

## Developmental parameters and voltinism of the painted apple moth, *Teia anartoides* Walker (Lepidoptera: Lymantriidae) in New Zealand

John G. Charles<sup>1</sup>, John M. Kean<sup>2</sup>, Asha Chhagan<sup>1</sup>

<sup>1</sup>HortResearch, Private Bag 92 169, Auckland, New Zealand. E-mail: jcharles@hortresearch.co.nz

<sup>2</sup>AgResearch Limited, PO Box 60 Lincoln, New Zealand.

### Abstract

Key developmental parameters, including the lower threshold temperature for development and thermal accumulation requirements, of *T. anartoides* reared on an artificial diet were determined. The median number of days required to complete development was measured for each life stage at constant mean temperatures of 6.7, 10.2, 12.6, 17.7, 21.9, 22.5 and 30°C. Rate of development was a linear function of temperature over a range that can be realistically expected in New Zealand, and minimum rates of development were estimated by extrapolation. Eggs failed to emerge at temperatures below 10.2°C. Some neonate larvae survived for 60 days at 6.7°C, but failed to develop. At higher temperatures, larvae usually developed through 4 and 5 instars to males and females respectively, with generation developmental times of 71 and 76 days at 17.7°C, and 33 and 34 days at 30°C (for males and females respectively). Optimum temperatures for development lay between 17.7 and 22.5°C. Female developmental requirements above a base temperature of 9.6°C were 616 day-degrees per generation, consisting of 119 day-degrees for egg hatch plus 497 day-degrees for larval and pupal development. Historical weather data from sites around New Zealand suggest that *T. anartoides* might develop through 1.4 generations/year in the south of the South Island and 4 generations/year in the north of the North Island. The data indicate that the moth might realistically establish at any coastal site around New Zealand, and vary from uni-voltine in the south to tri-voltine in the north, depending on a number of factors including host plant.

**Keywords:** threshold temperature, thermal requirements, pest status

### Introduction

The painted apple moth (PAM), *Teia anartoides* Walker (Lepidoptera: Lymantriidae) is native to the south-east of Australia (Common 1990). Its primary native host plants are species of wattles (*Acacia*, Mimosaceae), but it has been a minor pest of several exotic commercial and garden plants for more than 100 years. When PAM was found in New Zealand in 1999 its known host plants from Australia and New Zealand in the Mimosaceae, Fabaceae, Myrtaceae, Santalaceae and Solanaceae suggested that it might be a potentially severe economic and environmental pest, and an eradication programme was soon initiated.

The life-history and biology of PAM in Australia is largely unknown, apart from brief descriptions of life stages, damage and an initial note on development on "geranium" at ambient temperatures in Sydney (Smithers 1966). Unlike many pest Lymantriidae (e.g., gypsy moth, *Lymantria dispar*) in the Northern Hemisphere, PAM does not diapause but continues to develop slowly through the winter on evergreen hosts. The geographical range of PAM in Australia suggested that, should it establish in New Zealand, it would spread throughout the latitudinal limits of the country. However, with a climate varying from subtropical in the north to cool temperate in the south, the number of generations per year, and hence pest status, might vary substantially in different regions.

Research to support eradication aimed to measure key parameters for development of PAM, including the lower threshold temperature for development and thermal accumulation requirements, so that the potential voltinism of the insect in New Zealand could be described. These parameters, together with ecological data collected from the field, could then be used in subsequent population models to predict its potential pest status and help optimise the eradication or, should that fail, subsequent control strategies.

## Materials and Methods

### *Experimental procedure for measuring*

#### *PAM development at constant temperatures*

Experiments were initiated at the HortResearch Mt Albert Research Centre, Auckland, in March 2002, with PAM from a laboratory colony reared on artificial diet and maintained at 25°C. The colony was established in November 2001 from wild insects collected from Auckland. The artificial diet was that used for rearing gypsy moth (Odell *et al.*, 1984), modified by the addition of ferric phosphate (1 g/kg) and the antibiotics streptomycin, penicillin (both 0.15 g/kg) and fumagillin (1 g/kg) (A. Barrington, HortResearch, *pers. comm.*). Experimental eggs and neonate larvae, all obtained from the laboratory colony, were reared in different incubators with a 16 h:8 h photoperiod at nominal constant temperatures of 7, 10, 13, 17, 21, 25 and 30°C. Exact temperatures were recorded hourly by Tinytalk® temperature loggers.

