Development rates of the embryonic and immature stages of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), at constant and fluctuating temperatures

T.L. Blomefield[1] & J.H. Giliomee[2*]

[1]*ARC Infruitec-Nietvoorbij, Private Bag X5026, Stellenbosch, 7599 South Africa*
[2]*Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7062 South Africa*

Development rates of the egg, larval and pupal stages of codling moth, *Cydia pomonella* (Linnaeus), on apples were determined at constant temperatures of 15, 17, 20, 25 and 30 ± 1 °C and at fluctuating temperatures. There was a linear relationship between rate of development and temperature over the range of temperatures used. The lower threshold temperatures for embryonic, larval and pupal development were 11.1, 7.9 and 9.9 °C, respectively. The degree-days required to complete embryonic, larval and pupal development were 80.1, 345.5 and 280.0, respectively. The responses of the different stages of *C. pomonella* to constant temperatures were similar to those under fluctuating temperatures. It is suggested that a base temperature of 10 °C be used in South Africa for calculating degree-days in predicting phenological events such as first egg hatch.

Key words: *Cydia pomonella*, degree-days, developmental rates, phenology, minimum developmental temperature.

INTRODUCTION

The codling moth, *Cydia pomonella* (Linnaeus) (Tortricidae), is a major pest of apples and pears and to a lesser extent stone fruits in South Africa (Pettey 1925; Pettey & Joubert 1926; Myburgh 1963; Myburgh *et al.* 1973; Blomefield 1989).

Previous research has been directed toward determining seasonal occurrence, oviposition behaviour and egg hatch for the improved timing of insecticide sprays for codling moth control in South African pome fruit orchards (Pettey 1932; Nel 1940, 1941; Hattingh 1942, Blomefield *et al*. 1997, Giliomee & Riedl 1998). The identification of the codling moth female sex pheromone (Roelofs *et al.* 1971) made it possible to attract and trap male moths. This led to the development of a monitoring system, and the application of sprays according to a trap catch threshold (Myburgh & Madsen 1975). Despite an improvement in the management of codling moth, the continuing use and heavy reliance on insecticides, increasing concern regarding resistance to insecticides, and the decreasing number of insecticides suitable for an effective resistance management strategy have resulted in concern regarding the correct use and timing of insecticides (Blomefield 1994). The development of an integrated control programme for codling moth, based on minimum use and correct timing of insecticides, requires a thorough understanding of the pest's biology.

Although relative humidity (Shelford 1927), food quality (Hathaway *et al.* 1971) and photoperiod (Riedl & Croft 1978) have been shown to affect the development of codling moth, temperature is considered the most important factor (Wilson & Barnett 1983; Higley *et al.* 1986; Kneifl 1992). The relationship between temperature and development of codling moth was first investigated in detail in Illinois, U.S.A., by Glenn (1922), who used mean daily temperatures to establish the development rates of the various life stages. More recent studies have measured the development rates of codling moth under controlled temperatures (Rock & Shaffer 1983; Pitcairn *et al.* 1991). These field and laboratory studies have provided estimates of the lower threshold temperature for development of codling moth, which varied between 10 and 12 °C. At higher temperatures, Rock & Shaffer (1983) found no decline in the larval and pupal development rate up to 32 °C, while Pitcairn *et al.* (1991) suggested that the upper threshold temperatures for the egg and pupal stages were near 27.8 °C and for the larval stage 32.2 °C.

Using 10 °C as the lower threshold temperature, the average number of degree-days (°D) to complete a generation varied between 611.7 and 631.4 (Glenn 1922; Pitcairn *et al.* 1991). Degree-day

*To whom correspondence should be addressed.
E-mail: jhg@sun.ac.za

accumulations used in conjunction with pheromone trap catches are useful for predicting critical stages in a pest's development, such as egg laying, egg hatch and the seasonal phenology of the pest (Headlee 1931; Batiste *et al.* 1973; Riedl & Croft 1978; Welch *et al.* 1978; Pickel *et al.* 1986; Blago & Dickler 1990; Beers & Brunner 1992; Ahmad *et al.* 1995). Although most phenology models for codling moth use a base temperature of 10 °C as the developmental threshold for all the stages of codling moth (Glenn 1922), there are °D prediction models for egg hatch that use a base temperature of 11.1 °C (Hagley 1973). The objective of this study was to establish which threshold temperature for development should be used in a phenology model for codling moth in South Africa and to determine the °D required to complete the various developmental stages.

