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ABSTRACT

Models of phenology of the pine false webworm (PFW), *Acantholyda erythrocephala* and one of its parasitoids were developed from relationships between PFW spatial distribution and microweather.

Development of subterranean stages of PFW was simulated from rate-summation models developed from nonlinear regression equations describing the relationship between temperature and rate of development of post-diapause prepupae and pupae. Defoliation caused by PFW increased the soil's exposure to solar radiation resulting in higher soil temperatures and a corresponding reduction in development time of subterranean stages. Predictability was enhanced slightly when the distribution of insects and temperature of the soil were incorporated into the model. Increasing the time increment used in the model from 1 to 4 h did not adversely affect its resolution.

Mating and oviposition of PFW occur within a few hours of emerging from the soil and the majority of PFW eggs were mature and ready for deposition at female emergence. Potential fecundity of PFW was accurately predicted from adult wet and dry weights. The oviposition pattern of PFW was also described by a model based on temperature-dependent oviposition and ageing rate functions.
The effect of larval web construction on the development of arboreal stages was investigated. When exposed to sunlight, the web traps heat and raises the body temperature of its inhabitants. A model was developed and used to examine the significance of the web microclimate for development of larvae. Relationships between web temperatures, canopy temperatures and standard meteorological methods were developed to permit using data from standard weather stations to drive the model. Larval development increased by 1.4 to 2.8 d when estimated web temperatures were incorporated into the model, while development was retarded by 2.6 to 4.0 d when canopy temperatures were used instead of meteorological screen temperatures.

Two ichneumonid parasitoids, Sinophorus megalodontis and an undescribed species of Olesicampe were reared from eonymphs of PFW. Morphological methods for distinguishing the immature stages of the parasitoids were developed. A predictive model for subterranean development and adult longevity of Olesicampe sp. was used to describe and to compare phenological observations from emergence traps, Malaise traps and dissections of host larvae. The effectiveness of the parasitoids as natural control agents is discussed in relation to host synchrony, encapsulation, and multi- and superparasitism.
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1.1 Biology of Pine False Webworm

The pine false webworm (PFW), *Acantholyda erythrocephala* (L.) (Hymenoptera: Pamphiliidae), is endemic to the Palearctic Region, occurring in Great Britain, central and northern Europe to Lapland, and east to the Caucasus and western Siberia, Korea and Japan (Middlekauff 1958, Charles and Chevin 1977). This species was first reported in North America in 1925 from Pennsylvania (Wells 1926), and has since been reported in New Jersey (Soraci 1938), New York (Middlekauff 1938), Connecticut (Plumb 1945) and the Lake States (Wilson 1977). Larval PFW were first reported in Ontario in 1961 in Scarboro Township (Eidt and McPhee 1963). PFW now occurs throughout most of southern Ontario and in the Lake-of-the-Woods region in northwestern Ontario (Syme 1981).

The host plants of PFW are nine species of *Pinus*. *Pinus resinosa* Ait. (red pine) and *P. strobus* L. (white pine) are the most favored and *P. nigra* Arnold (Austrian pine) the least favored in North America (Middlekauff 1958). *Pinus sylvestris* L. (Scots pine) is preferred to *P. nigra* in mixed stands in...

Adult males precede females, in spring, from earthen cells in the soil (Schwerdtfeger 1944). Females mate soon after emergence. Unfertilized females can deposit viable eggs that develop into males. Eggs are laid in contiguous rows on the flattened surface of one year-old pine needles (Griswold 1939). A slit is cut in the needle by the ovipositor into which a crease of the chorion is inserted (Middlekauff 1958). Eggs obtain moisture from the vascular system of the plant (Schwerdtfeger 1941).

Newly hatched larvae descend needles to the twigs where they spin silk around the base of the needles and feed gregariously on the sides of needles above the fascicle. While maturing, larvae enlarge their web and feed on the basal ends of needles that they pull towards themselves (Griswold 1939). Accumulation of silk, frass, exuviae and uneaten needles forms a web enclosing the larvae. One to 35 (average 6 to 10) larvae inhabit silken tubes within this web (Schwerdtfeger 1944). Male larvae pass through five instars and females have six during the course of their arboreal development (Schwerdtfeger 1941).

Larvae fall to the ground and burrow into the soil upon completion of feeding in early summer. These larvae or eonymphs, mold earthen cells and enter summer diapause. Most eonymphs emerge from diapause and transform in autumn to
pronymphs which have characteristic pupal eyes visible through the larval skin (Schwerdtfeger 1941). A portion of eonymphs may remain in diapause for several years (Schwerdtfeger 1944). PFW is essentially univoltine (Griswold 1939), pronymphs and less commonly eonymphs in prolonged diapause are the overwintering stages. Pupation occurs in spring when soil temperatures increase.

1.2 Phenology and Biometeorology

Phenology is the study of the effects of climate and season on natural events (Stedinger et al. 1985). Insect phenology concerns the physiological processes governing development, dormancy, reproduction and ageing (Tauber and Tauber 1973). The temporal distribution of the insect's stages throughout the season determines the degree of synchrony of various stages with food resources and mortality agents such as parasitoids, predators and pathogens (Willmer 1982).

Although other variables, such as nutrition, moisture and photoperiod can affect development, the primary driving force is temperature (Curry et al. 1978, Baker 1980). Oviposition, fecundity, longevity (Hogg and Gutierrez 1980, Mason and Mack 1984) and processes at the population level (e.g., mating, migration) are also influenced by temperature. A phenological model is a description of the temporal progression of events in the life of insects as a function of environmental conditions. Phenological models based only on temperature provide
significant predictive power.

An understanding of phenology can provide information about species distribution (Tauber and Tauber 1973) and the more complex processes involved in population dynamics, for example the benefits that occur when reproduction and development are synchronized with favorable conditions. Ability to predict phenological events for pests allows precise timing of the application of control agents, be they chemical or biological. This is especially critical when the duration of susceptible stages is brief (de Reede and de Wilde 1986). Timing of surveys to determine abundance also requires a knowledge of when the developmental stages are present. Economic losses can be forecast if the onset of the destructive stage can be predicted (Dennis et al. 1986).

Process-oriented models are essentially hypotheses describing the predicted behavior of a system. Tests of these hypotheses include the degree to which the models mimic natural events under field conditions. A phenology model is not only a tool to predict seasonal activity of an insect population, but also provides a framework within which questions can be addressed about underlying mechanisms affecting that population and gaps in knowledge can be identified (Régnière 1982).

The major impediment to understanding the effects of weather and temperature on insects is the difficulty in relating
macroclimatic variables to the microclimate that impinges on the insect's habitat (Wellington 1957, Gilbert et al. 1976, Wellington and Trimble 1984). Although microclimatic temperatures have been measured, few studies have done so for a long enough period that meaningful comparisons may be made with meteorological standards (Baker 1981). Two possible approaches to relate Stevenson screen data and microclimate are: make measurements of the microclimate under various macroclimatic conditions and determine the thermal requirements for development of the insect in the laboratory and use the results to compare predicted development from Stevenson screen data with actual development of the insect in the field (Morris and Fulton 1970). The differences between observed and predicted events are then attributed to differences between macroclimate and microclimate. The first approach was used with European pine shoot moth, *Rhyacionia buoliana* (Green 1968). Temperatures of the insects' microhabitats were recorded and used to construct models which relate infested bud temperatures to Stevenson screen temperatures.

Wellington (1954) pointed out the value of shelter builders for studying the effects of weather on insect populations. Larvae of PFW live inside shelters in the canopy and eggs occur on the surface of the foliage. Eonymphs, pronymphs and pupae live in the soil, thus, PFW inhabits two different habitats. The adults, at different times in their lives move between both habitats. Its shelter-building behavior, abundance in southern
Ontario and its variety of habitats make PFW an excellent species for the study of the effects of microclimate on phenology.

The central theme of this thesis is to determine whether empirical relationships between the thermal conditions in the microhabitat of the insect and conventional meteorological measurements enhance the predictability of phenology models.

The present study involves the development of phenology models for PFW. Individual Chapters deal with the development of models for successive phenophases of PFW. Chapter 2 covers the period from spring thaw until adult emergence. Chapter 3 examines oviposition and fecundity in an attempt to predict the temporal distribution of egg laying. Chapter 4 investigates the development of the resulting arboreal stages of PFW and the role that microclimate plays in this development. In Chapter 5, the biology and phenology of two parasitoids of PFW are explored to understand the effects that interspecific synchrony have on population dynamics. Factors inducing and maintaining diapause states were not evaluated in this investigation.

1.3 Study Areas

Field investigations were conducted in red pine plantations in south central Ontario. In 1983-1985, studies were conducted in two sites in Simcoe County. One plantation, planted in 1969, was 1.2 km North of Anten Mills and another was 3.8 km East of
Craighurst. Two one-hectare plots (100 X 100 m) in the Anten Mills plantation (AM1 and AM2) and one plot in the Craighurst plantation (CR) were used. Each plot was marked off in a grid of 10-m intervals. During 1985-86 the study was conducted in a plantation (planted in 1970-72) 3.5 km NNW of Lakehurst (LA) in Peterborough County. Soils in all locations were loamy sands to sandy loams. The soil in the LA plantation was underlaid with calcareous rocks.

1.4 Meteorological Equipment

During 1983-85, standard aspirated Stevenson Screens (1.3 m above ground) [Atmospheric and Environment Service (AES), Environment Canada] were installed in clearings at the AM and CR plots, each with a maximum and minimum thermometer and a standard rain gauge (AES). Daily maximum and minimum temperatures and rainfall were recorded at about 0900 hours.

An electronic weather station and electronic data loggers (Campbell Scientific Inc. (CS), Logan, Utah) were used in conjunction with the Stevenson Screen at the AM location in 1984-85. The electronic station consisted of a tripod tower (CS, Model CM10K) to which meteorological sensors were fixed. A combined temperature and humidity probe (CS, Model 207) was mounted on the tower in a ventilated screen 1.5 m above the ground. Global solar radiation was measured using a pyranometer (Li-Cor Inc., Lincoln Nebraska, Model LI-200S) with cosine correction. Precipitation was measured with a Sierra tipping
bucket rain gauge (CS, Model RG2501). These sensors were monitored by a CR-7 (CS) data logger programmed to sample the sensors every 5 seconds and output the averages, maxima, minima or totals on the hour. At the LA plantation, only the electronic weather station was used in 1986. A second CR-7 data logger was added in 1985-86 allowing comparisons to be made between different sites within the plantations.

Copper-constantan thermocouples were used to measure the thermal microclimate of the insects' habitats within the plantations. The gauge of the wire depended on the application. Wire diameter used was smaller when direct solar radiation was greatest. Thermocouples were calibrated in an ice bath with a mercury-in-glass thermometer.
Chapter 2

Subterranean development and adult emergence of pine false webworm.

2.1 Introduction

PFW overwinters in the soil as pronymphs inside cells formed in late summer by body movements of eonymphs. As the soil warms in spring, overwintered pronymphs transform to pupae in the cells and pupae in turn emerge as adults.

The duration of the pupal stage is reported to last from 15-18 days (Prozorov 1925, Middlekauff 1958) and is influenced by temperature (Schwerdtfeger 1941). Peak emergence of males from the soil precedes (protandry) that of females (Schwerdtfeger 1944). The date of adult emergence depends on local weather. In France, adults appear in April and occasionally in the last days of March (Charles and Chevin 1977). In western Siberia, adults are first observed at the end of May (Prozorov 1925). Adult emergence, in New York, occurs from mid-April until mid-May (Middlekauff 1958), similar to the emergence period in Germany (Schwerdtfeger 1941) and Ontario (Syme 1981).

Development of subterranean insects is regulated by the thermal environment of the soil (Morse et al. 1985). Soil temperatures have temporal and spatial variation. It is essential to know the depth in the soil at which an insect dwells as temperature varies with soil depth (Logan et al. 1979,
Willmer 1982). Horizontal distribution of soil insects also influences developmental processes (Griffiths 1959) through changes in exposure to solar radiation (Wallace and Sullivan 1963).

Emergence patterns of insects may also be affected by variations in temperature (Tatar 1984). While functional advantages of protandrous emergence have been suggested, little information exists as to how the pattern is achieved (Lederhouse et al. 1982). Protandry may result from sex-related differences in developmental rates, spatial distribution or other factors.

The objectives of this phase of the study were to examine emergence patterns of PFW in the field; determine the spatial distribution of the subterranean stages of PFW; determine the variability of the soil thermal microclimate and relate it to the distribution of PFW in the soil; determine the relationship between temperature and development of the subterranean stages of PFW and examine the processes and stability of the emergence pattern using computer simulations.

2.2 Materials and Methods

Adult Emergence. Adult emergence patterns were determined using emergence traps. Traps were made from aluminum window screening shaped into cones wired at the bottom to steel hoops (0.25 m$^2$ basal area). Emerging adults climbed through a small hole at the top of the cone and were captured in collecting
bottles containing 70% ethanol.

Emergence was monitored during 1983-85 with 50 traps placed in each of the three sample grids (Section 1.3), according to computer-generated random coordinates. During 1986, 33 emergence traps were placed in each of three PFW-defoliation zones within the LA plantation. Defoliation zones were subjectively identified as heavy (H), moderate (M) and light (L). Traps were placed at 5-m intervals in three rows 5 m apart. Each trap was held down with three wire tent pegs. Soil and litter was forced up against the trap to prevent escape of insects. Adults were removed from collecting bottles and from the interior of traps each day at about 1000 hours.

Vertical Distribution of PFW in Soil. The vertical distribution of PFW eonymphs in the soil at the LA plantation was determined in August 1984. Soil litter was scraped away and a core 15 cm deep was extracted from the soil using a core sampler. The distance of each eonymph from the soil surface was measured to the nearest cm. Eonymphs were preserved in 70% ethanol for later sex determination based on head capsule size. Head capsules were measured using a calibrated ocular micrometer mounted on a stereo dissecting microscope.

Soil distribution of PFW in the AM plantation was compared with the distribution in the LA plantation in the following manner. Branches with larvae were collected at the Lakehurst
plantation in 1985 and kept in water-filled jars inside 40 by 40 by 40 cm screen cages on the soil surface at one of the Anten Mills plots (AM1). Tops of the cages were covered with chicken wire and the sides were buried in the ground to prevent larval escape. After larvae completed development, they dropped to the ground and burrowed into the soil. Soil in the enclosures was dug up in October and the vertical distribution of larvae was determined.

Pronymphs with larger head capsules were females, while smaller individuals were males (Schwerdtfeger 1941). The mean vertical distributions of each sex in the soil were compared. The vertical distribution of larvae in the soil was described by:

\[ V(z) = (1 - a)q^aw \]  

where \[ a = (z_L - z)/(z_L - z_U) \]

\( V(z) \) = cumulative proportion of individuals and \( z \) = soil depth. Depth was normalized between lower (\( z_L \)) and upper (\( z_U \)) limits. Parameters \( q \) and \( w \) were estimated by nonlinear regression.

Soil Temperature. Soil temperature was measured using 24-AWG copper-constantan thermocouple wire inserted through lengths of Tygon tubing. Thermocouple junctions were sealed to the end of tubes with epoxy resin. Square holes were dug in the soil to a depth of 20 cm. Thermocouples were placed on one side of each hole at 5 and 10 cm depths. Soil and humus were replaced and the thermocouples were wired as differential pairs.
to data loggers. Thermocouples were installed in autumn to allow soil to settle before temperature recordings were made the following spring.

Ten pairs of thermocouples were placed in a moderate to heavy defoliated zone and ten pairs were installed in a lightly defoliated zone at the LA plantation. Data loggers were used to monitor thermocouples every 5 s and calculate hourly average temperatures. Temperature recording began in winter prior to the disappearance of the snow cover while the ground was still frozen.

Soil temperatures at multiple depths were estimated from temperatures at the 5 and 10 cm depths incorporating temporal and spatial variability, a correction for asymmetry of the wave and a correction for phase lag resulting from the slower heating of the soil with increased depth. At each field location, the hourly average temperatures recorded by individual thermocouples were averaged at each depth (i.e., 5 and 10 cm). These average temperatures were used to estimate temperatures at other depths within the vertical distribution of PFW in the soil.

The hourly temperature differential \( (D_z) \) between the temperature at a depth of 10 cm and any other depth \( z \) was calculated (Régnière et al. 1981) using:
\[ D_Z = \begin{cases} 
\text{Delta}_z \cos\{180[1 + (t + 5)/16]\} \\
\text{when } 1 \leq t \leq 10 \\
\text{Delta}_z \cos\{180(t - 11)/8\} \\
\text{when } 10 < t < 20 \\
\text{Delta}_z \cos\{180[1 + (t - 19)/16]\} \\
\text{when } 20 \leq t \leq 24 
\end{cases} \] (2.2)

where \( \text{Delta}_z = (R_z - R_y)/2 \), \( t \) is time of day, \( R_y \) is the daily temperature range at 10 cm, and \( R_z \) is the daily temperature range at depth \( z \). \( R_z \) was calculated as a function of soil depth using:

\[ R_z = R_y / \exp[k(z - y)] \] (2.3)

where \( y \) is 10 cm and \( k \) is the reciprocal of the damping depth and is calculated daily (Rosenberg 1974) from:

\[ k = \frac{\ln(R_y/R_x)}{x - y} \] (2.4)

where \( R_x \) is the temperature range at 5 cm and \( x \) is 5 cm.

The preceding algorithm assumes the temperature wave at the unknown depth is symmetrically distributed around the reference temperature wave. However, temperature waves at the two observed depths were seldom symmetrical. The difference between the temperature maxima (\( T_{maxx} - T_{maxy} \)) was usually greater than the difference between minima (\( T_{minx} - T_{miny} \)). If this relationship holds true for all depths, the proportion (PD) of the temperature range at the unknown depth that occurs above the reference wave is computed daily from:

\[ PD = \frac{(T_{maxx} - T_{maxy})}{(T_{minx} - T_{miny}) + (T_{maxx} - T_{maxy})} \] (2.5)

and a corrected temperature difference (\( D_{corr} \)) is determined from:
\[ D_{\text{corr}} = D_z + \Delta z - PD (R_z - R_y) \]  
(2.6)

The temperature at any depth for any hour of the day is estimated from:

\[ T_z(t) = T_y(t) - D_{\text{corr}} \]  
(2.7)

The phase lag \((t_y - t_z)\) in temperature that occurs with increasing depth for the predicted and reference temperatures was determined from:

\[ t_y - t_z = \left((z-y)/2\right)\left(p/(\pi \alpha)\right)^{0.5} \]  
(2.8)

where \(p\) is the period of the wave in seconds (i.e., \(8.64 \times 10^4\) s) and the thermal diffusivity \(\alpha = \pi / k^2 p\) (Rosenberg 1974).

Temperature-dependent Development. Duration of the prepupal period (i.e., time for termination of diapause and morphogenesis to pupa) was determined using pronymphs collected in late October and early November. Pronymphs were placed in damp vermiculite in plastic boxes and gradually acclimatized to a \(-0.5^\circ\text{C}\) storage temperature. Individuals were removed from storage after about three months and placed in 1.9-mL shell vials stoppered with foam plugs. The vials were placed on their sides in plastic boxes and covered with moist paper towels. Boxes were put into paper bags and placed in one of a series of constant-temperature chambers set at 1.7, 5.8, 7.5, 10.7, 15.0, 19.1, 22.4, and 23.0°C. Another group of spring collected pronymphs was reared at 4.1°C. Preliminary investigations indicated that pupation did not occur at temperatures greater than 23.0°C. Pronymphs were examined twice daily until pupal
Pupae emerging from pronymphs described above were used to determine the duration of pupal development at constant temperatures. Pupae emerging from 15°C were distributed among 11 constant temperature chambers ranging from 2.3 to 31.7°C, while pupae emerging at other temperatures were left in the chambers in which they eclosed. One group of insects was alternated daily between 7.4 and 15°C chambers until adult eclosion to compare their developmental periods with pupae kept throughout the stage at 7.4 and 15°C. Pupae were examined twice daily until adult emergence. Sex of pupae was determined either by examination of emerged adults or from the shape of terminal abdominal segments of pupae (Kolomietz 1967). Adults produced at 7.4°C were weighed to determine the relationship between size and developmental rate.

Total duration of subterranean development (i.e., pronymph to adult) was determined in a similar manner. Laboratory overwintered pronymphs were placed in shell vials on their sides in transparent plastic boxes. Vials were covered with damp vermiculite and boxes were placed at 12 constant temperatures ranging from 1.8 to 31.0°C. Boxes at 1.8°C were moved to 15°C after 90 days to speed up development. Boxes were examined twice daily and newly emerged adults were removed.