Two egg clusters, of >100 eggs each, were held in 500 ml plastic containers at each temperature, and the time to eclosion recorded for all eggs that hatched. Similarly, daily development and mortality of 40 neonate larvae (<24 h old) were measured at each temperature. Neonate larvae were removed from egg batches and transferred to 30 ml plastic cups with ventilated plastic lids containing a c. 2 cm<sup>3</sup> block of artificial diet, where they were reared individually until pupation. Diet cubes were replaced before they dried out or as required to ensure a continuous food supply. Individual pupae were removed from their cocoons, then sexed, weighed and measured (length), before being held in new 30 ml plastic cups until emergence. The developmental time for each larval instar and pupa was recorded daily, and the total time from neonate larva to adult at each temperature was calculated.

#### *Thermal requirements for development*

The reciprocal of the median number of days required to complete development of each life stage,  $D$ , was used to estimate the developmental rate ( $d = 1/D$ ), at each temperature  $T$ . Developmental rate was assumed to be a linear function of temperature such that

$$d = (T-b)/q \quad (1)$$

where  $b$  is the threshold base temperature for development and  $q$  is the day-degree accumulation required to complete development. Therefore  $d$  was regressed on  $T$ , with  $b$  estimated as  $-y$ -intercept/slope, and  $q$  as  $1/\text{slope}$ . There was no need to fit more complicated non-linear developmental rate curves (e.g., Logan 1988) because the data were linear over the temperature range expected for most of the time in the wild. In some cases, fitting  $d$  as a function of  $T$  can lead to different results to those from fitting  $D$  to  $T$  (Kramer *et al.* 1991), so the estimate base temperature  $b$  and thermal requirement  $q$  were checked by fitting the hyperbolic relationship  $D = q/(T-b)$ .

The thermal requirements for development of each larval instar were estimated as proportions of the total larval requirement, using the data from those individuals that successfully completed development to adulthood. Some larvae died during development, mostly during moulting. Mortality was assumed to result from physiological complications at moulting, rather than an accumulated lack of fitness, and so the developmental times of immature larvae that died at different instars were taken as an independent data set. This data set was used to test the estimated developmental requirements for each larval stage and the base temperature for larval development.

The variability in the developmental rates of each life stage was quantified using the method of Wagner *et al.* (1984). Non-linear regression was used to fit the two-parameter logistic approximation for a cumulative Gaussian curve (Dennis *et al.* 1986) to cumulative normalised developmental rate data

$$y = \left( 1 + \exp \left[ \frac{-\pi(x - \mu)}{\sigma\sqrt{3}} \right] \right)^{-1} \quad (2)$$

where  $\mu$  is the midpoint (mean) and  $\sigma$  is the spread (standard deviation).

#### *Estimating voltinism throughout New Zealand*

The total number of day-degrees required for development from egg to adult emergence was estimated by fitting equation 1 to the developmental data for egg and female larva + pupa using a common base temperature,  $b_c$ . Because female

PAM oviposit within a few hours of emergence and mating, with effectively no pre-oviposition period after emergence, this summation estimated the thermal requirements required to complete a generation.

Temperature data were obtained from climate stations close to each of New Zealand's eleven major seaports, the most likely entry sites for future incursions. Long-term (in most cases 1985-2004) daily temperature data (National Institute for Water and Atmosphere (NIWA) database) were used to estimate daily thermal accumulation  $a$ , as a weighted mean:

$$a = \frac{[T_{min} - b_c] + [T_{max} - b_c] + 2[T_{mean} - b_c]}{4} \quad (3)$$

where  $T_{min}$ ,  $T_{max}$ , and  $T_{mean}$  are the daily minimum, maximum, and mean temperatures respectively, and the quantities inside square brackets are set to 0 if negative (Barlow and Dixon 1980). In the case of Lyttelton, the nearest climate station was Le Bons Bay, on the exposed hills of eastern Banks Peninsula, 236 m above the sea. On examination, it became clear that the readings from this station were not a good indication of conditions on the low Canterbury Plains to the west of Lyttelton. Therefore, analyses were carried out using temperatures from both Le Bons Bay to the east and Lincoln to the west, as indicators of potential climates in the vicinity of Lyttelton Harbour.

