THERMAL REQUIREMENTS FOR DEVELOPMENT OF THE ELM LEAF BEETLE, *PYRRHALTA LUTEOLA* (MÜLLER)

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THERMAL REQUIREMENTS FOR DEVELOPMENT OF

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LUTEOLA (MÜLLER)

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PREFACE

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I dedicate this work to my father and mother, Bob and Twyla, and my sister and brother, Robyn and Tim, for their encouragement and support which made this study possible.

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CHAPTER I

INTRODUCTION

The elm leaf beetle, Pyrrhalta luteola (Müller), is one of the most common pests of elm trees in the United States. Most species of elms are susceptible to attack. In Oklahoma, P. luteola prefers the Siberian elm, Ulmus pumila L. Adult and larval feeding on elms during the summer results in skeletonized leaves that dry up and drop prematurely. Occasionally, pure stands of elms are severely attacked; but for the most part elms grown as ornamentals in urban locations are more heavily infested.

As with many other ornamental pests, relatively few biological studies have been conducted on P. luteola compared to entomological research in other agricultural and commodity areas. Many landscape managers, pest control operators, and homeowners apply pesticides on elms with little knowledge of elm leaf beetle biology or life history. An accurate method for predicting P. luteola development could be useful in achieving more successful and effective control. The objectives of this study were to determine the effects of temperature on development and survival of the immature stages of the elm leaf beetle, and on the use of these data in predicting the development of field populations. In addition, temperature studies were also conducted to observe adult longevity and egg production.

CHAPTER II

REVIEW OF THE LITERATURE

P. luteola Biology and Life History

The elm leaf beetle, Pyrrhalta luteola (Müller), is a native of southern Europe and initially appeared in the United States near the vicinity of Baltimore, Maryland in 1835 (Fernald 1901). It was first recorded in Oklahoma at Shawnee in 1955 by L. H. Davis (Eikenbary and Raney 1968).

The adult elm leaf beetle is about 6.35 mm in length with an oval-shaped body twice as long as it is wide. Newly emerged beetles are reddish-yellow to bright yellow and turn yellowish-green after a few days. Adults of later generations, particularly the overwintering beetles, are dark olive-green. Each elytron has a wide black mark along the outside margin and a narrow black mark along the inside edge where the elytra joins together. Near the base of the elytra are oval black spots. The prothorax has a black T-shaped mark centrally and a circular black spot near each lateral margin. The vertex of the head is black. A black linear spot marks each of the segments of the legs and antennae which are yellow in color.

P. luteola overwinters in the adult stage and can be found in any natural situation that is sheltered and dry, including barns, church belfries, stone walls, cracks and crevices of fence posts, telephone poles, unused chimneys, attics, asbestos shingles, basements, piles of

rubbish, and loose bark on elm trees. The adults come out of hibernation in the spring after the elm leaves have emerged. This may occur any time from mid-March to early May, depending on geographic location and climatic conditions. Immediately after emerging from overwintering sites, adults begin feeding on the new leaves. Mating and egg laying begins shortly thereafter and may last up to four weeks.

The spindle-shaped eggs of the elm leaf beetle are orange-yellow and usually deposited in small compact clusters of 2 to 4 rows. The eggs, 1.6 mm long and .8 mm wide, are deposited with one end attached to the leaf with a glue-like material. The number of individual eggs in a cluster usually ranges from 1 to 25, but some have been found to contain as many as 47. Most of the eggs are laid on the undersides of the leaves, but occasionally an egg mass will be found on the upper surface. An individual female may deposit up to 800 individual eggs in a life span. Depending on temperature, the eggs hatch in approximately 5 to 12 days.

Newly hatched P. luteola larvae immediately begin migrating and feeding on elm leaves. The first instar larvae appear nearly black since the yellow color of the cuticle is obscured by dark tubercles and hairs. The full grown third instar larvae are approximately 12.7 mm long and dull yellow with two black stripes running down the dorsal area. There are two rows of tubercles between the black stripes and also two rows of lateral tubercles. The head, tubercles, and legs are all black.

After 2 to 3 weeks of feeding on the undersurfaces of leaves, the larvae begin migrating toward the base of the tree and seek crevices in the bark for pupation. Upon arrival at the pupation site the

larvae curl into a c-shaped position and remain in a quiescent state for 2 to 6 days.

P. luteola pupae are 6.35 mm long, bright orange-yellow, and covered with a few black setae. Although most are near the tree base or in bark fissures, they can also be found in upper layers of loose soil near the tree or in cracks of nearby pavement. Pupal development takes from 5 days to 3 weeks depending on climate.

Newly emerged adults usually begin feeding after one day and begin mating and ovipositing 8 to 14 days later. The average life span for a non-overwintering adult is approximately 30 days. The number of generations occurring each year varies upon geographical location, with 1 or 2 occurring in Connecticut, Massachussetts, and New York, 2 in Ohio, 3 or 4 in Kansas and Oklahoma, 4 or 5 in Arizona, and 3 to 5 in California.

The generalized life history and descriptions of this insect follow those reported by Fernald (1901), Houser (1918), Britton (1932), Herrick (1935), Parks (1936), Felt and Rankin (1938), Craighead (1950), Thompson (1963), U.S.D.A. (1964), Brown and Eads (1966), Wene (1968), Baker (1972), Weber and Thompson (1976), and Davidson (1979).

Damage Caused by P. luteola

Elm leaf beetle damage is of two types. Adult feeding is characterized by circular holes eaten completely through leaves. The larvae skeletonize the foliage by feeding on the epidermal tissue from the undersides of the leaves. The larvae are more damaging to an elm than adults and will cause leaves to curl, turn brown, and fall from the tree (Houser 1918; Herrick 1935). The first generation of the year is often

the most destructive (U.S.D.A. 1964). Trees which lose their foliage in the first part of the season will produce a new set of leaves; however, later generations will attack the new growth (Houser 1918; Herrick 1935; Thompson 1963). Two or three complete successive defoliations will usually injure or kill a tree (Fernald 1901; Houser 1918; Britton 1932; Herrick 1935). Generally only partial defoliation occurs, killing individual limbs or leaving the tree in a weakened condition. Such a condition leaves an elm susceptible to bark beetle and borer attack, as well as disease organisms (U.S.D.A. 1964). Weakened American elms, Ulmus americana L., can become a favorable breeding ground for the European elm bark beetle, Scolytus multristriatus (Marsham), which carries the Dutch elm disease Ceratocystis ulmi (Buis.) (Felt 1935; Felt and Bromely 1943; Brewer 1973). Herrick (1935) reported that elms weakened by defoliation were subject to further injury by leaky gas mains, pruning of roots for the laying of sidewalks, and lack of moisture due to covering the ground with impervious pavements.

The adult beetle can create a nuisance when they seek shelter in homes and other buildings for overwintering. During periods of warm weather in the winter many of the overwintering beetles will become active and cause considerable annoyance by crawling into living quarters and on windows. They rarely cause damage inside a home except occasionally staining curtains, wallpaper, and painted surfaces (Wheeler 1959; U.S.D.A. 1964; Koehler et al. 1965; Baker 1972).

P. luteola Host Preference

Although the food of the elm leaf beetle seems to be limited to elm species it has been known to deposit eggs on several other plants

(Fernald 1901). In California, the adult has been observed feeding on almond and bean plants (Herrick 1935). Elm species most seriously attacked include the English elm, Ulmus procera Salisb., Siberian elm, and American elm. In the Northeastern United States the English and American elms are the preferred hosts (Fernald 1901; Houser 1918; Britton 1932; Parks 1936; Felt and Rankin 1938; Baker 1972). Further west the Siberian elm is the major host (Thompson 1963; Baker 1972; Luck and Scriven 1976). In Oklahoma, Eikenbary and Raney (1968) observed Siberian elms as the primary host of P. luteola.

In a study conducted by Luck and Scriven (1979), five groups of 20 elm leaf beetle larvae and 20 pairs (male and female) of adults were reared on leaves from four species of elms: American, Siberian, English, and old and new leaves of the Chinese (lacebark) elm, Ulmus parvifolia Jacq. The leaves from English elm produced the highest larval survivorship (70%) but the shortest adult life expectancy. Low larval survivorship was found on the leaves of Siberian and American elm (25 and 15%, respectively) but caused the longest life expectancy of adults. Larvae failed to survive when fed old leaves of Chinese elm while those fed new leaves exhibited low levels of larval and adult survivorship. Luck and Scriven rated the four species of elms from most to least susceptible as follows: U. procera, U. pumila, U. americana, and U. parvifolia.