Data from individuals moved between low and high
temperatures were used to estimate time required to complete development at the low temperature using a interpolation technique. Briefly, the method used was:

\[ \hat{t}_L = \frac{t_L}{1 - (t_H / \bar{t}_H)} \] (2.10)

where \( \hat{t}_L \) is estimated time an individual requires to complete development at low temperature, \( t_L \) is actual time spent at low temperature, \( \bar{t}_H \) is average time required to complete development at high temperature (determined from individuals reared at high temperature for entire stage) and \( t_H \) is time that individuals actually spend at high temperature (Régnière 1987).

Individual development times were converted to development rates \((1/\text{time})\) and mean development rates \( (b_m) \) were computed for each experimental temperature \((T)\). Matched-asymptote equations (Logan et al. 1976) were used to describe the relationship between mean developmental rates and temperature. Parameters were estimated using program PAR of BMDP (Dixon 1983). Equation 2.11a is an exponential function coupled with a decay function, while Equation 2.11b is a logistic function combined with a decay function. The choice of equation was determined graphically by the shape of the relationship near the optimal temperature (Régnière et al. 1981). The equations are:

\[ \hat{b}_m(T) = P_1 \left\{ \exp(P_2 r) - \exp[P_2 - (1 - r)/P_3] \right\} \] (2.11a)

and

\[ \hat{b}_m = P_1 \left\{ [1 + \exp(P_2 - P_3 r)]^{-1} - \exp[(r - 1)/P_4] \right\} \] (2.11b)

where

\[ r = \frac{(T - T_B)}{(T_m - T_B)} \]

\( T_m \) and \( T_B \) are maximum and minimum temperatures above and below
which development did not occur, and $P_1-P_4$ are parameters estimated by nonlinear regression.

Variability in development rates for all temperatures can be mathematically described if the distribution of development rates can be normalized into standard units. The method developed by Régnière (1984) was used to describe developmental variability of all subterranean stages of PFW. This requires selecting an appropriate normalizing constant, in this case, the estimated mean development rate calculated using Equation 2.11. Individual rates at each constant temperature were divided by the temperature-dependent solution of Equation 2.11. Normalized data from each temperature were pooled and a cumulative distribution was constructed. A logistic function:

$$ Y = [1 + \exp(-K(X-C))]^{-1/Q} \quad (2.12a) $$

or a Poisson function:

$$ Y = [1 - \exp(-KX)]^{1/Q} \quad (2.12b) $$

was fitted to the cumulative frequency distribution using nonlinear regression. Parameters $K$, $Q$ and $C$ in Equation 2.12a describe the slope, skew and position of the sigmoid curve. Parameters $K$ and $Q$ behave similarly in Equation 2.12b, a function better suited for describing sigmoid distributions with extreme positive skews. The inverted forms of these equations are

$$ X = C - \ln(Y^{-Q} - 1)/K \quad (2.13a) $$

and

$$ X = -\ln(1 - Y^Q)/K \quad (2.13b) $$
for the logistic and Poisson curves, respectively. These describe the variability factor $X$ of the development rate for the $Y$th percentile of the population.

Pronymphs collected in the fall and overwintered in the laboratory were reared outdoors at the LA plantation inside 37 by 19 by 14.5 cm high plastic boxes partially filled with soil. This emulated subterranean development in natural conditions but eliminated spatial variability. A 29 by 15.5 cm hole was cut in the top of each box and covered with fine-mesh plastic screening. Drain holes were drilled in the bottoms of the boxes. Thermocouples were glued to the center of the bottoms of the boxes. Fifty shell vials each containing one larva were taped on their sides to the bottoms of six boxes and covered with soil to a depth of 11 cm. Three boxes were placed in a heavily defoliated zone and three were placed in a lightly defoliated zone. Each box was buried until the soil level in the box was even with the surrounding soil. Thermocouples were connected to data loggers programmed to record hourly average temperatures. Boxes were examined daily for adult emergence. A rate-summation model to predict the emergence of the adults from the soil boxes was constructed based on the FORTRAN program provided by Régnière (1984).

Phenology Model Construction. The modeling approach used is based on the assumption that development is an additive process (Logan et al. 1976). For each discrete time step ($\Delta t$), the
proportion of development completed was multiplied by the time step. For all subterranean stages of PFW, \( \Delta t = 0.0417 \) d. To incorporate developmental variability, the hourly development rate was multiplied by factor \( X_Y \) (from Equation 2.13) for each percentile \( (Y) \) of the population and development was accumulated until development reached unity (Regniere 1984). Thus, development of a percentile of the population \( (P_Y(t)) \) at time \( t \) was approximated by the difference equation

\[
P_Y(t) = P_Y(t - \Delta t) + b_m(T) \Delta t X_Y
\]  

(2.14)

The proportion of the population that had completed development at time \( t \) was then:

\[
P(t) = \frac{100}{Y = 1} \sum P_Y(t)
\]  

(2.15)

Development of PFW in soil cells following diapause termination consisted of prepupal and pupal phenophases. Subterranean development of PFW culminated in the emergence of adults from the soil. The model assumes that all overwintered pronymphs are at the same stage of development when soil temperatures rose above freezing. Development of each sex was computed independently and simultaneously since male and female subterranean stages of PFW have different temperature-dependent development rate and variability functions.

The number of developing cohorts \( (c) \) of PFW simulated during each stage of the multiple-cohort subterranean phenology model was determined by the number of days it took for the population
to complete the previous phenophase (Wagner et al. 1985). The limit of a class interval for the distribution of cohorts was set at 1000 hours since emergence traps were examined at this time. The first cohort \((c = 1)\) began development at the end of the day that the first individuals had completed the previous phenophase. The last cohort \((c = n)\) began development when the last of the population had completed the previous phenophase. Each daily cohort represented the proportion of the population beginning the phenophase \(\left( P_b_c \right) \) by time \(t_d\) which was incremented in daily steps. \(P(t_d)\) was derived from Equation 2.15, and:

\[
P_b_c(\Delta t_d) = P(t_d) - P(t_d - \Delta t_d) \tag{2.16}
\]

and

\[
\sum_{c=1}^{n} P_b_c = 1.0 \tag{2.17}
\]

The proportion of the cohort \(\left( P_f_c \right)\) finishing the phenophase by time \( t \) was also computed from the rate-summation model (Equation 2.14).

Each cohort simulation resulted in a separate cumulative frequency distribution of the proportion completing the phenophase. The cumulative proportion of the population \(\left( P_p(t) \right)\) that had completed development was the sum of the cohort distributions weighted by the proportion of the population in the cohort. When \( P_p(t) = 1.0 \) the population has completed the phenophase.

The model was written in FORTRAN. Input for the model
consisted of hourly average soil temperatures from the heavy to moderate-defoliation zone and from the light-defoliation zone of the LA plantation in 1986. Soil temperature files started 22 March when the ground was still frozen.

To determine if vertical distribution of the soil cells influenced emergence pattern of PFW, the model was modified to incorporate this element of spatial variability. The proportion \( p(\Delta z) \) of insects in 1.5 cm increments (i.e., \( \Delta z \)) of the soil from the surface to the bottom of the lowest interval containing larvae was determined from the depth-dependent solution to Equation 2.1 where:

\[
p(\Delta z) = V(z) - V(z - \Delta z) \tag{2.18}
\]

For simulations involving microclimatic stratification of development (i.e., depth in soil), soil temperature was calculated at the midpoint of each vertical stratum. Hourly temperature at six depths was used as the input for the model. The rate-summation model was then calculated for each stratum \( s \) and developmental status of the population \( P(t,z) \) was determined from:

\[
P(t,z) = \sum_{s=1}^{n} P_s(t) \ p(\Delta z) \tag{2.19}
\]

where \( P_s \) is the proportion of PFW in the stratum that had completed development.
2.3 Results

**Adult Emergence.** Peak female emergence occurred after peak of male emergence in most situations (Fig. 2.1). Onset of emergence was similar from 1983-1985, although, the pattern was obscured by low adult numbers during 1984 and 1985. Onset of male emergence in 1984-85 in the three plots ranged from 12 May (day 133) to 17 May (day 137), while the onset of female emergence ranged from 12 May to 19 May (day 140). Duration of emergence was 4 to 26 days in the same years. The emergence pattern was similar in 1986, but occurred earlier as a result of defoliation of the pine canopy and a warmer spring (Fig. 2.1). Observed onset of emergence in the heavy defoliation zone preceded the onset of emergence in the moderate defoliation zone by two days, which in turn preceded emergence from the light defoliation zone by seven days. Throughout the LA plantation the emergence period ranged from 27 April to 26 May. Female percentage of emerging adults from all locations (Table 2.1) varied from 16.7 to 56.9.

**Vertical Distribution of PFW in Soil.** Differences between the mean depth of male and female eonymphs were always less than the vertical sampling interval (1 cm) and not statistically significant, therefore frequencies of PFW of both sexes at each vertical depth increment were pooled. Similarly, the difference between mean depths of eonymphs at each location was less than the sampling interval, so the data were again pooled. Since the
Fig. 2.1. Cumulative emergence patterns of adults of PFW in 1983 and 1986.
upper limit of the distribution was the soil surface, $z_U = 0$. The lower limit was the maximum depth of the sample that contained larvae (9 cm) (Fig. 2.2). For these data, $q = 3.484$ and $w = 2.705$ (Equation 2.1) provided an equation which had excellent fit ($R^2 = 0.999$).

Soil Temperature. Maximum observed soil temperatures never exceeded 17°C prior to the completion of adult emergence at all locations. A simulated soil temperature profile is shown in Fig. 2.3A. Cumulative degree-days ($> 0°C$) at each observed and predicted depth in the soil are shown in Fig. 2.3B.

Temperature-dependent Development. No pupa emerged at temperatures greater than 23.0°C. Mean prepupal development period was longer for females than for males at all but the lowest temperature (Table 2.2). Lack of an observable difference at 1.7°C reflected the high variability at this temperature. Similarly, female pupal development took longer than male development at all but the lowest temperature (Table 2.3). Pupae from prepupae reared at 15°C and subsequently kept at another temperature during pupal development had a consistently shorter developmental period than individuals that experienced a lower temperature as prepupae (Table 2.3). For pupae reared at 7.4°C, there was no correlation between development times and female live weights ($r=-0.005$, $df=55$, $P=0.968$). There was a significant negative correlation ($r=-0.377$, $df=50$, $P=0.006$) between these variables for males.
Fig. 2.2. Cumulative vertical distribution of larvae of PFW in soil. Curve is regression (Equation 2.1) of pooled cumulative frequencies as a function of soil depth. Symbols are observed cumulative frequencies by sex, location and pooled.
Fig. 2.3. (A) Soil temperature profile for 2 April 1986 in a moderately- to heavily-defoliated zone at LA plantation. Solid lines are estimated temperatures at indicated depths (cm) and dotted lines are recorded average soil temperatures. (B) Cumulative degree-days (>0°C) at LA plantation. Solid lines are predicted temperatures and dotted lines are observed temperatures. Lines occur in order of depth in soil.
Table 2.1. Number of emerging adults of PFW captured in emergence traps in 1983-1986.

<table>
<thead>
<tr>
<th>Year</th>
<th>Plot</th>
<th>Number of adults</th>
<th>% Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>AM1</td>
<td>1882</td>
<td>45.6a</td>
</tr>
<tr>
<td></td>
<td>AM2</td>
<td>537</td>
<td>44.5a</td>
</tr>
<tr>
<td></td>
<td>CR</td>
<td>355</td>
<td>50.7</td>
</tr>
<tr>
<td>1984</td>
<td>AM1</td>
<td>153</td>
<td>22.9a</td>
</tr>
<tr>
<td></td>
<td>AM2</td>
<td>98</td>
<td>32.7a</td>
</tr>
<tr>
<td></td>
<td>CR</td>
<td>65</td>
<td>55.4</td>
</tr>
<tr>
<td>1985</td>
<td>AM1</td>
<td>26</td>
<td>53.8</td>
</tr>
<tr>
<td></td>
<td>AM2</td>
<td>18</td>
<td>16.7a</td>
</tr>
<tr>
<td></td>
<td>CR</td>
<td>21</td>
<td>28.6a</td>
</tr>
<tr>
<td>1986</td>
<td>LA(H)</td>
<td>832</td>
<td>52.0</td>
</tr>
<tr>
<td></td>
<td>LA(M)</td>
<td>2026</td>
<td>40.1a</td>
</tr>
<tr>
<td></td>
<td>LA(L)</td>
<td>262</td>
<td>56.9a</td>
</tr>
</tbody>
</table>

a significantly different from 50% ($\chi^2$; P < 0.05)

Table 2.2. Mean development times (days) and rates for post-diapause prepupal development of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. ('C)</th>
<th>Sex</th>
<th>n</th>
<th>Mean time (d)</th>
<th>SE</th>
<th>Mean rate (1/d)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.7</td>
<td>M</td>
<td>40</td>
<td>27.9</td>
<td>2.2</td>
<td>0.053</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>64</td>
<td>27.8</td>
<td>1.6</td>
<td>0.047</td>
<td>0.004</td>
</tr>
<tr>
<td>5.8</td>
<td>M</td>
<td>16</td>
<td>9.2</td>
<td>0.8</td>
<td>0.121</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>20</td>
<td>10.9</td>
<td>0.9</td>
<td>0.106</td>
<td>0.010</td>
</tr>
<tr>
<td>7.5</td>
<td>M</td>
<td>51</td>
<td>7.5</td>
<td>0.5</td>
<td>0.172</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>66</td>
<td>8.9</td>
<td>0.4</td>
<td>0.136</td>
<td>0.008</td>
</tr>
<tr>
<td>10.7</td>
<td>M</td>
<td>34</td>
<td>5.2</td>
<td>0.3</td>
<td>0.222</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>47</td>
<td>5.7</td>
<td>0.3</td>
<td>0.203</td>
<td>0.012</td>
</tr>
<tr>
<td>15.0</td>
<td>M</td>
<td>202</td>
<td>3.4</td>
<td>0.1</td>
<td>0.387</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>F</td>
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<td>4.0</td>
<td>0.1</td>
<td>0.295</td>
<td>0.008</td>
</tr>
<tr>
<td>19.1</td>
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<td>21</td>
<td>2.1</td>
<td>0.2</td>
<td>0.637</td>
<td>0.090</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>20</td>
<td>3.1</td>
<td>0.2</td>
<td>0.353</td>
<td>0.023</td>
</tr>
<tr>
<td>22.4</td>
<td>M</td>
<td>7</td>
<td>1.5</td>
<td>0.3</td>
<td>0.786</td>
<td>0.107</td>
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<tr>
<td></td>
<td>F</td>
<td>4</td>
<td>3.3</td>
<td>0.6</td>
<td>0.343</td>
<td>0.066</td>
</tr>
<tr>
<td>23.0a</td>
<td>M</td>
<td>3</td>
<td>1.7</td>
<td>0.2</td>
<td>0.611</td>
<td>0.055</td>
</tr>
</tbody>
</table>

a no female pupae eclosed at this temperature.
Table 2.3. Mean development times (days) and rates for pupae of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>Sex</th>
<th>n</th>
<th>Mean time (d)</th>
<th>SE</th>
<th>Mean rate (1/d)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.3</td>
<td>M</td>
<td>19</td>
<td>98.0</td>
<td>1.4</td>
<td>0.010&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>47</td>
<td>97.2</td>
<td>0.8</td>
<td>0.010&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.000</td>
</tr>
<tr>
<td>4.1</td>
<td>M</td>
<td>9</td>
<td>50.6</td>
<td>0.3</td>
<td>0.020&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>52.4</td>
<td>0.4</td>
<td>0.019&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.000</td>
</tr>
<tr>
<td>4.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>M</td>
<td>2</td>
<td>55.5</td>
<td>0.5</td>
<td>0.018</td>
<td>0.000</td>
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<tr>
<td></td>
<td>F</td>
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<td>58.8</td>
<td>0.4</td>
<td>0.017</td>
<td>0.000</td>
</tr>
<tr>
<td>5.8</td>
<td>M</td>
<td>16</td>
<td>36.1</td>
<td>0.2</td>
<td>0.028&lt;sup&gt;bc&lt;/sup&gt;</td>
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<tr>
<td></td>
<td>F</td>
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<td>37.4</td>
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<td>M</td>
<td>16</td>
<td>27.8</td>
<td>0.3</td>
<td>0.036</td>
<td>0.001</td>
</tr>
<tr>
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<td>0.000</td>
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<tr>
<td>11.0</td>
<td>M</td>
<td>39</td>
<td>15.8</td>
<td>0.1</td>
<td>0.063&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.000</td>
</tr>
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<td></td>
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<td>0.1</td>
<td>0.062</td>
<td>0.000</td>
</tr>
<tr>
<td>11.0&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>16.0</td>
<td>0.1</td>
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<td>0.001</td>
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<tr>
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<td>M</td>
<td>31</td>
<td>10.5</td>
<td>0.1</td>
<td>0.095&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>46</td>
<td>10.9</td>
<td>0.1</td>
<td>0.092&lt;sup&gt;b&lt;/sup&gt;</td>
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</tr>
<tr>
<td>15.4</td>
<td>M</td>
<td>37</td>
<td>9.9</td>
<td>0.1</td>
<td>0.101&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>42</td>
<td>10.4</td>
<td>0.1</td>
<td>0.097&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.001</td>
</tr>
<tr>
<td>18.6</td>
<td>M</td>
<td>23</td>
<td>7.8</td>
<td>0.1</td>
<td>0.129&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>27</td>
<td>8.4</td>
<td>0.1</td>
<td>0.120&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.002</td>
</tr>
<tr>
<td>18.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>M</td>
<td>34</td>
<td>7.6</td>
<td>0.1</td>
<td>0.132</td>
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<tr>
<td></td>
<td>F</td>
<td>58</td>
<td>7.9</td>
<td>0.1</td>
<td>0.127</td>
<td>0.001</td>
</tr>
<tr>
<td>23.1</td>
<td>M</td>
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<td>6.3</td>
<td>0.3</td>
<td>0.161</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4</td>
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<td>0.2</td>
<td>0.151</td>
<td>0.003</td>
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<tr>
<td>23.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>M</td>
<td>34</td>
<td>6.0</td>
<td>0.1</td>
<td>0.168&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>27</td>
<td>6.3</td>
<td>0.0</td>
<td>0.160&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.002</td>
</tr>
<tr>
<td>26.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>M</td>
<td>20</td>
<td>5.9</td>
<td>0.1</td>
<td>0.171&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>9</td>
<td>6.2</td>
<td>0.2</td>
<td>0.162&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.006</td>
</tr>
</tbody>
</table>

<sup>a</sup>pupae reared at these temperatures were from prepupae reared at 15°C.

<sup>b</sup>mean developmental rates used to construct temperature-dependent rate model.

<sup>c</sup>development rate significantly different (t-test; P < 0.05) than rate for pupae with different prepupal thermal history reared at comparable temperature.
Adults did not emerge from the vermiculite boxes at temperatures greater than 20.5°C. Adult males emerged prior to females at all but the highest temperatures (Table 2.4). Mortality in vermiculite boxes was high at all temperatures. Adult emergence was highest at intermediate temperatures. Insects died before reaching the pupal stage at the highest temperatures. At all temperatures, a portion of the insects died as adults before emerging from vials.

To test the interpolation technique, estimated times for pupal development at 7.4°C were calculated from the insects that were moved daily between 7.4 and 15.0°C. These times were compared with actual development times for pupae reared throughout the stage at 7.4°C (Table 2.3). Since the amount of time individuals spent at each temperature was variable, depending on when they pupated or eclosed as adults, these individual times were used instead of means in the computations. Estimated times for males (n=15) and females (n=22) were 27.0 and 26.5 days, respectively. Although the estimate for females was less than the estimate for males, mean estimated rates were not significantly different from actual rates (males; t=-0.31, p=0.76; females; t=-1.99, p=0.06). Development periods for total subterranean development at 1.8°C were also estimated using this technique (Table 2.4).