MATERIAL AND METHODS

Eggs, larvae and pupae were obtained from a laboratory colony. The colony was started in 1986 from fifth instar larvae collected in corrugated cardboard bands placed around the trunks of trees in an unsprayed apple orchard at the Elgin Research Farm, Elgin, Western Cape (34°09'S 19°02'E) at an elevation of 305 m. Larvae were reared on a wheat-germ diet (Guennelon *et al.* 1981) at 25 ± 3 °C, under continuous illumination by nine 36 watt fluorescent tubes and 50 ± 10 % relative humidity (RH). The moths and pupae were reared at 22 ± 3 °C, an RH of 70 ± 10 % and a photoperiod of 16:8 (L:D).

Egg stage

Egg development was observed at constant temperatures of 15, 17, 20, 25 and 30 ± 1 °C, in incubators with a 16:8 (L:D) photoperiod. The eggs were held in desiccators in which the RH was maintained at 70 % using a potassium hydroxide solution, following the method of Solomon (1951). Eggs of a similar age and quality were obtained by placing 3–5-day-old male and female moths in circular gauze cages 12 cm wide × 9 cm high placed on top of wax paper. After 30 min the wax sheets were removed and cut into 3 × 9 cm strips and the number of eggs per strip counted. Each strip of paper was numbered and attached to a circular wire gauze cage which was placed in a desiccator. Observations at each temperature were replicated four times with the number of eggs in each replicate varying from 60 to 250. Eggs were observed daily until the black-head stage of development and thereafter three times a day until egg hatch. With the commencement of egg hatch, observations were made every 1–3 hours during the light period. The laboratories in which the incubators were held were maintained at a similar temperature and humidity to the incubators.

To determine the effect of fluctuating temperatures (ambient) on egg development, the duration of the egg stage was also observed in an outdoor insectary. The insectary consisted of a wooden floor 30 cm off the ground and a roof covered with bituminous fibre sheeting. The walls consisted of plastic fly-screen. At regular intervals, mostly weekly from October to March, eggs were collected using the method described previously. The paper strips with eggs were attached to a wire gauze cage which was placed in a circular plastic container, 21 cm wide and 11 cm high. To reduce the effects of desiccation, the plastic container was filled with water to a depth of 3–4 cm. The gauze cage was placed on a plastic platform suspended above the water 5 cm from the top of the container. The method of observation was the same as that for constant temperatures. Daily maximum and minimum temperatures from a weather station approximately 100 m from the insectary were used to calculate the mean daily temperature and mean temperature for each incubation period.

Larval stage

Larval development was monitored under the same conditions of constant temperature and photoperiod as for the eggs in a growth chamber at 70 ± 5 % RH. The observations at each temperature were replicated five times and each replicate consisted of 50 mature Granny Smith apples. Each apple was washed in warm water, air-dried and placed in a 550 ml plastic container. Eggs collected from 3–5-day-old moths were maintained at 22 ± 3 °C and 70 ± 10 % RH. On hatching, each neonate larva was transferred individually with a fine brush to an apple. Depending on the size of the apple, the number of larvae per apple varied from 2 to 3. A strip of single-faced corrugated cardboard was placed in each container to provide cocooning sites for the mature larvae leaving the apples. All the containers and cardboard strips were inspected daily for cocoons. On finding a cocoon, the date was recorded and the cocoon

placed in a glass vial plugged with cotton wool. The glass vials were inspected twice daily until moth emergence, and the sex of the moth was recorded.

The duration of the larval stage was also monitored at fluctuating temperatures in the outdoor insectary described above. At fortnightly intervals, from November to March, neonate larvae were transferred to mature Granny Smith apples. Transfer of the larvae and all observations carried out were the same as those used at constant temperatures.

Pupal stage

Pupal development was monitored under the same range of constant temperatures as the larval stage. Each replicate consisted of a minimum of 20 individuals. To obtain cocoons, mature apples were placed in four wooden containers (740 × 510 × 200 mm) in a breeding room at 22 ± 3 °C and 70 % ± 10 % RH and each apple was artificially infested with three neonate larvae as above. Strips of single-faced corrugated cardboard were placed on the top of the apples and along the inside of the containers for pupation, and each container sealed with a screened lid. The cardboard strips were inspected daily between 08:00 and 09:00 and between 15:00 and 16:00. To obtain pupae of a similar age, the cocoons collected between 15:00 and 16:00 were discarded. The cocoons were placed in 300 ml containers sealed with screened lids to allow air flow. The containers were inspected twice daily for moth emergence and recorded.