Halperin (1971) noted that a correlation existed between soft, pubescent leaves and species susceptibility (e.g., U. procera), while small thick leaves were associated with resistance (e.g., U. parvifolia). Other species of elm noted to be seldom injured by P. luteola include

slippery elm, U. rubra Muhl., winged elm, U. alata Michx., and rock elm, U. thomasii Sarg. (Britton 1932; Herrick 1935).

In relation to damage on elm seedlings, size and position of seedlings seem to be a factor. Lemen (1980) found U. parvifolia seedlings growing directly under adult elms suffered 580 times more P. luteola damage than seedlings not directly under adult elms. It was difficult for elm seedlings to establish themselves near mature trees of their own species. Findings also revealed that below a total tree volume of 2.0×10^5 cm^3, seedlings were completely free from attack.

Natural Enemies of P. luteola

The elm leaf beetle has several types of natural enemies in the form of predators, parasites, and diseases. Eikenbary and Raney (1968) found 12 species of insects to be predaceous on P. luteola. These species include Brochymena cariosa Stal, B. quadripustulata (F.), Mineus strigipes Herrich-Schaeffer, Podisus maculiventris (Say), Stiretrus anchorago (F.), S. fimbriatus (Say), Arilus cristatus (L.), Sinea diadema (F.), Chrysopa carnea Stephens, Hippodomia convergens Geurin-Meneville, Collops quadrimaculatus (F.), and Calosoma sp. With the exception of C. quadrimaculutus, all species were found to be predaceous on larvae. C. carnea, H. convergens, and C. quadrimaculutus were observed feeding on eggs; P. maculiventris, S. fimbriatus, and Calosoma sp. were found predaceous on pupae; M. strigipes, P. maculiventris, S. fimbriatus, and S. diadema were observed attacking adults. Despite the number of species found, field observations indicated that predators were unable to control P. luteola populations below damaging levels. This ineffectiveness was probably due to

the transient nature of most of the predators and their lack of host specificity.

Other insect predators of P. luteola are Apateticus maculiventris Say (Houser 1918), Perrilus confluens (Herrich-Schaeffer) (Wene 1968), and Coleomegilla maculata Degeer (Weber and Holman 1976). Predators other than insects include several species of birds and toads (Britton 1932; U.S.D.A. 1964; Davidson 1979).

Four species of parasites have been reported on the elm leaf beetle. An egg parasite, Tetrastichus xanthomelaenae (Rond.), was introduced from France in 1908 into the eastern United States (Howard 1908). Its effectiveness has not been determined. A tachinid, Erynniopsis antennata (Rond.) was introduced into California in 1939 and is parasitic on both larvae and overwintering adults (Flanders 1940). Flanders also observed a native tachinid of the West coast, Synaplomyia galerucellie (Villeneue) occasionally attacking the larval stage of P. luteola. A native chalcid parasite, Tetrastichus brevistigma Gaham has been found effective against pupae (Berry 1938).

Luck and Scriven (1976) studied the degree of biological control achieved by T. brevistigma and E. antennata against the elm leaf beetle in southern California. Only 10% of P. luteola larvae sampled were parasitized by T. brevistigma. E. antennata killed a high proportion (65-88%) of overwintering adults but larval mortality was low.

Perhaps the most important natural check on the abundance of P. luteola is the fungus Beaveria bassiana (Bals.). This fungus is prevalent during moist conditions and attacks both pupae and adults. After the spores gain access to the insect they germinate, sending white mycelial threads throughout the body. After death the fungal

growth completely envelopes the body of the host, obscuring the details of its anatomy and making it appear as a shapeless snow-white mass (Herrick 1912, 1935; Houser 1918; Britton 1932; Parks 1936; U.S.D.A. 1964; Baker 1972; Davidson 1979). Broudii (1973) suggested placing mulches around the base of elms in order to increase moisture conditions which enhance the growth of B. bassiana.

Insecticidal Control

Insecticides have been the primary means for controlling P. luteola infestations. Early chemicals suggested for control included arsenate of lead and nicotine sulfate (Fernald 1901; Herrick 1912, 1935; Britton 1932; Parks 1936; Graham 1939; U.S.D.A. 1939; Pinone 1959). Arsenate of lead was recommended as a spray against larvae while nicotine sulfate was suggested for use as either a spray or drench for control of the pupae. Fernald (1901) and Houser (1918) prescribed a mixture of hot water and kerosene for killing pupae.

Various rates and formulations of DDT were observed to be effective against P. luteola (Wheeler 1959; Thompson 1963; Koehler et al. 1965; Brown and Eads 1966). Koehler et al. (1965) and Price et al. (1978) found a single spray application of Sevin® (carbaryl) providing control for several months. Trunk injections of Bidrin® (dicrotophos) and Meta-Systox® (oxydemetomethyl) have provided protection against P. luteola for periods of four weeks or longer (Wene et al. 1968; Wene 1970; Saunders 1971; King et al. 1984). Soil drenches observed to be successful include Meta-systox, Bidrin, and Cygon® (dimethoate) (Wene 1970; Saunders 1971; Brewer 1973). Brewer (1973) found high efficacy with sprays of Sevin, Meta-systox, Orthene® (acephate), and soil im-

plantations of Furadan® (carbofuran). Other insecticides effective in reducing elm leaf beetle populations include Mesurol® (methiocarb), Ficam® (bendiocarb) (Price et al. 1980), Ammo® (cypermethrin) (King et al. 1983), and Advantage® (carbosulfan) (King et al. 1984).

Current recommendations by the Oklahoma State University extension service (Anonymous 1984) suggest Orthene 15.6% EC and Sevin 50% WP or 27% EC for larval control with sprays being applied after egg hatch. Di-syston® (disulfoton) 15G is also recommended for use.

Modeling Insect Development

The theory that insect growth and development is dependent on temperature was formulated during the mid-1700's (Wilson and Barnett 1983). A general growth curve for most insects, with development rate plotted as a function of temperature, shows that an insect takes a long time to develop through successive stages at low temperatures. As temperatures increase, development rates become proportional to temperature resulting in a linear response curve. This region is known as the normal growth zone where development is at an optimum (Young and Willson 1984). Insect development falls off sharply when temperatures approach and go beyond the optimum rate of growth, resulting in increased mortality (Wagner et al. 1984).

The thermal requirements for development are often used as a basis for predicting the insect response curve. One method for predicting insect growth is the degree-day approach which has been developed by several researchers (Glenn 1922; Peairs 1927; Lindsey and Newman 1956; Arnold 1960; Baskerville and Emin 1968; Allen 1976; Hartstack et al. 1976; Sevacherian et al. 1977).

The use of degree-day equations is widespread since it requires minimal data for formulation, is easy to calculate and apply, and often produces approximately correct values (Wagner et al. 1984). Degree-day formulas have been developed on a large variety of insects, including pests of field crops, vegetables, fruits, nuts, trees, and shrubs (Ives 1973; Reissig et al. 1978; Wall and Berberet 1980; Potter and Timmons 1983). Degree-day requirements have also been determined for several important predators and parasites (Powell et al. 1981; Obrycki and Tauber 1982).

The degree-day approach is valid only over intermediate temperatures since the rate of development is assumed to be linear. The number of degree-days may be too low or high when estimated below or above the optimum temperature range (Howe 1967).

Numerous empirical functions have been developed and used to describe the effects of temperature on insect development rates including a logistic equation (Davidson 1944), a modified sigmoid formula (Stinner et al. 1974), and a model formulated by the technique of matched asympotic expansion (Logan et al. 1976). These and many other functions describe part or all of the response curve, but most have their shortcomings. While some functions have a foundation in theory, their parameter values have little or no biological meaning (Wagner et al. 1984).

Some investigators have attempted to explain the thermodynamics of complex biological processes that affect organism development. Johnson and Lewin (1946), working with bacteria, formulated one of the first complex biophysical models describing development rates. Their model provided a good fit to data at optimum temperatures, but did not

accurately describe development near the lower threshold. Hultin (1955) described the influence of temperature on the rate of inactivation of the enzymes lipase, saccharase, and trypsin and provided a theory for modeling development rates at low temperatures. Sharpe and DeMichele (1977) consolidated the work of Johnson and Lewis (1946), Hultin (1955), and other investigators to formulate a complex biophysical model that describes the nonlinear response in development rates at both high and low temperatures as well as the linear response at intermediate temperatures. Schoolfield et al. (1981) modified the original form of the Sharpe and DeMichele equation for use in nonlinear regression techniques. To extend this model to entomologists, Wagner et al. (1984) developed a computer program from the Statistical Analysis System (SAS) Library (Helwig and Council 1979).