T_b for all subterranean stages was set at 0°C since
Table 2.4. Mean development times (days) and rates for pronymph to adult development of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>Sex</th>
<th>n</th>
<th>Mean time (d)</th>
<th>SE</th>
<th>Mean rate (1/d)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.8(^a)</td>
<td>M</td>
<td>14</td>
<td>138.1</td>
<td>7.5</td>
<td>0.008</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>25</td>
<td>146.2</td>
<td>5.8</td>
<td>0.007</td>
<td>0.000</td>
</tr>
<tr>
<td>5.8</td>
<td>M</td>
<td>11</td>
<td>54.1</td>
<td>1.8</td>
<td>0.019</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>24</td>
<td>58.1</td>
<td>0.9</td>
<td>0.017</td>
<td>0.000</td>
</tr>
<tr>
<td>7.4</td>
<td>M</td>
<td>10</td>
<td>40.4</td>
<td>1.4</td>
<td>0.025</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>20</td>
<td>43.3</td>
<td>1.0</td>
<td>0.023</td>
<td>0.001</td>
</tr>
<tr>
<td>11.0</td>
<td>M</td>
<td>11</td>
<td>22.4</td>
<td>0.8</td>
<td>0.045</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>16</td>
<td>26.7</td>
<td>0.8</td>
<td>0.038</td>
<td>0.001</td>
</tr>
<tr>
<td>12.5</td>
<td>M</td>
<td>18</td>
<td>22.9</td>
<td>0.6</td>
<td>0.044</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>25</td>
<td>23.6</td>
<td>0.4</td>
<td>0.043</td>
<td>0.001</td>
</tr>
<tr>
<td>15.0</td>
<td>M</td>
<td>13</td>
<td>15.8</td>
<td>0.4</td>
<td>0.064</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>28</td>
<td>16.9</td>
<td>0.3</td>
<td>0.060</td>
<td>0.001</td>
</tr>
<tr>
<td>15.5</td>
<td>M</td>
<td>8</td>
<td>14.9</td>
<td>0.4</td>
<td>0.069</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>16</td>
<td>15.4</td>
<td>0.5</td>
<td>0.066</td>
<td>0.002</td>
</tr>
<tr>
<td>18.6</td>
<td>M</td>
<td>2</td>
<td>11.5</td>
<td>0.0</td>
<td>0.087</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>11.0</td>
<td>0.1</td>
<td>0.092</td>
<td>0.003</td>
</tr>
<tr>
<td>20.5</td>
<td>M</td>
<td>2</td>
<td>12.3</td>
<td>0.8</td>
<td>0.082</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>15</td>
<td>11.9</td>
<td>0.4</td>
<td>0.086</td>
<td>0.003</td>
</tr>
</tbody>
</table>

\(^a\) estimated development times by interpolation technique.
development progressed at the lowest temperatures tested. \( T_m \) was set at temperatures just greater than the highest temperatures at which development was observed. The three-parameter equation (Equation 2.11a) was fitted to prepupal and pronymph to adult subterranean development data (Fig. 2.4A, C), while pupal development (Fig. 2.4B) was better described using the four-parameter model (Equation 2.11b). The initial model for female prepupal development did not adequately reflect the observed data at low temperatures (Fig. 2.4A), temperatures critical for development in the field. Since sample sizes used to develop the function were disproportionate between groups, a weighted regression based on sample size was substituted. Parameter estimates for the equations are listed in Table 2.5. Although the \( R^2 \)-values for the weighted models suggested a poorer fit than the unweighted models (Table 2.5), deviations between predicted and observed development rates for the former were smaller at low temperatures.

Pupal and pronymph to adult developmental variability were described using Equation 2.12a (Fig. 2.5B, C), while the positive skewed distribution of prepupal variability was described by Equation 2.12b (Fig. 2.5A). Parameter estimates for these equations are in Table 2.6. Only the middle 90% of the variability functions for prepupal development was used in the simulations. This eliminated individuals with extreme developmental rates unrealistically suggested by Equation 2.12b.
Fig. 2.4. Development rates of male (solid lines) and female (dashed lines) (A) post-diapause prepupae, (B) pupae and (C) pronymphs to adults of PFW at constant temperatures. Circles and triangles are mean observed rates for males and females, respectively. Curves are regressions from Equations 2.11a and b. Both weighted (dotted line) and unweighted (dashed line) regressions are shown for female prepupal development.
Fig. 2.5. Developmental variability of male (solid lines) and female (dashed lines) (A) post-diapause prepupae, (B) pupae and (C) pronymphs to adults of PFW at constant temperatures. Circles and triangles are cumulative frequencies of observed individual rates/predicted rates from development rate regressions (Equation 2.11) for males and females, respectively. Curves are regressions from Equations 2.12a (B, C) and b (A).
Table 2.5. Estimated parameters and goodness-of-fit statistics of models for development of subterranean stages of PFW.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Sex</th>
<th>Parameters</th>
<th>P1</th>
<th>P2</th>
<th>P3</th>
<th>P4</th>
<th>Tm</th>
<th>Tb</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prepupae M</td>
<td>0.057</td>
<td>3.071</td>
<td>0.041</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prepupae M</td>
<td>0.060</td>
<td>2.984</td>
<td>0.038</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.995</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prepupae F</td>
<td>0.066</td>
<td>2.264</td>
<td>0.061</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.969</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prepupae F</td>
<td>0.051</td>
<td>3.184</td>
<td>0.134</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.895</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pupae M</td>
<td>0.209</td>
<td>2.981</td>
<td>5.470</td>
<td>0.031</td>
<td>29.0</td>
<td>0.0</td>
<td>0.999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pupae F</td>
<td>0.199</td>
<td>2.927</td>
<td>5.369</td>
<td>0.031</td>
<td>29.0</td>
<td>0.0</td>
<td>0.998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pronymph M</td>
<td>0.008</td>
<td>3.374</td>
<td>0.105</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.993</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pronymph F</td>
<td>0.007</td>
<td>3.481</td>
<td>0.092</td>
<td>-</td>
<td>24.0</td>
<td>0.0</td>
<td>0.996</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.6. Estimated parameters and goodness-of-fit statistics for development variability functions for subterranean stages of PFW.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Sex</th>
<th>Parameters</th>
<th>K</th>
<th>C</th>
<th>Q</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prepupae M</td>
<td>2.398</td>
<td>-</td>
<td>0.274</td>
<td>0.995</td>
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</tr>
<tr>
<td>Prepupae F</td>
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<td>-</td>
<td>0.317</td>
<td>0.999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pupae M</td>
<td>34.849</td>
<td>1.009</td>
<td>0.684</td>
<td>0.999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pupae F</td>
<td>38.254</td>
<td>1.022</td>
<td>0.564</td>
<td>0.999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pronymph M</td>
<td>14.281</td>
<td>0.983</td>
<td>1.905</td>
<td>0.998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pronymph F</td>
<td>18.037</td>
<td>1.006</td>
<td>2.148</td>
<td>0.999</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a parameters estimated for regressions weighted by sample size.
Adult emergence was 43% of the initial 300 pronymphs placed in the soil boxes. The emergence pattern of these adults was used to validate the subterranean development model under variable-temperature regimes measured in the boxes from the two defoliation zones. The model predicted emergence as much as 12 days too late in the heavily defoliated zone (Fig. 2.6A), while predictions (Table 2.7) were in closer agreement to observed emergence in the lightly defoliated zone (Fig. 2.6B).

**Phenology Model Validation.** For both defoliation zones and both sexes (Fig. 2.7), predicted adult emergence from single and multiple-strata models were only slightly different. Although the results for the 10, 50, and 90% percent emergence classes were variable (Table 2.8), in general the incorporation of multiple strata into the model slightly enhanced accuracy. Increasing the time increment of the multiple-strata model from 1 to 4 h (i.e., $\Delta t=0.167$ d) did not adversely affect resolution of the model.

2.4 Discussion

Wellington (1957) suggested that comparisons between two extreme habitats provided a more reliable method of assessing the effects of weather on insect populations than long-term studies in one habitat. In the present instance, degree of exposure to sunlight in the habitat was clearly an important variable that had to be taken into account. Defoliation opens
Fig. 2.6. Simulated emergence of PFW males (solid lines) and females (dashed lines) from soil boxes in (A) heavily-defoliated and (B) lightly-defoliated zones. Symbols are observed emergence of males (triangles) and females (circles).
Fig. 2.7. Simulated (lines) and observed (circles) emergence of adults of PFW from LA plantation in 1986: (A) males and (B) females from moderate- to heavily-defoliated zone and (C) males and (D) females from lightly-defoliated zone. Consecutive lines of the same type represent pupal eclosion and adult emergence, respectively. Different line types depict simulations using one depth (solid), multiple depths (short dash), and multiple depths with four-hour increments (long dash).
Table 2.7. Deviations (dev.) in days of observed adult emergence from simulated emergence and the deviation as a proportion (pro.) of total simulation time for adults emerging from soil boxes.

<table>
<thead>
<tr>
<th>Percent emergence</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10%</td>
<td>50%</td>
<td>90%</td>
</tr>
<tr>
<td>Plot</td>
<td>Sex</td>
<td>dev.</td>
<td>pro.</td>
</tr>
<tr>
<td>L</td>
<td>M</td>
<td>1.5</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.5</td>
<td>0.04</td>
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<tr>
<td>H</td>
<td>M</td>
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<tr>
<td></td>
<td>F</td>
<td>9.6</td>
<td>0.27</td>
</tr>
</tbody>
</table>

Table 2.8. Deviations (dev.) in days of observed adult emergence from simulated emergence and the deviation as a proportion (pro.) of total simulation time.

<table>
<thead>
<tr>
<th>Percent emergence</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10%</td>
<td>50%</td>
<td>90%</td>
</tr>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>one depth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>M</td>
<td>0.4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.7</td>
<td>0.04</td>
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<td>six depths</td>
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<td></td>
</tr>
<tr>
<td>B</td>
<td>M</td>
<td>0.2</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.6</td>
<td>0.04</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>M</td>
<td>0.6</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>F</td>
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<td>0.04</td>
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<td></td>
</tr>
<tr>
<td>B</td>
<td>M</td>
<td>2.6</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2.0</td>
<td>0.05</td>
</tr>
</tbody>
</table>
the canopy and changes the pattern of light penetration to the understory (Schowalter et al. 1986). Defoliation by the pine moth, *Dendrolimus pini*, increased the magnitude and range of diurnal soil temperatures (Ierusalimov 1973), as occurred in the three defoliation zones examined in the present study. Defoliation by PFW affected soil temperatures and consequently the temporal pattern of emergence of the adults, but did not alter the sexual sequence of emergence. Protracted emergence of *Hyphantria cunea* could be partially attributed to variable degrees of solar radiation on overwintering sites in the soil (Morris and Bennett 1967). Temperature differentials between shaded and exposed sites resulted in a 2-3 week difference in the emergence of *N. swainei* (Tripp 1965). Observed difference in emergence of adults of PFW from the habitat extremes examined in the present investigation was approximately one week.

The variable sex ratio of PFW observed in this investigation suggested differential mortality between the sexes or differential sex determination mechanisms. Female PFW generally predominate in less heavily-infested habitats (Jahn 1967). Where the insects were more numerous, the sex ratio was even or favored males, in agreement with this study. For the three defoliation zones examined in the LA plantation, males predominated where the insects were most abundant (M-zone) and females were more numerous where the the sawflies were least abundant (L-zone). Where densities were intermediate (H-zone) the sex ratio was 1:1. These differences may have resulted from
the failure of some females to mate prior to ovipositing at high densities.

Eonymphs were found below the humus layer at depths of 5 to 11 cm in Europe (Schwerdtfeger 1941, Jahn 1967). Here, eonymphs were found from just below the soil surface to a depth of 9 cm. The mean depth was less than the 5 cm minimum suggested in earlier studies. Vertical distributions of the soil cells of PFW were not significantly different at the two locations sampled. Eonymphs of Acantholyda posticalis, in some climatic zones, overwinter deeper in the soil in response to reduced snow cover and soil desiccation (Kolomietz 1967). Since the two plantations were only separated by a distance of 112 km, climatic effects on overwintering depths between the two sites were minimal. Since red pines are planted only on loamy sands and sandy loam soils (Bassett 1984), the effects of soil type would be minimal. Although the vertical distribution of females was consistently deeper than the vertical distribution of males, the sampling interval employed in the study was not adequate to detect the differences. Increasing the resolution of the sampling interval, however, would not enhance the utility of the soil distribution function since soil temperatures do not vary greatly over the short distances involved.

Soil temperatures in spring have been described as a monotonically increasing function of time (Logan et al. 1979). While not strictly true, since soil temperatures fluctuate
diurnally, the net effect over a period of days or weeks is a rising temperature. Although degree-days are not used here, rate summations are analogous to degree-day summations and the latter are a more standardized means of comparing heat accumulations. Soil in the lightly-defoliated zone accumulated heat at a slower rate than did soil in the moderately- to heavily-defoliated zone. Accumulations of heat slowed as depth increased, even within the top 10 cm of the mineral soil. PFW inhabiting soil cells at different vertical depths experience different microclimates.

Soil temperatures predicted from air temperatures would be the most practical approach for pest management purposes since soil-temperatures records are rarely available. Although some progress has been made in this direction (Morse et al. 1985), accurate predictions for forested soils are difficult (Novak and Black 1985). The model of soil temperature presented here imparts the needed resolution for use in process-oriented phenological models and could be easily modified to predict hourly soil temperatures from maximum and minimum soil temperatures.

The microclimate of soil-inhabiting insects can be considerably different than that experienced by dwellers above ground. Several authors have used soil temperatures to predict phenological events for subterranean insects (Logan et al. 1979, Régnière et al. 1981, Morse et al. 1985). Phenological
predictions based on air temperature are not appropriate for insects in the soil (Collier and Finch 1985). Soil and air temperature inputs provided similar results for simulation models of the black cutworm, *Agrotis ipsilon* (Kaster and Showers 1984). Bare and grass-covered soils accumulated heat faster than a conventional meteorological screen (Baker 1981). In the present investigation, however, soil temperatures under the plantation canopy never approximated the extremes of the air temperatures. The 5-cm depth at which soil temperatures were recorded was near the median depth of the insects in the soil. If the thermocouples were at another depth the multi-stratum model might have provided much better predictions than the single-stratum model.

The curvilinear nature of the temperature versus development rate functions was evident for all stages of PFW. Rates departed from linearity at both the highest and lowest temperatures. Prepupal development and pupal eclosion began soon after soil temperatures rose above freezing. Similarly pupal development also progressed when the soil temperature had only moderately warmed. The determination of development rates at low temperatures was crucial for the construction of predictive phenological models for PFW. Maximum soil temperatures observed during subterranean development of PFW never approached the temperature maxima for development. The inhibition of development at high temperatures observed in the laboratory would rarely occur in the field.
Development rates of male prepupae and pupae were greater than those of females. The accelerated rate of male development explains the protandry observed in the field. Differences in development were unrelated to size differences within a sex. Therefore, size differences between the sexes is not related to differences in development rates (Lederhouse et al. 1982).

High mortality of insects in the vermiculite boxes was similar to the mortality of subterranean stages of PFW in the laboratory experiments. The insects are extremely susceptible to desiccation and infection once removed from their soil cells and placed in artificial environments. Exarate pupae are also very fragile and easily damaged.

The interpolation technique was a useful method for determining development rates at low temperatures and critical in predicting the phenology because development begins early in the spring when temperatures are very low. Alternating temperatures reduced the developmental period in calendar time and hence the exposure of insects to pathogens and desiccating conditions. The technique is valid if developmental variability is not affected by temperature and developmental rates of individuals are constant during a stage. The construction of variability functions by pooling standardized rates from all temperatures suggested that the first assumption was valid. Exposure of insects to high temperatures early in a stage may
retard subsequent development (Turnock et al. 1986). This did not occur with the pupae of PFW that were moved daily between low and intermediate temperatures. However, incubation of the prepupa at moderate temperatures did result in retardation of pupal development when reared at lower temperatures.

Diapause is the most significant synchronizing element in insect life cycles (Tauber and Tauber 1981) especially for regulating voltinism. But the termination of diapause and subsequent morphogenesis of prepupae of PFW was more variable than pupal development. For PFW and some other insects (e.g., Hyphantria cunea) (Morris and Fulton 1970), prepupal development imparts a high degree of variability to the phenology. This variability, although dramatic in physiological time, is negligible in calendar time since spring soil temperatures are constantly increasing, which in turn increases developmental rates and obscures the differences accumulated at low temperatures.

The single-stage (i.e., pronymph to adult) model provided an adequate prediction of adult emergence of PFW from the soil boxes for only one of the defoliation zones. Temperatures recorded in the boxes in the heavily-defoliated zone exceeded the upper threshold for pronymph to adult development late in the development period. As has been demonstrated, subterranean development is a combination of several temperature-dependent processes, each with its own maximum and minimum for
development. This model treated subterranean development as one process. The temperatures were often less than the optimal for pupal development, but greater than the maximum for prepupal development, and thus predicted slow or no development when rates would actually be near the maximum. Temperatures experienced by the insects in the artificial environments of the boxes were often higher than those that would be normally encountered by the subterranean stages under natural conditions.

The slightly better fit achieved by incorporating vertical distribution into the simulation model did not justify the increased computational complexity and time required. Increasing the time increment decreased the computational time without affecting the resolution of the simulation.

The protracted emergence pattern of PFW adults resulted from: inherent variability in development rates of prepupae and pupae, and microclimatic differences resulting from the vertical and horizontal distribution of insects in the soil. The vertical distribution determined the temperatures of the insects' habitat via the diurnal fluctuations and seasonal increases in soil temperature during spring. Differential shading of the soil surface, due in part to degree of defoliation, had a profound effect on soil temperatures and hence emergence patterns.

The stability of the protandrous emergence pattern resulted
from the differential rates of prepupal and pupal development between the sexes and to a lesser degree from their differential vertical distribution.

PFW has become more common in recent years in Ontario (Syme 1981). Although not widespread, PFW has been locally abundant in pine plantations. Even in low numbers, PFW is especially destructive in Christmas tree plantations, where the webs and defoliation reduce the trees' market value. The characteristically small tree size and lack of crown closure in Christmas tree plantations would result in a very different soil microclimate than those found in other kinds of plantations. Since soil temperatures are employed in the model, it should therefore provide adequate predictions of adult emergence in the Christmas tree areas. Although there is currently no insecticide registered for use against this species (Syme 1981), the present model will be useful for timing control operations.
Chapter 3
Oviposition-fecundity models for pine false webworm.

3.1 Introduction

Temperature during the oviposition period has a profound effect on oviposition rates of most species examined. The pattern of oviposition influences the age distribution of subsequent stages and therefore must be included in phenological models. Oviposition pattern is determined by the emergence pattern, survival and behavior of female sawflies and modified by weather (Rumphorst and Goosen 1960).

Flight period of PFW is reported to extend from 21 days (Rumphorst and Goosen 1960) to a month (Jahn 1967). Adults are diurnal and peak flight activity occurs between 1100 and 1500 hours on sunny, calm days with only minimal activity on cool, rainy or windy days (Rumphorst and Goosen 1960).

Little is known about the fecundity of PFW. Three females prevented from ovipositing and dissected contained 27, 37 and 41 eggs (Schwerdtfeger 1941). Several immature eggs were also found. Reported fecundities for PFW vary from 16 (Middlekauff 1958) to 35 (Rumphorst and Goosen 1960) eggs per female.

Oviposition and fecundity result from a complex interaction of several processes all affected by temperature. The objective of this investigation was to examine these processes in the field and in the laboratory, to determine the effects of
temperature on the processes and to develop a model of reproduction.

3.2 Materials and Methods

Oviposition Pattern in Field. Terminals of twenty branches were examined daily at about 1000 hours for newly deposited eggs during 1986. Ten branches at a height of 3.5 m and another ten branches at 1.5 m were selected around a small opening in the plantation. Needles with new eggs were marked at each observation and the number recorded.

Pairs of newly emerged adults from emergence traps were placed on red pine foliage in lantern-chimney rearing containers. The lantern chimneys rested on the lids of 225-mL ointment jars filled with water. Cut ends of branches were inserted into the jars through holes in the lids. Tops of the chimneys were covered with muslin. An absorbant-cotton wick provided drinking water and honey was smeared on the muslin top. The rearing containers were housed in a screened insectary situated in a large clearing in the LA plantation.

A total of 90 pairs of adults was set up in the rearing containers on 4, 5, 6 and 8 May 1986. Containers were examined daily in the morning, and eggs and dead females were removed and recorded. Temperature in the insectary was recorded from thermocouples hanging from the ceiling. Rearing containers were shaded by white sheets.
Potential Fecundity. Females collected from the emergence traps in the three plots in 1983 (Section 2.2) were used to determine the relationship between potential fecundity and body weight. Females were briefly dipped in acetone and weighed. Females were then dissected and the number of mature oocytes in the ovarioles was counted. Dissected females and oocytes were placed for a minimum of 24 h in an oven at 70°C and weighed again. The number of eggs dissected from females was regressed against wet and dry weights. Square-root transformations of number of eggs, and wet and dry weights stabilized the variance and yielded linear relationships. Regression lines were compared by analysis of covariance using the SAS GLM procedure (SAS Institute 1985). Potential fecundity of females collected from emergence traps in 1986 was estimated from their weights using the regressions and compared with observed potential fecundity from dissections.