The duration of the pupal stage was also determined at fluctuating temperatures in the insectary. Larvae were reared on the wheat germ diet in clear plastic containers that were kept in the insectary. Larvae which had emerged the previous night from the artificial rearing medium, and spun cocoons in the corrugated cardboard, were collected every 10 to 14 days from 2 December 1988 to 21 February 1989. The cocoons were placed in 300 ml plastic containers covered with a fine gauze cloth, and inspected daily for moth emergence. The number and sex of each moth was recorded.

Statistical analysis

The lower threshold temperature for development of the embryonic and other immature stages was estimated by linear regression, using the model $1/y = a + bx$, where x = temperature, y = time in days required to complete development, and a and b are regression constants. The threshold temperature for development was obtained by solving for x in $1/y = 0 = a + bx$ (Arnold 1959). The thermal constant for development was calculated as the reciprocal of the slope of each regression equation. The thermal constant was compared to the mean number of °D required for development of each life stage at constant temperatures and at fluctuating temperatures. The mean °D for the development of the embryonic and each immature stage was estimated using the formula of Jackson & Elliott (1988):

$$°D = T(c - T_{min}) ,$$

where T is the mean number of days taken to complete development at a constant temperature (c) and T_{min} is the lower threshold temperature. The estimated development time in days at fluctuating temperatures was obtained by solving for y in $1/y = a + bx$, where x = mean of the maximum and minimum temperatures recorded during each observation period. The number of °D required to complete development at fluctuating temperatures was calculated, using the sine-wave model of Baskerville & Emin (1969), based on daily maximum and minimum temperatures.

RESULTS

Egg stage

The development rates in days and °D at the five constant temperatures are given in Table 1. The number of days required for egg hatch decreased as temperature increased, the means ranging from 19.39 days at 15 °C to 4.23 days at 30 °C. The lower threshold temperature for embryonic development was estimated at 11.06 °C. The mean °D estimate for egg development was 80.1 °D (Table 1), which is comparable to the thermal constant of 80.5 °D as determined in this study.

There was a strong positive linear relationship between the reciprocal of the duration of the egg stage and temperature (Fig. 1). At fluctuating temperatures between 14.87 °C and 17.09 °C the observed incubation period was shorter than the estimated period (Table 2), the difference decreased with increasing temperature. Between 19.26 °C and 27.46 °C the difference between the estimated and observed incubation period was less than 0.58 days and 5.2 °D, respectively. The observed mean °D for development at fluctuating temperatures (Table 2) was similar to the thermal

Table 1. Mean development time in days and degree-days (°D) for *Cydia pomonella* eggs, larvae and pupae at five constant temperatures. Degree-days were calculated using the lower threshold temperature for development determined for each stage (egg = 11.1°C, larva = 7.9 °, pupa = 9.9 °) and also for a base temperature of 10°C.

Stage	Temp (°C)	*n*	Developmental time (days ± S.D.)	Range	°D ± S.D.	°D ± S.D. (base 10°C)
Egg	15	570	19.39 (± 0.622)	18.6–20.8	76.43 (± 2.45)	97.00 (± 3.11)
	17	505	13.76 (± 0.581)	12.0–15.8	81.59 (± 3.45)	96.15 (± 4.07)
	20	574	9.19 (± 0.433)	8.0–10.7	82.15 (± 3.87)	91.90 (± 4.33)
	25	515	5.75 (± 0.220)	5.0–6.9	80.18 (± 3.06)	86.27 (± 3.29)
	30	474	4.23 (± 0.312)	3.8–4.9	80.19 (± 5.91)	84.68 (± 6.24)
Mean					80.1	91.2
Larva						
	15	179	48.94 (± 6.711)	38.0–70.0	347.50 (± 47.60)	244.72 (± 33.55)
	17	196	39.68 (± 6.476)	29.0–61.0	361.12 (± 59.70)	277. 79 (± 45.99)
	20	235	26.19 (± 3.423)	18.0–38.0	316.92 (± 41.40)	261.91 (± 34.23)
	25	224	21.07 (± 3.653)	15.0–34.0	360.25 (± 62.40)	316.00 (± 54.80)
	30	266	15.46 (± 2.316)	12.0–26.0	341.55 (± 54.40)	309.10 (± 49.56)
Mean					345.5	281.9
Pupa						
	15	215	56.25 (± 10.065)	42.0–109.0	288.41 (± 51.60)	281.28 (± 50.79)
	17	164	37.90 (± 3.510)	31.0–53.0	270.20 (± 25.00)	265.27 (± 24.58)
	20	156	27.48 (± 3.474)	22.0–43.0	278.38 (± 35.00)	274.81 (± 34.63)
	25	166	18.88 (± 4.082)	14.0–34.0	285.64 (± 61.70)	282.18 (± 60.01)
	30	173	13.78 (± 2.233)	11.0–27.0	277.40 (± 44.90)	275.61 (± 44.66)
Mean					280.0	275.8

constant obtained for constant temperatures. The variation between the estimated and the observed incubation period at the lower temperatures is probably a reflection of the nonlinear relationship between temperature and rate of development at the lower temperatures (Higley *et al.* 1986; Pitcairn *et al.* 1991), although a linear model is used for determining the estimate. At all constant tempera-