CHAPTER III

METHODS AND MATERIALS

Introduction

Development of Pyrrhalta luteola eggs, larvae, and pupae were monitored in constant temperature cabinets (Percival® Model I 35 LVL) to determine mean development rates. Adults were reared in order to determine longevity and egg production. Each life stage was held at five different constant temperatures: 15.6°, 22.2°, 28.8°, 32.2°, and 36.1°C. Photoperiod was set at a 16:8 (day:night) ratio for all studies. In addition, all life stages (except adults) were monitored for development on either elm trees or in an outdoor insectary so that laboratory findings could be validated. A Weathertronics® HI-Q Thermograph (Model 4110) was used to monitor daily maximum and minimum temperatures in the outdoor studies. All laboratory and field studies were conducted from May to August, 1983.

Egg Studies

Newly deposited eggs obtained from infested Siberian elms were used in the laboratory studies. This procedure was conducted by using plastic flagging to randomly tag elm branches free of egg deposits. Each branch, tagged at 30 to 60 cm intervals from the terminal end, was inspected for egg clusters twice a day. When a freshly oviposited egg cluster was found, it was immediately transferred to a temperature

cabinet maintained at one of the five respective temperatures. The egg cluster and the leaf that it was laid on was held in a Falcon® plastic petri dish (100 x 15 mm) and covered with a plastic lid. Filter paper moistened with a 5% cubric sulfate solution was placed on the bottom of each dish to keep the leaf fresh and prevent fungal development. Ten to 30 egg clusters were held at each temperature. Eggs were checked twice a day for hatching.

Outdoor studies of egg development were conducted on three different Siberian elms located on a roadside in Stillwater, Oklahoma. Branches free of egg deposits were randomly tagged with plastic flagging in the same manner as previously described. Leaves found with egg deposits on the branches under surveillance were marked with a laundry tag for identification purposes. Eggs were monitored twice a day. In order to obtain realistic temperature data, the thermograph used to monitor daily temperatures was placed in an instrument shelter directly under one of the trees being observed. The instrument shelter, 45.72 cm x 33.02 cm x 50.8 cm, rested on wooden legs approximately 121 cm in height.

Larval Studies

Terminal shoots of Siberian elm were used in laboratory studies of larval development to simulate field conditions. Newly hatched larvae reared from egg clusters held at 28.8°C were placed on freshly cut foliage. This procedure involved placing two terminal branches approximately 10 cm in length inside a Nalgene® 100 mm propylene powder funnel and then inserting the cut end of the branches into a 120 ml juice jar containing Hoaglands solution (Hoagland and Arnon 1950).

Tissue paper was utilized to seal stems in the funnel and prevent larvae from falling into the solution. A rubber stopper was placed around the stem of the funnel in order to hold it securely in the mouth of the jar. A paper towel was wrapped over the top of the funnel with a rubber band to prevent larval escape. Fifteen replications were held at each constant temperature, consisting of 75 newly hatched larvae per replication. Branches were replaced when the leaves began to dessicate or were defoliated from larval feeding. Larvae were transferred to new foliage with a Simmons® size 00 camel's hair paint brush. Development was observed daily until all larvae pupated.

A storage shed served as an outdoor insectary for larval development. Terminal branches measuring 15.2 to 17.8 cm from a Siberian elm were utilized for rearing in the same manner as previously described, with the exception that funnels were not used to contain the larvae. Two terminal branches were securely placed in the juice jar through a hole in a rubber stopper. The jar containing the branches was placed inside a paper cup (10 cm x 20.5 cm). A Lexan® plastic cylinder was then placed over this rearing apparatus. Two circular openings approximately 2.5 cm in diameter were present on each side of the cylinder to allow for ventilation. Nylon sheer fabric was placed over the holes and the top of the cylinder to prevent escape. Fifteen replications with 75 newly hatched larvae per replication were utilized. Development was observed daily. A thermograph was placed inside the outdoor insectary to monitor daily temperatures.

Pupal Studies

Laboratory studies of pupal development were conducted by collecting

field populations of pre-pupal third instar larvae and holding them in petri dishes at a constant temperature of 28.8°C. Immediately following pupation, pupae were transferred to one of the five experimental temperatures. Pupae were incubated in Conex® 30 ml graduated medicine cups with cardboard lids and checked twice a day for adult emergence. Fifteen replications with 15 pupae per replication were held at each temperature. The outdoor insectary study was conducted in the same manner as in the laboratory.

Adult Studies

Adult P. luteola were observed for longevity and egg production under the five respective temperatures noted earlier. Newly emerged adults were reared on Siberian elm foliage in the same manner as in the larval experiments. Five replications were held at each temperature, with five pairs of female and male beetles per replicate. Males and females were identified by the method described by Weber (1976). Replications were checked daily for mortality and number of egg clusters oviposited. The number of individual eggs per cluster was also recorded. Foliage was changed daily.

Modeling and Analysis Procedures

Two procedures were utilized for describing the median development rates of P. luteola. One approach used was the biophysical rate-summation model of Sharpe and DeMichele (1977). The equation for this model, modified by Schoolfield et al. (1981) is:

$$r(T) = \frac{RHO25 \frac{T}{298.15} \exp\left[\frac{HA}{R}\left(\frac{1}{298.15} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{HL}{R}\left(\frac{1}{TL} - \frac{1}{T}\right)\right] + \exp\left[\frac{HH}{R}\left(\frac{1}{TH} - \frac{1}{T}\right)\right]}$$

where $r(T)$ = mean development rate at temperature T (°K), R = the universal gas constant (1.987 cal deg^{-1} $mole^{-1}$), RHO25 = development rate at 25°C (298.15°K) assuming no enzyme inactivation, HA = enthalpy of activation of the reaction that is catalyzed by a rate controlling enzyme, TL = Kelvin temperature at which the rate controlling enzyme is one-half active and one-half low temperature inactive, HL = change in enthalpy associated with low temperature inactivation of the enzyme, TH = Kelvin temperature at which the rate controlling enzyme is one-half active and one-half high temperature inactive, and HH = change in enthalpy associated with high temperature inactivation of the enzyme.

The equation has six parameters: two that dominate at intermediate temperatures (RHO25 and HA), two that dominate at low temperatures (TL and HL), and two that dominate at high temperatures (TH and HH). The computer program used for this model was assembled by Wagner et al. (1984) from the Statistical Analysis System (SAS) library (Helwig and Council 1979).

Inputs for this program consisted of constant temperature (°C) and development rate ($time^{-1}$) data from each life stage. Each data entry consisted of one temperature and its associated rate. The program then identified the form of the model that best described the data, e.g., a six-parameter model with low and high temperature inhibition of the rate-controlling enzyme, a four-parameter model with low or with high temperature inhibition, or a two-parameter model without low and high temperature inhibition. Next, the starting values for each parameter

were determined and used as inputs for regression analysis. This analysis used Marquardt (1963) methods of non-linear regression to select the least square estimates of the parameters.

A degree-day system for P. luteola development was calculated according to Arnold (1959). The reciprocals of time required for egg, larval, and pupal development were regressed on temperature to establish respective developmental thresholds. The general linear models (GLM) procedure from the SAS library (Sall 1982) was used for the regression analysis.

Degree-days (^{o}C) required for life stage development at each temperature were calculated by the formula:

$$\text{Degree-days} = (T - TL) \times \text{days to develop}$$

where T = experimental constant temperature and TL = lower developmental threshold temperature (^{o}C). A maximum-minimum equation (Arnold 1960) was utilized to calculate degree-days for P. luteola development during the field study. The equation is:

$$\text{Degree-days} = \frac{\text{Max} + \text{Min}}{2} - TL$$

where max = maximum daily temperature, min = minimum daily temperature, and TL = lower developmental threshold temperature (^{o}C).

Chi-square methods (Little and Hill 1978) were applied in the same manner as Taylor and Harcourt (1978) for determining if the degree-days required in the outdoor studies differed significantly from the degree-days predicted from the laboratory experiments.

Summary statistics for immature, adult, and ovipositional data was computated by using univariate procedures from the SAS library (Sall 1982). Analysis of variance procedures were also utilized to determine

least significant differences (LSD) between development times or egg cluster sizes.

All analysis procedures in this study were made in the Oklahoma State University Computer Center.

CHAPTER IV

RESULTS AND DISCUSSION

Immature Development

The average number of days required for P. luteola egg development are presented in Table I[1]. Development ranged from an average of 18.9 days at 15.6° to 3.8 days at 32.2°C. Ranges in development time for each temperature are also presented in Table I. Significant differences (P = 0.05) were found in the length of embryogenisis between each temperature.