Oogenesis. Samples of 50 newly-emerged females was weighed and randomly assigned to one of three treatments. One group (I) was confined with males on red pine branches in lantern-chimney rearing containers and another group (II) was confined with males without foliage. Containers were placed in a controlled-environment chamber at 23.4°C with a 15:9 (L:D) photoperiod. The number of residual oocytes was determined by dissection and the number of eggs deposited by group-I individuals was counted daily. After three days, group-II
individuals were killed and preserved in 70% ethanol. The last group (III) was killed and preserved in ethanol.

Oviposition at Constant Temperatures. Adults, collected from the soil at the LA plantation, were shipped on ice to the laboratory where they were used for oviposition studies. Females were weighed and confined with males on red pine branch tips in chimney rearing containers.

Containers were placed in four constant-temperature chambers (14.9, 18.1, 23.4 and 26.6°C) with a 15:9 (L:D) photoperiod. Branches were examined daily at the end of the scotophase (0800 hours) and all eggs were removed and counted. Death dates of females were recorded and cadavers were preserved in 70% ethanol for later dissection to determine residual oocyte content. To determine the pattern of egg laying for a group of females incubated at 14.9 (n=24) and 23.4°C (n=17), eggs were removed at the end of the scotophase and at 5-h intervals during the photophase, culminating at the start of the next scotophase, for the first seven days of their oviposition periods.

Mean time to 50% fecundity of each individual was calculated at each temperature. Times were transformed to rates (1/time) and means calculated for each temperature. Mean rates, weighted by sample size, were regressed as a function of temperature. To describe oviposition pattern around the means, a two-parameter Weibull function (Equation 3.1) was fitted to the cumulative
distribution of eggs per females as a function of normalized time (oviposition times/mean oviposition times).

\[ F(x) = 1 - \exp\left(-\frac{x}{\eta}\right)^\beta \]  

(3.1)

where \( F(x) \) = the proportion of eggs deposited by normalized time \( x \), and \( \eta \) and \( \beta \) are parameters estimated by nonlinear regression (SAS Institute 1985).

Mean ageing rates (averages of reciprocals of individual longevities), weighted by initial number of females, were regressed against temperature. Cumulative distribution of female longevities was described as a function of normalized time (longevity/mean longevity).

Reproductive potential was calculated as the sum of age specific fecundities (eggs/female/day) for each temperature.

Simulation of Oviposition-Longevity. A model to describe the egg-laying pattern was constructed from oviposition and ageing rate functions. The model employed two physiological time scales, one for the rate females aged and the other for ovipositional rate. Temperature-dependent ageing rate was calculated for each hour of the day and the physiological age of the cohort mean was accumulated (physiological age = \( \Sigma [\text{ageing rate per day} \times 1/24] \)). The cumulative proportion of the cohort that had died by normalized time \( x \) was solved from the cumulative distribution function (Equation 3.1). When the physiological age of the cohort mean equaled one, the proportion
of the cohort that had died was 0.50. Proportion of the cohort alive at each time interval is \( 1 - F(x) \). The number of insects alive at time \( t \) is the product of the proportion alive and the initial number of insects in the cohort. Chronological time of events was determined by keeping track of the hour of the day that was input into the model.

Similarly, temperature-dependent hourly oviposition rate was computed and the physiological age of the cohort mean was accumulated. The cumulative proportion of eggs deposited by the cohort was estimated from the distribution of cumulative eggs/female function. The cumulative number of eggs deposited by an average individual was the product of the cumulative proportion and reproductive potential.

For each cohort, the number of eggs deposited daily by an average female was calculated at 1000 hours. Total egg production during the daily interval was determined from the number of eggs per individual times the number of surviving females. The model was used to predict number of eggs deposited, pattern of egg deposition and relative abundance of females in the screened insectary. Four cohorts, one for each starting date, were simulated. Temperatures recorded by thermocouples in the insectary were used as model input.

The cumulative proportional oviposition of natural populations was also simulated. This simulation was initialized
with the observed emergence times of the females in the LA plantation in 1986 (Fig. 2.1B). The number of cohorts ovipositing equaled the number of days females emerged, while the proportion emerging each day represented the proportion of the population in each cohort. Air temperatures recorded from the meteorological screen were used as input for this component model. Simulation results were compared with egg depositions on the high and low branches in the LA plantation in 1986.

3.3 Results

Oviposition Pattern in the Field. Initial cumulative deposition of eggs occurred sooner in the lower branches than in the high branches (Fig. 3.1). Egg accumulation was about the same in both strata towards the later half of the oviposition period.

No eggs were deposited on 3 May (day 124). The maximum temperature on that day was 7.4°C, while the maximum temperature the previous and following days were 10.2 and 20.9°C, respectively.

Potential Fecundity. The relationships between the number of mature oocytes dissected from newly emerged females and their wet or dry weights were highly significant (P<0.0001) for females from the three plots trapped in 1983. Since the slopes (wet weight, F=1.20, df=2,1206, P=0.30; dry weight, F=0.71, df=2,1195, P=0.49) and the distances (wet weight, F=1.82,
Fig. 3.1. Cumulative oviposition frequency by PFW on high and low red pine branches at LA plantation in 1986.
between the regression lines were homogenous for both relationships, the data were pooled to yield the following:

\[
\text{oocytes} = -1.11 + 0.77 \text{ wet weight} \quad (r^2=0.88)
\]
\[
\text{oocytes} = -0.13 + 1.09 \text{ dry weight} \quad (r^2=0.91)
\]

Mean number of oocytes, and mean wet and dry weights were significantly different (Table 3.1) between the three defoliation zones trapped in 1986, indicating that increased defoliation resulted in a reduction in female weight and oocytes/female.

To test the models ability to describe fecundity from body weight, potential fecundities of the females emerging from the three defoliation zones of the LA plantation in 1986 were estimated from their wet and dry weights using the appropriate pooled regression. Estimated potential fecundities approximated observed potential fecundities (Table 3.2). Not only were the models able to predict potential fecundity of pooled samples for the three LA zones, the models were rigorous enough to predict the potential fecundities of females from each defoliation zone (Table 3.2). Mean deviations of the predicted from observed were smallest for the heavily-defoliated zone. The dry-weight model consistently yielded smaller deviations from observed than the wet-weight model, although the difference was only significant for the lightly-defoliated zone (t-test, P<0.05).
Table 3.1. Mean wet and dry body weights, and number of mature oocytes of dissected females of PFW trapped in 1983 and 1986.

<table>
<thead>
<tr>
<th>Plot</th>
<th>n</th>
<th>Mean (SE) wet weight (mg)</th>
<th>Mean (SE) dry weight (mg)</th>
<th>Mean (SE) no. of oocytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AM1</td>
<td>822</td>
<td>67.1c (0.62)</td>
<td>23.5b (0.26)</td>
<td>26.9b (0.31)</td>
</tr>
<tr>
<td>AM2</td>
<td>221</td>
<td>84.6a (0.94)</td>
<td>30.8a (0.39)</td>
<td>35.3a (0.48)</td>
</tr>
<tr>
<td>CR</td>
<td>170</td>
<td>70.4b (1.12)</td>
<td>24.5b (0.47)</td>
<td>28.0b (0.60)</td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>135</td>
<td>51.0c (1.31)</td>
<td>16.2c (0.54)</td>
<td>18.7c (0.77)</td>
</tr>
<tr>
<td>M</td>
<td>170</td>
<td>61.6b (1.07)</td>
<td>21.2b (0.49)</td>
<td>25.9b (0.68)</td>
</tr>
<tr>
<td>L</td>
<td>120</td>
<td>76.5a (0.86)</td>
<td>29.4a (0.39)</td>
<td>35.0a (0.55)</td>
</tr>
</tbody>
</table>

Means within columns and within years followed by same letter were not significantly different (Duncan's [1955] multiple range test, P > 0.05).

Table 3.2. Predicted potential fecundities from wet- and dry-weight regressions for females of PFW trapped in LA plantation in 1986.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Predicted mean (SE) no. of oocytes</th>
<th>Mean (SE) deviation from observed no. of oocytes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Wet weight</td>
</tr>
<tr>
<td>H</td>
<td>19.1 (0.61)</td>
<td>0.5 (0.38)</td>
</tr>
<tr>
<td>M</td>
<td>24.0 (0.50)</td>
<td>-1.8 (0.35)</td>
</tr>
<tr>
<td>L</td>
<td>31.2 (0.41)</td>
<td>-3.7 (0.37)</td>
</tr>
<tr>
<td>Pooled</td>
<td>24.5 (0.38)</td>
<td>-1.6 (0.22)</td>
</tr>
<tr>
<td>H</td>
<td>18.3 (0.63)</td>
<td>-0.4 (0.36)</td>
</tr>
<tr>
<td>M</td>
<td>24.2 (0.57)</td>
<td>-1.7 (0.29)</td>
</tr>
<tr>
<td>L</td>
<td>33.7 (0.46)</td>
<td>-1.5 (0.35)</td>
</tr>
<tr>
<td>Pooled</td>
<td>25.0 (0.44)</td>
<td>-1.2 (0.19)</td>
</tr>
</tbody>
</table>
Oogenesis. Mean numbers of oocytes dissected from females of the three treatment groups and their mean live weights are shown in Table 3.3. For group I females, the number of oocytes is the total of the deposited eggs plus the residual number of mature eggs present in their abdomens at death. Of the 50 group II individuals, only 28 survived to the third day following introduction into the rearing containers. For each treatment, the square roots of the number of eggs were regressed against the square roots of the live weights (Table 3.3) and the regression lines (Fig. 3.2) were compared using analysis of covariance. Increases in square root of number of eggs resulted in comparable increases in square roots of wet and dry weights ($F=1.64$, $df=2,118$, $P=0.20$), but the distances between the relationships were different ($F=44.66$, $df=2,120$, $P=0.0001$). Group I and II females contained significantly more mature oocytes than did group III females (Table 3.3). Initial mean live weight of group I and III females were not significantly different, but initial weights of surviving group II females were significantly larger.

Oviposition at Constant Temperatures. Females failing to oviposit were eliminated from further analysis. Oviposition at all temperatures began the day females were introduced into the rearing containers. Hence, the preoviposition period of PFW was less than one day at these temperatures and is thus smaller than the observation interval employed. At each temperature, egg laying was characterized by an initial burst of depositions
Fig. 3.2. Regressions for square root of fecundities of groups I-III females of PFW as a function of square root of their live weight.
followed by a sharp decline in the egg-laying rate. Fecundities at the four experimental temperatures were not significantly different, but longevity was inversely proportional to temperature (Table 3.4). Maximum fecundity was 73 eggs by one female at 18.1°C.

Ovipositions at 14.9 and 23.4°C occurred predominately during photophase although occasionally eggs were observed at the end of the scotophase (Fig. 3.3). Ovipositions were concentrated at the beginning of the photophase at 23.4°C.

Oviposition rate increased with temperature (Fig. 3.4A) as follows: \( y = -0.230 + 0.034x \) where \( y \) = rate to 50% fecundity (days\(^{-1}\)) and \( x \) = temperature (°C) \((r^2=0.918; F=22.28; df=1,3; P=0.042)\). Estimated parameters for the cumulative distribution (Fig. 3.4B) of oviposition times (Equation 3.1) were \( \eta=1.7488 \) and \( \beta=0.9228 \) \((R^2=0.983)\).

Temperature-dependent ageing rate function (Fig. 3.5A) for female PFW was \( y = -0.101 + 0.014x \) where \( y \) = mean ageing rate (days\(^{-1}\)) and \( x \) = temperature (°C) \((r^2=0.962; F=50.57; df=1,3; P=0.019)\). Cumulative mortality (Fig. 3.5B) as a function of normalized time was \( y = 0.092 + 0.435x \) where \( y \) = cumulative mortality and \( x \) = normalized time \((r^2=0.964; F=1712.06; df=1,65; P<0.0001)\).

Observed reproductive potentials at 14.9, 18.1, 23.4 and
Table 3.3. Regression statistics for relationships between number of mature oocytes and live weight for PFW.

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Mean (SE) no. oocytes</th>
<th>Mean (SE) live weight (mg)</th>
<th>Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean (SE)</td>
<td></td>
<td>Slope</td>
</tr>
<tr>
<td>Ia</td>
<td>46</td>
<td>36.3a (2.26)</td>
<td>60.1a (2.55)</td>
<td>0.95</td>
</tr>
<tr>
<td>II</td>
<td>28</td>
<td>39.4a (1.68)</td>
<td>72.9b (2.96)</td>
<td>0.74</td>
</tr>
<tr>
<td>III</td>
<td>50</td>
<td>26.8b (1.27)</td>
<td>63.3a (2.37)</td>
<td>0.82</td>
</tr>
</tbody>
</table>

*a Mean number of oocytes for group I individuals is sum of deposited and retained eggs. Means followed by same letter are not significantly different (Duncan's [1955] multiple range test; P > 0.05).

Table 3.4. Mean longevities and fecundities of PFW females reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>n</th>
<th>Mean (SE) longevity (days)</th>
<th>Mean (SE) fecundity (eggs/female)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.9</td>
<td>24</td>
<td>27.5a (3.17)</td>
<td>32.9a (3.81)</td>
</tr>
<tr>
<td>18.1</td>
<td>20</td>
<td>14.3b (2.11)</td>
<td>33.7a (4.49)</td>
</tr>
<tr>
<td>23.4</td>
<td>75</td>
<td>9.2bc (0.68)</td>
<td>34.6a (1.94)</td>
</tr>
<tr>
<td>26.6</td>
<td>11</td>
<td>7.1c (1.33)</td>
<td>42.0a (3.46)</td>
</tr>
</tbody>
</table>

Means followed by same letter are not significantly different (Duncan's [1955] multiple range test; P > 0.05).
Fig. 3.3. Diel pattern of egg laying by PFW females at 23.4 and 14.9°C. Light and dark bands under histograms are photophases and scotophases, respectively. Vertical lines are standard errors of means.
23.4°C
n=17

14.9°C
n=24

MEAN NO. OF EGGS/SURVIVING FEMALE

TIME (DAYS)
Fig. 3.4. (A) Mean oviposition rate (±SE) to 50% fecundity for PFW as a function of temperature and (B) cumulative eggs per female at each constant temperature as a function of normalized time. Lines are regressions.
A. RATE TO 50% FECUNDITY (1/DAYS)

TEMPERATURE (°C)

B. CUMULATIVE EGGS/FEMALE

NORMALIZED TIME (TIME/MEAN TIME)

- 14.9
- 18.1
- 23.4
- 26.6
Fig. 3.5. (A) Mean ageing rate (±SE) of PFW females as a function of temperature and (B) cumulative proportion of dead females as a function of normalized time at each constant temperature. Lines are regressions.
26.6 °C were 43.2, 43.3, 44.3 and 51.1 eggs/female, respectively. Since fecundities at these temperatures were not significantly different, it was assumed that these values were not different. For modeling purposes a pooled mean of 44.6 eggs/female, based on initial number of females, was used.

**Simulation of Oviposition-Longevity.** The distribution pattern of egg deposition predicted by the model was very similar to the observed pattern (Fig. 3.6A). Similarly, the pattern of female availability for oviposition (Fig. 3.6B) was similar for observed and predicted, except the rate of removal of females from the predicted population was more gradual than the rate of removal of the observed population. Both observed and simulated populations were all dead at about the same time. Sum of fecundities for all females predicted by the model was 2465 eggs, while the observed number of deposited eggs was 2015. This translates to a predicted fecundity of 27 eggs/female and an observed fecundity of 22 eggs/female. The difference between observed and expected fecundity reflects the more gradual disappearance of the simulated population with a greater proportion of females available for oviposition towards the end of the oviposition period.

For simulations of egg deposition in the field (Fig. 3.6C), low temperatures at the beginning of the oviposition period resulted in little or no predicted oviposition while observed ovipositions were taking place in the field. The rate of
Fig. 3.6. (A) Predicted number of eggs (dotted line) compared with observed number of eggs (solid line) deposited by PFW in outdoor insectary, (B) simulated (dotted line) compared with observed (solid line) number of ovipositing females and (C) simulated oviposition pattern (solid line) for PFW compared with observed oviposition pattern (dotted line) of natural populations and pattern of female emergence (dashed line) at Lakehurst in 1986.
predicted ovipositions increased dramatically when the temperature sharply increased, but the majority of natural egg depositions had occurred by this time. The oviposition pattern in the field was very similar to the pattern of emerging females (Fig. 3.6C).

3.4 Discussion

Egg deposition in the field stopped when maximum air temperatures were 7.4°C. This was close to the threshold predicted by the linear regression for oviposition rate. Maximum air temperatures of 10.2°C resulted in ovipositions. The ability of females to oviposit at such low temperatures is probably enhanced by their dark color. Females began ovipositing as they moved up the trees resulting in lower branches accumulating eggs sooner than upper branches. The low ambient temperatures during the beginning of the oviposition period accentuated this trend.

Female body weight is an unreliable estimate of potential fecundity in some sawflies due to varying degrees of fat utilization by maturing females (Heron 1966). However, both wet and dry weights were accurate predictors of potential fecundity for PFW. Dry weights produced closer agreement between observed and expected potential fecundities, but the increased resolution probably would not justify the extra effort required in determining dry weights. As demonstrated in the previous chapter, the degree of defoliation of the host trees had a
profound effect on the phenology of emerging adults of PFW via alteration of soil microclimate. In addition, associated with this depletion of the foliage resource was a reduction in the mean weight of emerging females which resulted in a reduced potential fecundity. Consequently, the earliest females to emerge were those with the lowest potential fecundities. Since the fecundity models retained their predictive abilities for females from all defoliation zones, it was clear that stunted females from heavily defoliated zones were unable to shunt other reserves to egg production following starvation stress of the larvae. A few females at emergence contained no mature eggs.

Sawflies vary in their reproductive state at adult emergence. Although most females are ready to oviposit, the proportion of mature to immature oocytes present in their abdomens varies from species to species. For some species the number of oocytes does not change after emergence (Wilkinson et al. 1966, Lyons 1970), and thus dissections of newly emerged females provided a reliable estimate of fecundity. Eggs of other species (Prebble 1941, Lyons 1964, Heron 1966, Ives et al. 1968) undergo some postemergence maturation. A few immature oocytes were always observed during dissections of newly emerged females of PFW. Evidence presented here suggests that females underwent post-emergence maturation of these immature eggs. Females that were allowed to oviposit, produced more mature eggs than did females sacrificed at emergence. Poor survival of females inhibited determination of whether or not females kept
alive and prevented from ovipositing mature eggs. The larger size of surviving females of this group biased the results so that an estimate of egg maturation for this group was unreliable.

At all experimental temperatures, PFW began ovipositing within the first 24 h after emergence. Thus, PFW possesses a negligible preoviposition period. Females are diurnal and even at constant temperatures in the laboratory restrict ovipositions to daylight hours. Fecundity of PFW was not dependent on temperature over the range of temperatures examined. This does not hold true for all insects (Hogg and Gutierrez 1980, Mason and Mack 1984). Conversely, ageing and oviposition rates of PFW were significantly temperature dependent as was the resultant pattern of oviposition.

Oviposition and ageing are temperature-dependent phenomenon and can be treated using rate-summation techniques (Régnière 1984). Models incorporating these functions for PFW reared in an outdoor insectary provided reasonable estimates for absolute fecundity, oviposition pattern and female abundance. For these models to be incorporated into population dynamics models a functional relationship between degree of defoliation and fecundity needs to be developed. Only intrinsic survival (Curry and Feldman 1987), in the absence of other mortality agents, is utilized in the present model. Models like this one that keep mortality and oviposition as separate processes can be used to
test other population mortality factors (Curry and Feldman 1987). Attempts to model the relative oviposition pattern of natural populations resulted in poor estimates of cumulative emergence. During the beginning of the oviposition period in the field, temperatures were below 10.2°C. These temperatures were below the lowest experimental temperature. The model predicted little or no oviposition while observed females were laying eggs. Oviposition rates as a function of these low temperatures may be nonlinear and higher than extrapolated rates. Conversely, females which have dark bodies may increase their temperature behaviorally. For practical purposes, accurate estimates of cumulative oviposition to predict phenology can be obtained from cumulative adult emergence.