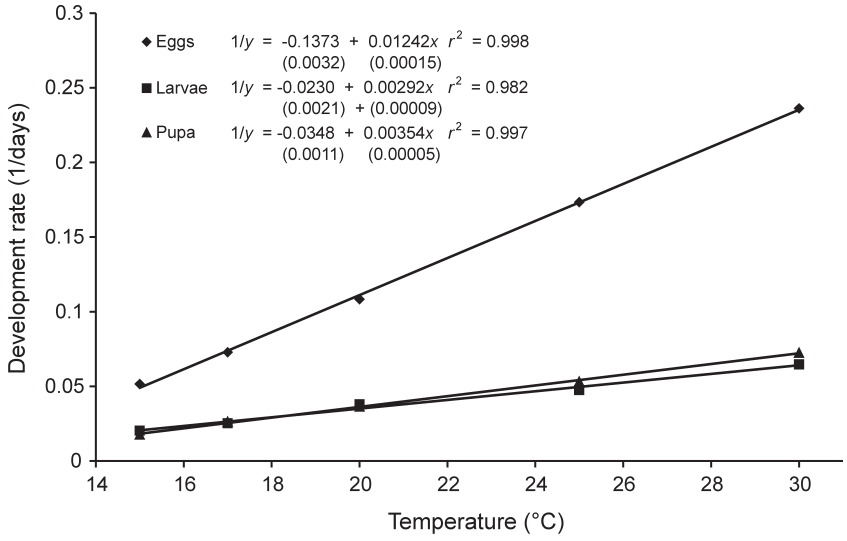

Fig. 1. Rate of *Cydia pomonella* eggs, larvae and pupa development at five constant temperatures. The symbols represent the mean development rate at each temperature with the standard errors in brackets.

Table 2. Mean observed development times, estimated development times, and mean observed degree-days (°D) required for development of *Cydia pomonella* eggs, larvae and pupae at fluctuating temperatures. Degree-days were calculated using the lower threshold temperature for development determined for each stage (egg =11.1 °C, larva = 7.9 °C, pupa = 9.9 °C).

Stage	Mean temperature (°C)	*n*	Observed development time (days ± S.D.)	Estimated development time (days)	Observed °D (±S.D.)
Egg	14.87	115	15.51 (± 0.161)	21.11	72.04 (± 7.964)
	15.47	117	13.90 (± 0.390)	18.24	68.54 (± 2.645)
	16.10	138	12.49 (± 0.588)	15.96	72.37 (± 8.660)
	17.09	138	11.63 (± 0.117)	13.34	66.72 (± 1.459)
	19.26	122	9.23 (± 0.382)	9.81	82.77 (± 4.090)
	20.15	169	8.95 (± 0.171)	8.85	84.95 (± 4.841)
	20.66	159	8.57 (± 0.207)	8.38	93.04 (± 4.976)
	22.27	188	6.97 (± 0.216)	7.18	87.50 (± 6.011)
	23.08	156	6.95 (± 0.272)	6.70	78.80 (± 5.628)
	27.46	123	6.67 (± 0.054)	6.49	78.81 (± 0.001)
Mean			10.09	11.61	78.55
Larva	19.67	62	30.06 (± 4.602)	29.28	30.06 (± 4.602)
	20.17	88	29.72 (± 4.741)	28.09	29.72 (± 4.741)
	21.03	74	24.20 (± 3.990)	26.25	24.20 (± 3.990)
	22.01	73	25.52 (± 3.069)	24.43	25.52 (± 3.069)
	22.15	133	24.68 (± 5.140)	24.19	24.68 (± 5.140)
	22.99	95	23.26 (± 3.955)	22.84	23.26 (± 3.955)
	23.38	90	23.67 (± 3.573)	22.27	23.67 (± 3.573)
	23.40	119	23.33 (± 3.811)	22.24	23.33 (± 3.811)
Mean			22.56	24.95	367.19
Pupa	22.30	191	23.88 (± 2.743)	22.47	279.62 (± 39.480)
	22.26	143	24.07 (± 2.838)	22.54	291.98 (± 47.648)
	23.30	97	20.33 (± 2.947)	22.79	289.33 (± 37.093)
	22.97	124	21.04 (± 3.933)	21.27	290.40 (± 31.698)
	22.67	164	21.14 (± 2.036)	21.83	274.77 (± 27.459)
	23.15	127	20.19 (± 1.607)	21.02	276.72 (± 21.904)
	23.70	163	19.20 (± 1.825)	20.18	282.37 (± 26.450)
Mean			21.41	21.72	283.60

tures a sharp increase in egg hatch was observed 1–2 hours after commencement of the light phase.