A higher percentage of eggs hatched at the lower temperatures, with a peak of 77.6% developing to larvae at 22.2°C (Table II). No hatching occurred at 36.1°C. There was partial embryonic development at this temperature, with some of the egg clusters turning gray in color. In one case a larval head penetrated the egg chorion.

Larval development (Table III) ranged from an average of 61.7 days at 15.6° to 12.1 days at 36.1°C. No significant difference (P = 0.05) was found between mean development times at 32.2° and 36.1°C, but significant differences were found among development times at all other temperatures.

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[1] All tables can be found in Appendix A.

The optimum temperature for larval survival was at 28.8°C where 60% of the larvae pupated (Table IV). Only 1.3% were reared to pupae at 36.1°C. It was not suprising to find low numbers of larvae pupating at the lower two temperatures, as Luck and Scriven (1979) found only 25% survival when P. luteola were fed leaves of U. pumila at 22°C.

The mean development time for the pupal stage (Table V) ranged from 21.2 days at 15.6° to 3.7 days at 36.1°C. Significant differences (P = 0.05) were found among the average number of days to develop at all temperatures.

Adult emergence ranged from 96 to 100% (Table VI). The low mortality at 36.1°C indicated that the pupal stage may be able to withstand higher temperatures than the egg and larval stages. In nature it is doubtful that such a high emergence rate would occur since P. luteola pupae are usually attacked by fungus diseases, predators, and parasites (U.S.D.A. 1964).

Nonlinear regression of the data by the Sharpe and DeMichele model did not indicate enough deviation from linearity at the temperature extremes to exhibit low and high temperature inhibition. Therefore, a two-parameter model was chosen for describing P. luteola development. This form of the model was not desired, since it cannot accurately determine the lower and upper developmental thresholds. Furthermore, a two-parameter model will predict unrealistically high development rates beyond the temperature extremes.

Another weakness found in the Sharpe and DeMichele model is that no modifications exist for mortality factors. The relationship between the rate of egg development (%/1 day) and temperature is plotted in

Figure 1[2]. The actual upper developmental threshold for the egg stage probably exists between 32.2° and 36.1°C, since egg hatching was not observed at 36.1°C. However, this model was not designed to handle occurrences of extreme mortality and continued to predict increasing development rates beyond 36.1°C. Additional constant temperature studies for egg development at 33°, 34°, and 35°C would have produced a more accurate estimate of the upper threshold.

The larvae reared at 36.1°C were probably exposed to a temperature approaching the upper developmental threshold. The paucity of larvae reaching pupation at this temperature were still developing faster than larvae reared at other temperatures (Figure 2). Additional temperature studies at ± 0.1°, 0.2°, and 0.3°C intervals from 36.1°C may have been needed to indicate where the downward trend of the response curve occurs.

The pupal stage (Figure 3) appears to have an upper developmental threshold exceeding 36.1°C, since development rates were still increasing at this temperature with minimal mortality. Further studies at 37° and 38° could have helped in determining the upper threshold.

Additional studies at ± 1°, 2°, and 3°C intervals from 15.6°C might have aided the biophysical model in determining the lower developmental threshold for the three immature life stages. Unfortunately, insufficient numbers of temperature cabinets prohibited additional constant temperature studies.

The second approach used to analyze the development rate data was

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[2] All figures can be found in Appendix B.

the "linear approximation" method. Summary statistics for linear regression of development rate on temperature for each life stage are presented in Tables VII through IX. The relationship between development and temperature is plotted in Figures 4 through 6. The theoretical developmental threshold (C^{O}) is shown by the x-intercept of the regression line. The theoretical lower threshold temperatures for embryonic, larval, and pupal development were 11.3^{O}, 11.0^{O}, and 11.1^{O}C, respectively.

A base temperature of 11.1^{O}C was used as the lower threshold of development for all degree-day (C^{O}) calculations. Table X shows the degree-days (C^{O}) required for P. luteola development at each of the five constant temperatures. Mean degree-day accumulations required for completion of life stages were: 78.9-egg, 268.1-larva, and 89.3-pupa.

The reliability of using degree-days for predicting P. luteola development in the field was assessed using temperature and development data from outdoors. The average number of days required for development of each life stage in the outdoor study are presented in Table XI. The observed degree-days (C^{O}) accumulated for each life stage did not differ significantly from those expected when tested by Chi-square methods (Table XII).

It appears that the degree-days formulated from the laboratory studies are reasonably accurate in predicting elm leaf beetle development during the growing season. However, the thermal requirements for the emergence of overwintering adults must be determined before this degree-day system can be accurately utilized to predict initial larval activity. Presently, the only way available to predict larval emergence is by estimating the peak of egg oviposition. This may be difficult to

do on a large scale. Further studies are needed to determine the degree-days required for emergence of overwintering adults.

Adult Longevity

The average duration of an elm leaf beetle adult is shown in Table XIII and presented graphically in Figure 7. The length of an adult's lifespan ranged from an average of 54.0 days at 15.6°C to 9.7 days at 36.1°C. There was no significant difference (P = 0.05) between the average lifespan at 28.8° and 32.2°C, but significant differences were found among the average lifespans at all other temperatures. The range in duration at 15.6°C was quite extreme, with one adult living 130 days.

The average length of adult longevity in this study was shorter than findings by other researchers. Wene (1968) observed an average lifespan of 30 days for adults reared at approximately 25°C. Luck and Scriven (1979) found 50% of a test population of P. luteola adults remaining alive for 9 to 11 weeks when reared at 22°C. However, Luck and Scriven reared only one pair of adults per oviposition cage as compared to five pair in this study. There may have been a higher degree of competition for food or space in this experiment which could have shortened the lifespan.

Another observation noted in the adult study was a difference in coloration that occurred with increasing temperatures. Adults at 15.6°C resembled the dark olive-green appearance of an overwintering adult. Individuals reared at 22.2°, 28.8°, and 32.2°C possessed the normal yellow-green colors prevalent during summer-time conditions. Adults were almost orange-yellow when reared at 36.1°C.

Egg Production

The total number of egg clusters and individual eggs oviposited in this study was at an optimum during the three intermediate temperatures and relatively low at the two extreme temperatures (Table XIV). Although more egg clusters were laid by adults reared at 32.2°C significantly larger egg cluster sizes were found at 22.2° and 28.8°C (Table XV). Means of field-collected egg cluster sizes cited in the literature were larger than those observed in the laboratory experiments. Wene (1968) and Weber and Thompson (1976) reported average egg cluster sizes of 14.8 and 18.9, respectively. In our research, egg clusters averaging 17.9 eggs were found while monitoring field development. The largest egg cluster observed in the laboratory study occurred at 22.2°C and contained 44 eggs. An egg cluster found in the field study possessed 39 eggs. Weber and Thompson (1976) reported a field-collected egg cluster containing 47 eggs.

CHAPTER V

SUMMARY

The objectives of this study were to (1) determine the effects of temperature on development and survival of the immature stages of Pyrrhalta luteola; (2) use these data in predicting development of field populations, and (3) observe the effects of temperature on adult longevity and egg production.

The development of all P. luteola immature life stages increased with rise in temperature. Eggs did not hatch at 36.1°C. Larvae survived at all five constant temperatures but exhibited high mortality at 36.1°C. Pupae survived at all temperatures with minimal mortality.

Nonlinear regression of the data with the Sharpe and DeMichele biophysical model produced a two-parameter model which predicted accurate development rates for most of the temperature range in this study. Additional constant temperature studies at the temperature extremes are needed to generate a six-parameter model that could determine developmental thresholds. Modifications for the biophysical model should be developed to deal with cases of extreme mortality that may occur at high temperatures.

The theoretical threshold temperatures for development of egg, larval, and pupal stages were 11.3°, 11.0°, and 11.1°C, respectively when estimated from linear regression techniques. Mean degree-day (C°) accumulations required for completion of life stages were: 78.9-egg,

268.1-larva, and 89.3-pupa. Accumulated degree-days (C°) above a base of 11.1°C during outdoor development of P. luteola did not differ significantly from life-stage thermal requirements. However, the thermal requirements for overwintering adult emergence need to be determined before this degree-day system can be accurately utilized.

Life expectancy of elm leaf beetle adults decreased with rising temperature. Increasing temperatures brought changes in color, with adults appearing dark olive-green at 15.6°C, yellow-green at the three intermediate temperatures, and orange-yellow at 36.1°C. Egg production was optimal at the three intermediate temperatures and minimal at the two extreme temperatures. Egg cluster sizes in the laboratory were smaller than those found in the field.