PFW deposits a low number of large high quality eggs. The majority of eggs is mature and ready to be oviposited when the female ecloses and emerges from the soil. Even at low temperatures, most eggs are deposited shortly after emergence. The black bodies of the females probably allow them to be active at low temperatures. This rapid deposition of eggs means that if females succumb to a mortality agent, the eggs are already deposited. As a result, survival of females has little effect of generation survival. Defoliation affects fecundity by reducing egg numbers and thus acts as a feedback system in regulating population numbers.
Chapter 4

Arboreal development of pine false webworm.

4.1 Introduction

Eggs of PFW are deposited on pine needles of the previous-year's foliage. Eggs hatch, under field conditions, after five to eight days (Prozorov 1925) usually during late May (Middlekauff 1958) or after as long as three weeks of incubation (Griswold 1939). Upon hatching the larvae form conspicuous webs in which they feed and develop. The ultimate-instar larvae drop to the ground from mid- to late June (Middlekauff 1958). These observations are of little value for predicting seasonal timing of PFW since development is a temperature-dependent process. Local weather during the development of these arboreal stages may have an effect on these processes. To accurately predict development, heat accumulations must be known in the microhabitats where PFW develop.

Meteorologists use conventional methods for measuring weather to permit comparisons between sites. Temperatures are recorded from instruments placed in standardized ventilated screens (e.g. Stevenson screen). Any insect habitat is made up of a mosaic of microclimates fluctuating dynamically over time and space (Baker 1980), consequently, extreme differences may exist between these meteorological standards and temperatures in insect habitats (Wellington 1950, Smith 1954, Morris and Fulton 1970).
Vertical strata of plant canopies often have different microclimates (Strong et al. 1984), which may result in differences in development of the arboreal stages of PFW. Also, the webs of PFW may act like heat sinks (Wellington 1950, Shepherd 1958), thereby affecting insect phenology.

The purpose of this study was to determine the development of PFW relative to the spatial distribution of arboreal stages; the relationships between the temperatures in the microhabitats of PFW and meteorological standards; the role of temperature on behavior of PFW larvae; and the effect of temperature on egg and larval growth and development. The effects of temperatures in the arboreal habitats on PFW development was determined through the use of phenological simulations.

4.2 Materials and Methods

Spatial Distribution and Development of Arboreal Stages. Larval development in the field was assessed using a regular sampling program. All 2781 trees within plot AM1 were numbered with aluminum tags nailed to their boles and semiweekly, 50 trees were selected at random from this plot. Red pines have a uniform growth form and flush a new vertical whorl of branches from the bole each year, allowing easy division of the canopy into three vertical strata. The leader and first whorl of branches comprised the uppermost stratum. The next eight whorls
were divided equally into high and low strata. The upper stratum and one branch randomly chosen by whorl number and cardinal direction from each of the other strata were sampled. One branch was selected at random according to cardinal direction from the fourth whorl of each tree in 1984. Branches were examined and all stages of PFW were removed and preserved in 70% ethanol.

Due to the collapse of the PFW population at Anten Mills in 1985, all branch sampling during 1986 was conducted in 3 plots at the LA plantation. The largest plot (900 trees) was established in a heavily-defoliated zone, while two smaller plots (100 trees) were established in moderately- and lightly-defoliated zones. Branches, excluding leaders, were sampled semiweekly and the insects were picked off and preserved in alcohol. Larval instars were determined using head capsule measurements. Comparisons were made between development of the arboreal stages in different spatial dimensions. Mean development stage in each strata on each day was computed (egg = 0, larval instars = 1 to 6).

Larval Drop. The period of larval drop was determined using inverted adult emergence traps (Section 2.2) suspended from three wooden stakes. Glass collecting bottles were fixed to the funnel stems at the bottom of the cones via tight-fitting holes punched in the plastic lids of the bottles.
Fifty traps were placed in plots AM1 and AM2 in 1983-85 as described for the emergence traps. During 1986, 25 traps were placed in each of the heavily-defoliated and moderately-defoliated zones at the LA plantation. Traps were arranged at 5-m intervals in 2 rows 5 m apart. Traps were checked each morning and all PFW larvae were removed and preserved in 70% ethanol. Sex of the ultimate-instar larvae was determined from head capsule measurements.

**Micrometeorology.** Maximum and minimum daily air temperatures were recorded from thermometers housed in a conventional AES Stevenson screen in 1983-85. Maximum and minimum daily temperatures, as well as hourly temperatures, were recorded from a temperature probe in a CS meteorological screen in 1984-86. Linear regression was used to determine the relationship between daily maximums and minimums recorded in the AES screen and daily maximums and minimums recorded in the CS screen in 1984-85. Temperatures recorded in the CS screen during 1986 were corrected using this linear regression.

Temperatures in the plantation canopy were recorded using three thermocouples (36-AWG) positioned vertically, in branch whorl numbers 3, 5.5, 8 from the top of the trees, at two locations in plot AM1 during 1985. Thermocouples were suspended under tinfoil pie plates, the upper surfaces of which were painted white to increase the emissivity and the undersides were painted black to inhibit reflection. Extension wires near the
junctions were painted white or covered with aluminum foil to shield them from solar radiation. The vertical distribution of thermocouples was dependent on tree height. Canopy temperature differentials ($\Delta T_o$) were determined by 1) converting CS screen temperatures to AES standard temperatures using the regression determined earlier and 2) subtracting these converted temperatures from the canopy temperatures ($T_o$) for each height in the canopy. Average canopy temperature differentials for the period of egg and larval development were then determined for each hour of the day. Canopy temperatures for 1985 were estimated from air temperature pooled for all heights using linear regression.

Differential pairs of thermocouples (36-AWG) were used to compare temperatures inside and outside the webs of PFW. Outside thermocouples were positioned adjacent to the webs, shielded by pie plates positioned to minimize the interception or reflection of solar radiation to the web. Web temperature differentials ($\Delta T_w$) were computed from:

$$\Delta T_w = T_w - T_C$$ (4.1)

where $T_w$ = web temperature ($^\circ$C).

The effect of different weather conditions on web temperatures, PFW larval body temperatures and air temperatures was determined by periodically recording temperatures using thermocouple probes attached to a portable potentiometer. The body-temperature probe was made by inserting a 40-AWG
thermocouple junction into a hypodermic needle. Thermocouple leads ran through a porcelain tube. The probe was inserted into the anus of the larvae or into the thorax. Web surface temperatures were recorded with an Instatherm infrared thermometer (Model 14-220D-15, Barnes Engineering Co., Stamford, Conn.).

**Egg Development at Constant Temperatures.** The effect of constant temperatures on egg development was determined using eggs obtained from mating pairs of PFW confined on red pine branches in lantern globe rearing containers (Section 3.2) at 23°C. Branches with eggs laid within 24 h were removed and placed in constant-temperature chambers (3.9, 5.8, 7.0, 10.7, 14.9, 18.4, 23.8, 26.7 and 30.3°C) with 15:9 L:D photoperiods. Branches at the lowest three temperatures were moved to 14.9°C after 50 days of incubation to allow the eggs to complete their development and to prevent excessive mortality at these temperatures. Eggs at the five highest temperatures were examined every 12 h until larval eclosion was completed. Eggs at lower temperatures were examined daily.

**Larval Development at Constant Temperatures.** Larval development rates were determined at several constant temperatures. Branches with eggs were collected from the LA plantation and stored at 4°C until use. Twigs were cut to fit rearing containers. Cut ends of the twigs were inserted through holes in the tops of 450-mL ointment jars. The tops of the jars
were made by riveting two lids together end to end. The upper lid held the lantern globe enclosing the foliage.

Branches were placed at 23°C and examined daily for larval eclosion. Newly hatched larvae were held in the rearing containers distributed among seven constant-temperature chambers (7.3, 10.4, 14.9, 18.1, 24.0, 26.7 and 29.0°C) and a fluctuating-temperature chamber set to alternate between 27 and 8°C (i.e., square wave, average 20.3°C) with the day-night light cycle. Larvae were examined daily until they dropped when they were preserved in 70% ethanol for sex determination by head capsule measurement. Dry weight of ultimate-instar larvae was determined.

Egg Development in the Field. Since eggs in the field are of variable and unknown age, eggs of known age were used to validate models of egg development under field conditions. Eggs were obtained from mated females placed in plastic bags enclosing red pine branches. Females were removed after 24 h; eggs were marked and examined daily until hatch. Females were bagged at two heights in the canopy in 1984 and thermocouples (24-AWG) were fastened to the underside of the branches to record hourly average temperatures near the eggs. Similarly in 1985, females were allowed to oviposit over a three-day period and eggs that were deposited each day were observed throughout their development. Temperatures in 1985 were measured using pie-plate-shielded thermocouples placed at the same height in
Behavior of Larvae at High Temperature. Individual branches containing late-instar larvae were placed in front of a General Electric sunlamp (275 W) in the laboratory. A thermocouple attached to a potentiometer was placed adjacent to a larva in the web. The activity of the larva was noted when the light was turned on and the temperature in the web rose.

4.3 Results

Spatial Distribution and Development of Arboreal Stages. The modes of the polymodal frequency distributions of larval head capsule measurements (Fig. 4.1) representing larval instars occurred at about the same head capsule widths in all years. The size limits (mm) of the six larval instars were: I < 1.005; 1.006 < II < 1.255; 1.256 < III < 1.555; 1.556 < IV < 1.955; 1.956 < V < 2.355; and VI > 2.356.

All insects were in the egg stage on 3 and 7 June (days 154 and 158) (Fig. 4.2A). Hatch began in the leader and high strata by 10 June (day 161) and in the low stratum by 14 June (day 165). As the season progressed, the insects high in the tree were more advanced than lower insects. Although the insects in the high stratum were slightly advanced compared to those in the low stratum, the differences were not as pronounced as the differences between the leader and upper strata. There was no significant difference in mean development of insects among the canopy.
Fig. 4.1. Frequency distributions of larval head capsule widths of PFW collected from AM in 1983 and 1984, and from LA in 1986. Modes corresponding to the larval instars are indicated by Roman numerals.
Fig. 4.2. Mean stage (±SE) of development of PFW from (A) three vertical strata at the AM1 plantation in 1983 and (B) three defoliation zones in the LA plantation in 1986.
different cardinal points of the tree in 1984. Development in the heavily- and moderately-defoliated zones was not significantly different in 1986 (Fig. 4.2B), however, development was slightly slower in the lightly-defoliated zone.

Larval Drop. Frequency distributions of head capsule measurements of larvae dropping from trees had two well-defined modes. The pattern of larval drop of the sexes was determined (Fig. 4.3), assuming that the larger individuals were females and the smaller larvae were males. The median time of male drop preceded the drop of females by 1 to 2 days in both 1983 and 1986. There were only slight differences in the timing of larval drop between plots in both years.

Micrometeorology. The relationship between the temperatures recorded in the AES Stevenson screen and the CS screen temperatures was $y = 0.554 + 0.928x$ ($F=9467.8; \text{df}=1.206; P<0.0001; r^2=0.979$) where $y =$ AES screen temperatures ($^\circ\text{C}$) and $x =$ CS screen temperatures ($^\circ\text{C}$). The slope was significantly different from 1 ($t=5.090; \text{df}=206; P=0.0001$) and the intercept was not significantly different from zero ($t=-1.159; \text{df}=206; P=0.2478$), indicating a slight temperature elevation in the CS screen at high temperatures. All temperatures recorded in the CS screen were corrected using the regression equation.

The relationship between the canopy temperature ($T_c$), pooled for all heights, and the standardized air temperature in the
Fig. 4.3. Cumulative drop of ultimate instars of PFW in sample plots in (A) 1983 at the Anten Mills plantation (plots AM1 and AM2) and in (B) 1986 in the H and M zones of the Lakehurst plantation.
The graphs show the cumulative drop of different groups over the days of the year for two years: 1983 and 1986. The groups include Male AM1, Female AM1, Male AM2, Female AM2, Male H, Female H, Male M, and Female M. The x-axis represents the day of the year, and the y-axis represents the cumulative drop.
meteorological screen \( (T_a) \) was:

\[
\hat{T}_c = -0.244 + 0.967T_a
\]  

\((F=522482.1; \, df=1,8218; \, P<0.0001; \, r^2=0.985)\).

Maximum differential recorded between the web and outside air temperatures in 1984 was 13.0°C, but the mean difference \((\pm SE)\) was only 0.7±0.02°C. The maximum temperature recorded in the canopy was 30.2°C, while web temperatures peaked at 42.5°C. Mean web temperature difference \((\Delta T_w)\) was described by:

\[
\Delta T_w(t) = \begin{cases} 
  a(b + \sin \left[2\pi(t - c)/24\right]) & \text{when } 0700 \leq t \leq 2200 \text{ hours} \\
  -0.215 & \text{when } 2200 < t < 0700 \text{ hours}
\end{cases}
\]

\((4.3)\)

where \( t = \) time of day, \( a = \) amplitude \((1.833)\), \( b = \) period \((0.269)\), and \( c = \) phase \((8.419)\) of the wave \((R^2=0.971)\).

Estimated web temperature was also described as a linear function of canopy temperature using:

\[
\hat{T}_w = -1.789 + 1.147T_c
\]

\((F=192789.1; \, df=1,7549; \, P<0.0001; \, r^2=0.962)\). The slope and intercept of the regression line were significantly different from 1 \((t=56.19; \, df=7549; \, P=0.0001)\) and 0 \((t=-37.45; \, df=7549; \, P=0.0001)\), respectively.

Table 4.1 lists some representative temperatures associated with webs of PFW. Temperature variation at each reading resulted from the small time constants of the fine thermocouple probes. Web temperature on a clear day \([18\, \text{June (day 169)}]\) was as much as 7°C in excess of ambient air temperatures recorded
Table 4.1. Representative temperatures in webs of PFW and associated meteorological variables.

<table>
<thead>
<tr>
<th>Day of year</th>
<th>Time of day</th>
<th>Ta (°C)</th>
<th>S (W m⁻²)</th>
<th>W (ms⁻¹)</th>
<th>To (°C)</th>
<th>Tw (°C)</th>
<th>Ti (°C)</th>
<th>Ts (°C)</th>
<th>Weather</th>
<th>Web</th>
</tr>
</thead>
<tbody>
<tr>
<td>169</td>
<td>1117</td>
<td>17.8</td>
<td>0.823</td>
<td>3.12</td>
<td>15.8-16.6</td>
<td>24.0-24.2</td>
<td>18.7</td>
<td>clear</td>
<td>old</td>
<td></td>
</tr>
<tr>
<td>1118</td>
<td>1117</td>
<td>16.1</td>
<td>17.1</td>
<td>22.0</td>
<td>22.2</td>
<td>21.5-21.7</td>
<td>clear</td>
<td>new</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1126</td>
<td>1117</td>
<td>16.3</td>
<td>16.7</td>
<td>17.9</td>
<td>18.3</td>
<td>clear</td>
<td>shaded/new</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1130</td>
<td>1117</td>
<td>16.3</td>
<td>16.5</td>
<td>22.8</td>
<td>23.6</td>
<td>20.3-20.6</td>
<td>19.2</td>
<td>clear</td>
<td>new</td>
<td></td>
</tr>
<tr>
<td>1550</td>
<td>1117</td>
<td>19.5</td>
<td>0.739</td>
<td>3.58</td>
<td>19.8</td>
<td>20.5</td>
<td>22.0-24.1</td>
<td>23.4-23.5</td>
<td>clear</td>
<td>new</td>
</tr>
<tr>
<td>1600</td>
<td>1117</td>
<td>18.2</td>
<td>18.3</td>
<td>19.0</td>
<td>19.7</td>
<td>18.8-19.0</td>
<td>cloud</td>
<td>new</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1627</td>
<td>1117</td>
<td>18.8</td>
<td>0.606</td>
<td>3.63</td>
<td>19.0</td>
<td>19.7</td>
<td>20.1-20.6</td>
<td>21.9-22.1</td>
<td>clear</td>
<td>new</td>
</tr>
<tr>
<td>170</td>
<td>1407</td>
<td>23.5</td>
<td>0.586</td>
<td>1.72</td>
<td>22.6</td>
<td>22.8</td>
<td>24.4-25.5</td>
<td></td>
<td>clear</td>
<td>new</td>
</tr>
<tr>
<td>1429</td>
<td>1407</td>
<td>21.6</td>
<td>22.1</td>
<td>25.0</td>
<td>26.7</td>
<td>23.5-23.8</td>
<td>cloud</td>
<td>new</td>
<td></td>
<td></td>
</tr>
<tr>
<td>175</td>
<td>1356</td>
<td>12.6</td>
<td>0.340</td>
<td>3.72</td>
<td>11.3</td>
<td>11.9</td>
<td>11.2-12.4</td>
<td>12.8</td>
<td>overcast</td>
<td>new</td>
</tr>
<tr>
<td>1415</td>
<td>1356</td>
<td>12.1</td>
<td>0.328</td>
<td>3.35</td>
<td>11.7</td>
<td>12.5</td>
<td>12.4-13.0</td>
<td>12.8</td>
<td>overcast</td>
<td>new</td>
</tr>
<tr>
<td>178</td>
<td>1150</td>
<td>18.2</td>
<td>0.139</td>
<td>2.06</td>
<td>18.0</td>
<td>18.1</td>
<td>19.2-19.9</td>
<td>19.3-19.5</td>
<td>18.7</td>
<td>overcast/rain</td>
</tr>
</tbody>
</table>

- Ta: average air temperature for hour in which the web temperature was recorded
- S: average solar radiation for hour in which the web temperature was recorded
- W: average wind velocity during hour in which the web temperature was recorded
- To: air temperature from thermocouple placed adjacent to web
- Tw: web temperature from thermocouple inserted into web
- Ti: body temperature of PFW larva in web from thermocouple-syringe probe inserted into anus
- Ts: web surface temperature from infrared thermometer
outside the web. Temperatures recorded in the older, usually uninhabited webs were consistently higher than the temperatures recorded in newer webs. Older webs were darker than newer webs. Newer portions of webs usually contained green, freshly cut needles and living needles. Temperatures of the larvae approximated the temperatures in the webs under clear sunny skies and were in excess of ambient air temperatures.

Artificial shading of the web or the passing of a cloud in conjunction with the high wind velocities on 18 June (day 169) rapidly cooled the web to near ambient air temperatures. Web temperatures remained above web temperatures on 19 June (day 170), with the lower wind velocity, even when thick clouds were present. Web temperatures recorded from the shaded side of the web were closer to ambient temperatures than temperatures on the side exposed to direct solar radiation. Web temperatures and PFW body temperatures were only slightly elevated above ambient air temperatures under overcast skies or wet conditions. The angle of incidence of the solar radiation profoundly influenced web temperatures. Under a constant radiant load, webs with their long axis tilted from an acute to an obtuse angle to the sun increased in temperature by as much as 4°C.

High Temperature Behavior. As web temperatures reached 33-35°C, under the radiant heat load produced by the U.V. lamp, the larvae on the radiated side of the web moved out of their silken tubes. Larvae initially fastened silk strands to nearby
needles, but assumed resting positions among the strands with their heads oriented towards the light. Larvae in tubes leading away from the lamp moved towards the shaded side of the web, but as temperatures in the front of the web increased, these larvae also vacated the webs. Some larvae dropped from the web on silken threads if the temperature rose above 33°C, while others writhed erratically and died.

**Constant-temperature Development.** The mean times for egg hatch at each experimental temperature and the corresponding development rates are given in Table 4.2. All eggs incubated at 30.3°C failed to hatch. Since the survival of eggs at 26.7°C was noticeably reduced, the value of the temperature maximum \((T_m)\) was estimated to be 30.0°C. Development rates of eggs at 3.9, 5.8, and 7.0°C were estimated by the interpolation technique (Section 2.3). Since mean rates of egg development after transfer of eggs to 14.9°C were all significantly different than the mean development rate of eggs reared throughout the stage at 14.9°C (t-test; \(P < 0.0001\)), all eggs had undergone development at the lower temperatures prior to transfer. The value of the temperature minimum \((T_b)\) was set at 3.0°C since the difference at 3.9°C was small. Eggs remaining at low temperatures had developed at 3.9 and 5.8°C and although head capsules were evident, the eggs failed to hatch.