The mean annual thermal accumulation for each location was calculated from a mid-winter biofix (1 July – 30 June) to capture the entire New Zealand growing season. The average annual thermal accumulation was then divided by the total generational day-degree requirement to estimate the number of generations per year that might be expected at each location. The annual variation in thermal summations gave some indication of how variable these estimates might be from one year to the next. The resulting estimates of voltinism represent probable maxima, since they are based on laboratory results on an artificial diet designed to be highly nutritious and lacking inhibitory plant defensive compounds.

## Results

Actual mean temperatures recorded by data loggers in the different incubators over the course of the experiment were 6.7, 10.2, 12.6, 17.7, 21.9, 22.5 and 30°C.

### *PAM development at constant temperatures* Eggs

No eggs emerged at either 6.7 or 10.2°C. At 12.6°C, eggs emerged during a ten-day period from 34 days after oviposition. Eggs developed and emerged apparently normally over the temperature range from 17.7 to 30°C, but only a few larvae hatched at 30°C. Microscopic examination of the remaining eggs showed that most had completed development to a fully formed larva, which had then failed to completely cut open the eggshell to emerge. Hence measured mortality may have been due to other sub-optimal experimental conditions at 30°C (e.g., low humidity) rather than temperature inhibition of development *per se*.

### Larvae and pupae

Neonate larvae reared at 6.7°C were sufficiently active to feed. Many survived for >60 days but none developed beyond first instar. The temperature *per se* was sub-lethal, because individual 60 day-old first instar larvae, when transferred to 23°C, developed apparently normally to adults. At 10.2°C, 50% of neonate larvae moulted to second instar before ultimately dying at various ages up to 102 days. At 12.6°C, almost 50% of the larval cohort developed to final instar. Of these, about 12% spun cocoons or pupated, but none was able to complete development to adult emergence.

Over the temperature range from 17.7 to 30°C, generation developmental times (from oviposition to adult emergence) varied from 71 and 76 days at 17.7°C to 33 and 34 days at 30°C for males and females respectively (Table 1). For the cohorts at different temperatures survival to adult emergence ranged from 68-80%, and highest mortality occurred during the early larval and pupal stages. Larvae usually developed through 4 and 5 instars to adult males and females respectively, although an additional instar in each sex was sometimes recorded. Development times for eggs and larval instars 1-3 were the same for both sexes, but development times for the final instars of females were longer than for males, while pupal

development was longer for males (Figure 4).

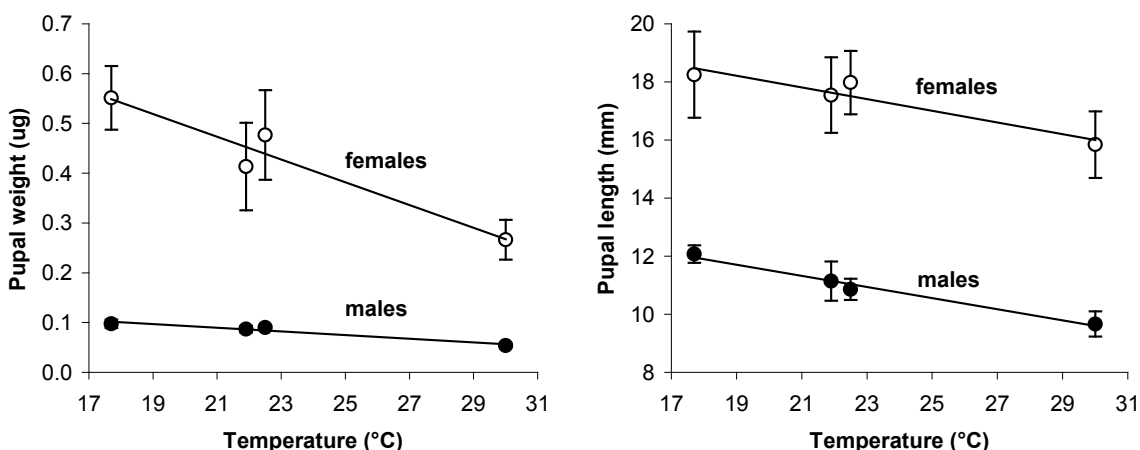
Female PAM pupae (and hence adults) were consistently heavier and larger than males at all temperatures (Figure 1). Both sexes were larger at lower temperatures, and both pupal weights and lengths declined linearly with higher temperatures (♂ pupal wt =  $-0.003697t + 0.1677$  [n= 64  $R^2 = 0.61$ ,  $p < 0.001$ ]; ♀ pupal wt =  $-0.2272t + 0.95$  [n=38,  $R^2 = 0.35$ ,  $p < 0.001$ ]; ♂ pupal length =  $-0.1912t + 15.32$  [n=64,  $R^2 = 0.42$ ,  $p < 0.001$ ]; ♀ pupal length =  $-0.2022t + 22.1$  [n=38,  $R^2 = 0.14$ ,  $p < 0.013$ ]) (Figure 1).