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APPENDIX A

TABLES

TABLE I

DURATION (DAYS) OF PYRRHALTA LUTEOLA EGG STAGE AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	Mean±S.E.[1]	Range
15.6	18.9±0.076[A]	17.0-20.6
22.2	7.1±0.022[B]	5.5- 8.3
28.8	4.2±0.032[C]	3.0- 5.4
32.2	3.8±0.029[D]	2.9- 4.7

[1] Means followed by the same letter are not significantly different (P=0.05) LSD.

TABLE II

PYRRHALTA LUTEOLA EGG SURVIVAL AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	No. Eggs Observed	No. Hatching	% Hatching
15.6	255	152	59.6
22.2	720	559	77.6
28.8	728	352	48.3
32.2	625	292	46.7
36.1	428	0	0.0

TABLE III

DURATION (DAYS) OF PYRRHALTA LUTEOLA LARVAL STAGE AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	Mean±S.E.[1]	Range
15.6	61.7±0.262[A]	50-76
22.2	23.8±0.102[B]	20-28
28.8	14.8±0.039[C]	13-19
32.2	13.1±0.080[D]	12-15
36.1	12.1±0.165[D]	11-13

[1]Means followed by the same letter are not significantly different (P=0.05) LSD.

TABLE IV

PYRRHALTA LUTEOLA LARVAL SURVIVAL AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	No. Initially Reared	No. Pupating	% Pupating
15.6	1125	350	31.1
22.2	1125	283	25.1
28.8	1125	681	60.5
32.2	1125	121	10.7
36.1	1125	15	1.3

TABLE V

DURATION (DAYS) OF PYRRHALTA LUTEOLA PUPAL STAGE AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	Mean±S.E.[1]	Range
15.6	21.2±0.082[A]	15.5-23.9
22.2	8.1±0.020[B]	6.9- 8.4
28.8	4.6±0.007[C]	4.5- 4.8
32.2	4.1±0.019[D]	3.6- 4.7
36.1	3.7±0.013[E]	3.5- 4.5

[1]Means followed by the same letter are not significantly different (P=0.05) LSD.

TABLE VI

PYRRHALTA LUTEOLA PUPAL SURVIVAL AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	No. Initially Reared	No. Emerging Adults	% Emergence
15.6	225	221	98.6
22.2	225	225	100.0
28.8	225	217	96.4
32.2	225	216	96.0
36.1	225	220	97.7

TABLE VII

SUMMARY STATISTICS FOR LINEAR REGRESSION
OF PYRRHALTA LUTEOLA EGG DEVELOPMENT
ON TEMPERATURE

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C V.
MODEL	1	6 68355178	6 68355178	7369 62	0 0001	0 844886	16.2835
ERROR	1353	1 22704325	0 00090691		ROOT MSE		R MEAN
CORRECTED TOTAL	1354	7 91059503			0 03011487		0.18494070

SOURCE	DF	TYPE I SS	F VALUE	PR > F	DF	TYPE III SS	F VALUE	PR > F
T	1	6 68355178	7369 62	0 0001	1	6 68355178	7369 62	0.0001

PARAMETER	ESTIMATE	T FOR HO PARAMETER=0	PR > |T|	STD ERROR OF ESTIMATE
INTERCEPT	-0 15030615	-37 67	0 0001	0.00398996
T	0 01321888	85 85	0 0001	0 00015398

TABLE VIII

SUMMARY STATISTICS FOR LINEAR REGRESSION
OF PYRRHALTA LUTEOLA LARVAL DEVELOPMENT
ON TEMPARATURE

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V
MODEL	1	0.72604434	0 72604434	43695 59	0 0001	0 967925	7.9518
ERROR	1448	0.02405992	0 00001662		ROOT MSE		R MEAN
CORRECTED TOTAL	1449	0 75010425			0 00407627		0 05126219

SOURCE	DF	TYPE I SS	F VALUE	PR > F	DF	TYPE III SS	F VALUE	PR > F
T	1	0 72604434	43695 59	0 0001	1	0 72604434	43695.59	0 0001

PARAMETER	ESTIMATE	T FOR HO. PARAMETER=0	PR > |T|	STD ERROR OF ESTIMATE
INTERCEPT	-0 04133555	-90 70	0 0001	0 00045573
T	0 00374553	209 03	0 0001	0 00001792

TABLE IX

SUMMARY STATISTICS FOR LINEAR REGRESSION
OF PYRRHALTA LUTEOLA PUPAL DEVELOPMENT
ON TEMPERATURE

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C V
MODEL	1	7 56619899	7 56619899	42066.83	0 0001	0 974585	7 4451
ERROR	1097	0 19730795	0 00017986		ROOT MSE		R MEAN
CORRECTED TOTAL	1098	7 76350694			0 01341124		0 18013407

SOURCE	DF	TYPE I SS	F VALUE	PR > F	DF	TYPE III SS	F VALUE	PR > F
T	1	7 56619899	42066 83	0 0001	1	7 56619899	42066.83	0.0001

PARAMETER	ESTIMATE	T FOR HO: PARAMETER=0	PR > |T|	STD ERROR OF ESTIMATE
INTERCEPT	-0 12497048	-81 07	0 0001	0 00154160
T	0.01132379	205 10	0 0001	0 00005521

TABLE X

DEGREE-DAYS ($^{\circ}$C) REQUIRED FOR DEVELOPMENT OF IMMATURE STAGES OF PYRRHALTA LUTEOLA

Temp. ($^{\circ}$C)	Eggs±S.E.	Larvae±S.E.	Pupae±S.E.
15.6	84.4±0.340	274.9±1.169	94.5±0.368
22.2	78.8±0.254	264.4±1.138	89.9±0.222
28.8	75.1±0.571	263.8±0.699	82.3±0.125
32.2	81.1±0.630	276.3±1.692	86.4±0.398
36.1	---	303.0±4.132	92.3±0.324
$\bar{x}$±S.E.	78.9±0.230	268.1±0.509	89.3±0.136

TABLE XI

DURATION (DAYS) OF PYRRHALTA LUTEOLA IMMATURE STAGES UNDER FLUCTUATING OUTDOOR TEMPERATURES AT STILLWATER, OKLA. (MAY TO JULY, 1983)

Stage	No. Observed or Reared	Mean
Egg[1]	665	5.5
Larval[2]	402	24.7
Pupal[2]	224	7.0

[1]Development observed on elm trees.

[2]Reared in an outdoor insectary.

TABLE XII

COMPARISON BETWEEN OBSERVED AND EXPECTED DEGREE-DAYS (°C) FOR DEVELOPMENT OF PYRRHALTA LUTEOLA AT STILLWATER, OKLA. (MAY TO JULY, 1983)

Stage	Observed	Expected	Chi-Square[1]
Egg	77.1	78.9	0.041
Larval	260.5	268.1	0.215
Pupal	102.0	89.3	1.806
Total	439.6	436.3	2.062

[1]Observed and expected degree-days are not significantly different (P>0.25).

TABLE XIII

DURATION (DAYS) OF PYRRHALTA LUTEOLA ADULTS AT FIVE CONSTANT TEMPERATURES[1]

Temp. (°C)	Mean±S.E.[2]	Range
15.6	54.0±3.237[A]	16-130
22.2	25.5±0.990[B]	5- 42
28.8	14.9±0.689[C]	4- 26
32.2	14.2±0.872[C]	2- 29
36.1	9.7±0.367[D]	8- 21

[1]25 females and 25 males per constant temperature.

[2]Means followed by the same letter are not significantly different (P=0.05) LSD.

TABLE XIV

EGG PRODUCTION BY PYRRHALTA LUTEOLA FEMALES AT FIVE CONSTANT TEMPERATURES[1]

Temp. (°C)	Total No. Egg Clusters	Total No. Eggs
15.6	47	429
22.2	294	3828
28.8	250	3527
32.2	479	3457
36.1	49	325

[1]25 females per constant temperature.

TABLE XV

MEAN NUMBER OF EGGS PER EGG CLUSTER LAID BY PYRRHALTA LUTEOLA FEMALES AT FIVE CONSTANT TEMPERATURES

Temp. (°C)	Mean±S.E.[1]	Range
15.6	9.1 ± 1.099^{B}	1-28
22.2	13.0 ± 0.466^{A}	1-44
28.8	14.1 ± 0.518^{A}	1-35
32.2	7.2 ± 0.253^{B}	1-36
36.1	6.6 ± 0.732^{B}	1-22

[1]Means followed by the same letter are not significantly different (P=0.05) LSD.