Larvae developed at all experimental temperatures (Table 4.3). However, newly eclosed larvae failed to establish on all
### Table 4.2. Mean development times (days) and rates for eggs of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>n</th>
<th>Mean time (d)</th>
<th>SE</th>
<th>Mean rate (1/d)</th>
<th>SE</th>
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<tbody>
<tr>
<td>3.9</td>
<td>18</td>
<td>16.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.4</td>
<td>0.053</td>
<td>0.000</td>
</tr>
<tr>
<td>282.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>5.8</td>
<td>0.004</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>5.8</td>
<td>49</td>
<td>12.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.2</td>
<td>0.067</td>
<td>0.000</td>
</tr>
<tr>
<td>126.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>1.6</td>
<td>0.008</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>7.0</td>
<td>13</td>
<td>6.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.4</td>
<td>0.173</td>
<td>0.004</td>
</tr>
<tr>
<td>73.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>5.0</td>
<td>0.015</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>10.7</td>
<td>265</td>
<td>35.9</td>
<td>0.2</td>
<td>0.028</td>
<td>0.000</td>
</tr>
<tr>
<td>14.9</td>
<td>254</td>
<td>20.4</td>
<td>0.1</td>
<td>0.049</td>
<td>0.000</td>
</tr>
<tr>
<td>18.4</td>
<td>239</td>
<td>14.1</td>
<td>0.1</td>
<td>0.071</td>
<td>0.000</td>
</tr>
<tr>
<td>23.8</td>
<td>258</td>
<td>8.5</td>
<td>0.0</td>
<td>0.118</td>
<td>0.001</td>
</tr>
<tr>
<td>26.7</td>
<td>109</td>
<td>7.9</td>
<td>0.0</td>
<td>0.127</td>
<td>0.001</td>
</tr>
<tr>
<td>30.3</td>
<td></td>
<td>No development</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Mean times to completion of development after transfer to 14.9°C.

<sup>b</sup> Estimated mean development times using interpolation technique.

### Table 4.3. Mean development times (days) and rates for larvae of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>Sex</th>
<th>n</th>
<th>Mean time (d)</th>
<th>SE</th>
<th>Mean rate (1/d)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.3</td>
<td>M</td>
<td>4</td>
<td>73.3</td>
<td>1.8</td>
<td>0.014</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2</td>
<td>75.5</td>
<td>6.5</td>
<td>0.013</td>
<td>0.001</td>
</tr>
<tr>
<td>10.4</td>
<td>M</td>
<td>9</td>
<td>60.3</td>
<td>1.6</td>
<td>0.017</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>9</td>
<td>66.0</td>
<td>1.7</td>
<td>0.015</td>
<td>0.000</td>
</tr>
<tr>
<td>14.9</td>
<td>M</td>
<td>17</td>
<td>36.7</td>
<td>1.5</td>
<td>0.028</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>36</td>
<td>40.2</td>
<td>0.9</td>
<td>0.025</td>
<td>0.001</td>
</tr>
<tr>
<td>18.1</td>
<td>M</td>
<td>42</td>
<td>22.2</td>
<td>0.3</td>
<td>0.045</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>52</td>
<td>25.6</td>
<td>0.4</td>
<td>0.039</td>
<td>0.001</td>
</tr>
<tr>
<td>20.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>M</td>
<td>7</td>
<td>17.6</td>
<td>0.9</td>
<td>0.058</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>8</td>
<td>20.0</td>
<td>0.5</td>
<td>0.050</td>
<td>0.001</td>
</tr>
<tr>
<td>24.0</td>
<td>M</td>
<td>20</td>
<td>15.8</td>
<td>1.0</td>
<td>0.066</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>26</td>
<td>17.0</td>
<td>0.3</td>
<td>0.059</td>
<td>0.001</td>
</tr>
<tr>
<td>26.7</td>
<td>M</td>
<td>24</td>
<td>14.0</td>
<td>0.2</td>
<td>0.072</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>47</td>
<td>16.4</td>
<td>0.3</td>
<td>0.062</td>
<td>0.001</td>
</tr>
<tr>
<td>29.0</td>
<td>M</td>
<td>31</td>
<td>13.5</td>
<td>0.4</td>
<td>0.076</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>39</td>
<td>15.5</td>
<td>0.3</td>
<td>0.065</td>
<td>0.001</td>
</tr>
</tbody>
</table>

<sup>a</sup> Average of alternating temperatures.
but two branches at 7.3°C. Consequently, the value for $T_b$ utilized for modeling purposes was set at 7°C. The value of $T_m$ was estimated from preliminary experiments to be about 33.0°C.

Development rates as functions of temperature for the egg and larval stages were developed as described in Section 2.2. Parameter estimates for Equation 2.11a for egg development were $P_1=0.008$, $P_2=4.393$ and $P_3=0.131$ ($R^2=0.996$). Functions (Equation 2.11b) for larval development were developed separately for each sex with parameter estimates of $P_1=0.094$, $P_2=2.051$, $P_3=4.446$ and $P_4=0.048$ ($R^2=0.995$) for males and $P_1=0.084$, $P_2=1.977$, $P_3=4.191$ and $P_4=0.053$ ($R^2=0.992$) for females. Estimated parameters for developmental variability functions for eggs and larvae were obtained as described in Section 2.3 using Equation 2.12a. Estimated parameters for eggs were $K=16.257$, $C=0.994$ and $Q=0.796$ ($R^2=0.997$). Parameters for male larvae were $K=18.257$, $C=1.043$ and $Q=2.112$ ($R^2=0.999$) and for female larvae were $K=16.540$, $C=0.969$ and $Q=1.378$ ($R^2=0.999$).

The means of the distribution of head capsule widths of the last-instar larvae at the lowest temperatures were smaller than at intermediate temperatures (Fig. 4.4). Head capsule sizes at the alternating temperature (average 20.3°C) more closely resembled head capsule sizes of larvae reared at the higher of the two temperatures. Mean dry weights of larvae were larger at higher temperatures with a maximum at 24.0°C (Table 4.4). A significantly lower dry weight of females was evident at the
Fig. 4.4. Frequency distributions of head-capsule widths of larvae of PFW reared at seven constant temperatures and an alternating temperature regime.
highest temperature. Mean dry weights of the larvae reared at the alternating temperature were less (not significant) than would be anticipated for larvae reared at the average of the fluctuating temperatures.

Validation of Egg Phenology Model. A computer simulation based on the described development rate and variability functions was used to compare observed egg development in the field in 1984 with predicted egg development. A FORTRAN algorithm modified from the program developed by Régnière (1984) was used. The simulation began on 1 June (day 152) when eggs were deposited on branches by the bagged females.

Two independent sets of temperature data were used as input for the model: average hourly air temperatures recorded from the CS temperature probe and hourly temperatures computed from maximum and minimum temperatures recorded in the Stevenson screen, using half-cosine functions (Régnière 1982). Predicted emergence was within three days of observed emergence (Fig. 4.5A) for both simulations. The simulation using recorded hourly temperatures was in closer agreement with observed results than the simulation using estimated hourly temperatures, but the difference in deviations of observed from simulated hatch was small (Table 4.5). The deviations between observed and expected for both simulations were greatest at the time of 50% emergence for the three egg hatch percentages compared. However, the deviations were less than 16% of the total
Fig. 4.5. Predicted (lines) and observed (symbols) egg hatch of PFW (solid lines) for (A) single-cohort simulation and multiple-cohort simulations using (B) observed hourly air temperatures, (C) estimated hourly air temperatures and (D) observed canopy temperatures. Solid line in (A) is simulation results using observed hourly temperatures and dashed line is results using estimated hourly temperatures from daily maximum and minimum temperatures. Solid lines in (B-D) are simulation results for individual cohorts and the dashed lines are results for population.
Table 4.4. Mean\textsuperscript{a} dry weights (±SE) of larvae of PFW reared at constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Wt. (mg)</td>
</tr>
<tr>
<td>7.3</td>
<td>1</td>
<td>8.3d</td>
</tr>
<tr>
<td>10.4</td>
<td>9</td>
<td>18.2 ± 0.75c</td>
</tr>
<tr>
<td>14.9</td>
<td>17</td>
<td>20.1 ± 2.21bc</td>
</tr>
<tr>
<td>18.1</td>
<td>42</td>
<td>24.7 ± 0.64ab</td>
</tr>
<tr>
<td>20.3\textsuperscript{b}</td>
<td>7</td>
<td>20.8 ± 0.50bc</td>
</tr>
<tr>
<td>24.0</td>
<td>20</td>
<td>27.2 ± 0.83a</td>
</tr>
<tr>
<td>26.7</td>
<td>24</td>
<td>23.7 ± 0.74abc</td>
</tr>
<tr>
<td>29.0</td>
<td>31</td>
<td>23.0 ± 0.72abc</td>
</tr>
</tbody>
</table>

\textsuperscript{a} means in the same column followed by the same letter are not significantly different (Duncan's [1955] multiple range test, P < 0.05).  
\textsuperscript{b} average of fluctuating temperature.

Table 4.5. Deviations (dev.) in days of observed egg hatch from simulated egg hatch and the deviation as a proportion (pro.) of total simulation time for the 1984 single-cohort simulation and the 1985 multiple-cohort simulation pooled for all three days.

<table>
<thead>
<tr>
<th>Percent emergence</th>
<th>10%</th>
<th>50%</th>
<th>90%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dev.</td>
<td>pro.</td>
<td>dev.</td>
</tr>
<tr>
<td>Year</td>
<td>Model input</td>
<td>1984</td>
<td>Obs. Air Temp.</td>
</tr>
<tr>
<td></td>
<td>Est. Air Temp.</td>
<td>0.5</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Obs. Canopy Temp.</td>
<td>-0.8</td>
<td>0.03</td>
</tr>
<tr>
<td>1985</td>
<td>Obs. Air Temp.</td>
<td>-3.9</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Est. Air Temp.</td>
<td>-1.9</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Obs. Canopy Temp.</td>
<td>-0.8</td>
<td>0.03</td>
</tr>
</tbody>
</table>
As a test of modeling multiple cohorts, the development of the eggs deposited 14 to 16 June (days 165 to 167) in the field during 1985 by bagged females was simulated. The results were compared with actual egg development over the same period of time deposited by bagged females. The proportion of eggs deposited on each day (i.e., 0.555, 0.287, and 0.158, respectively) was used as the proportion in each cohort starting development. Three sets of temperature data were used to drive the model: 1) hourly temperature averages (Fig. 4.5B); 2) estimated hourly temperatures (Fig. 4.5C); and 3) average hourly temperatures recorded from thermocouples at the same height in the canopy as the eggs (Fig. 4.5D). Estimated egg hatch for each of the three daily cohorts were pooled and compared with the pooled observed egg hatch (Table 4.5). Simulations driven by both estimated air temperature and canopy temperatures produced smaller deviations from observed than did the simulation based on observed air temperature. The canopy temperature simulation better predicted the onset of egg hatch when compared with the estimated air temperature simulation, but deviated more towards the termination of the egg hatch period.

**Arboreal Development Simulations.** A model was used to simulate the combined development of eggs and larvae. The simulation was initialized with the observed oviposition pattern of wild females at the LA plantation in 1986 (Fig. 3.1). The
observed proportion of eggs laid each day represented the proportion of insects in the daily cohorts. Eggs began development during a 14-day period, consequently, 14 cohorts were simulated simultaneously and the completion of development of the larvae was proportioned accordingly. Model input was the corrected air temperature recorded in the meteorological screen at the LA plantation during 1986. After a preliminary simulation with no corrections for microclimatic differences, the model was modified to incorporate: i) a canopy temperature correction function from the pooled canopy temperatures in 1985 (Equation 4.2), ii) the linear web correction function (Equation 4.4), iii) the non-linear web correction function (Equation 4.3) and iv) a combination of i and iii. In addition, only the fastest developing 90 percent of the population was simulated to determine its effect on the distribution of dropping times. This was accomplished by dividing the upper 90 percent of the variability function into percentile categories.

The output of the model was predicted drop of last-instar male and female larvae from the trees. The predicted drop was compared to observed captures in the traps, pooled for H- and M-defoliation zones, from the LA plantation in 1986.

Results of the simulation (Fig. 4.6A) without correction for microclimatic differences provided an adequate prediction of the onset of larval drop (Table 4.6), but was less accurate in predicting the termination of the arboreal stage. Introducing
Fig. 4.6. Observed (circles=males, triangles=females) and predicted (lines) larval drop of male and female PFW from the H- and M-defoliated zones of LA plantation in 1986; (A) CS screen temperatures, (B) canopy temperature correction, (solid line=males, dashed line=female) (C) linear (solid line=males, dashed line=females) and nonlinear (dotted line=males, dotted-dashed line=females) web temperature corrections and (D) web and pooled canopy corrections (solid line=males, dashed line=females).
Table 4.6. Deviations (dev.) in days of observed larval drop from simulated drop and the deviation as a proportion (pro.) of simulation time.

<table>
<thead>
<tr>
<th>Microclimatic correction</th>
<th>Sex</th>
<th>10%</th>
<th>20%</th>
<th>90%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>dev.</td>
<td>pro.</td>
<td>dev.</td>
</tr>
<tr>
<td>none</td>
<td>M</td>
<td>2.5</td>
<td>0.05</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2.6</td>
<td>0.05</td>
<td>5.6</td>
</tr>
<tr>
<td>T&lt;sub&gt;C&lt;/sub&gt; (pooled)</td>
<td>M</td>
<td>5.4</td>
<td>0.10</td>
<td>6.9</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>6.6</td>
<td>0.12</td>
<td>9.5</td>
</tr>
<tr>
<td>T&lt;sub&gt;W&lt;/sub&gt; (Equation 4.4)</td>
<td>M</td>
<td>1.2</td>
<td>0.02</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.7</td>
<td>0.03</td>
<td>4.3</td>
</tr>
<tr>
<td>T&lt;sub&gt;W&lt;/sub&gt; (Equation 4.3)</td>
<td>M</td>
<td>0.8</td>
<td>0.02</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.4</td>
<td>0.03</td>
<td>3.8</td>
</tr>
<tr>
<td>T&lt;sub&gt;C&lt;/sub&gt; and T&lt;sub&gt;W&lt;/sub&gt;</td>
<td>M</td>
<td>3.6</td>
<td>0.07</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4.4</td>
<td>0.08</td>
<td>6.9</td>
</tr>
<tr>
<td>T&lt;sub&gt;C&lt;/sub&gt; and T&lt;sub&gt;W&lt;/sub&gt; (90% variability)</td>
<td>M</td>
<td>3.7</td>
<td>0.07</td>
<td>4.1</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.9</td>
<td>0.07</td>
<td>6.2</td>
</tr>
</tbody>
</table>
the canopy-temperature correction function into the model (Fig. 4.6B) resulted in larger deviations between observed and predicted larval drop. Inclusion of either web-temperature correction functions into the model (Fig. 4.6C) resulted in predictions with slightly smaller deviations from observed than the basic model. Using nonlinear correction function for web temperature predicted slightly faster development than did the linear function, and was in closer agreement with predicted drop. When both microclimatic correction functions were employed (Fig. 4.6D), the results were more accurate than when only the canopy function was used, but were not an improvement over basic or web-temperature corrected models. The number of days between male and female drop was much greater for all simulated development (4.3-5.1 d at 50% drop) than for observed development (2.1 d at 50% drop). In addition, deviations between predicted and observed increased from the onset to the termination of larval drop for all simulations. The difference in deviations between the onset and termination of larval drop was reduced by using 90 percent of the developmental variability.

Inclusion of estimated web temperatures into the model reduced development time from 1.2 to 2.8 d over corrected screen temperatures. Including estimated canopy temperature into the model, however, retarded development by 2.6 to 4.0 d. Simulation results combining both canopy and web correction functions suggested that higher temperatures are required to
reduce the deviations between simulated and observed larval drop.

4.4 Discussion

The results corroborated the observation that PFW males and females have five and six larval instars, respectively (Schwerdtfeger 1941). The class intervals for instars occurred at about the same head capsule widths for the three years for which frequency distributions were compared. However, the head-capsule sizes for North American populations were considerably larger than head capsules of a European population (Schwerdtfeger 1941). The width of ultimate larval head capsules in the laboratory study also increased with temperature to a maximum, after which it was inversely correlated with increases in temperature. Low and high temperature effects on head capsule size have been reported for other insects (Uvarov 1931, Guppy 1969). Differences in head capsule sizes observed in the constant temperature rearings suggest that the European population either experienced different temperatures or are genetically different.

The weight of last-instar larvae also varied with temperature. Thus, the temperature experienced by the larvae affected their ability to assimilate food and their ability to accumulate resources for fecundity. The growth rate of PFW, like Colias larvae (Sherman and Watt 1973), is probably greatest at or near its optimal range of temperatures for feeding.
Ostrinia nubilalis had significantly larger heads and greater weight when reared in variable temperatures than larvae reared under comparable constant temperatures (Beck 1982). This was not the case with PFW. However, the maximum and minimum temperatures used in the variable regime were outside the range for efficient weight gain. Head capsule sizes of field collected larvae were comparable to larvae reared in the intermediate constant temperatures in the laboratory.

Larvae collected from webs from the four cardinal quadrants of trees developed at the same rate. Larvae developed slower in the least defoliated trees of the same plantation. The difference in development of the larvae in the defoliation zones probably resulted from differences in adult emergence and degree of exposure of the webs to solar radiation. The lightly defoliated zone also produced the heaviest larvae so that the slower development was not because of inadequate nutrition. Slight differences in development were observed in different canopy strata. The fastest development occurred near the top of trees. The differences in development rate were related to the degree of exposure of the webs to solar radiation. While sampling programs to determine PFW developmental status can ignore cardinal direction, they must incorporate vertical stratification.

Plant canopies experience a different microclimate than the standards of conventional meteorology. The red pine canopies in
which PFW reside were generally cooler than clearings used for meteorological screens. Temperatures of canopies underwent a diurnal temperature pattern with the deviations dependent upon time of day and height in the canopy.

Several functions have been proposed for shelters built by phytophagous insects. These include protection from enemies (Morris 1976), desiccation (Henson 1958, Willmer 1980, Strong et al. 1984) and phototoxicants (Berenbaum 1978). However, the salient feature of these shelters is that the internal temperature differs from the temperature of the surrounding air (Wellington 1950, Barbosa et al. 1963). Insect shelters have been likened to greenhouses that mitigate spring temperatures in the Temperate Zone (Wellington and Trimble 1984). Solar radiation has a profound effect on elevating temperatures of exposed plant structures, feeding insects and the inside of these insect-built shelters (Wellington 1950, Wellington 1954). The relationship between the external and internal climates of these structures is complex. The webs of PFW exhibit a diurnal pattern of heating and cooling related to the diurnal intensity of solar radiation (Henson and Shepherd 1952, Shepherd 1958). As with other shelter-building insects (Henson 1958), the magnitude of the pattern was modified by the degree of cloud cover, rain, wind and the color, orientation, and size of the web. Elevations of web temperatures may be due in part to reflected and transmitted radiation in addition to global solar radiation.
As with other shelter-building insects (Wellington 1954, Henson 1958, Green 1968), PFW larvae vacate the web to avoid critical high temperatures. Temperatures in webs of PFW occasionally rise above tolerable levels for the larvae. The larvae then respond by moving away from these overheated areas. When they leave the web, the larvae also leave its boundary layer and thus improve their convective heat exchange. Finally, the larvae reduce the surface area exposed to the radiation by positioning themselves with their heads towards the radiation source.

The shelters built by some early-emerging insects are aids to exploiting the cold temperatures of early spring (Wellington 1950). Yet when PFW hatches from the egg, eastern tent caterpillar (*Malacosoma americanum*) in the same plantation had completed the tent-building phase. Other non-webbing pine-feeding sawflies in the same plantation (*Neodiprion nanulus nanulus*, *Diprion similis* and *D. frutetorum*) were in more advanced stages of development than PFW. *Neodiprion n. nanulus* males were dropping and forming cocoons several days in advance of the PFW larval drop. Although the web-building habit of PFW accelerates development other adaptations do not allow PFW to take advantage of early spring temperatures in its present distribution in North America.

The web of PFW is multifunctional. In addition to
thermoregulation, the silkspinning habit of the larvae serves to facilitate mobility (Kolomietz 1967) and attachment to the food plant (Strong et al. 1984). The larvae move along the substrate (i.e., a needle, a branch or any other surface) on their backs by moving their heads from side to side and attaching a silk ladder under which they travel. This behavior was observed on numerous occasions in the present study in all but the ultimate instar. Some pine-feeding sawflies feed from the distal tips of the needles towards the base (Ghent 1958). However, PFW larvae are unable to grasp their food and bite off the needles at the base and feed as the needles are drawn into the web. Disturbed PFW larvae retract into the web away from the food and need a method of securing the needles. Examination of a number of webs containing intact needles revealed that the larvae had guyed the needles with strands of silk prior to feeding on them. Severed needles were fixed in position with silk strands. These silk guys also could serve to slow the movement of parasitoids around the web.

Male PFW larvae begin development at the same time as females, but because they pass through one less instar, they precede the females from the trees. Thus, sampling after the onset of larval drop will be biased towards the larger females.