**Thermal requirements for development**

The rates of development of PAM life stages were linear up to 23°C, but usually decreased at 30°C (Figure 2). As the data at 30°C suggested that this temperature was sub-optimal for development, they were excluded from further analyses. Equation 1 fitted to the remaining data suggests a base temperature for development of  $b_c = 9.6^\circ\text{C}$  (Table 2). This was corroborated by the independent results from larval instars 1 to 3 that failed to complete their development (Table 2).

**Table 1: Mean developmental period  $\pm$  95% confidence value (days) for PAM life stages at different temperatures. Dashes indicate that eggs and/or larvae failed to develop at these temperatures.**

Temperature °C	egg	larva		pupa		total (egg + larva + pupa)	
		female	male	female	male	female	male
6.75	-	-	-	-	-	-	-
10.24	-	-	-	-	-	-	-
12.6	37.1 $\pm$ 0.8	-	-	-	-	-	-
17.7	14.7 $\pm$ 0.1	50.0 $\pm$ 2.4	36.5 $\pm$ 2.1	11.7 $\pm$ 0.9	19.7 $\pm$ 0.5	76.4 $\pm$ 2.2	70.9 $\pm$ 1.9
21.9	10.3 $\pm$ 0.1	32.4 $\pm$ 1.8	23.9 $\pm$ 1.7	8.3 $\pm$ 0.7	13.7 $\pm$ 0.4	50.8 $\pm$ 2.3	47.7 $\pm$ 1.6
22.5	9.4 $\pm$ 0.1	31.7 $\pm$ 2.5	21.2 $\pm$ 0.6	7.3 $\pm$ 0.4	12.7 $\pm$ 0.3	48.8 $\pm$ 2.5	43.3 $\pm$ 0.9
30	7.8 $\pm$ 0.3	20.2 $\pm$ 2.0	16.3 $\pm$ 1.0	6.0 $\pm$ 0.4	8.6 $\pm$ 0.8	34.1 $\pm$ 2.0	32.7 $\pm$ 1.1



**Fig. 1.** Influence of temperature on PAM pupal weight (left) and length (right). ● = mean values for males; ○ = mean values for females. Error bars show 95% confidence intervals. Error bars for males lie within the dots.

Equation 2 modelled the variability in the development of PAM life stages very well (Table 3, Figure 3), and provided a better fit than the alternative logistic functions of Régnière (1984) or the Weibull function (Wagner *et al.* 1984),

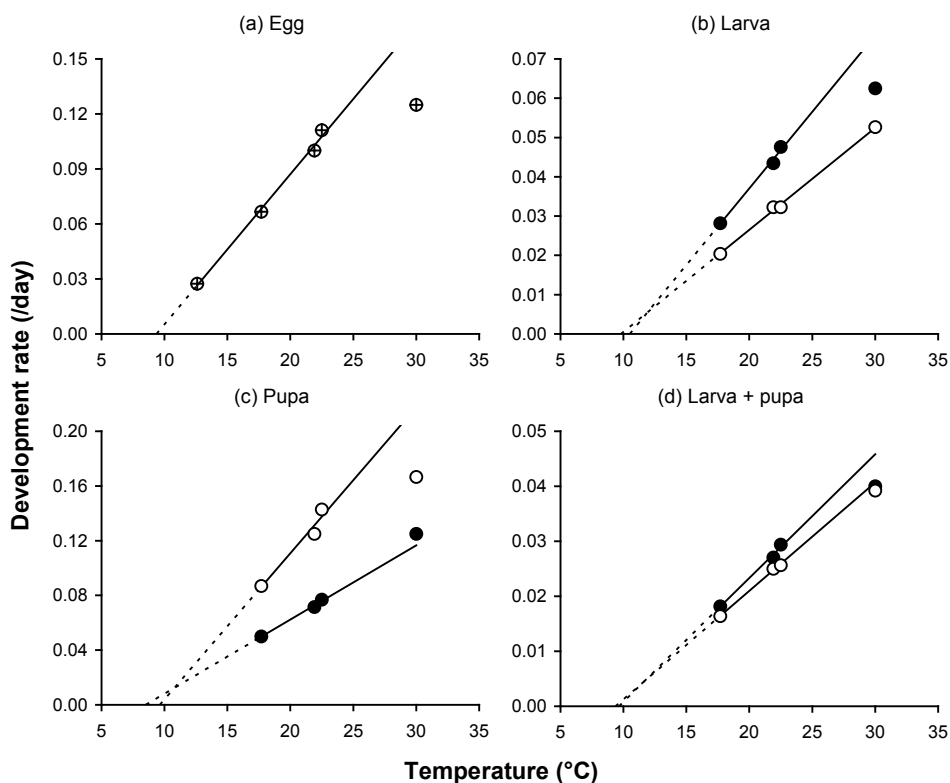
according to Akaike's information criterion (Akaike 1973). The degree of spread around the mean (95% confidence range estimated as  $2\sigma$  or visually from Figure 3) was 13 to 23% of the median developmental time, across all life stages.