APPENDIX B

FIGURES

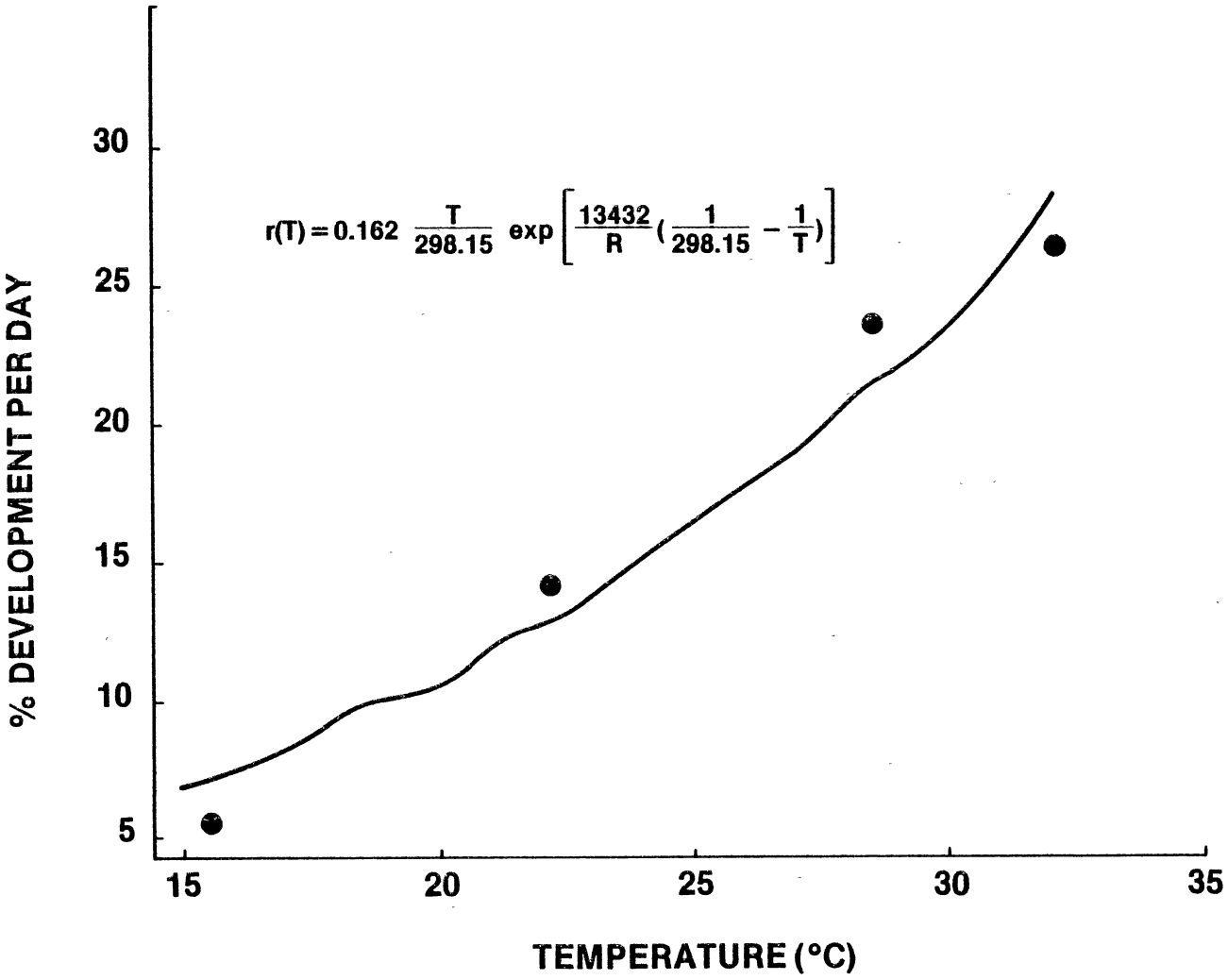

Figure 1. Relationship Between Pyrrhalta luteola Egg Development and Temperature as Predicted by the Sharpe and DeMichele Biophysical Model

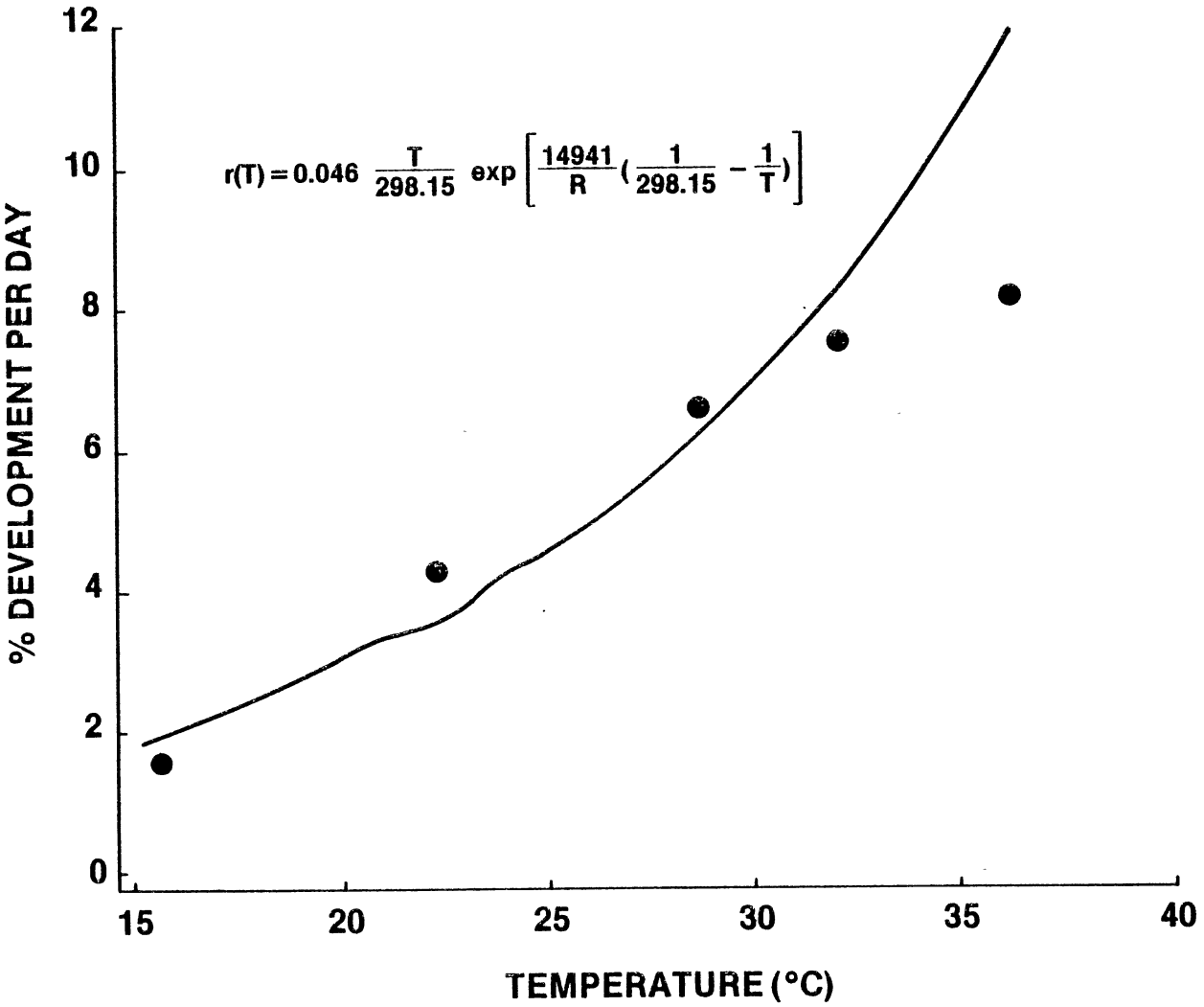

Figure 2. Relationship Between Pyrrhalta luteola Larval Development and Temperature as Predicted by the Sharpe and DeMichele Biophysical Model

