H1,5X,6A4,5X,3A8)
WRITE(61,20) LOCATION,DATES
30 FORMAT(6F6.2)
READ(60,30) STSMAX(1), ST2MAX(1), ST4MAX(1), SUMDEV5, SUMDEV2, SUMDEV4
40 FORMAT(1HC,7 DATE ATMIN ATMAX STSMIN STSMAX DEV5 SUMDEV
CS ST2MIN ST2MAX DEV2 SUMDEV2 ST4MIN ST4MAX DEV4 SUMDEV4
C#)
WRITE(61,40)
50 FORMAT(I3,1X,I3)
READ(60,50) NDGRASS,NDAYS
NDGPASS=NDGPASS+1
NDAYS=NDAYS+1
60 FORMAT(10(F4.2,2F2.0))
PEAK(60,60) (DATE(I),ATMIN(I),ATMAX(I),I=2,NDAYS)
DO 1 I=2,NDGPASS
ATMIN(I)=5./9.*(ATMIN(I)-32.)
ATMAX(I)=5./9.*(ATMAX(I)-32.)
STSMIN(I)=1.4352+.89006*(STSMAX(I-1)+.66233*(ST2MAX(I-1)-
CSTSMAX(I-1))+.51055*(ATMIN(I)-STSMAX(I-1))
ST2MIN(I)=1.0864+.91793*(ST2MAX(I-1)+.30801*(ST4MAX(I-1)-
CST2MAX(I-1))+.70453*(STSMIN(I)-ST2MAX(I-1))
ST4MIN(I)=.26324+.97723*(ST4MAX(I-1)+.85749*(ST2MIN(I)-ST4MAX(I-1))
STSMAX(I)=.3.4273+1.2562*STSMIN(I)+1.6516*(ST2MIN(I)-
CSTSMIN(I))+.78558*(ATMAX(I)-STSMIN(I))
ST2MAX(I)=.24951+.97751*ST2MIN(I)+.22415*(ST4MIN(I)-
CST2MIN(I))+.69377*(STSMAX(I)-ST2MIN(I))
ST4MAX(I)=.29981+.98538*ST4MIN(I)+.74772*(ST2MAX(I)-ST4MIN(I))
1 CONTINUE
K=NDGPASS+1
DO 2 I=K,NDAYS
ATMIN(I)=5./9.*(ATMIN(I)-32.)
ATMAX(I)=5./9.*(ATMAX(I)-32.)
STSMIN(I)=0.
ST2MIN(I)=-1.6981+1.0551*ST2MAX(I-1)+1.9786*(ST4MAX(I-1)-ST2MAX
C(I-1))+.25933*(ATMIN(I)-ST2MAX(I-1))
ST4MIN(I)=-.88526+.9323*ST4MAX(I-1)+.77791*(ST2MIN(I)-ST4MAX(I-1))
STSMAX(I)=0.
ST2MAX(I)=-2.8927+1.2999*ST2MIN(I)+.44703*(ST4MIN(I)-ST2MIN(I))
C+.87671*(ATMAX(I)-ST2MIN(I))
ST4MAX(I)=-.51471+.93634*ST4MIN(I)+.70016*(ST2MAX(I)-ST4MIN(I))
2 CONTINUE
CALL TEMPS(NDAYS,STSMIN,STSMAX,STS)
CALL TEMPS(NDAYS,ST2MIN,ST2MAX,ST2)
CALL TEMPS(NDAYS,ST4MIN,ST4MAX,ST4)
CALL DEV(NDAYS,PCDEV5,SUMS,STS)
CALL DEV(NDAYS,PCDEV2,SUM2,ST2)
CALL DEV(NDAYS,PCDEV4,SUM4,ST4)
70 FORMAT(1H0,F5.2,2X,F6.2,2X,F6.2,3X,3(F6.2,2X,F6.2,2X,F6.4,2X,F6.4,
C2X))
WRITE(61,70) (DATE(I),ATMIN(I),ATMAX(I),STSMIN(I),STSMAX(I),
PCDEV5(I),SUMS(I),ST2MIN(I),ST2MAX(I),PCDEV2(I),SUM2(I),ST4MIN(I),
CST4MAX(I),PCDEV4(I),SUM4(I),I=2,NDAYS)
CALL EXIT
END

```

(Appendix G, continued)

```

SUBROUTINE TEMPS(NDAYS,STXMIN,STXMAX,STX)
  DIMENSION STXMIN(150),STXMAX(150),STX(150,12)
  PI=3.1416
  DO 1 I=2,NDAYS
    DO 2 J=1,5
      T=FLOAT(J)*.2
      STX(I,J)=STXMIN(I)+.5*(STXMAX(I)-STXMIN(I))*(1.-COS(PI*T))
    2 CONTINUE
    DO 3 J=6,12
      T=(FLOAT(J)-5.)*.14286
      STX(I,J)=STXMAX(I)-.5*(STXMAX(I)-STXMIN(I+1))*(1.-COS(PI*T))
    3 CONTINUE
  1 CONTINUE
  RETURN
END
SUBROUTINE DEV(NDAYS,PCDEVX,SUMX,STX)
  DIMENSION STX(150,12),PCDEVX(150),SUMX(150)
  SUMX(1)=0.
  DO 1 I=2,NDAYS
    PCDEVX(I)=0.
    DO 2 J=1,12
      DEVX=0.
      IF(STX(I,J).GE. 9. .AND. STX(I,J).LE. 20.4) DEVX=
C 1./12.*(EXP(-6.2661+.12931*STX(I,J)))
      IF(STX(I,J).GT. 20.4 .AND. STX(I,J).LE. 30.) DEVX=
C 1./12.*(-.45377+.04003*STX(I,J)-.00081*(STX(I,J)**2.))
      PCDEVX(I)=PCDEVX(I)+DEVX
    2 CONTINUE
    SUMX(I)=SUMX(I-1)+PCDEVX(I)
  1 CONTINUE
  RETURN
END

```