**Table 2. Thermal requirements for development of PAM sexed at pupation, and for three larval instars (undifferentiated sex) that died before pupation; all regressions exclude the 30°C data; b = base temperature required for development; q = day-degrees above b required to complete the stage; R<sup>2</sup> = correlation coefficient (Figure 1); q<sub>c</sub> = day-degrees required above a common base temperature of 9.6°C.**

Life stage	Sex	b (°C)	q (°day)	R <sup>2</sup>	q <sub>c</sub> (°day)
Egg	undifferentiated	9.4	121.9	0.995	119.4
Total larva	male	10.5	256.3	0.992	278.3
	female	9.8	384.8	0.987	391.8
Pupa	male	8.5	184.4	0.994	168.4
	female	9.6	93.5	0.959	93.8
Total larva + pupa	male	9.7	443.8	0.992	446.2
	female	9.4	507.2	0.997	497.1
1 <sup>st</sup> larva	undifferentiated	8.7	82.3	0.992	76.0
2 <sup>nd</sup> larva	undifferentiated	8.2	69.7	0.993	61.5
3 <sup>rd</sup> larva	undifferentiated	9.4	56.9	0.961	55.9

**Table 3. Fitted parameters for the logistic approximation for the cumulative Gaussian function for variation in PAM developmental times: n = number of data points used in the regression;  $\mu$  = midpoint (mean) of the curve;  $\sigma$  = spread (standard deviation) of the curve; R<sup>2</sup> = correlation coefficient for observed versus predicted values (Figure 3).**

Life stage	Sex	n	$\mu$	$\sigma$	R <sup>2</sup>
Egg	undifferentiated	28	0.963	0.072	0.876
Larva	male	27	0.984	0.095	0.960
	female	28	1.001	0.115	0.904
Pupa	male	16	0.954	0.065	0.953
	female	15	0.955	0.105	0.959
Larva + pupa	male	31	0.987	0.071	0.959
	female	27	0.983	0.095	0.941