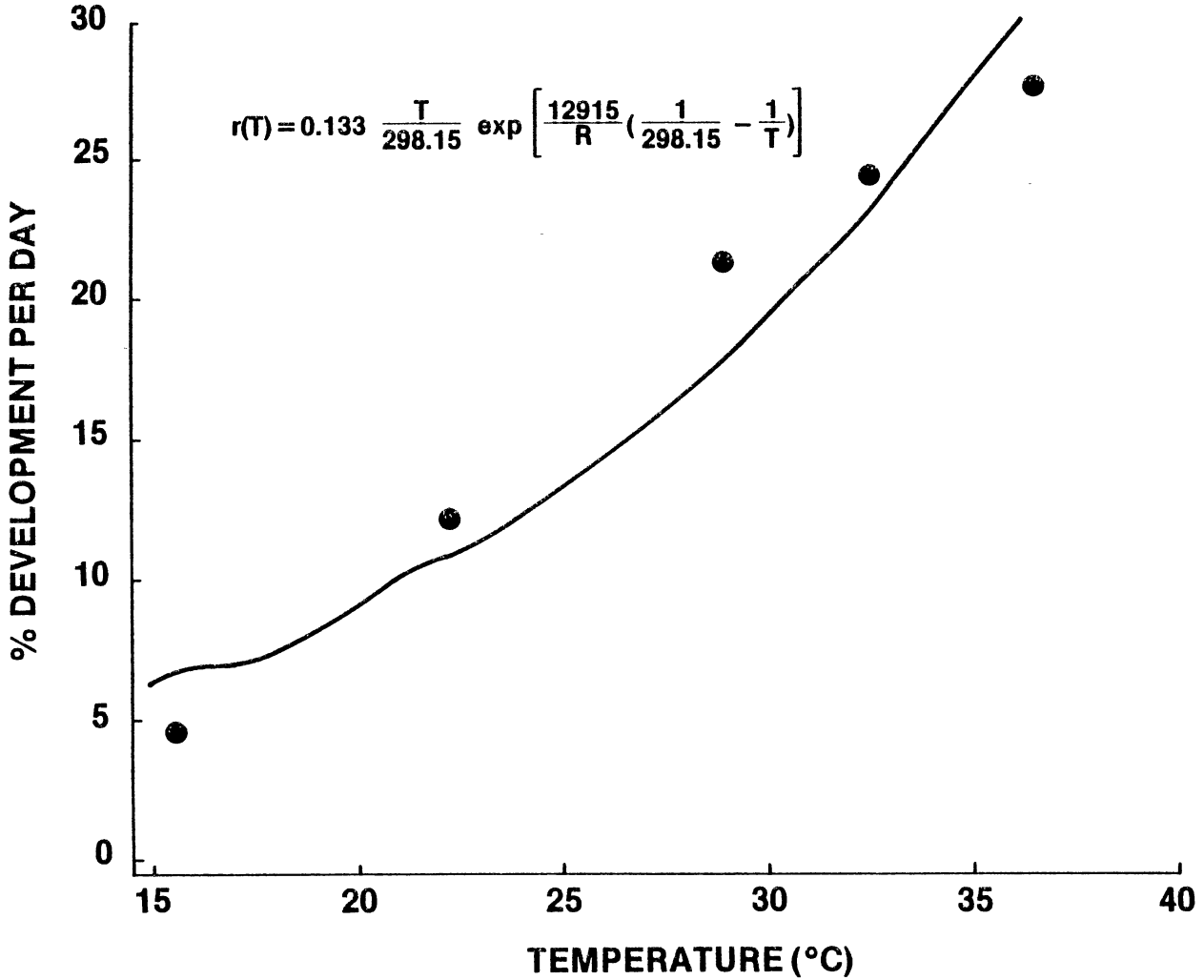

Figure 3. Relationship Between Pyrrhalta luteola Pupal Development and Temperature as Predicted by the Sharpe and DeMichele Biophysical Model

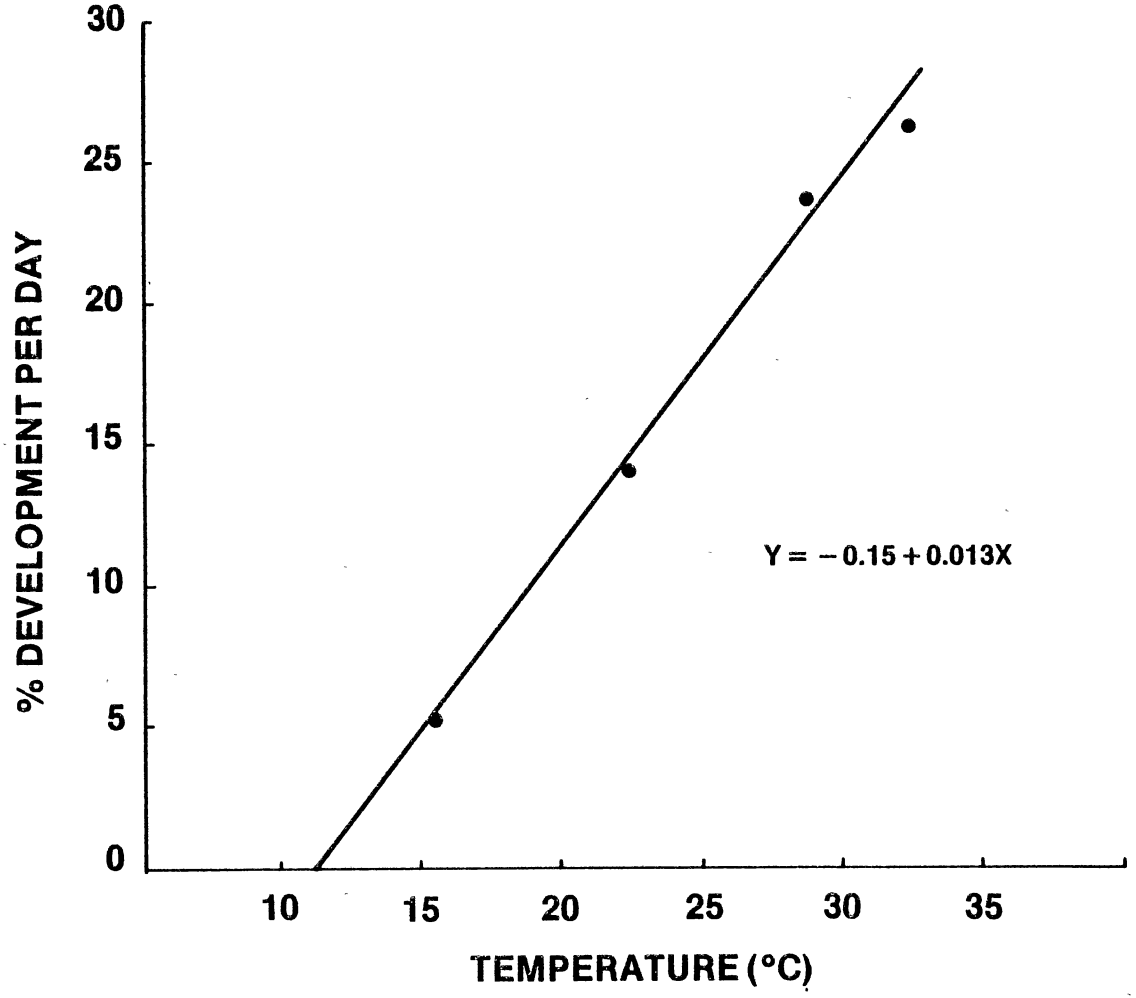

Figure 4. Derivation of the Threshold Temperature by the X-intercept Method for Pyrrhalta luteola Egg Development