Larval stage

The duration of larval development decreased from 48.94 days at 15 °C to 15.46 days at 30 °C (Table 1). Males and females required approximately an equal number of days at each constant temperature to complete development (Table 3) and for this reason male and female data were pooled when determining the °D requirements for the larval stage. The estimated lower threshold temperature for larval development was 7.89 °C and the mean °D estimate for development was 345. 5 °D (Table 1), which is comparable to the thermal constant of 344.9 °D. There was a strong positive linear relationship between the reciprocal of the duration of the larval stage and temperature (Fig. 1). At varying temperatures the difference between the observed development times and estimated larval development times was mostly less than 2 days or 28.5 °D (Table 2). Male and female development rates under fluctuating temperatures were also very similar (Table 4).

Pupal stage

The duration of pupal development ranged from 56.25 days at 15 °C to 13.78 days at 30 °C (Table 1). The estimated lower threshold temperature for pupal development was 9.89 °C and the mean °D estimate for development was 280 °D, which is comparable to the thermal constant of

Table 3. Mean development time (days) of *Cydia pomonella* male and female larvae and pupae at five constant temperatures.

Temperature (°C)	Development time (days ± S.D.)			
	Male			
	n	Larva	*n*	Pupa
15	81	47.80 (± 6.435)	111	56.25 (± 9.915)
17	100	38.87 (± 6.326)	88	37.91 (± 3.358)
20	123	25.85 (± 3.234)	65	27.94 (± 3.588)
25	121	20.66 (± 3.572)	81	19.69 (± 4.443)
30	135	15.15 (± 2.796)	86	13.99 (± 2.364)
	Female			
	n	Larva	*n*	Pupa
15	63	49.05 (± 6.797)	102	56.07 (±10.305)
17	81	40.05 (± 6.569)	76	37.88 (± 3.702)
20	110	26.58 (± 3.626)	91	27.13 (± 3.702)
25	102	21.53 (± 3.799)	83	17.98 (± 3.407)
30	126	15.84 (± 2.207)	87	13.59 (± 2.084)

278.6 °D (Table 1). The mean °D accumulations at each of the temperatures tested were comparable with the mean degree-day estimate, differing by 9 °D**.** There was a strong positive linear relationship between the reciprocal of the duration of the larval stage and temperature (Fig. 1). Development rates for males and females at each constant temperature were also very similar (Table 3). At fluctuating temperatures the observed and estimated development times were very similar (Table 2), differing by between 3.2 and 35.0 °D. Male and female development rates were also very similar (Table 4).

DISCUSSION

The relationships between temperature and the development rate of codling moth eggs, larvae and pupae were strongly linear over the range of temperatures tested. The marked increase in the development time at 15 °C indicated that this and lower temperatures fall in the unfavourable range for codling moth development. Estimates of the lower threshold temperature for the egg, larval, and pupal development were 11.06 °C, 7.89 °C, 9.89 °C, respectively, suggesting that the egg stage

Table 4. Mean development times (days) of *Cydia pomonella* male and female larvae and pupae at fluctuating temperatures.

Stage	Mean temp. (°C)	Mean development time (days ± S.D.)			
		n	Male	*n*	Female
Larva	21.03	21	22.57 (± 2.821)	26	24.46 (± 4.420)
	21.67	25	21.12 (± 4.693)	31	22.16 (± 4.576)
	22.01	28	26.18 (± 3.031)	37	26.62 (± 2.994)
	22.99	33	22.33 (± 3.663)	40	23.34 (± 3.759)
	23.38	15	23.53 (± 4.749)	27	23.44 (± 3.388)
Pupa	22.26	92	24.48 (± 3.307)	51	23.33 (± 1.451)
	22.67	112	21.40 (± 2.165)	51	20.57 (± 1.510)
	22.97	82	21.55 (± 2.846)	42	20.67 (± 1.748)
	23.15	72	20.15 (± 1.607)	55	20.24 (± 1.621)
	23.30	60	20.67 (± 2.995)	39	19.95 (± 2.724)
	23.70	90	19.30 (± 1.748)	71	19.07 (± 1.923)

Table 5. Summary of mean °D requirements for the egg, larva and pupa of *Cydia pomonella* from its present study and for comparison purposes those of Glenn (1922), Pitcairn (1991) and Riedl & Croft (1978).