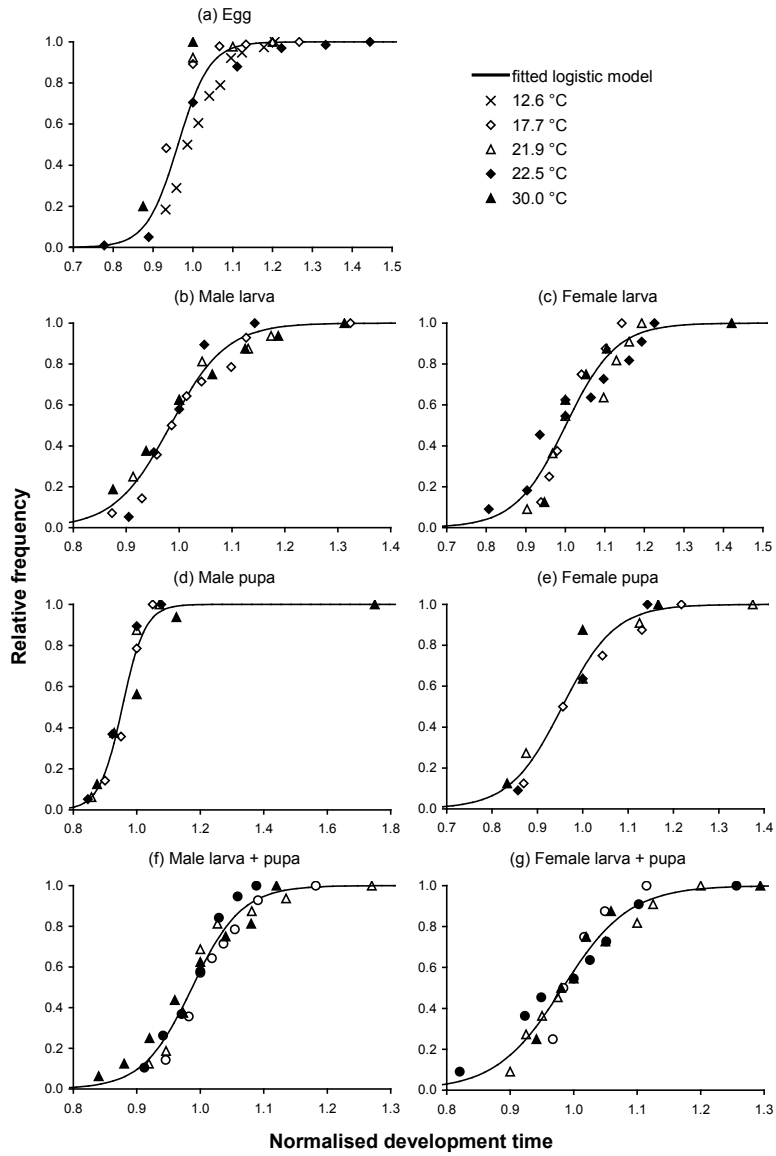
**Fig. 2.** Median developmental rates of PAM life stages at constant temperatures. ● = males; ○ = females; ⊕ = undifferentiated results. — = linear regressions (excluding 30°C results) which are extrapolated (---) to estimate the lower developmental threshold.

### Predicting voltinism throughout New Zealand

Developmental requirements were expressed relative to a common base temperature of  $b_c = 9.6^\circ\text{C}$ . Female maturation required 119.4 day-degrees for egg hatch (undifferentiated between males and females) plus 497.1 day-degrees for development of larva + pupa, for a total generation time of 616.5 day-degrees (Table 2, Figure 4). Males developed more rapidly, requiring 565.6 day-degrees for development. Hence adult males from any one egg batch are likely to emerge from pupation and disperse in search of other females before their sisters complete development. The New Zealand locations provide from 835 day-degrees above  $9.6^\circ\text{C}$  in the far south, to 2250 day-degrees in the north, allowing time for an estimated 1.4 generations /year in the south, to almost 4 generations /year in the north (Table 5).

### Discussion

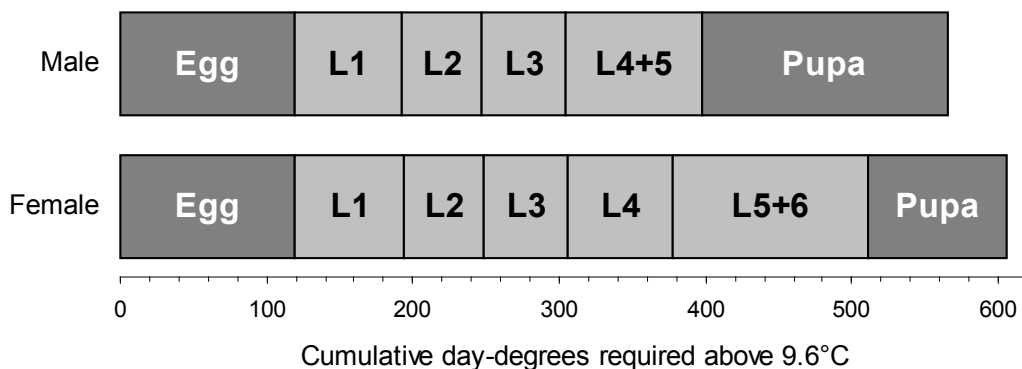
The threshold temperature for larval development of PAM ( $9.6^\circ\text{C}$ ) contrasts with that of  $c. 6^\circ\text{C}$  for two other well known species of pest lymantriids, gypsy moth *Lymantria dispar*, and nun moth *L. monacha* (Zwolfer 1935, Casagrande *et al.* 1987). If the base temperatures for these two species are standardised to PAM's  $9.6^\circ\text{C}$  (using the method proposed by Morris & Fulton 1970), then the standardised day-degrees above base required for full larval development ( $=q_c$ ) are 500 ( $\sigma$ ) and 587 ( $\text{f}$ ) for gypsy moth and 651 (undifferentiated) for nun moth. Hence PAM larvae (with  $q_c$  of 272 ( $\sigma$ ) and 390 ( $\text{f}$ )) developed much faster than gypsy or nun moth. PAM males developed more rapidly than females (1.43 $\sigma$ : 1 $\text{f}$ ) relative to gypsy moth (1.17  $\sigma$ : 1 $\text{f}$ ). Although all three species are polyphagous, the developmental differences reflect the different life-histories evolved in response to