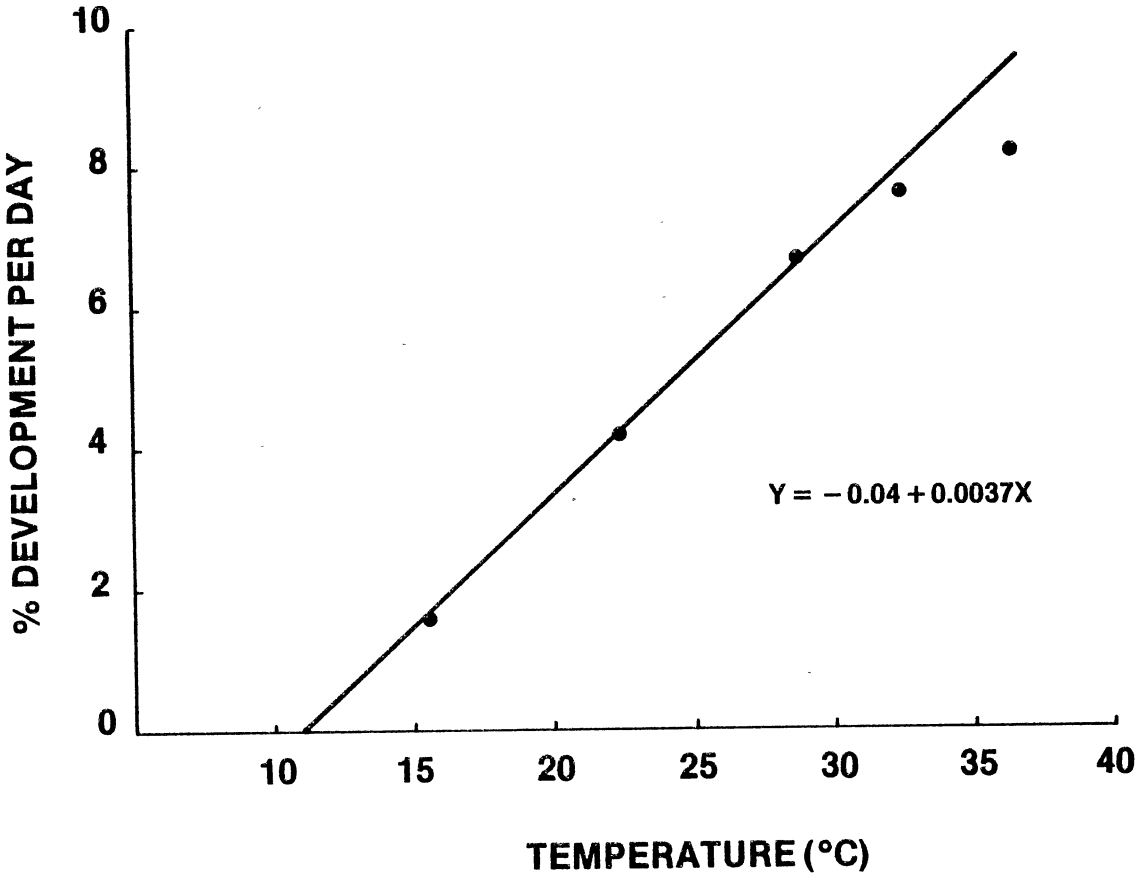

Figure 5. Derivation of the Threshold Temperature by the X-intercept Method for Pyrrhalta luteola Larval Development

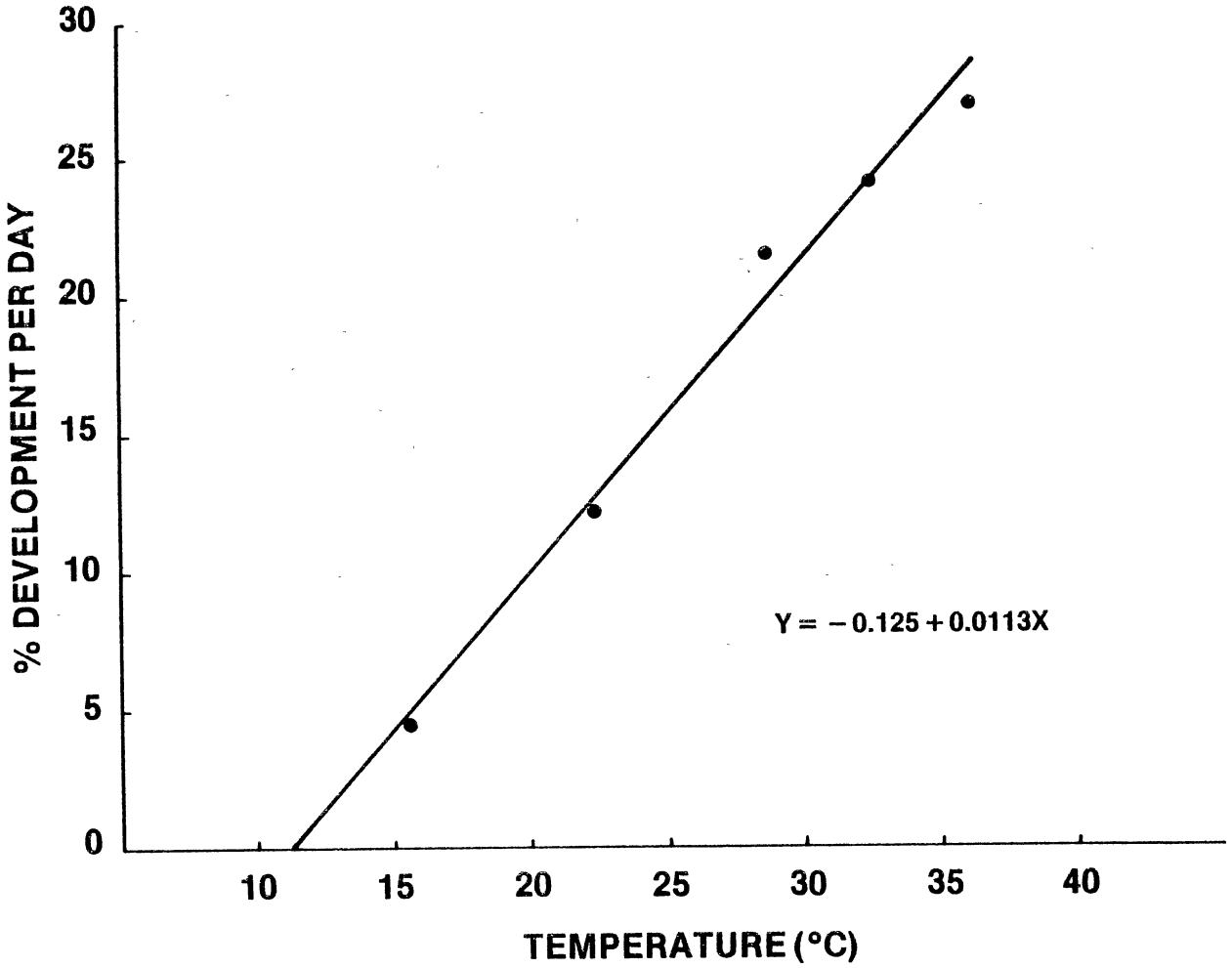

Figure 6. Derivation of the Threshold Temperature by the X-intercept Method for Pyrrhalta luteola Pupal Development

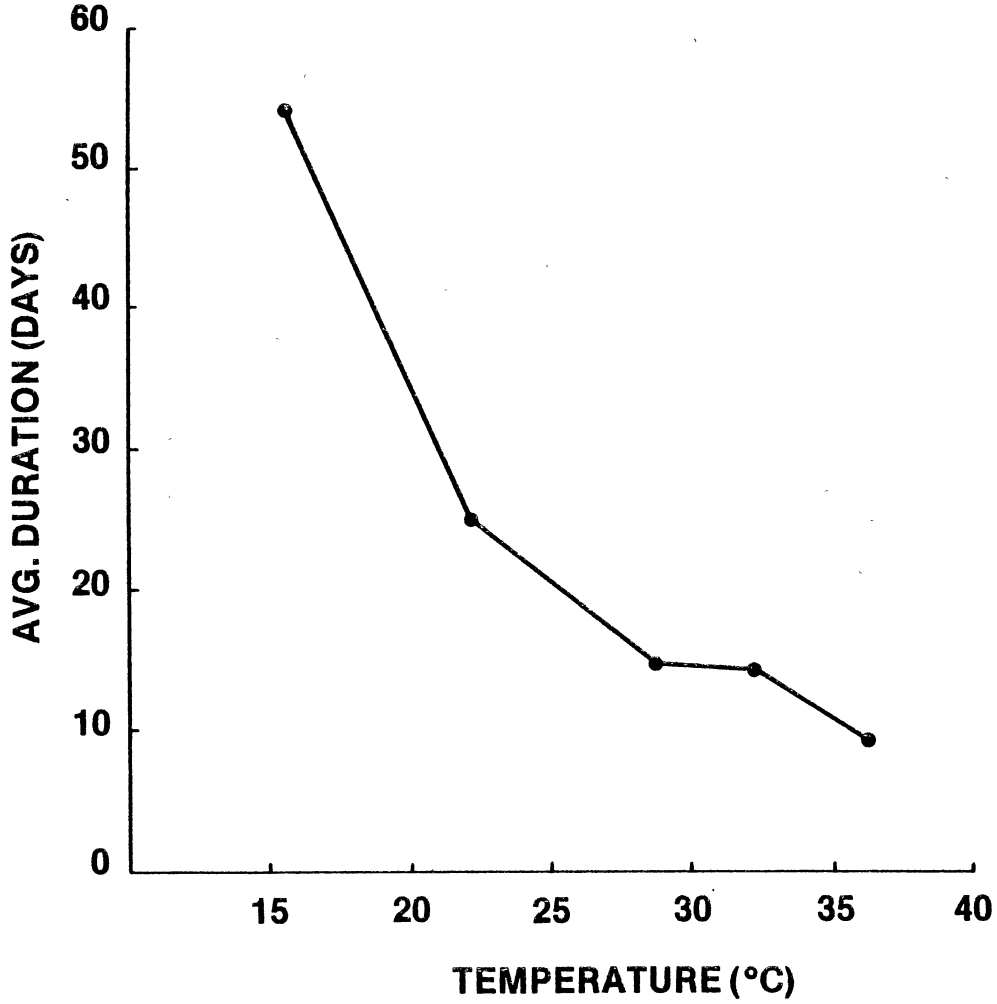

Figure 7. Average Duration of Pyrrhalta luteola Adults at Five Constant Temperatures

VITA

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