The described model treats larval development as one stage. Differences in the development of individual instars may have affected model predictions. In some insects, different instars
have different developmental rate limiting parameters (Beck 1982). The cryptic habits of PFW made it difficult to observe the rates of development of the different instars.

Nonlinear equations employed in this study provided realistic descriptions of the development rates of eggs and larvae of PFW. Unlike the subterranean stages of PFW, the arboreal stages experience both high and low temperature extremes. Insect embryogenesis can occur at temperatures below which eggs can hatch (Morris and Fulton 1970, Beck 1983), and this happened with PFW. Interpolation techniques allowed this low temperature development to be incorporated into the development rate equations.

Observed canopy temperatures provided an accurate estimate of egg development when used as input to the model. This indicates that egg development on the surface of pine needles was not significantly influenced by radiant heating or cooling. Temperatures of conifer foliage have been reported to be as much as 5.6°C warmer than the surrounding air when exposed to solar radiation and as much as 3°C below ambient temperatures on clear nights (Wellington 1954). Temperature elevations of as much as 6.3°C in the mines of needle mining insects have also been observed (Henson and Shepherd 1952). In addition, differences in egg development of the moth, *Orgyia pseudotsugata*, between thinned and unthinned Douglas fir canopies were attributed to differences in solar radiation (Wickman and Torgersen 1987).
Although the slight difference between observed and predicted PFW egg hatch thus may have resulted from compensatory diurnal heating and nocturnal cooling of the foliage, it may also have been a result of an averaging of temperatures from convection within the canopy. For example, use of infrared thermometry showed that needle temperatures did not differ greatly from air temperatures in well-ventilated Douglas fir canopies (Tan et al. 1978).

The most accurate prediction for onset and median egg hatch was provided using ambient temperatures recorded in the plantation canopy as model input. Estimated air temperatures from maximum and minimum thermometers provided estimates of egg hatch in 1984 and 1985 as accurate as uncorrected observed air temperatures recorded in the CS screen. Employing uncorrected observed air temperature predicted egg development too early. Overheating of the CS screen would explain this discrepancy.

Vertical differences in canopy temperatures were not responsible for the observed faster development of PFW in the upper canopy. Furthermore, the oviposition pattern as a function of tree height did not result in the accelerated development in the upper canopy since female PFW begin oviposition in the lower canopy. Therefore, the faster development in the upper canopy probably resulted from the increased exposure of these webs to solar radiation.
Behavior of monarch butterfly caterpillars reduced the larval period by 10 to 50% by affecting the thermal environment (Rawlins and Lederhouse 1981). This reduction decreased the period larvae were exposed to predators, parasitoids and pathogens. Elevations of web temperature in the present study reduced the developmental period in calendar time by only 1.2 to 2.8 days over screen temperatures. Conversely, canopy temperatures increased the developmental period when compared with screen temperatures. Simulations suggested that observed larvae experienced more thermal units than was predicted by the model. For example, the extreme defoliation encountered in the Lakehurst plantation in 1986 was very different from defoliation in the plantation on which the empirical microclimatic relationships were based. Severe defoliation at Lakehurst opened the canopy to such an extent that PFW webs were exposed to intense solar radiation for longer periods.

The climate experienced by PFW arises from a series of compensatory processes in their microhabitats. PFW webs constructed from frass, exuviae, and needle fragments act like heat sinks in direct sunlight and raise the body temperatures of the inhabitants, while red pine canopies lower the air temperatures outside the webs below screen temperatures. The microclimate is further modified by the insects' own activities. Empirical relationships designed to describe these processes in predictive models for PFW will not be very accurate if the degree of defoliation in the stand is not taken into account.
The duration of simulated larval drop was considerably longer than observed. This discrepancy appeared at the end of the larval development, suggesting that problems may still exist in the variability functions developed from constant-temperature laboratory rearings. Simulations using only the fastest 90 percent of the population partially alleviated this problem. Because foliage quality in the laboratory deteriorated as the larvae grew, the development of the slower individuals may have been further retarded by qualitative changes in their food. This factor may also explain the disparity between predicted and observed larval drops for males and females, since females took longer to develop than males in the laboratory.

Larvae of PFW, unlike the eggs and subterranean stages, can actively respond to changes in thermal conditions. Larvae can move to avoid critical high temperatures and their behavior also may improve their developmental rate. In this type of simulation, the thermal maximum for development is a sensitive parameter (Gold et al. 1987). The estimated thermal maximum for larval PFW is very near the high temperature at which active avoidance is elicited, so that errors in estimating this parameter could have serious effects on model predictions. Since the current version of the model uses mean temperature deviations, not extremes, thermal maxima would rarely be encountered in the simulations.
Chapter 5

Biology and phenology of Sinophorus megalodontis and Olesicampe sp. (Hymenoptera: Ichneumonidae), parasitoids of pine false webworm.

5.1 Introduction

A parasitoid must coincide temporally and spatially with its host to cause significant mortality of the host population (Griffiths 1969, Huffaker et al. 1977). Asynchrony between host and parasitoid has been suggested as the cause of failure of many biological control programs (Hoy 1976, Huffaker et al. 1977, Ehler and Andres 1984), as has releasing adult parasitoids when suitable hosts were unavailable (Griffiths and Lyons 1968, Hoy 1976). Inability of parasitoids to exploit hosts in all host habitats can also result in failures (Miller 1983).


Two species of ichneumonids were reared from the sawfly host during the present investigation. Sinophorus megalodontis Sanborne belongs to a species group that attacks web-spinning sawflies (Sanborne 1984). Another member of the species group, S. crassifemur (Thomson), attacks PFW larvae and related species in the Palearctic region (Schwerdtfeger 1944). Only the
biologies of S. validus and S. turionis (S. rufifemur) have been studied in any detail (Timberlake 1912, Tothill 1922, Juillet 1959, Morris 1976).

Another ichneumonid reared from PFW is an undescribed species (H. Townes pers. comm.) of the poorly known genus Olesicampe (Billany et al. 1985). Some species of this very large cosmopolitan genus are responsible for significant mortality of sawfly populations (Price and Tripp 1972, Billany et al. 1985) and some have been successfully introduced as biological control agents against sawflies (Turnock and Muldrew 1971, Quednau and Lim 1983, Drooz et al. 1985).

The objective of this investigation was to study the life history and the temporal and spatial activity patterns relative to the host of these ichneumonids, and to estimate parameters for developing temperature-dependent development rate and ageing rate functions to be incorporated into a predictive phenology model. Methods for differentiating the immature stages of the two species were investigated. Three methods of determining the phenology of the adult parasitoids were compared.

5.2 Materials and Methods

Description of Immature Stages. Egg morphology was determined by dissecting adult females of the two parasitoids species. Eggs dissected from host larvae were compared with these eggs. The morphology of the two species of parasitoids
was determined by examining larvae that had partially emerged from the egg and by associating $S$. megalodontis larvae with empty chorions. Parasitoid eggs and larval head capsules were measured with an ocular micrometer mounted on a stereo microscope.

**Adult Emergence and Flight Period.** The temporal pattern of parasitoid emergence from the soil was determined using traps (Section 2.2). Traps were examined daily during the parasite emergence period in late May and early June.

Adult parasitoid activity was monitored with Malaise traps (D.A. Focks Ltd., Gainesville Florida). Traps were positioned at the edge of a clearing adjacent to plot AM1 in 1983 and in the heavily- and moderately-defoliated zones within the LA plantation in 1986. Adults of Olesicampe sp. and $S$. megalodontis were removed daily at 1000 hours and preserved in 70% ethanol for later identification.

**Temporal and Spatial Distribution of Parasitism.** To determine the host stage attacked and the spatial distribution of parasitism, all the host larvae collected by branch sampling and larval drop trapping at the AM1 plantation in 1983 and by branch sampling at the H plot in 1986 (Section 3.2) were dissected and the incidence of parasitoid eggs and larvae was noted. Total number of $S$. megalodontis was determined from the sum of the unhatched eggs plus larvae or hatched eggs, whichever
was greater. The number of *Olesicampe* sp. was estimated as the sum of the eggs and larvae, since hatched eggs were undetectable. To determine the spatial distribution of parasitism, host larvae were pooled for all sample days from the three vertical strata in the plantation canopy sampled in 1983. To determine the effect of time of host drop on incidence of parasitism, samples of dropping larvae were dissected and pooled at three-day intervals for the first 12 days of the drop period while the last eight days made up the final sample.

**Subterranean Development and Adult Longevity of *Olesicampe* sp.** Post-diapause development rates and adult longevity of *Olesicampe* sp. at constant temperatures were determined using parasitized PFW larvae collected in late autumn from the soil of the LA plantation and parasitoid adults reared from these larvae. Parasitized larvae are distinguishable from unparasitized hosts because they retain eonymphal characteristics and are distinguished from eonymphs in prolonged diapause by their yellow coloration. Parasitized larvae were stored as described previously for unparasitized pronymphs (Section 2.2). Upon removal from cold storage the larvae were placed in 1.9-mL shell vials and incubated at nine constant temperatures (1.8, 4.3, 7.1, 10.6, 15.6, 18.6, 23.3, 27.1 and 29.9°C).

Temperature-dependent development rate and variability functions for *Olesicampe* sp. were determined using nonlinear
regression of individual development rates (Régnière 1984).

Freshly emerged adults of *Olesicampe* sp. were placed individually in rearing vials and randomly assigned to eight constant-temperature chambers (4.1, 5.8, 11.0, 15.0, 19.0, 23.0, 27.0 and 31.0°C) to determine the effect of temperature on longevity. Vials were made by gluing together the lids of two 52-mL plastic snap-on cap vials. The bottom of one vial was removed and replaced with muslin. A hole was drilled through the lids into which an absorbent cotton wick was inserted, running from the upper insect vial to the lower water-filled vial. Honey was smeared on the muslin. Parasitoids were examined daily and time of death recorded.

Mean ageing rates (i.e., mean of reciprocals of longevity) of parasitoid females at each constant temperature was determined and regressed as a linear function of temperature (Section 3.2). Normalized longevity times were obtained by dividing individual longevities by mean longevity for each temperature. The cumulative distribution of normalized times pooled for all temperatures was fitted to a two parameter Weibull function (Section 3.2).

A model of subterranean development and longevity of *Olesicampe* sp. was developed (Section 2.2 and 3.2). Overwintered larvae of *Olesicampe* sp. were assumed to be at an equal stage of development as spring soil temperatures began to
increase. For modeling purposes, subterranean development of *Olesicampe* sp., in spring, consisted of: 1) post-diapause development of the larvae of *Olesicampe* sp. within the host and 2) emergence of the parasitoid larvae from the host, cocoon formation and adult emergence.

Two types of soil temperature data were used in the subterranean development model: average hourly soil temperatures recorded at a 5-cm depth at the LA plantation in 1986 and soil temperatures at six depths, estimated from soil temperatures recorded at two depths (5 and 10 cm) from the same locations (Section 2.2). It was assumed that the vertical distribution of parasitized hosts in the soil was similar to the distribution of unparasitized hosts. Insects in each 1.5 cm increment of soil developed at a rate determined by the estimated temperature for that stratum. For every time step in the simulation the rate-summation model was simultaneously solved for all six spatially distributed groups. Then, total development was apportioned for the entire population. Temperature data from the moderately- and lightly-defoliated zones of the plantation were employed in the simulations. The model incremented time in intervals of 1 or 4 h.

Average hourly air temperatures were used to estimate longevity in the model. The number of cohorts simulated in the longevity model was determined by the number of days that adults emerged from the soil. For each time step, mean ageing rate of
the cohort was determined and the fractional age of the cohort was accumulated. The cumulative proportion of the cohort dying was calculated from the Weibull function. The proportion surviving was one minus the proportion dying. The proportion of the population surviving was the product of the proportion of the cohort surviving and the proportion of the population in the cohort. Observed emergence was used to initialize the longevity component of the model. Simulated adult longevity was compared to Malaise trap captures of adult parasitoids scaled to match the proportion of living adults.

5.3 Results

Description of Immature Parasitoids. Eggs of S. megalodontis were brown, smooth and broader at one end than the other (Fig. 5.1A). Mean length of eggs dissected from host larvae was 0.968 mm (S.D.=0.048, n=30) and mean width at the broadest point was 0.238 mm (S.D.=0.020). Eggs of S. megalodontis were visible through the integuments of the host larvae. Eggs of Olesicampe sp. (Fig. 5.1B) were clear, curved and broader at one end than at the other. Mean length of 30 eggs of this species was 0.566 mm (S.D.=0.041) and mean width was 0.167 mm (S.D.=0.028). Chorions from hatched S. megalodontis were discernible. Empty chorions of Olesicampe sp. were never encountered.

First-instar larvae of both parasitoid species were of the ichneumonid mandibulate-caudate type (Quednau and Lim 1983).
Fig. 5.1. Immature stages of PFW parasitoids: (A) larva of *S. megalodontis* emerging from the egg; (B) egg of *Olesicampe* sp.; (C) first-instar larva of *Olesicampe* sp.; (D) cocoons of *S. megalodontis* (right) and *Olesicampe* sp. (left).
Head capsules of *S. megalodontis* (Fig. 5.1A) were generally larger than those of *Olesicampe* sp. (Fig. 5.1C), but with some overlap in both height and length. However, the diagonal length of the larvae from the tip of the mouthparts to the dorsal end of the head capsule was consistently longer in the former species. The head capsule of *S. megalodontis* was darker, its deeper shade of yellow probably resulting from a greater degree of sclerotization. In addition, the length of the tail in *S. megalodontis* was about as long as the body, while the length of the tail in *Olesicampe* sp. was about half the body length. The cocoon of *S. megalodontis* was longer, darker, smoother and more tubular than the *Olesicampe* sp. cocoon (Fig. 5.1D).

**Adult Emergence and Flight Period.** Parasitoids collected from the emergence traps were pooled for heavily- and moderately-defoliated zones. Only six individuals, three of each species, were captured in the lightly-defoliated zone and were subsequently disregarded. The proportion of females of *S. megalodontis* collected was not significantly different from 50% ($n=42, \%\text{female}=52.4, \chi^2=0.10, P>0.05$), however, collections of *Olesicampe* sp. contained significantly more males ($n=56, \%\text{female}=35.7, \chi^2=4.57, P<0.05$). Adults of both species were captured in emergence traps beginning 23 May (day of year 143) (Figs. 5.2A, B). Emergence periods for *Olesicampe* sp. and *S. megalodontis* lasted 16 and 17 days, respectively. Mean (SE) emergence of male *S. megalodontis* preceded emergence of females by 3.1 (1.03) days; males of *Olesicampe* sp. preceded females by
1.6 (0.81) days. There were no significant differences in time of emergence of comparable sexes for the two parasitoid species (males; $t=1.77$, df=40, $p=0.084$; females; $t=0.09$, df=54, $p=0.930$). Peak adult emergence coincided with about average instar 1.5 and lasted until about average instar 3.8 in 1986 (Fig. 4.2B).

Parasitoids from the Malaise traps, in the moderately defoliated- and heavily-defoliated zones, were pooled. The onset of the observed flight periods of the two species (Figs. 5.2C, D) coincided with the onset of emergence from the soil. Malaise traps collected significantly more males than females of both parasitoid species (Olesicampe sp.; $n=637$, %female=30.6, $\chi^2=95.78$, $p<0.05$; S. megalodontis; $n=538$, %female=16.9, $\chi^2=235.57$, $p<0.05$). Although percentages of females in the emergence traps were greater than in the Malaise traps for both species, the difference was only significant for S. megalodontis (Olesicampe sp. $\chi^2=0.626$, $p=0.429$; S. megalodontis $\chi^2=31.24$, $p<0.001$). The flight period for both species lasted 28 days until 18 June (day 169). The mean (SE) flight period of male S. megalodontis preceded the mean flight period of females by 2.7 (0.55) days; males of Olesicampe sp. preceded females by 2.0 (0.30) days. The flight periods of the two parasitoids were also significantly different (males; $t=9.72$, df=887, $p<0.001$; females; $t=5.33$, df=284, $p<0.001$). The depression in trap collections in the middle of the flight period occurred during a period of low temperature and rainfall.
Fig. 5.2. Emergence (A, B) and Malaise (C, D) trap catches of parasitoids of PFW from the LA plantation in 1986.
Collections from the Malaise trap in 1983 yielded a maximum of five adults of one sex and species per day. Females of *Olesicampe* sp. were caught from 15 to 29 June, while the males' flight extended from 13 June to 6 July. For both sexes of *S. megalodontis*, the flight period lasted from 18 June to 6 July. Flight period of adults was coincident with average host instars 0.9 to 4.8 in 1983 (Fig. 4.2A).

**Temporal and Spatial Distribution of Parasitism.** Unhatched eggs of *S. megalodontis* were found in all instars of PFW (Fig. 5.3A) in 1983 and 1986. The majority of eggs was found in the fourth instar in 1983 and in the first instar in 1986. Similarly, the eggs of *Olesicampe* sp. were distributed among all host instars in 1983 (Fig. 5.3B), but were limited to host instars I-III in 1986. Larvae of both parasitoid species were found only in instars II-VI in 1983, but in all host instars in 1986. There were encapsulated larvae of *S. megalodontis* in all host instars, but they occurred mainly in host instars IV-VI (Fig. 5.3C). Encapsulated larvae of *Olesicampe* sp. were found only in the last three host instars (Fig. 5.3D). Eggs of *S. megalodontis* were also found in ultimate host instars V and VI and eggs of *Olesicampe* sp. were found in ultimate host instar V collected in drop traps in 1983. A similar comparison was not available for 1986.

The total number of parasitized PFW larvae increased
Fig. 5.3. Mean numbers (±SE) of parasitoid eggs (A, B) and encapsulated larvae (C, D) per PFW larval instar collected by branch sampling at Anten Mills in 1983 (A, C) and Lakehurst in 1986 (B, D).
dramatically (Fig. 5.4) throughout the host larval period in 1983 as a result of the oviposition of both parasitoids. The incidence of parasitism by Olesicampe sp. remained relatively constant during the larval period in 1986, indicating that the majority of parasitoid eggs were deposited early in the host larval period. The incidence of parasitism by S. megalodontis was initially high and only slowly increased in 1986.

The greatest incidence of parasitism for both S. megalodontis and Olesicampe sp. was in the low canopy stratum (Table 5.1) followed by the high stratum. The host larvae in tree leaders and the first whorl of branches had the lowest incidence of parasitism. The percentage of PFW larvae parasitized by S. megalodontis was not significantly different in the upper two strata. There were no significant differences in percent parasitism for pooled samples collected from two heights in 1986 (Table 5.1). Host larvae were concentrated in the high strata in 1983, but the number of hosts collected from the two strata were approximately the same in 1986.

The greatest concentration of parasitism by S. megalodontis was in the southern and western quadrants of the trees (Table 5.2). The eastern quadrant had the lowest incidence of parasitism, while the northern aspect was intermediate. The percentage of hosts parasitized, however, was only significantly lower in the eastern quadrant. The incidence of Olesicampe parasitism was significantly greater in the western quadrant.
Fig. 5.4. Mean numbers (±SE) of total immature parasitoids, parasitoid eggs, and encapsulated parasitoid larvae per PFW larvae collected by branch sampling at Anten Mills in 1983 (A, C) and Lakehurst in 1986 (B, D). The numbers over the symbols are number of host larvae.
Table 5.1. Mean number of parasitoids per host ($\bar{x}$) and percent parasitized of PFW larvae collected by branch sampling from vertical strata at Anten Mills (AMI) in 1983 and Lakehurst (H) in 1986.

<table>
<thead>
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<th>Year</th>
<th>Height</th>
<th>No. hosts</th>
<th>$\bar{x}$</th>
<th>SE</th>
<th>%a</th>
<th>SE</th>
<th>$G^2$</th>
<th>P</th>
</tr>
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<td>S. megalodontis</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>Leader</td>
<td>2870</td>
<td>0.037</td>
<td>0.004</td>
<td>3.2a</td>
<td>0.3</td>
<td>92.031</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td></td>
<td>High</td>
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<td>0.051</td>
<td>0.003</td>
<td>4.1a</td>
<td>0.2</td>
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</tr>
<tr>
<td></td>
<td>Low</td>
<td>3750</td>
<td>0.128</td>
<td>0.010</td>
<td>7.8b</td>
<td>0.4</td>
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<tr>
<td>1986</td>
<td>High</td>
<td>2129</td>
<td>0.116</td>
<td>0.009</td>
<td>9.8a</td>
<td>0.7</td>
<td>3.578</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>2014</td>
<td>0.089</td>
<td>0.007</td>
<td>8.1a</td>
<td>0.6</td>
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<tr>
<td>Olesicampe sp.</td>
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</tr>
<tr>
<td>1983</td>
<td>Leader</td>
<td>2870</td>
<td>0.009</td>
<td>0.002</td>
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<td>High</td>
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<td>0.001</td>
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<td>Low</td>
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<td>0.003</td>
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<td>0.4</td>
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* Percentages within the same year and within a species followed by the same letter are not significantly different ($G^2$, $P$>0.05)

Table 5.2. Mean number of parasitoids per host ($\bar{x}$) and percent parasitized of PFW larvae collected by branch sampling from cardinal directions at Anten Mills (AMI) in 1983.