**Fig. 3.** Variability in the developmental times of PAM life stages. Lines show logistic models fitted to the experimental data (parameter values are listed in Table 2).

**Table 4. Potential number of PAM generations/year throughout New Zealand, based on female development on artificial diet and a common threshold for development of 9.6°C. 95% confidence values are given.**

Weather station	Location (°S; °E)	Altitude (m)	No. years met. data	°d above 9.6°C /yr	Potential generations /yr
Whangarei	35.767; 174.367	37	13	2250 ± 93	3.6 ± 0.2
Auckland	37.007; 174.789	33	19	2211 ± 60	3.6 ± 0.1
Tauranga	37.667; 176.200	4	14	2014 ± 86	3.3 ± 0.1
Napier	39.461; 176.859	3	13	1831 ± 92	3.0 ± 0.1
New Plymouth	39.000; 174.167	27	12	1654 ± 75	2.7 ± 0.1
Wellington	41.322; 174.804	43	19	1620 ± 73	2.6 ± 0.1
Nelson	41.283; 173.233	2	12	1537 ± 82	2.5 ± 0.1
Lincoln	43.650; 172.483	12	44	1237 ± 50	2.0 ± 0.1
Le Bons Bay	43.746; 173.119	236	19	948 ± 60	1.5 ± 0.1
Timaru	44.417; 171.250	17	19	1089 ± 59	1.8 ± 0.1
Dunedin	45.900; 170.517	2	19	974 ± 55	1.6 ± 0.1
Bluff	46.587; 168.376	5	19	835 ± 44	1.4 ± 0.1



**Fig. 4.** Total temperature accumulation requirements of PAM pre-imaginal stages fitted to a common 9.6°C base temperature.

different environments. Gypsy moth and nun moth live in continental climates with long harsh winters, with gypsy moth preferring deciduous hosts, and nun moth evergreen hosts. They are uni-voltine and spend most of the year in a diapause stage. PAM, on the other hand, has an evergreen natural host, is multi-voltine and does not diapause. It is adapted to the cool-temperate climates of coastal southern Australia and New Zealand, which have rather benign climates throughout the year. Even though temperatures may often fall below 10°C for

short periods, there are sufficiently long periods above 10°C, even in winter, to allow larvae to develop throughout the year. The ability of neonate larvae to survive for > 2 months at 6.7°C (almost 3°C below the minimum required for development) and then complete their development to adult when transferred to a higher temperature in the laboratory shows that larvae can readily survive extended periods of cool temperatures.

Males within a larval cohort took less time to develop to adults than females. Wild male PAM are

known to be capable of flying for many kilometres (Suckling *et al.* 2005), so male dispersal coupled with earlier emergence than females helps to ensure gene flow among and between populations. PAM adult females are wingless and essentially immobile, so cannot search for food or mates. They are protected only by the remains of their cocoon, and are vulnerable to predation (particularly by birds in the wild in Australia, JGC, *pers. observation*). Rapid reproduction is clearly advantageous, and the pro-ovigenic females (i.e., they emerge with a fully formed complement of eggs) attract males for mating with a sex pheromone (El-Sayed *et al.* 2005) and complete oviposition within about 24 h of mating (A. Barrington, HortResearch, *pers. comm.*)

The laboratory generated data at constant temperatures provided here give only an approximation of development under field temperatures. Inhibition at the lower end of the developmental curve is always especially difficult to measure experimentally, not least because movements of the extrapolated linear intercept are influenced greatly by data at higher temperatures. However, the estimates are very useful for planning a response to a new eradication, even though the actual developmental rates at low or diurnally fluctuating temperatures may be crucial for the more accurate threshold estimates required for subsequent population modelling. The data suggest that female PAM require fewer day-degrees above 9.6°C to develop through a generation than there are available annually in lowland areas throughout most of the country, indicating that the insect could colonise all of coastal New Zealand and complete at least one generation each year. Further inland, distribution would be limited at least partly by lower temperatures at increasing altitude, especially in the central plateau of the North Island and the mountain ranges in the South Island. Conservatively, PAM populations might be only uni-voltine in the south of the South Island, bi-voltine from mid-Canterbury north to the central North Island, and tri-voltine in the northern half of the North Island.