Stage	Present study	Glenn (1922)	Pitcairn *et al.*(1991)	Riedl & Croft (1978)
Egg	80.1	90.6	93.9	87.8
Larva	345.5	373.9	280.6	295.5
Pupa	280.0	147.2	256.0	142.2
Total	705.6	611.7	631.5	525.5

is more sensitive to low temperatures than either the larval or pupal stages. Estimates of the lower threshold temperatures obtained for egg and pupal development are comparable to those of Glenn (1922), who concluded from thermal summations under varying temperature conditions that the lower threshold temperature for the egg and larva was approximately 10 °C, while that for the pupa was 11 °C. However, he suggested that the lower threshold temperature for the egg may be greater than 10 °C.

Hagley (1972) reported a lower threshold temperature of 11 ± 1 °C for the egg stage. By contrast to our data, Pitcairn *et al.* (1991) found that the estimates of the lower threshold temperature for the egg, larva and pupa were 10.56, 11.54 and 12.49 °C, respectively, suggesting that the larval and pupal stages, and not the egg stage as in the present study, were the most sensitive stages to low temperatures. Rock & Shaffer (1983), who studied developmental times from neonate larvae to newly emerged adults, obtained a lower threshold temperature of 9.9 °C for the larval and pupal stage. This estimate is very similar to the lower threshold temperature estimated for the pupal stage in this study. Howell & Neven (2000) reported lower threshold temperatures of 6.9, 9.3 and 10.3 °C for the larval stage depending on how many points that deviated from linearity were used to calculate the lower threshold. These authors suggest that codling moth development time can be more accurately determined in the field using field-simulated temperature data than constant temperatures.

The mean °D estimates required to complete development of the egg, larval and pupal stages in this study were 80.1, 345.5 and 280 °D, respectively representing 11.35, 48.97 and 39.68 % of the mean duration of a total developmental period of 705.6 °D. The °D requirements for the egg, larval and pupal stages and mean duration for total development of codling moth were higher in this study than those given by other researchers (Table 5). The °D requirements presented by Glenn (1922), Riedl & Croft (1978), Rock & Shaffer (1983) and Pitcairn *et al.* (1991) are all based on a threshold temperature of 10 °C. Using the most commonly reported lower threshold temperature for development of 10 °C (Pitcairn *et al.* 1991), the average number of °D required to complete development of the egg, larval and pupal stages in this study would be 91.2, 281.9 and 275.8 °D, respectively (Table 1). The mean duration of total development would be 649.10 °D, which is comparable to that of Pitcairn *et al.* (1991) and Glenn (1922). Using a lower threshold temperature of 10 °C and the five fastest development times for each replication in this study of each life stage, the development times for the egg, larvae and pupae were 82.20, 215.38 and 239.58 °D, respectively. Based on these figures the minimum period for a generation was 505 °D, which is very similar to the minimum generation time of 525.5 °D given by Riedl & Croft (1978). At a base of 10 °C the larval and pupal development times are similar to those of Rock & Shaffer (1983).

At fluctuating temperatures the egg, larval and pupal stages required a mean of 78.55, 367.19 and 283.60 °D, respectively, to complete development with a mean duration of 729.6 °D for the total development period. The average number of °D to complete a life cycle, from egg to adult, under variable temperature conditions was similar to that obtained at constant temperatures (705.6 °D). The greatest variation occurred during the incubation period at average ambient temperatures below 17.19 °C. This is attributed to night and early morning temperatures on numerous occasions falling below 8.5 °C, which is below the developmental threshold of the egg, and a decrease in the linear relationship between temperature and time at temperatures below 17 °C. However, the similarity in °D requirements under constant and variable temperature conditions suggests that the estimates

of the lower threshold temperatures can be incorporated into a phenology model.

It is important to decide on the lower threshold temperature for development to be used in calculating °D for predicting phenological events such as first egg hatch, median egg hatch and the emergence of further generations. In the literature this has been reported to range from 8 °C to 11.1 °C (Howell & Neven 2000), but the most commonly reported temperature is 10 ° (Pitcairn *et al.* 1991). In this study it varied from 7.89 °C for the pupal stage to 11.06 °C for the egg stage. Although a lower threshold temperature was determined for each of the immature stages of codling moth in this study, it would be more practical to select the most universally applied lower threshold temperature for codling moth, 10 °C, incorporate it in a phenology model and evaluate the model's accuracy to predict key events in the seasonal occurrence of codling moth under field conditions. Using the mean development time taken from egg oviposition to adult emergence at the five constant temperatures, a minimum threshold temperature was estimated by the linear regression model $1/y = a + bx$. A minimum developmental temperature of 9.3 °C was estimated ($1/y = -0.1330 + 0.00143$, $r^2 = 0.006$). The authors consider this to be sufficiently close to 10 °C to justify using the universally applied lower threshold temperature in a phenology model in South Africa.