<table>
<thead>
<tr>
<th>Aspect</th>
<th>No. hosts</th>
<th>$\bar{x}$</th>
<th>SE</th>
<th>%a</th>
<th>SE</th>
<th>$G^2$</th>
<th>P</th>
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<tbody>
<tr>
<td>S. megalodontis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>3506</td>
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<td>5.4a</td>
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<td>74.266</td>
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<td>East</td>
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<td>0.040</td>
<td>0.004</td>
<td>2.9b</td>
<td>0.3</td>
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<tr>
<td>South</td>
<td>3713</td>
<td>0.095</td>
<td>0.007</td>
<td>6.8a</td>
<td>0.4</td>
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<td></td>
</tr>
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<td>1999</td>
<td>0.108</td>
<td>0.013</td>
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<td>0.5</td>
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<td>Olesicampe sp.</td>
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<td>North</td>
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<td>0.003</td>
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<tr>
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<td>0.005</td>
<td>2.7a</td>
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* Percentages within a species followed by the same letter are not significantly different ($G^2$, $P$>0.05)
compared with the eastern quadrant. Fewer host larvae were collected from the western aspect of the host trees.

The period of PFW larval drop lasted for 20 days (Section 4.3). The mean number of parasitoids (Table 5.3) of each species per host, from both sexes of the host larvae, increased over time, so that later-dropping larvae exhibited a greater incidence of parasitism. For the entire larval drop period, the proportion of parasitized larvae was similar between the sexes. The proportion (0.184, SE=0.013, n=894) of male PFW larvae parasitized by *S. megalodontis* was not significantly different than the proportion (0.163, SE=0.019, n=367) of females parasitized (*G^2=0.797, df=1, P>0.05*). Similarly, the proportion of males (0.060, SE=0.008, n=894) and females (0.065, SE=0.013, n=367) parasitized by *Olesicampe* sp. did not significantly differ (*G^2=0.143, df=1, P>0.05*).

The effectiveness of both parasitoid species was limited by superparasitism, multiparasitism and encapsulation by the host. Although both parasitoids species superparasitized hosts, the occurrence of superparasitism was greatest for *S. megalodontis*. The proportion (SE) of parasitized *S. megalodontis*, collected by branch sampling in 1983, branch sampling in 1986, and larval drop trapping in 1983, that were superparasitized were 0.185 (0.013), 0.107 (0.015), and 0.247 (0.024), respectively, while the proportion of *Olesicampe* sp. that were superparasitized were 0.017 (0.004), 0.000 (0.000), and 0.006 (0.005), respectively.
Table 5.3. Mean number of parasitoids per host ($\bar{x}$) and percent parasitized of PFW larvae collected from drop traps at Anten Mills (AMI) in 1983.

<table>
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<th>No.</th>
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<th>SE</th>
<th>%a</th>
<th>SE</th>
<th>$G^2$</th>
<th>P</th>
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<td>184-186</td>
<td>293</td>
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a Percentages within a species and sex and followed by the same letter are not significantly different ($G^2$, P>0.05)
Host larvae contained up to nine immature *S. megalodontis*. The greatest number of *Olesicampe* sp. found in one host was three. The proportion (SE) of parasitized PFW larvae from the same collections that were multiparasitized were 0.165 (0.012), 0.125 (0.016), and 0.172 (0.022), respectively.

Subterranean Development and Adult Longevity of *Olesicampe* sp. Subterranean post-diapause development of *Olesicampe* sp., in the spring, involved two observable phenophases; maturation of the larva within the host body culminating in the emergence of larva from the host ('within host' development) and subsequent cocoon spinning by the parasitoid larva, pupation, and ultimately the adult eclosion and emergence from the cocoon ('within cocoon' development). Since *S. megalodontis* cocoons were collected from the soil in fall and not reared from overwintering host larvae, post-diapause development for this species only entails within cocoon development.

Since there were no discernible differences between the development periods of males and females within host or within cocoon development of *Olesicampe* sp., the sexes were pooled for analysis. Within host development was completed at a much broader temperature range (1.8 - 29.9°C) than within cocoon development (7.1 - 23.4°C), because parasitoid larvae did not spin cocoons at high (> 27.1°C) and low (1.8°C) temperatures. Larvae were capable of cocoon formation at 5.8°C and successfully emerged after transfer to 15.6°C. For these
parasitoids, development periods were estimated using the interpolation technique (Section 2.2). Larvae allowed to spin cocoons at 15°C and moved to 27.1°C failed to emerge.

Equation 2.11b adequately described both within host (Fig. 5.5A) and within cocoon (Fig. 5.5B) development rates of Olesicampe sp. Estimated parameters were $P_1=0.327$, $P_2=2.546$, $P_3=5.568$, $P_4=0.017$, $T_m=31.0$, and $T_b=1.0$ ($R^2=0.848$) for within host development and $P_1=0.085$, $P_2=2.285$, $P_3=4.411$, $P_4=0.015$, $T_m=25.0$ and $T_b=5.0$ ($R^2=0.848$) for within cocoon development. Variability functions for development of these stages were also developed as described previously (Section 2.2). Parameters for Equation 2.12a were $K=6.373$, $C=0.753$, and $Q=0.365$ ($R^2=0.997$) for within host development and $K=44.928$, $C=1.017$, $Q=2.511$ ($R^2=0.999$) for within cocoon development.

The temperature-dependent ageing rate function (Fig. 5.6A) for adults of Olesicampe sp. was: $y = -0.034 + 0.011x$ ($r^2 = 0.784$) where $y =$ ageing rate and $x =$ temperature (°C) ($F=21.8; df=1,7; P=0.003$). The parameter estimates for the Weibull function describing the cumulative distribution of normalized times to death (Fig. 5.6B) were $\eta=0.997$ and $\beta=1.471$ ($R^2=0.991$).

Predicted emergence from the moderately-defoliated zone preceded the emergence from the lightly defoliated zone by seven and eight days for larvae and adults, respectively (Figs. 5.7A, B). Deviations of predicted emergence from observed emergence,
Fig. 5.5. Post-diapause temperature-dependent development rates for (A) within host and (B) within cocoon development of Olesicampe sp. Circles are individual observed rates and lines are regressions curves (Equation 2.11b).
Fig. 5.6. (A) Temperature-dependent ageing rate of Olesicampe adult females as a function of temperature and (B) cumulative distribution function of normalized death times. Circles are (A) observed mean ageing rates (±SE) and (B) cumulative mortality at each normalized time. Regression lines are indicated.
Fig. 5.7. Simulated development of subterranean stages of Olesicampe sp. from moderately- (A) and lightly-defoliated (B) plots of LA plantation in 1986. Solid lines (A, B) represent results using temperatures from one depth while the dashed lines represent summed development of insects at several depths in soil. First curves are emergence of parasitoid larvae from hosts and second curves are emergence of adults from soil. Circles are observed emergence of adults from soil. (C) Simulated relative abundance (solid line) of females and Malaise trap captures scaled to size (dotted line).
A. 

PROPORTION EMERGING

B. 

C. 

RELATIVE ABUNDANCE

NUMBER CAPTURED

DAY OF YEAR
in the moderately-defoliated zone was 3.2 days for 50% of the population in the single-stratum and 2.5 days in the multiple-stratum simulations. Increasing the time increment of the multiple-stratum model from 1 to 4 h had no effect on the deviations. Since emergence of parasitoid larvae from the hosts occurs in soil and parasitoids were rare in the soil, this event was not observed directly. Low numbers of emerging adults in the lightly defoliated zone also prevented comparisons between observed and predicted emergence.

The longevity models predictions (Fig. 5.7C) closely approximated the observed flight period of adults of Olesicampe sp. However, weather affected flight behavior, resulting in peaks and troughs of trap captures throughout the adult period, obscuring the pattern of longevity.

5.4 Discussion

Sinophorus megalodontis and Olesicampe sp. are solitary endoparasitoids of PFW and, like their hosts, are univoltine. Unlike Olesicampe lophryi, which overwinters in its host, Neodiprion swainei, as an egg or first instar larva (McLeod 1975), Olesicampe sp. overwinter in the host larvae as late-instar larvae. The parasitoid larvae prevent the hosts from transforming into pronymphs. Larval development is completed in the spring when larvae emerge from host cadavers. All that remains of the host is the empty cuticle. The parasitoid larvae spins a cocoon in the earthen cell, pupates
and emerges as an adult. *Sinophorus megalodontis* emerges from the host in fall and overwinters in its own cocoon within the host's earthen cell. This overwintering mode was also reported in *S. validus* (Morris 1976).

Parasitoid adults, like their sawfly hosts, emerge protandrously from the soil as seen in both emergence and Malaise traps. The emergence and flight periods of the two ichneumonid species were contemporaneous, despite the different strategies for subterranean development. The flight period of *S. megalodontis* adults was somewhat longer than that of *Olesicampe* sp. The higher proportion of males in Malaise traps, compared with emergence traps, reflected sex-related differences in flight behavior. Males spent their time searching near the ground for females, while females searched the trees. Malaise traps positioned near the ground intercepted a greater number of flying males. A similar bias was reported in flight trap captures of cocoon parasitoids of *N. swainei* (Price 1971).

There was considerable year-to-year variation in the date of adult emergence, as there was with host development. The onset of emergence in 1986 of both parasitoid species was synchronized with the host's early instars and with later instars in 1983. Dissections of parasitoids from host larvae confirmed that yearly variations in host-parasitoid temporal coincidence occur, resulting in differences in host stage attacked.
The females of both species oviposit into all instars of host larvae. Parasitoid eggs hatch soon after deposition, as evidenced by the presence of parasitoid larvae in first-instar host larvae. Larvae remain as first instars until the last instar of the host. Adults mated and began ovipositing soon after emergence as indicated by the coincidence of the onset of emergence and the occurrence of parasitized host larvae. Parasitoid attacks are distributed equally between the sexes of the host. Thus, the parasitoids do not affect the sex ratios observed in PFW populations.

The synchrony of Olesicampe sp. with specific host stages is not as consistent as in other species of Olesicampe attacking early instars of their hosts (Ives et al. 1968, McLeod 1975, Thompson and Kulman 1976, Billany and Brown 1980). Similarly, the stage attacked by S. megalodontis is variable, unlike S. validus (Morris 1976) and its sibling species, S. crassifemur, which also attacks Acantholyda spp. (Kolomietz 1967). The majority of species of Sinophorus that attack web-spinning insects have long ovipositors (Sanborne 1984). Sinophorus megalodontis and its Palearctic counterpart S. crassifemur have long ovipositors and are well adapted for attacking late instars in webs. Sinophorus crassifemur has been observed attacking third and fourth instars of the congeneric species A. posticalis (Kolomietz 1967). Silkspinning behavior of the sawfly and long ovipositors of parasitoids are probably coevolutionary responses to similar insects. Olesicampe sp. does not have a comparably
extensive ovipositor and is probably better suited for attacking earlier instars that are not well concealed in their webs.

Females of *Olesicampe* sp. are apparently unable to discriminate between previously parasitized hosts (i.e., superparasitism) and hosts attacked by *S. megalodontis* (i.e., multiparasitism). Encapsulation of the parasitoid larvae by hemolymph inclusions of the host was common. Encapsulation, regardless of the degree of host synchrony, was mainly restricted to late instars of the host.

Parasitized hosts may develop more slowly than unparasitized insects (Miller 1983). Larvae of the European pine sawfly, *N. sertifer*, developed slower when parasitized by *Lophyroplectus luteator* (Griffiths 1975). *Sinophorous validus* had little effect on the development rate of its host *H. cunea* (Morris and Bennett 1967). The increasingly greater incidence of parasitism in later dropping host larvae in 1983 suggested that development of PFW larvae may be retarded by parasitization. This observation is confounded by the coincidence of attacking parasitoids and late instars of PFW in that year and the possibility that earlier developing larvae escaped parasitism. The high proportion of later dropping larvae that were parasitized, compared with the proportion parasitized observed during branch sampling, supports the developmental retardation supposition.
The distribution of individual parasitoid species within forest canopies differs with respect to microclimate (Weseloh 1976). PFW larvae were seldom seen on branches outside of webs, unless they had completely defoliated the branch or until they were ready to drop. Both parasitoid species were most abundant in the high stratum and least abundant in the leader and first whorl of branches and intermediate in the lower stratum. The distribution of parasitoids is influenced by the distribution of the host larvae. In the heavily defoliated plantation sampled in 1986, the host larvae were equally distributed in the high and low strata and the parasitoids were also equally distributed among the hosts. Parasitized hosts were fairly evenly distributed around the sides of the tree.

Larvae of Olesicampe sp. were not capable of cocoon-forming behavior at the two lowest temperatures used in the constant temperature rearings. In variable temperatures in the field, larvae probably survive these temperatures and form cocoons during periods of higher soil temperature.

Observed parasitoid emergence was within 3 to 5 days of predicted emergence. Incorporating vertical distribution of temperatures in the soil into the model reduced the deviations between observed and predicted emergence by about one day. Reducing the number of time steps utilized in the model had no effect on the deviations between observed and expected events.
The longevity component of the parasitoid model provided close agreement between the observed flight period of females of *Olesicampe* sp. and the simulated longevity. This occurred even when other sources of mortality were not included in the model and the model was based on parasitoid longevity in the laboratory in the absence of hosts.

The transcontinental distribution of *S. megalodontis* (Sanborne 1984) suggests that this species is endemic to North America. Unidentified species of *Olesicampe* and *Sinophorus* have been reported from species of *Cephalcia* in Canada (Eidt 1969). It is likely that the species of *Olesicampe* described here originated in the New World. Even though members of these genera attack PFW in the Old World, these Nearctic species are poorly adapted to their recently introduced host. The evidence presented here suggests that these parasitoids, as a result of lack synchronization with the host, poor searching ability, and encapsulation are not having much impact on the host populations.

Techniques developed here will be useful for evaluating potential candidates for future biological control of PFW. The developed models will assist in synchronizing releases of potential biological agents.
Chapter 6

General Conclusion

The ability to predict temporal occurrence of stages of PFW has pragmatic implications for control of this pest species. Although there are no insecticides registered for control of PFW, Christmas tree growers apply chemicals to eradicate this sawfly in Scots pine plantations. For effective control, sprays should be applied when susceptible stages are available. Spray 'windows' are narrow due to the cryptic behavior of the larvae and a knowledge of the sawfly's phenology is required for effective control. In addition, biological control agents such as entomophagous insects must be released when suitable stages are present. Understanding phenology also imparts an understanding of processes at the population level.

To investigate the phenology of PFW a systems approach was adopted. Process-oriented phenology models were constructed to predict the development of stages of the sawfly. The existence of subterranean and arboreal stages, and the shelter-building habits of the larvae made PFW in red pine plantations an interesting system in which to study the effects of microclimate on phenological predictions. Models of phenology of PFW and one of its parasitoids were developed from relationships between PFW spatial distribution and microweather.

Protandrous emergence of adults from the soil, observed in
natural populations, resulted from differential rates of development between the sexes for post-diapause pronymphs and pupae. Defoliation caused by PFW increased the soil's exposure to solar radiation resulting in higher soil temperatures and a corresponding reduction in development time of prepupae and pupae. Consequently, adult emergence was accelerated by about one week between habitat extremes. PFW occurred at depths of 0-9 cm in the soil. No differences were detected between vertical distributions of the sexes, nor were differences detected between sites. Developmental rate differences and lack of microhabitat differences for the sexes indicated that alteration of the microclimate by defoliation would not affect the sequence of adult emergence.

Development of subterranean stages of PFW was simulated from rate-summation models developed from nonlinear regression equations describing the relationship between temperature and rate of development of subterranean stages. Developmental variability was described by fitting nonlinear regressions to cumulative development as a function of normalized rates. Adult emergence was satisfactorily predicted from soil temperatures recorded at 5 cm. A model was developed that accurately estimated soil temperatures at multiple depths from soil temperatures recorded at two depths. Predictability was enhanced slightly when the distribution of insects and temperature of the soil were incorporated into the model. Increasing the time increment used in the model from 1 to 4 h
did not adversely affect predictability.

Female PPW mate and begin ovipositing soon after emergence from the soil and the majority of PPW eggs were mature and ready for deposition at female emergence. Potential fecundity of PPW at emergence from the ground was accurately predicted from linear relationships with adult wet and dry weights. However, laboratory experiments indicated that PPW females mature some eggs following emergence from the ground. Increased degrees of defoliation by the sawfly resulted in reductions in size of adults emerging from defoliated zones. Consequently, the earliest emerging females had the lowest potential fecundity.

Fecundity of PPW was independent of temperature over the range of temperatures examined. Oviposition and ageing rates of PPW were temperature dependent. Females of PPW are diurnal and oviposition occurred during daylight hours. Oviposition pattern of PPW was also described by a model based on temperature-dependent oviposition and ageing rate functions. Although the model was of value for evaluating population processes, oviposition pattern in the field was more accurately represented by the emergence pattern of adult females from the soil.

The effect of larval web construction on the development of arboreal stages was investigated. When exposed to sunlight, the web traps heat and raises the body temperature of its
inhabitants. Larvae of PFW behaviorally thermoregulate and avoid critical high temperatures by vacating webs. A model was developed and used to examine the significance of the web microclimate for development of larvae. Relationships between web temperatures, canopy temperatures and standard meteorological methods were developed to permit using data from standard weather stations to drive the model. A small dynamic temperature gradient existed within the vertical canopy strata, but the net difference in heat accumulation between strata was minimal. Observed differences in development of larvae of PFW in different canopy strata were therefore attributed to varying degrees of exposure of webs to solar radiation. Egg development was not affected by solar radiation since egg development was accurately predicted using canopy temperatures. Larval development increased by 1.4 to 2.8 d when estimated web temperatures were incorporated into the model, while development was retarded by 2.6 to 4.0 d when canopy temperatures were used instead of meteorological screen temperatures.

As a prerequisite to biological control of this sawfly it was deemed necessary to know what parasitoids attack Ontario populations of the sawfly, their biology and how efficient they were at reducing host populations. Understanding the biology of the existing parasitoid fauna required that immature stages of the parasitoids be distinguishable. Coincidence of host and parasitoid stages in time and space are critical for successful population regulation. Thus, an investigation of the phenology
of the parasitoids was undertaken.

Two ichneumonid parasitoids, *Sinophorus megalodontis* and an undescribed species of *Olesicampe* were reared from eonymphs of PFW. The species are solitary endoparasitoids and univoltine. Although both species have adopted different strategies for subterranean development, the phenology of adults was contemporaneous. The two species of parasitoids were differentiated by morphology of eggs, first-instar larvae and cocoons. Malaise and adult emergence traps indicated the pattern of adult emergence. Malaise traps collected many more adults and also provided information on adult flight period, but were biased towards captures of males. Dissections of host larvae indicated that both parasitoids oviposit in all instars of the host, and temporal and spatial variations occur in synchronization with host instars. Effectiveness of the parasitoids in controlling host populations was also limited by encapsulation, and multi- and superparasitism. There was some indication that parasitism resulted in retardation of host development.

A predictive model for subterranean stages and adults of *Olesicampe* sp. was developed. Predicted emergence was within 3-5 days of observed emergence. Incorporating vertical soil distribution into the model only slightly enhanced the predictions. Reductions in the number of time steps in the model did not change predictions.
Pine false webworm is a suitable candidate for biological control attempts. Few North American parasitoids attack this introduced species and established parasitoids are ineffectual at reducing PFW populations. The biologies of native parasitoids are known and sampling methodologies for assessing success are developed. Phenological models have been developed to accurately predict development of all life stages of PFW during the growing season. Thus, introductions can be made when suitable host stages are available.

Rate-summation models provided accurate estimates of phenological events in the life history of PFW. Development as well as ageing and oviposition could be described using temperature-dependent rate regressions. Inherent variability in development was described as a function of normalized rates. Oviposition and ageing because of their greater variability were more accurately described as functions of normalized time. For most stages, incorporation of empirical functions relating microclimate to meteorological standards greatly increased computational complexity and only slightly enhanced predictions.
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