The actual number of generations per year in different environments or parts of the country can also be expected to be influenced by the host plants upon which PAM larvae feed. Host plants can be expected to support larval development of

wild PAM differentially. Even though PAM is a very polyphagous species, defensive chemicals in some plants may inhibit larval development while other host plants may be deficient in essential nutrients. Hence a multi-species plant diet may have considerable impacts on PAM seasonal phenology, inter-generation and inter-population natality, voltinism and population dynamics. Nevertheless, even allowing for probably slower development when feeding on natural host plants, this study provides strong evidence that, should it ever establish in New Zealand and feed on economically or environmentally important plants, multi-voltine PAM could become a serious pest through a significant proportion of the country.

## Acknowledgements

PAM larvae were provided by Anne Barrington and the Insect Rearing team at HortResearch, Auckland. The research was funded by MAF Biosecurity (now Biosecurity New Zealand).

## References

- Akaike H. 1973.** Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory* (eds BN Petrov and F Csaki), pp. 267-281. Akademiai Kiado, Budapest.
- Barlow ND, Dixon AFG. 1980.** Simulation of Lime Aphid Population Dynamics. Pudoc, Wageningen. 165 pp.
- Common IFB. 1990.** Moths of Australia. Melbourne University Press, Carlton, Victoria. 535 pp.
- Casagrande RA, Logan PA, Wallner WE. 1987.** Phenological model for gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae and pupae. *Environmental Entomology* 16: 556-562.
- Dennis B, Kemp WP, Beckwith RC. 1986.** Stochastic model of insect phenology: estimation and testing. *Environmental Entomology* 15: 540-546.
- El-Sayed A, Gibb AR, Suckling DM, Bunn B, Fielder S, Comesky D, Manning LA, Foster SP, Morris BD, Ando T. 2005.** Identification of sex pheromone components of the painted apple moth: a tussock moth with a thermally

- labile pheromone component. *Journal of Chemical Ecology* 31: 633-657.
- Kramer DA, Stinner RE, Hain FP. 1991.** Time versus rate in parameter estimation of nonlinear temperature-dependent development models. *Environmental Entomology* 20: 484-488.
- Logan JA. 1988.** Toward an expert system for development of pest simulation models. *Environmental Entomology* 17: 359-376.
- Morris RF, Fulton WC. 1970.** Models for the development and survival of *Hyphantria cunea* in relation to temperature and humidity. *Memoirs of the Entomological Society of Canada* 70: 60pp.
- Odell TM, Bell RA, Mastro VC, Tanner JA, Kennedy LF. 1984.** Production of the Gypsy Moth, *Lymantria dispar*, for research and biological control. In: *Advances and Challenges in Insect Rearing* (eds E G King, NC Leppla) pp. 156-166. Agricultural Research Service (Southern Region), U. S. Department of Agriculture, New Orleans.
- Régnière J. 1984.** A method of describing and using variability in development rates for the simulation of insect phenology. *Canadian Entomologist* 116: 1367-1376.
- Smithers CN. 1966.** A note on *Orgyia anartoides* (Walk.) (Lepidoptera: Lymantriidae). *Australian Zoologist* 13: 394-398.
- Suckling DM, Charles JG, Allan DJ, Chagga A, Barrington A, Burnip GM, El-Sayed AM. 2005.** Performance of irradiated painted apple moth (Lepidoptera: Lymantriidae) in urban Auckland, New Zealand. *Journal of Economic Entomology* 98(5): 1531-1538.
- Wagner TL, Wu H-I, Sharpe PJH, Coulson RN. 1984.** Modelling distributions of insect development time: a literature review and application of the Weibull function. *Annals of the Entomological Society of America* 77: 475-487.
- Zwölfer W. 1935.** Die Temperaturabhängigkeit der Entwicklung der Nonne (*Lymantria monacha* L.) und ihre bevölkerungswissenschaftliche Auswertung. *Zeitschrift für angewandte Entomologie* 21: 333-384.