Under cool conditions egg hatch may occur several weeks after full-bloom and commencement of the spring flight. The use of a phenology model to accurately predict the commencement of first flight and first egg hatch, can improve the timing of the installation of pheromone traps, mating disruption applications, cover sprays and reduce spraying and spray costs. Information on °D requirements will also lead to a better understanding of the seasonal occurrence of codling moth and assist growers in determining the reasons for control failure. Future studies will be undertaken under field conditions using the lower threshold temperature of 10 °C to evaluate the validity of the phenology model under South African conditions with respect to determining first egg hatch of the spring eggs, the number of accumulated °D from biofix to first egg hatch and full-bloom, prediction of the commencement of the second and third flights, and the accuracy of °D predictions based either on hourly or minimum and maximum temperatures. All of these aspects are critical to the sustainable management of codling moth.

ACKNOWLEDGEMENTS

We would like to thank F. Calitz of the Agricultural Research Council's Agrimetrics Institute and K.L. Pringle of the University of Stellenbosch for their assistance with the statistical analyses.

REFERENCES

AHMAD, T.R., ALI, M.A. & HAMAD, B. SH. 1995. Using degree-days model to determine the optimum spray timing for the codling moth *Cydia pomonella* (L.) (Lep., Olethreutidae). *Journal of Applied Entomology* **119**: 143–144.

ARNOLD, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. *Proceedings of the American Society for Horticultural Science* **74**: 430–445.

BASKERVILLE, G.L. & EMIN, P. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology* **50**: 514–517.

BATISTE, W.C., BERLOWITZ, A., OLSON, W.H., DETAR, J.E. & JOOS, J.L. 1973. Codling moth: Estimating time of first egg hatch in the field – a supplement to sex-attractant traps in integrated control. *Environmental Entomology* **2**: 387–391.

BEERS, E.H. & BRUNNER, J.F. 1992. Implementation of the codling moth phenology model on apples in Washington State, U.S.A. *Acta Phytopathologica et Entomologica Hungarica* **27**: 97–102.

BLAGO, N. & DICKLER, E. 1990. Effectiveness of the Californian prognosis model 'Bugoff 2' for *Cydia pomonella* L. (Lepidoptera, Tortricidae) under Central European conditions. 2nd International Symposium on Computer Modelling in Fruit Research and Crop Management. *Acta Horticulturae* **276**: 53–62.

BLOMEFIELD, T.L. 1989. Economic importance of false codling moth, *Cryptophlebia leucotreta,* and codling moth, *Cydia pomonella* on peaches, nectarines and plums. *Phytophylactica* **21**: 435–436.

BLOMEFIELD, T.L. 1994. Codling moth resistance: is it here, and how do we manage it? *Deciduous Fruit Grower* **44**: 130–132.

BLOMEFIELD, T.L., PRINGLE, K.L. & SADIE, A. 1997. Field observations on oviposition of codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Olethreutidae), in an unsprayed apple orchard in South Africa. *African Entomology* **5**: 319–336.

GILIOMEE, J.H. & RIEDL, H. 1998. A century of codling moth control in South Africa 1. Historical perspective. *Journal of the Southern African Society for Horticultural Sciences* **8**: 27–31.

GLENN, P.A. 1922. Relation of temperature to development of the codling moth. *Journal of Economic Entomology* **15**: 193–198.

GUENNELON, G., AUDEMARD, H., FREMOND, J. & EL IDRISSI AMMARI, M.A. 1981. Progrès réalisés dans l'élevage permanent du *Carpocapse* (*Laspeyresia pomonella* L.) sur milieu artificiel. *Agronomie* **1**: 59–64.

HAGLEY, E.A.C. 1972. Observations on codling moth longevity and egg hatchability. *Environmental Entomology* **1**: 123–125.

HAGLEY, E.A.C. 1973. Timing sprays for codling moth (Lepidoptera: Olethreutidae) control on apple. *Canadian Entomologist* **105**: 1085–1089.

HATHAWAY, D.O., CLIFT, A.E. & BUTT, B.A. 1971. Development and fecundity of codling moths reared on artificial diets or immature apples. *Journal of Economic Entomology* **64**: 1088–1090.

HATTINGH, C.C. 1942. A study of codling moth oviposition in a mixed pear orchard. *Journal of the Entomological Society of Southern Africa* **5**: 137–146.

HEADLEE, T.J. 1931. Performance of the thermal constant as an indicator of the time to apply cover sprays for codling moth. *Journal of Economic Entomology* **24**: 291–296.

HIGLEY, L.G., PEDIGO, L.P. & OSTLIE, K.R. 1986. DEGDAY: a program for calculating degree-days, and assumption behind the degree-day approach. *Environmental Entomology* **15**: 999–1016.

HOWELL, J.F. & NEVEN, L.G. 2000. Physiological development time and zero development temperature of the codling moth (Lepidoptera: Tortricidae). *Environmental Entomology* **29:** 766–772.

JACKSON, J.J. & ELLIOTT, N.C. 1988. Temperature-dependent development of immature stages of the western corn rootworm, *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae). *Environmental Entomology* **17**: 166–171.

KNEIFL, V. 1992. A temperature-based method for the aimed chemical control of codling moth (*Laspeyresia pomonella* L.) *Acta Phytopathologica et Entomologica Hungarica* **27**: 349–352.

MYBURGH, A.C. 1963. The codling moth – the background to the problem. *Deciduous Fruit Grower* **13**: 313–316.

MYBURGH, A.C., WHITEHEAD, V.B. & DAIBER, C.C. 1973. Pests of deciduous fruit, grapes and miscellaneous other horticultural crops in South Africa. *Department of Agricultural Technical Services, Republic of South Africa. Entomology Memoir* **27**: 1–38.

MYBURGH, A.C. & MADSEN, H.F. 1975. Interpretation of sex trap data in codling moth control. *Deciduous Fruit Grower* **25**: 272–275.

NEL, R.I. 1940. The validity of the bait-trap method of spray timing in codling moth control. *Department of Agriculture and Forestry, Union of South Africa. Entomology Memoirs* **2**: 55–76.

NEL, R.I. 1941. Varietal interplanting in relation to control of the codling moth. *Journal of the Entomological Society of Southern Africa* **4**: 111–134.

PETTEY, F.W. 1925. Codling moth in apricots. Preliminary report on the biology of the codling moth and its control in apricots, Wellington, during the 1924–25 fruit season. Union of South Africa. *Journal of the Department of Agriculture* **11**(1): 56–65; **11**(2) 137–152.

PETTEY, F.W. 1932. The codling moth and measures for its control in South Africa. *Department of Agriculture, Union of South Africa. Bulletin* **108**: 1–36.

PETTEY, W.C. & JOUBERT, C.J. 1926. Codling moth in apricots: report of studies of codling moth at Wellington during the 1925–26 fruit season. *Union of South Africa, Journal of Department of Agriculture* **12**: 461–483.

PICKEL, C. BETHELL, R.S. & COATES W.W. 1986. Codling moth management using degree-days. University of California IPM Publication **4**: 1–7.

PITCAIRN, M.J., PICKEL, C., FALCON, L.A. & ZALOM, F.G. 1991. Development and survivorship of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) at ten constant temperatures. *Pan-Pacific Entomologist* **67**: 189–194.

RIEDL, H. & CROFT, B.A. 1978. The effects of photoperiod and effective temperatures on the seasonal phenology of the codling moth (Lepidoptera: Tortricidae). *Canandian Entomologist* **110**: 455–470.

ROCK, G.C. & SHAFFER, P.L. 1983. Developmental rates of codling moth (Lepidoptera: Olethreutidae) reared on apple at four constant temperatures. *Environmental Entomology* **12**: 831–834.

ROELOFS, W.L., COMEAU, A., HILL, A. & MILICEVIC, G. 1971. Sex attractant of the codling moth: characterization with electroantennogram technique. *Science* **174**: 297–299.

SHELFORD, V.E. 1927. An experimental investigation of the relations of the codling moth to weather and climate. *Bulletin of the Illinois Natural History Survey* **16**: 311–440.

SOLOMON, M.E. 1951. Control of humidity with potassium hydroxide, sulphuric acid or other solutions. *Bulletin of Entomological Research* **42:** 543–554.

WELCH, S.M., CROFT, B.A., BRUNNER, J.F. & MICHELS, M.F. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. *Environmental Entomology* **7**: 487–494.

WILSON, L.T. & BARNETT, W.W. 1983. Degree-days: an aid in crop and pest management. *California Agriculture* **37**: 4–7.

Accepted 30 July 2009